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The ecology of macrozoobenthos and sea ducks
in the Pomeranian Bay

by

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Contents

Summary

1. The Pomeranian Bay (southern Baltic Sea), a large shallow offshore bay, is the transition zone between the Oder Estuary and the Baltic Proper. Sandy bottoms, between 0-20 m water depth, cover an area of 8.800 km². The rivers Oder and Peene transport about 20 km^3a^{-1} freshwater into the bay. In the last decades the area has been influenced by increasing anthropogenic discharges. The study area has undergone significant eutrophication. Riverine nitrogen loads were five times higher in the 1990s than in the 1960s. Phytoplankton and primary production have roughly doubled during the last 20 years. Accumulation of organic matter was observed in sediments locally. A joint Polish and German research project (TRUMP) was started in 1993 to evaluate the impact of the riverine material on the ecosystem of the Pomeranian Bay. Investigations focus on the distribution, transport, and modification of biogenic and anthropogenic inputs from the Oder River. Benthic macrofauna studies form a major part of these investigations.

2. This phD thesis aimed at 1) describing the recent distribution of macrozoobenthos communities and sea ducks in the Pomeranian Bay in relation to the prevailing abiotic and biotic factors, 2) developing and applying efficient methods for the analysis of low diverse sublittoral benthic communities, 3) to analyse short-term and long-term changes in the macrozoobenthos in relation to fluctuations and long-term trends in the environmental conditions.

3. Quantitative samples of benthic macrofauna were taken at 34 stations (6 to 30 m water depth) in the Pomeranian Bay in the period April 1993 to April 1995. Two different sampling methods were applied: 1) Van Veen grab (23kg/70 kg, 0.1 m², 1.0 mm mesh size) and 2) modified 'Reineck' box corer (190 kg, 0.0225 m², 0.5 mm mesh size). Methodological comparisons between both methods were performed. Species distribution patterns, species numbers, abundances, and biomasses were analysed. Univariate and multivariate statistics were used to compare the precision of results of both procedures in terms of species richness, abundance, biomass and size-frequency distribution. Conclusions are made about the applicability and efficiency of the two methods. Five replicate samples of method two are demonstrated to be the most efficient method for routine monitoring purposes in respect to data precision and laboratory sorting-time. Recommendations are given for the treatment of data on mobile epifauna species, which can not be sampled precisely with less than ten replicate grab samples. The identification of oligochaetes to species level seems to be renouncable for multivariate statistical analyses of community structures.

4. Fourty-five macrofauna species were identified. *Mya arenaria*, *Macoma balthica* and *Marenzelleria viridis* are the most important species with respect to biomass. Mean total biomass values decreased from about 100 g $AFDW\,m^{-2}$ in the Southwest of the bay to only about 10 g $AFDW\,m^{-2}$ in the North. Multivariate analyses suggest distinct assemblages within the shallow bay and at the slope to the adjacent deeper zones. Loose structuring was found for communities of the shallow parts. They are all dominated by filter-feeders. Surface deposit-feeders are dominant at the northern boundary of the study area adjacent to the Arkona Basin. The small range of sediment variation could not explain distribution pattern of species with a large tolerance for sediment parameters. Physical disturbance and available food supply are proposed to be important in structuring the benthic community.

5. The population structure of *Mya arenaria* has been investigated during a 1.5-year period in 1993/94 to follow changes in the size and age structure of the clam populations in different parts of the study area. Large spatial differences in the population structure were found between the sheltered Southwest of the bay and the shallow and exposed Oder Bank in the centre. The clam stock of the Oder Bank was formed by two different clam types. A slow growing cohort was assumed to be autochtonous on the Oder Bank. A fast growing one was assumed to have been introduced from the surrounding area. Their contribution to the total density varied seasonally and was probably denpendent on the intensity of bedload transport events. Erosion was supposed to be of minor importance in the Southwest of the Pomeranian Bay. High mortality rates during the first two years of life were assumed to be caused by predation. Mortality rates of older cohorts remained stable until old age. Variations in the density of cohorts were related to interannual differences in the reproductive success. A mild winter presumably lowers the reproductive success in the subsequent summer.

6. Spatial variations in individual growth rates of *Macoma balthica* and *Mya arenaria* were investigated in the Pomeranian Bay in 1993/94. Compared to full marine environments, growth rates of bivalves were considerably lower in this brackish area (salinity about 8‰). Growth of *M. balthica* correlated significantly with phytoplankton concentration. Growth of *M. arenaria* was assumed to be negatively effected by intensive physical disturbances. It is supposed that reduced salinities affect the growth of *M. arenaria* more than that of *M. balthica*.

7. The distribution and abundance of *Marenzelleria viridis*, a North American spionid polychaete which was first recorded in the Pomeranian Bay in the late 1980s, was studied in the southwestern part of the Baltic Sea in 1993/94 in relation to environmental factors. All available macrozoobenthos samples from German Baltic waters were used to construct a general distribution map. Highest abundances and biomasses were found in semi-enclosed lagoons (39.000 ind. m^{-2} and 70 g ash free dry weigth m^{-2}). The western horizontal distribution border and the vertical distribution range were following the 15 ‰ isohaline. Neither a horizontal nor a vertical limit was found to the East. Dense settlement was restricted to sediments with an organic content of less than 5 % and a silt content of less than 10 %. Simultaneous population studies were carried out in the Pomeranian Bay, the Oder Estuary and the Darss-Zingst Bodden from April 1993 to April 1994. Three different age groups were identified throughout the year. Settlement of larvae took place in autumn. Successful larval settlement was restricted to areas with a salinity above 5 ‰ and a winter phytoplankton concentration above 5 g Chl a m^{-3}. Benthic stages were found to be highly motile. Adults occurred up to 50 km away from recruitment areas.

8. Long-term changes in the macrofauna of the Pomeranian Bay were studied by comparing survey data from the 1950s, 1980s and 1990s. Biomass of filter-feeding bivalves increased significantly. Spatial distribution patterns of the investigated species have changed. Strong decreases in species richness were caused by oxygen depletion at stations deeper than 15 m. *Saduria entomon*, *Monoporeia affinis* and *Pontoporeia femorata* vanished entirely between 1981 and 1993. Although a causal relationship between simultaneous increases of nutrient levels and macrobenthic biomass cannot be verified, eutrophication is proposed to be the major process affecting changes in macrofauna assemblages. In addition, changes in hydrography and climate increased frequency and severity of oxygen depletion events in the Pomeranian Bay since the mid 1980s.

9. Between January 1992 and April 1995 the distribution and abundance of long-tailed ducks, *Clangula hyemalis*, were studied, and the extent to which these can be explained by benthic food supply and disturbance by an international shipping lane. Long-tailed ducks arrive in the study area in late fall and leave in early May. Maximum numbers of 800.000 birds were recorded in winter. About the half of these birds was still present in March-April. The spatial distribution of long-tailed ducks is best explained by the harvestable biomass of prevalent prey species. Bird densities were highest in areas providing a harvestable biomass > 10 g AFDW m^{-2}. Long-tailed ducks were more or less evenly distributed in the study area during winter. In spring, they seemed to be able to narrow the selection of feeding habitats to the most profitable patches and avoided areas providing a harvestable biomass < 5 g AFDW m^{-2} and disturbance by ship traffic.

1. Introduction
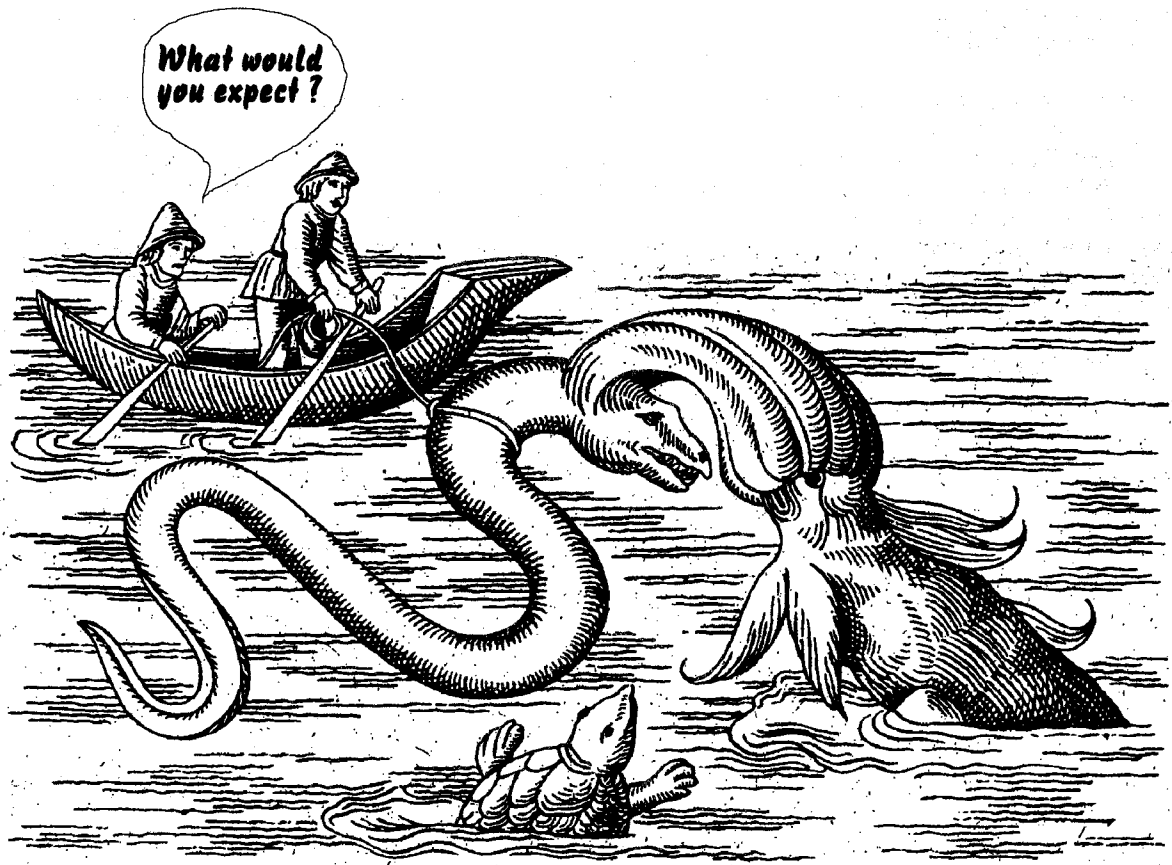
Gessner, 1583

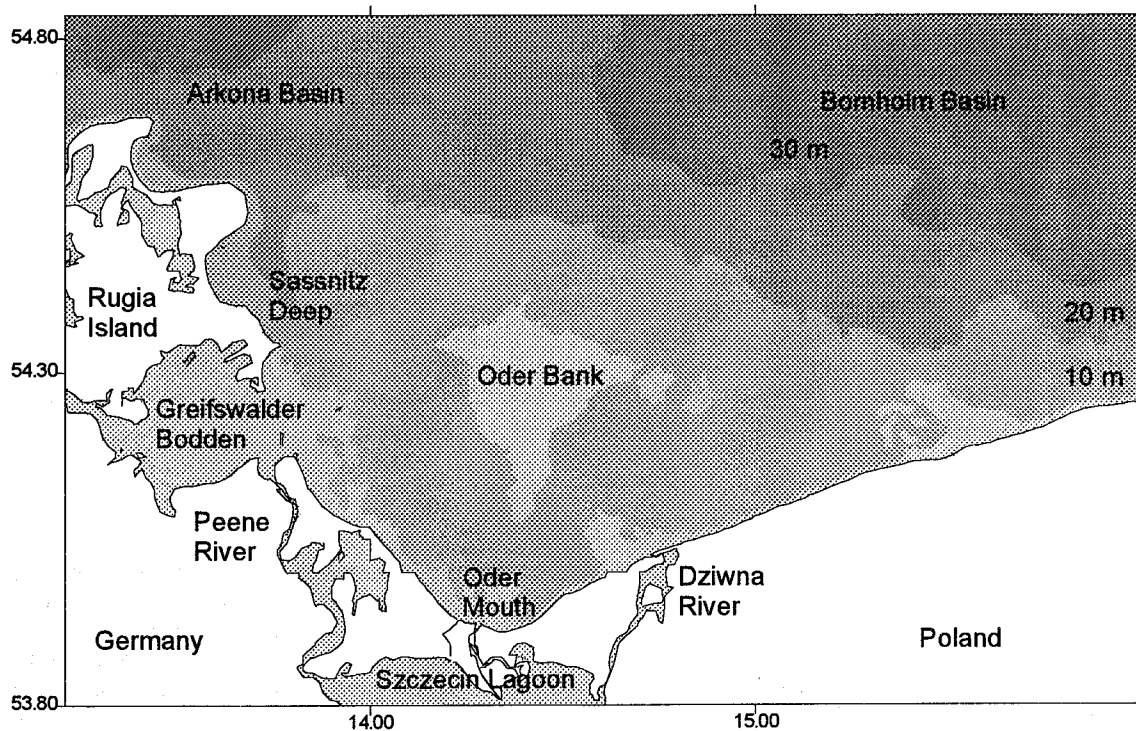# An assessment of environmental changes in the Pomeranian Bay

Fig. 1.1: Map of the study area.

About 40 % of all human beings spend their lives near estuaries and coasts. They exploit the large marine food supply, which results from a high biological productivity due to a permanent input of nutrients originating from both, the continent and the sea. However, coastal areas are also used intensively for many other activities such as transportation, settlement, mining and recreation. The dramatic growth of human populations in the coastal zones, the increasing economical pressure to increase agricultural production by the use of fertilizers, deforestation and increasing industrialisation have caused many environmental problems which have become increasingly acut in recent decades. Besides habitat degradation, erosion, and pollution, eutrophication was recognized as the major cause of the observed negative changes in coastal marine environments (Gray, 1992).

In Europe, two areas have received much attention with respect to marine pollution and eutrophication, the Adriatic and the Baltic Sea (e.g. HELCOM, 1990; Ott, 1992). Both areas are semi-enclosed with small exchanges of water with surrounding areas. Hence, the effects of discharged nutrients and pollutants are more severe. Estuaries and coastal zones near river mouths were identified as the most strongly affected parts. Large amounts of nutrients and other chemical substances are introduced via rivers. Inputs from land go into river mouths, into shallow lagoons and into coastal waters. They are partly deposited there in the sediment and partly transported into offshore areas. In fact, especially the Baltic Sea may be viewed as a continuation of many rivers which drain an area of 1.670.000 km² with a population of more than 71 Mio. people (HELCOM, 1990).

Seven major rivers contribute about the half of the mean annual freshwater discharge to the Baltic Sea (HELCOM, 1990). The Oder river is one of them. Regarding to its runoff volume, it is one of the most contaminated rivers in middle Europe (Lampe, 1993). Though the Oder river supplies only 3-4 % (18 km³) of the fresh water flowing annually into the Baltic Sea it accounts for about 15 % of the nutrient discharge and 10 % of the heavy metal inputs (Trzosinska, 1992). These loads are filtered and reduced before reaching the Baltic proper during the passage of the water through coastal lagoons and the shallow Pomeranian Bay, a large, sandy coastal area (Fig. 1.1). Lampe (1993) and Trzosinska (1992) recently summarized the present knowledge about the environmental state and material fluxes in the Oder estuary and proposed conclusions for further investigations. As of now little is known about the consequences of the input of nutrients and pollutants for the structure of the affected coastal ecosystems and about their functional response. Therefore, a research projekt (TRUMP) was launched in 1993 with the aims to analyse the distribution, turnover and deposition of

nutrients and chemical pollutants discharged by the Oder river into the Pomeranian Bay. The main task of the projekt is to describe the quality and quantity of environmental forces distributing, trapping and recycling the riverine loads (Bodungen et al., 1995).

This thesis is a contribution to the TRUMP-projekt. In it the structure of the benthic fauna in the Pomeranian Bay, its long-term changes, and its importance for the overall ecosystem function are described.

Eutrophication and Macrozoobenthos

As marine sediments often represent the final sink for organic matter and contaminants discharged to the sea, benthic macrofauna seems an appropriate target for the investigations of anthropogenic disturbances. Macrofauna species are relatively long-lived and sedentary, and can thus serve as indicators of the effects of discharges over time (Rees et al., 1991). Furthermore, macrofauna species are relatively easy to sample quantitatively and use has been made of a wide range of their responses in assessments of the effects of anthropogenic inputs. Benthic communities have been demonstrated to respond to pollution in a predictable manner (Bayne et al., 1988).
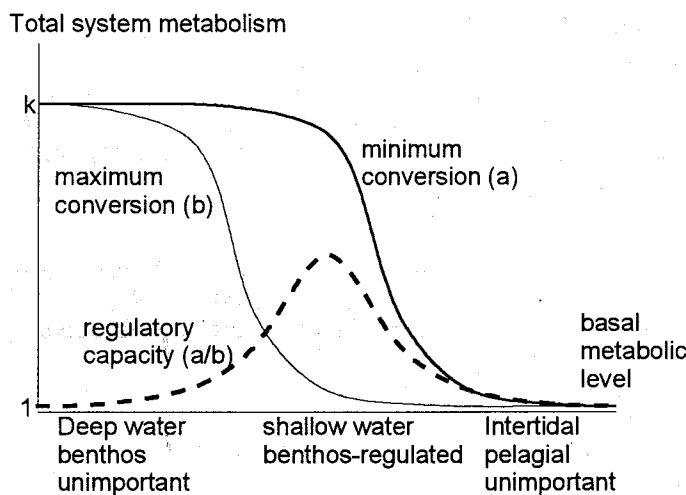

Fig. 1.2: Model of the regulatory capacity of the benthos with regard to system metabolism. The two sigmoid curves show the increase of total system metabolism (pelagic+benthic) when the pelagic component gains. The upper curve represents a case where nothing of the pelagic biomass is cropped by the benthos. The lower curve assumes that benthic organisms feed inputs from the pelagic compartment at a maximum rate and converts it to benthic biomass. The curves are almost identical when the pelagic component greatly outweighs the benthos or when the pelagic component is insignificant and the benthos dominates the total system metabolism in all cases. The greatest difference between the curves is found in shallow-water systems with rich filter-feeding benthic fauna (from Ott & Fedra, 1977).

Since the Pomeranian Bay is one of the largest shallow sublittoral areas in Central Europe (8.800 km²) it was thought that macrobenthic filter-feeders may also here effectively control pelagic production and buffer external nutrient inputs, due to a permanent mixing of the whole water column. This assumption was based on the conceptual model published by Ott & Fedra (1977) demonstrating that the conversion of planktonic biomass into the biomass of large, long-lived benthic organisms can stabilize the overall ecosystem behaviour (Fig. 1.2).

Hargrave (1973) described a comparable model in which oxygen demand of the sediment is related to pelagic primary production and the depth of the mixed layer in the water column (Fig. 1.3).

Eutrophication of marine environments is usually defined as a complex of responses ultimately triggered by an addition of limiting nutrients. The primary effect is an increase in primary production. The increased amounts of organic material subsequently deposited in sediments are assimilated by heterotrophic benthic organisms. This may eventually lead to increases in benthic biomass but also to anoxic conditions in sediments and mass-mortality among benthic animals. Changes in macrozoobenthos due to organic enrichment have been reviewed several times (e.g. Gray, 1992; Heip, 1995; Pearson & Rosenberg, 1978).

carbon equivalent of sediment
oxygen uptake (g C/m²a)
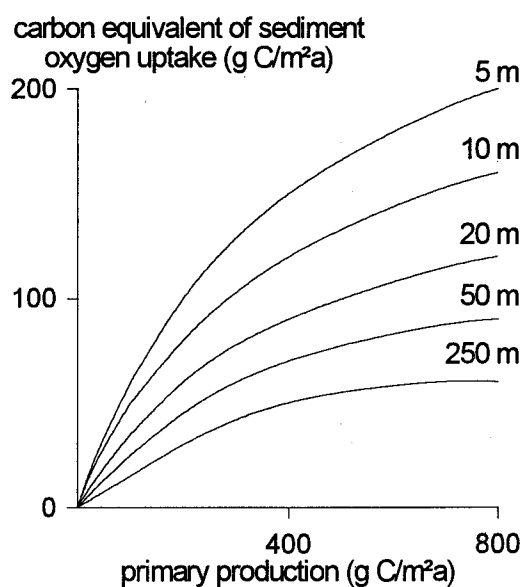
Fig. 1.3: Model of benthic-pelagic coupling. Benthic oxygen consumption is related to surface primary production and to the mean annual mixed layer depth (from Hargrave, 1973).

The classical model of Pearson & Rosenberg (1978) shows that the first changes that can be observed are an increase in the number of species, followed by an increase in biomass and then an increase in abundance. If loading continues, finally all macrofauna will disappear (Fig. 1.4). The concentration of oxygen is the most important factor controling the final dramatic changes. The model was later interpreted as a general response of benthic assemblages to various kinds of anthropogenic disturbances (Warwick, 1986). Unfortunately, it is not quantitative.
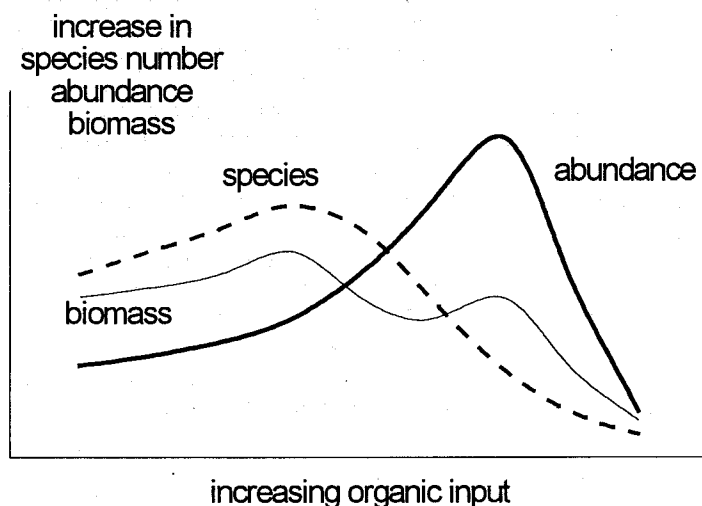
Fig. 1.4: The Pearson & Rosenberg (1978) model of effects of increased organic inputs on macrozoobenthos.

Besides changes in diversity, abundance and biomass, various other resposes to organic inputs were observed. Warwick (1986) described a shift from low numerical and high biomass dominance to a situation of high numerical and low biomass dominance, as short-lived and small-sized opportunistic species become more important. As a consequence, average macrofauna individual weights decrease (Beukema, 1991; Cederwall & Elmgren, 1980; Weigelt, 1991).

Arntz & Rumohr (1986) demonstrated that the amplitude of seasonal and annual numerical changes are large and erratic during early successional stages following a pertubation, while, at a later stage of recovery, amplitudes of oscillations show a greater regularity.

According to their mode of feeding, it was observed that the dominance by filter-feeding species may shift to a dominance by deposit-feeders (Beukema, 1991; Word, 1980). Otherwise, Warwick & Clarke (1994) showed that the changes in species composition under eutrophication stress were caused by a shift in dominance between phyla, but within phyla only by species shifts in the polychaetes.

Methods for analysing changes in benthic communities

Many biological effect studies have been applied to marine NE Atlantic areas during the last decades. Investigations of the benthic fauna often formed a major part of these investigations. There are several key references dealing with general issues of benthic sampling and analytical methods, notably Baker & Wolff (1987) and Holme & McIntyre (1984).

Attention has been payed to the examination of spatial pollution gradients at one point in time and to time series of observations where the significance of an impact is assessed with time (Clarke & Warwick, 1994). The community level became the most popular level for environmental impact studies, since microcomputers and the appropriate software are no longer a time-consuming and expensive problem.

The wide variety of different statistical methods applied in the analysis of changes in benthic communities may be summarized in main categories (Clarke & Warwick, 1994):
- Univariate statistical analyses (e.g. diversity indices),
- Distributional techniques (e.g. ABC (k-dominance) curves),
- Multivariate statistical analyses (e.g. cluster analysis, PCA-principal component analysis, MDS-multidimensional scaling).

Methods employing lower structural levels (biochemicals, cells, individuals) often require experimental approaches which reflect the condition of the organisms just at the time of sampling, whereas the structure of an assemblage of organisms reflects the integrated conditions over a period of time (Warwick, 1993). But also individual organisms can supply structures into which a vast range of biological data can be fitted (Bartholomew, 1986). Measures of 'fitness' (e.g. fecundity, growth rate, physiological condition) can be used to determine effects of environmental and anthropogenic stress at or below the level of the individual organism. Such measures may allow the detection of effects at stages prior the onset of population or community changes (Bayne et al., 1980). Research into physiological and biochemical norms and ranges has yielded techniques such as the 'scope for growth' measurements. The 'scope for growth' is an integrated physiological parameter reflecting the energetic balance between processes of energy acquisition (feeding and absorption) and energy expenditure (metabolism and excretion, Widdows & Johnson, 1988). But unfortunately there is still a need to calibrate the scale of response and to identify relationships between single measurable responses. Therefore, the complementary application of a variety of techniques suitable for detecting stress effects at individual, population and community level is recommended.

The applied techniques must be adapted to the natural environmental variables of the area under investigation. Such natural modifications are not always easy to separate from anthropogenic effects (Rees et al., 1991).

In the following paragraph I will describe the different approaches used in this study. Both, macrozoobenthos and sea ducks were subject of our investigations in the Pomeranian Bay. Some logistical constraints we had to consider while planning and running our investigations are also described.

What to assess in the Pomeranian Bay ? - the concept of an environmental impact study

„With sufficient time, money and taxonomic expertise, a properly designed and replicated sampling programme followed by sorting and identification of the organisms to species level is the ideal to be aimed for, but this is rarely achievable. Measurements of changes in the structure of natural marine communities are almost always a compromise between the scientific ideal and political, financial and logistical constraints." (Warwick, 1993)

At the very first beginning, in spring 1993, planning an environmental impact study on benthic communities in the Pomeranian Bay was almost like diving into the dark. Since 1945, the Pomeranian Bay is devided politically into a German and a Polish part. Assessments of oceanographic and biological parameters were only conducted on national scales. Existing scattered data sets were never calibrated or evaluated comprehensively until the 1990s.

Although the macrozoobenthos had been investigated several times, only little information on species composition could be obtained from the literature (Demel & Mulicki, 1954; Hagmeier, 1926; 1930;

Hertling, 1928; Löwe, 1963). The original data sets of Hagmeier were lost in 1944, those of Löwe had also disappeared.

From the lack of knowledge, it was almost impossible to formulate suitable hypotheses about changes in biological measures. We considered the importance of pilot samples to ensure the application of sensible measurements at a variety of levels of biological organisation. Thirtyfour stations were sampled with attention to different strata, depth, sediment types and potential dicharge sources in April 1993. Different sampling techniques were applied to describe the recent benthic communities and to select proper sampling methods and sites for a time-series sampling (see chapter 2). The compiled data set could later be used for an analysis of long-term changes in benthic communities of the Pomeranian Bay as the original data of Löwe turned up in a private library in 1994.

Ten stations were selected for a time-series sampling to study the dynamics of benthic populations and to measure the amplitude of seasonal and year-to-year oscillations of abundance and biomass. Unfortunately, we had to restrict our investigations to the western part of the bay, because it was impossible to obtain a sampling permission for Polish coastal waters between autumn 1993 and summer 1994.

To obtain a data set large enough for reliable quantifications, our field investigation was planned to continue for two years, from April 1993 until April 1995. Already after 1.5 years, this time-series was interrupted by a massive die-off of macrofauna caused by severe oxygen depletion in bottom waters in the southwest of the bay in summer 1994. Since then, we payed our attention to the recreation process of a macrofauna community, which is lacking typical opportunistic species.

Besides monitoring the benthic community, we encouraged the application of alternative measures at the population and individual level, since the use of statistical analyses of community data was almost restricted to multivariate statistics. Analyses of diversity indices, k-dominance curves and phylum-level approaches were impractical because of the low species richness in the Pomeranian Bay (only between 10 and 20 macrofauna species were found per station).

As a measure of the relative functional importance of species, biomass is usually a better measure than abundance, and production in turn is a better one than biomass. All macrofauna assemblages found in the study area in 1993 were dominated by the soft-shell clam, *Mya arenaria*, in terms of biomass. Thus we estimated annual production of *M. arenaria* by assessing its population structure, the population dynamics and individual growth. Since published data about environmental variables controlling the individual growth and the population dynamics of this filter-feeding bivalve in sublittoral habitats are scarce, related measurements were made simultaneously in different parts of the Pommeranian Bay.

Areas poor in species such as estuaries in the southern Baltic Sea, are considered to be very receptive to the introduction of new species. The geological history of the coastal lagoons is short (2.000 to 6.000 years). Diversity is usually low. The original fauna can be severely affected following successful introductions. For instance, the bivalve species *Dreissena polymorpha* and *M. arenaria* are today the predominant with respect to biomass in many coastal waters (Jansson, 1994). Five macrofauna species have been reported to be introduced to the southern Baltic Sea in total (Leppäkoski, 1984). The latest, the American polychaete *Marenzelleria viridis*, became established in the 1980s (Bick & Burckhardt, 1989). This species has spread rapidly and is now a dominant element of many macrozoobenthic communities. Gruszka (1991a), who observed this filter-feeding spionid worm in the Pomeranian Bay, suspected a detrimental impact on other members of the zoobenthos. An analyses of the population dynamics of *M. viridis* became an important part of our studies to describe its niche in the field in relation to various environmental factors.

In February 1993, just while planning our sampling programme, Danish ornithologists discovered that the complex of coastal lagoons in the Oder estuary and the shallow parts Pomeranian Bay are the most important wintering areas for seabirds in the Baltic Sea (Durinck et al., 1994). In particular, the coastal lagoons are important to the piscivorous smews, *Mergus albellus*, and goosanders, *Mergus merganser*, whereas the offshore waters are significant for benthophagous sea ducks. On average, 1.25 Mio. sea ducks (mainly long-tailed ducks, *Clangula hyemalis*, velvet scoters, *Melanitta fusca*, and Common scoters, *Melanitta nigra*) were recorded during the mild winters of 1991/92 and 1992/93. Apparently, this is the largest concentration of wintering seaducks in Europe. The ecological importance of these large sea duck concentrations are still far from clear.

Sea ducks feed on benthic invertebrates, of which bivalves comprise the most important prey (e.g. Madsen, 1954). Only nearshore areas which may not be optimal feeding habitats for seaducks were studied in the past to estimate the predation pressure of sea ducks on their prey stocks in the Baltic Sea (e.g. Kirchhoff, 1979, Leipe, 1985; Nilsson, 1972).

The feeding ecology of waders, a genus of benthophagous shorebirds, has been studied much more intensively during the last decades (e.g. Zwarts & Wanink, 1993). Waders are known to remove substantial parts of the benthic biomass production from intertidal areas. Their mean annual consumption rates usually range from 10-20 % of total benthic biomass, but even much higher values have been reported (see overview in Meire, 1993). In such circumstances birds often consume more than can be replaced by production and, therefore, these shorebirds are sometimes able to deplete their food recources completely within a few years. To obtain an estimate of the predation pressure of sea ducks in the Pomeranian Bay, we analysed the major components of the offshore winter habitat of long-tailed ducks and common scoters and estimated the impact of these species on local bivalve stocks.

Outline of the thesis

The aim of my thesis is to gain more information on the wide variety of both natural and anthropogenic environmental forces shaping the dynamics of macrofauna species and their avian predators in shallow coastal waters in the southern Baltic Sea.

The thesis contains four main chapters. Three of which consist of a general part and one or more research papers. The papers were prepared as individual publications, some of which are already accepted, others are submitted. In the first parts of each chapter, I tried to develop some additional aspects of our research project, which were not reported in the respective papers. These parts are based on published and unpublished findings.

The second chapter presents a methodological approach discussing various aspects of sampling design which was partly published in Powilleit et al. (1995). The third chapter starts with a description of the macrozoobenthic communities of the Pomeranian Bay and environmental impacts structuring the macrofauna in space and time. The population dynamics of two important filter-feeding animals, the soft-shell clam, *M. arenaria*, and the polychaete, *M. viridis*, are discussed in the fourth chapter. Spatial variations in the growth of bivalves are described. These results were used to obtain preliminary estimates of benthic production. The thesis continues by an examination of the ecological role of the most numerous sea duck wintering in the study area, the long-tailed duck, by focusing on its distribution, feeding ecology and food consumption.

Although the description of structural and functional responses of the macrozoobenthos on eutrophication and pollution of the Pomeranian Bay was the immediate aim of our research project, this thesis does not analyses these impacts comprehensively. Several of our studies are still under process, since many of the nessessary data on other compartments of the ecosystem under investigation have not been analysed yet.

2. Methodological approach
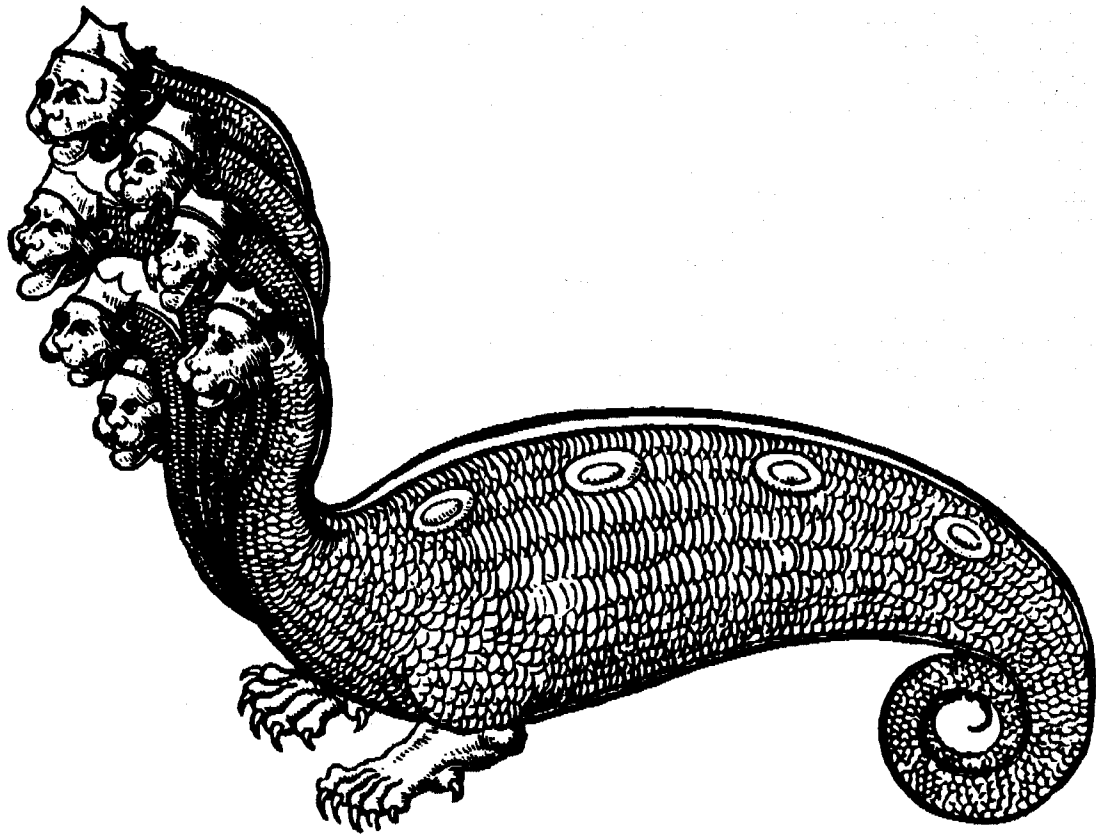
Gessner, 1575

Designing a sampling programme: collection and treatment of data

Sampling strategy

The sampling strategy has a strong influence on the options for later statistical analyses. Stratified sampling, randomized sampling, single-spot sampling, grid sampling and transect sampling are the basic procedures used in spatial benthos investigations (Rumohr, 1990). The idealised sampling strategy for a benthic monitoring of effects of point-source discharges assesses spatial gradients of response (transect sampling). However, such a strategy needs a good knowledge of the discharge transport pathways and the lateral extent of benthic changes in relation to the plume (Rees et al., 1991).

The Pomeranian Bay is the transition zone between the Oder estuary and the Baltic proper. Its environment is strongly effected by both bordering ecosystems. The freshwater input flows through the Swina mouth (60-70 %), through the Dziwna river in the east (15 %), and the Peene river via the neighbouring Greifswalder Bodden in the west (15 %). There are at least three main discharge point-sources. The pelagic transport patterns of the inputs are forced by local winds (Lampe, 1993; Siegel et al., 1994).

The application of a transect sampling design is impractical in the Pomeranian Bay, also because of the spatial heterogeneity of its bottom topography. As a rule the sediment consists of fine sand, but coarse sand and gravel prevail at some places, especially in the Polish part. Silty sediments occur off the Swina mouth. The sediment of the Sassnitz Deep, near the Isle of Rugia in the west, is muddy sand (Koine, 1995; Neumann & Bublitz, 1969).

The bottom water salinity varies between 6-8 ‰ near the coast and between 8-10 ‰ in the Sassnitz Deep.

We considered therefore a depth-related stratified sampling design as the only practical solution, because a suitable grid design was impossible with our time and laboratory recources.

Sampling method

Benthologists are used to apply many different sampling techniques in response to the large variety of marine sediments, and the different aims of the investigation in question. In order to ensure confidence in the precision of results and to allow intercomparability of the collected data, several method intercomparisons were made in the North Sea and the Baltic Sea and recommendations, especially for the monitoring of marine soft-bottom macrofauna, have been published (e.g. Rees et al., 1991; Rumohr, 1990). But generally there are no commonly accepted guidelines employed outside the Baltic and even within the Baltic different sampling gear continues to be used. The HELCOM monitoring programme for the Baltic Sea concentrates mainly on long-term changes in community structures of the deeper offshore basins (HELCOM, 1988; 1990). These basins are often characterized by muddy sediments with low densities of macrobenthic species. Therefore, the Van Veen grab ($0.1 m^2$) and a 1 mm sieve is recommended for collection of samples.

We focussed our attention on a coastal marine environment. Shallow nearshore habitats in the Pomeranian Bay are mainly sandy and harbour high densities of small polychaete species and deep burying bivalves. The use of deeply penetrating box corers in combination with a 0.5 mm sieve is necessary to collect these infauna species quantitatively. Because of high abundances the covered sampling area is usually smaller than $0.1 m^2$ to minimize laboratory sorting time (Jensen, 1981).
The differences between these two sampling techniques in terms of effectivness and univariate and multivariate sample statistics have been intercalibrated. Both, the Baltic Sea standard monitoring sampling technique and a modified 'Reineck' box corer (Reineck, 1963) in combination with a 0.5 mm sieve were used. Established univariate and multivariate statistical analyses were applied for data comparison.

Comparison of sampling methods applied in the Pomeranian Bay

Benthic sampling usually involves four basic parameter which determine sampling efficiency: sample size, penetration depth, sieve mesh size and number of independent replicates. The following account presents results of a cumulative approach which does not aims to measure the effects of grabs and sieves separately.

Simultaneous sampling was performed at nine stations in April and again at four stations in October 1993. Sampling locations, geographical positions, water depth and methods applied are given in Table 2.1 (see also Fig. 3.1 in paper 1). Samples taken with the Van Veen grab (70 kg, 0.1 m², 8-12 cm penetration depth) were sieved through a 1 mm metal gauze and box corer samples (0.0225 m², 15-25 cm penetration depth) were sieved through a 0.5 mm metal gauze. All samples were stained with Rosé Bengal. Fixation, sorting, species and biomass determination were analysed following the HELCOM-guidelines (HELCOM, 1988).

The mean abundance and biomass, RCL (relative 95 % confidence limits expressed as a percentage of the sample average) were calculated for every set of subsamples. The relative differences between the means of Van Veen grab and box corer samples were tested for all species with a density > 100 Ind./m² by using a pairwise Student-t-Test (Weber, 1980).

Table 2.1: Sampling sites in the Pomeranian Bay 1993/1994 (internal station codes are given in brackets; station No. 25 is identical to the HELCOM macrobenthos monitoring site 'K3'). Methods: (1) Van Veen grab/1.0 mm sieve; (2) modified 'Reineck' box corer/0.5 mm sieve.

station	latitude (N)	longitude (E)	depth (m)	method
1 (10)	53°56.30'	14°16.20'	6	1,2
2 (BA1)	53°59.10'	14°14.20'	10	1
3 (165)	54°00.70'	14°12.20'	11	1,2
4 (164)	54°06.80'	14°06.70'	14	2
5 (162)	54°08.30'	14°11.70'	14	2
6 (H17)	54°16.30'	14°09.20'	16	2
7 (160)	54°14.40'	14°04.10'	14	2
8 (133)	54°12.20'	13°54.30'	11	1,2
9 (992)	54°13.70'	13°42.00'	10	1
10 (31A)	54°20.50'	13°46.30'	15	1
11 (132)	54°20.90'	13°50.80'	17	1,2
12 (130)	54°23.20'	13°55.80'	15	1,2
13 (131)	54°26.50'	13°43.60'	21	1,2
14 (952)	54°33.00'	13°50.50'	20	1,2
15 (BA3)	54°00.00'	14°20.60'	11	1
16 (5A)	54°05.00'	14°20.10'	13	1
17 (6)	54°05.00'	14°27.50'	14	2
18 (163)	54°09.70'	14°27.60'	13	1
19 (BA9)	54°12.00'	14°30.00'	13	2
20 (20)	54°14.00'	14°26.30'	6	2
21 (39)	54°20.30'	14°31.30'	9	1,2
22 (911)	54°22.10'	14°23.30'	8	2
23 (948)	54°31.90'	14°26.20'	15	1,2
24 (BA23)	54°33.80'	14°21.80'	21	1
25 (152)	54°38.00'	14°17.00'	30	1
26 (56)	54°40.70'	14°07.80'	27	1
27 (BA15)	54°11.00'	14°40.60'	13	1
28 (23)	54°14.00'	14°38.30'	14	2
29 (43)	54°20.30'	14°52.30'	12	2
30 (BA25)	54°25.70'	14°59.20'	22	1
31 (BA11)	54°02.60'	14°43.10'	10	1
32 (927)	54°06.20'	14°42.30'	11	2
33 (48)	54°10.40'	15°03.80'	17	1
34 (74)	54°14.10'	15°27.20'	16	2

Several comparisons were made to estimate a representative minimum number of sampling units for each grab. An index of precision (D) was calculated with:

$$D = 1/mean*sd\sqrt{n}.$$

The HELCOM-guidelines recommend a D-value < 0.2 to require an acceptable precision of samples (HELCOM, 1988). An index of clumping (b) was measured for a better interpretation of RCL values (b expressed as slope of $sd^2 = mean^b$ indicating 'random distribution' for b = 1, 'some clumping' for b = 1.5, and 'clumped distribution' for b = 2; Elliott & Drake, 1981).

The relationship between the number of species and the number of sampling units (species number 's' = an^b, a is slope, b is intercept) was calculated for stations 3 and 21 for all subsets of samples (means of all possible combinations; Weinberg, 1978). The predictable maximum number of species for these two stations was estimated as the intercept of the function after a reciprocal and linear transformation. Additionally, a cumulative Bray-Curtis-Index of similarity was calculated for the box corer sub samples (means of all possible combinations for increasing sampling area; Weinberg, 1978).

At nine sites choosen for methodological comparisons, 20 species were found in Van Veen grab samples as well as in box corer samples. Table 2.2 shows the presence, abundance and biomass values of all species obtained with the two sampling methods. The small-sized polychaetes *Manayunkia aestuarina* and *Fabricia sabella* were found in greater numbers in box corer samples. Epibenthic crustaceans (e.g. *Gammarus spp.*) occurred in greater numbers in Van Veen grab samples. Higher abundance and biomass values were found in box corer samples for all abundant species, exept for the cockle, *Cerastoderma lamarcki*. Especially with the polychaetes these differences were significant.

No differences were found for the index of precision. D was < 0.2 for all sample means > 100 individuals/m² (equivalent to 3 specimens per sampling unit of box corer samples and 10 specimens per sampling unit of Van Veen grab samples, respectively), except for *M. edulis* and *C. lamarcki* (Table 2.3). The index was always > 0.2 for lower sample means.

The index of clumping (b) of Elliott & Drake (1981) was > 1 for *M. edulis* and *C. lamarcki* (indication of 'some clumping') and equal to 1 for all other species (indication of 'random distribution'). The RCL values for *M. edulis* and *C. lamarcki* are > 100 % of sample means. RCL values of all other species are mainly in a range of 30-60 % of sample means. Differences between grabs are insignificant in most cases. RCL values of abundance means of the amphipod *Corophium volutator*, the baltic tellin, *Macoma balthica*, and biomass means of *C. lamarcki* are significantly larger for box corer samples (Table 3, pairwise t-test, p < 0.05).

Fig. 2.1 shows the relative numbers of species present at stations 3 and 21 in relation to the covered sampling area. The predicted total numbers were 23 and 17, respectively, in April 1993.

The total number of species ever found at these two stations during six sampling cruises in 1993/1994 was 24 and 19, respectively. 69 % and 72 % of the total number of species estimated occurred in the three subsamples of each sampling method at station 3, respectively. 86 % and 82 % of the total number of species estimated occurred in the three subsamples of each sampling method at station 21, respectively.

Furthermore, a comparative size-frequency analysis of the population structure was made for the polychaete *M. viridis* and the bivalves *C. lamarcki*, *M. balthica* and *M. arenaria*. Of *M. viridis* the cohorte of juveniles was never found in Van Veen grab samples. Adult cohorts were more abundant in box corer samples. Only the first two age classes of *M. balthica* were quantitatively less represented in Van Veen grab samples, sieved with a 1 mm sieve. For *M. arenaria* smaller densities were detected for juveniles and also for the oldest age groups (> 10 years old). No typical comparative pattern was found for *C. lamarcki*.

Table 2.2: Occurence of species at 9 stations sampled simulteaniously in April 1993 with box corer/0.5 mm sieve and Van Veen grab/1 mm sieve and differences between abundance and biomass values for infaunal species with a minimum density of 100 individuals/m² given for Van Veen grab samples (expressed as mean percentage of the box corer average; significant values: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

species	occurence box corer (total number of samples)	occurence Van Veen grab (total number of samples)	mean density % ± sd	mean biomass % ± sd
Halicryptus spinulosus	2	2		
Antionella sarsi	3	1		
Eteone longa	1			
Scoloplos armiger	1	1		
Nereis diversicolor	8	7	* 74±29	77±47
Marenzelleria viridis	9	7	*** 52±20	43±13
Pygospio elegans	9	9	*** 43±26	47±24
Streblospio shrubsoli	6	2	*** 3±5	
Manayunkia aestuarina	4	1	*** 2±3	
Fabricia sabella	3	2	*** 2±2	
Gammarus zaddachi	3	4		
Gammarus salinus	5	8		
Corophium volutator	4	5	* 78±8	82±21
Bathyporeia pilosa	2	3		
Hemimysis lamornae		1		
Cyathura carinata	1	1		
Hydrobia ulvae	9	9	*** 57±22	101±34
Cerastoderma lamarcki	7	7	113±54	3745±7709
Mytilus edulis	8	8		
Macoma balthica	8	8	84±65	107±75
Mya arenaria	9	8	77±43	68±57

Table 3: D-values (Index of precision) of density and RCL (relative confidence limit) for density and biomass of dominant species (minimum density used for box corer: 3 individuals per sampling unit; for Van Veen grab: 10 individuals per sampling unit).

| species	box corer D±sd	RCL (%±sd) density	RCL (%±sd) biomass	Van Veen grab D±sd	RCL (%±sd) density	RCL (%±sd) biomass
Nereis diversicolor	0.17±0.11	39±27	68±61	0.15±0.10	39±25	48±20
Marenzelleria viridis	0.19±0.14	38±23	48±26	0.12±0.10	27±29	32±28
Pygospio elegans	0.16±0.07	31±12	41±16	0.15±0.09	54±48	55±46
Corophium volutator	0.21±0.12	52±23	57±23	0.11±0.10	17±16	23±20
Hydrobia ulvae	0.18±0.14	39±29	42±29	0.18±0.08	39±19	52±31
Mytilus edulis	0.48±0.16	85±41	100±62	0.58±0.18	141±50	145±62
Cerastoderma lamarcki	0.30±0.12	56±31	119±67	0.28±0.08	58±14	53±18
Macoma balthica	0.23±0.11	57±33	70±40	0.10±0.07	21±16	37±34
Mya arenaria	0.17±0.10	37±11	74±43	0.14±0.07	33±16	52±39
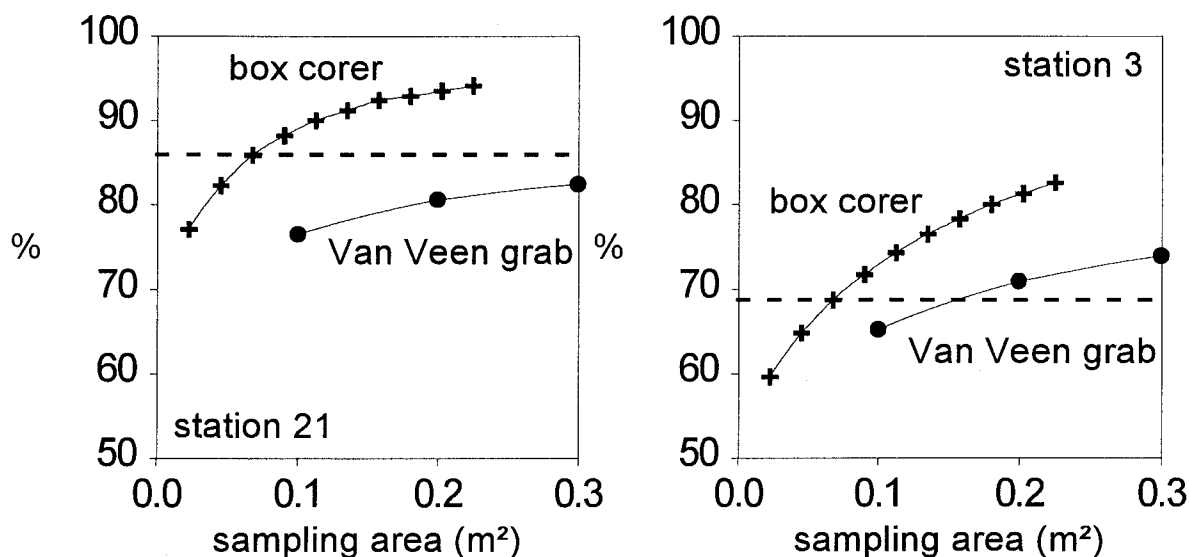
Fig. 2.1: Relationship between the relative number of species and number of sampling units (expressed as sampling area). The predicted total number of species = 100 %, was computed to be 17 at station 21 and 23 at station 3, respectively. The predicted total number is defined as the intercept of a reciprocal and linear transformed function for the box corer data sets. The dotted line shows the percentage value of three box corer subsamples for an easier comparison between methods.

Three subsamples with a size of 0.0225 m² are necessay to cover more than 80 % of the total number of species at sites with less than 20 species. Sites with more than 20 species require five subsamples of the same size to obtain a similar percentage.

Intensive physical disturbance at the sediment surface causes a random distribution pattern for most of the species living in shallow offshore waters (e.g. Gage, 1974). Three sampling units of 0.0225 m² reached relative confidence limits (RCL) of 40-60 % for abundant species (5-10 specimens per sampling unit) and of 20-30% for very abundant species (50-100 specimens per sampling unit). These results agree with estimates of an appropriate number of sampling units in relation to sample means and species clumping (Elliott & Drake, 1981; Holme & McIntyre, 1984).

RCL values for abundances of large species were slightly larger in box corer samples compared to Van Veen grab samples. Data for the small spionid polychaete *Pygospio elegans* presented an inverse result. This effect can be explained by a better adjustment of the catching area of the Van Veen grab to the distribution of large animals, and in the case of *Pygospio elegans* by the smaller sieve mesh size, used for method 2. A minimum of three subsamples with a size of 0.1 m² or five subsamples with a size of < 0.05 m² has to be taken to require biomass RCL values ≤ 50 %. Three box corer sampling units are not enough to ensure biomass RCL values ≤ 50 % for the clumpy distributed cockle. After Elliott & Drake (1981), 5-10 replicates would be appropriate to reach RCL values ≤ 50 %. Again three Van Veen grab subsamples yielded more precise results.

The use of a 0.5 mm sieve is recommended for the collection of small polychaete species, oligochaetes and first-year bivalves at any time of the year. The summer generation of *Bathyporeia spp.* will pass through the meshes of a 1 mm sieve too. The results show also differences in biomass values for the larger polychaetes and *M. arenaria*. These differences are related to the penetration depth of the grabs. Large adults of the polychaetes *Nereis diversicolor* and *M. viridis* are known to burrow 10-20 cm deep in sandy sediments and even deeper in mud (e.g. Esselink & Zwarts, 1989; Zettler et al., 1994; own obs.). They were more quantitatively captured by the box corer which penetrated the sediment on average 5 cm deeper than the Van Veen grab. Although the penetration depth of the Van Veen grab was sufficient to collect most of the large bivalves, they were not sampled quantitatively for the whole sampling area of 0.1m² because of the lower depth range of the grab buckets during the initial penetration. The loss of about 30 % of the total biomass of *M. arenaria* is at the same level as estimated by Brey (1984) who estimated a 40 % loss in his Van Veen grab.

Data treatment: the importance of determining oligochaetes to species level

Species richness is very low in the investigation area. The shallow sandy parts of the brackish Baltic Sea host only about 60-70 species compared with several hundreds of species in marine environments. Not more than 10-20 species occur at a single site. The number increases if oligochaete are taken into account. Their identification requires taxonomic expertise and is very time consuming. Including oligochaete species into statistical analysis can perhaps provide more sensitive discriminations.

In macrofauna monitoring programmes oligochaetes caught using a 1 mm sieve were often not determined to species level. Most taxa living in the Baltic Sea pass through the meshes of the sieve and in many occasions the numbers found do not reflect their true densities in the field. During the data analysis they were usually classified as meiofauna and rejected from the dataset or summarised at higher taxonomic level.

All oligochaetes found in our box corer samples, which had been sieved with 0.5 mm, were determined to species level. We performed MDS ordinations (multidimensional scaling) excluding and including oligochaetes to test wether a dataset with 23 species contains more discriminating information than a set of 19 species or not. We assumed that additonal species cause lower similarity values between stations, but the computed MDS plots were nearly identical (Fig. 2.2) for both data sets and similarity values of the multivariate ordination including oligochaetes were only slightly smaller then those without them.
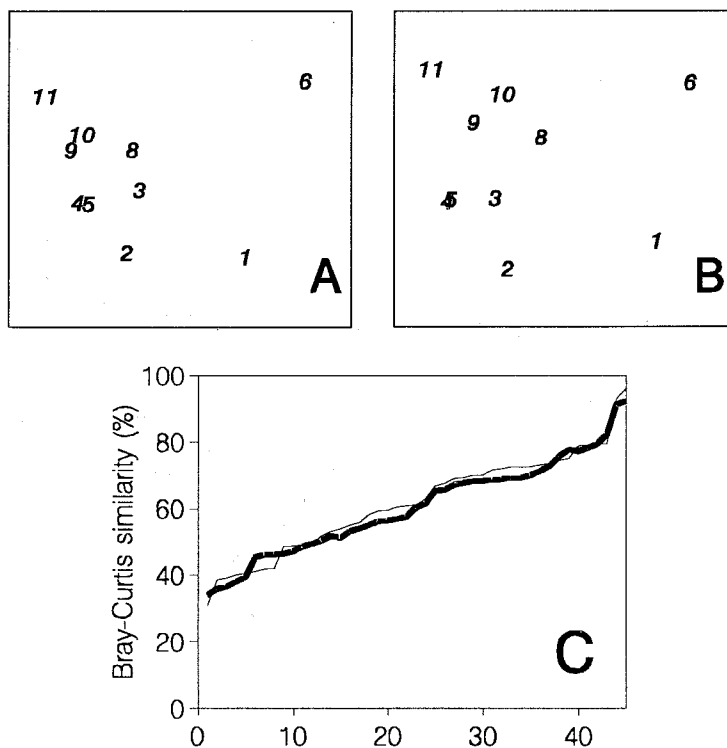

Fig. 2.2: MDS plots (A, B) and ranked Bray-Curtis similarities values (C) for ten sampling sites (45 pairs of comparison, see Fig. 1 in paper 1 for the location of sites). Ordinations were performed with √√-transformed abundances after exclusion of all hyperbenthic species living in *Mytilus*-clumps and *Mytilus edulis* itself. Stress ranges from 0,01 to 0,04. A: box corer data excluding Oligochaetes (19 species), B: box corer data including oligochaetes (23 species), C: thick solid line - box corer data including oligochaete species, thin solid line - box corer data excluding oligochaete species.

Data treatment: *Mytilus*-clumps and related epifauna species

Mytilus-clumps caused various problems during the data analysis. Significant differences were found between subsamples with and without *Mytilus*-clumps by multivariate analyses of abundance data (Fig. 2.3). Total biomass values differed also among subsamples and between sample means of a time series from a single site calculated from three subsamples only. Both three replicate samples of Van Veen grab and box corer supplied RCL values > 100 % for the blue mussel. Own observations with a dredge and video technique and the estimates of Elliott & Drake (1981) for clumped distributed species indicate that a minimum of 10 replicates is required, even for related epifauna species. Especially the occurence of epibenthic amphipodes are related to these patches (Fig. 2.4). Due to the larger sample size epifaunal crustaceans living in *Mytilus*-clumps were sampled more commonly in Van Veen grab samples.
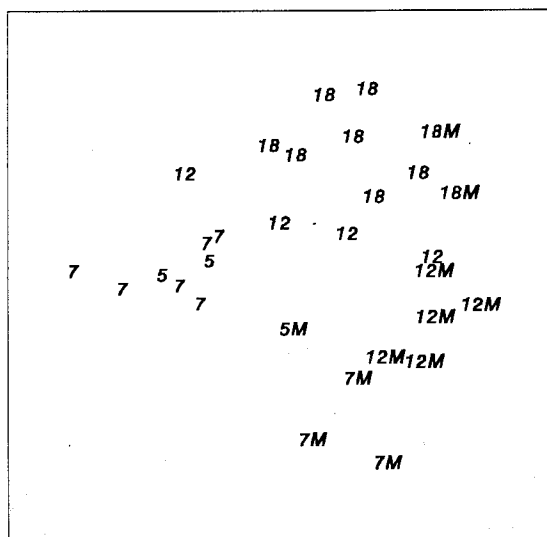

Fig. 2.3: MDS ordination of species √√-transformed abundances for single box corer subsamples from 4 sites with patches of Mytilus-clumps (see Fig. 3.1 in paper 1 for the location of sites). Subsamples containing *Mytilus*-clumps are labeled with M (20 species, Stress = 0,16).

Bathyporeia pilosa
Corophium volutator
Nais elinguis
Jaera albifrons
Gammarus zaddachi
Gammarus salinus
Mytilus edulis
Manayunkia aestuarina
Fabricia sabella
Tubificoides benedeni
Enchytraeidae
Cerastoderma lamarcki
Streblospio shrubsoli
Macoma balthica
Marenzelleria viridis
Pygospio elegans
Hydrobia ulvae
Tubifex costatus
Nereis diversicolor
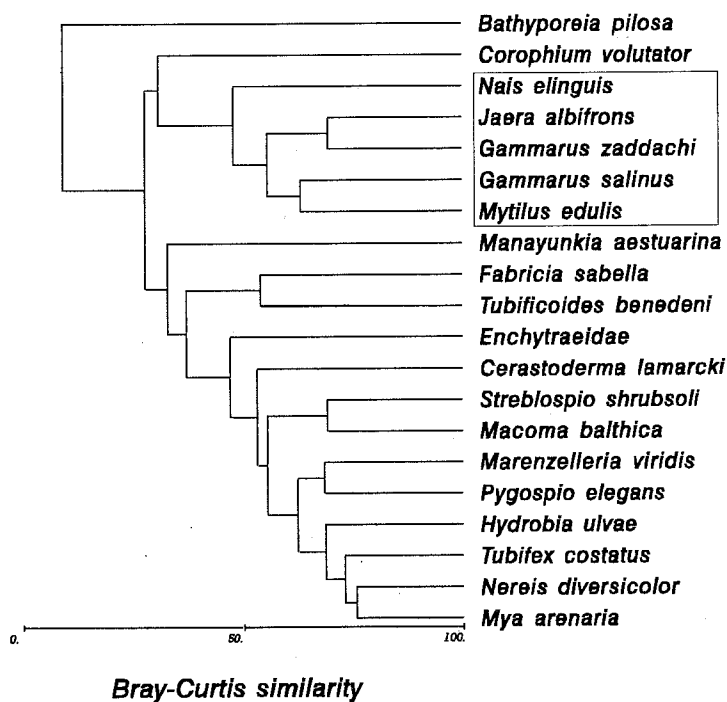Mya arenaria

Bray-Curtis similarity

Fig. 2.4: Dendrogram for hierarchical clustering of 20 species from stations 5, 7, 12, 18 (30 subsamples) with mussel patches. Bray-Curtis similarities calculated on standardized abundance data (minimum used dominance = 1 %).

Data treatment: the repeatability of sites

We compared the means of box corer samples from 7 sites taken in April and October 1993 and April 1994, a period without severe oxygen deficiencies, to get an information about the repeatability of sampling a certain site. The computed MDS (Fig. 2.5) showed pronounced differences between the similarities within the samples of single site. Samples collected at stations A,B,G were more similar to each other than samples taken at site D and F.

Differences in the variability among samples collected from any single site identified by the non-metric MDS are difficult to interprete. Huge variabilities among samples can be caused by problems in geographical and depth positioning of the research vessel (Holme & McIntyre, 1984). Samples of this study were collected with two different research vessels using the same GPS navigation system with an accuracy of ± 20 m. Differences in the practice of positioning were estimated not to be larger than ± 200 m. Depth finding by using echo sounder was possible with an accuracy of ± 0,5 m due to temporal variation in sea level and wave action.

In other cases this variability in itself can be also discussed to be a symptom of perturbated situations (Warwick & Clarke, 1993). Hence, we compared the relative intensity of six abiotic and biotic disturbance factors at each site and an index of relative dispersion between samples, established by Clarke & Warwick (1994). Results are shown in Table 2.4. The data provide a positive relationship between the index of dispersion and the total disturbance value, but this was not very obvious. Probably, variability was mainly caused by problems in depth finding on slopes, because great variability was found at sites D and E (stations 8 and 11). Both sites were located at slopes. Depth measurements varied between the samples for these sites within a range of ± 0,5-1 m. This range is nearly identical to the estimated accuracy of depth measurements due to the variation of the mean sea level and is therefore impossible to improve. Natural community gradients at slopes in the investigated area were obviously to strong along short depth ranges for an appropriate repeatability of the samples.
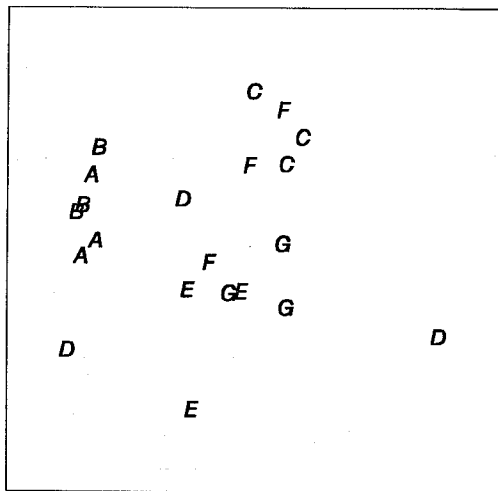

Fig. 2.5: MDS ordination of species √√-transformed abundences for seven stations (A-G). Stations were sampled three times, in April and October 1993 and April 1994. Note the differences in the variability between samples from a single station (23 species, Stress = 0.18).

Tab. 2.4: Index of relative dispersion within three samples from a certain station collected between April 1993 and April 1994 in relation to the relative intensity of various causes of ecological disturbance (the level of a disturbance factor is ranked among the stations). Stations are labelled after Fig. 5 and ranked by the level of their relative dispersion index.

station	Index of relative dispersion	physical sediment turbidity	input of organic matter	oxygen stress	steepness of the sea floor	sea duck predation	density of Mytilus-clumps	Sum of relative disturbance levels
G	0,52	2	6	4	1	1	4	18
B	0,67	6	2	1	1	5	2	17
A	0,76	7	1	2	1	4	5	20
C	0,97	4	3	3	1	2	7	20
E	1,09	1	7	7	2	1	1	19
F	1,18	3	4	6	1	3	6	23
D	1,82	5	5	5	3	1	3	22

Conclusions

Finally, I will give some recommendations for the design of coastal monitoring programms and the analysis of macrofauna data within the shallow parts of the Baltic Sea or comparable low diverse brackish environments:

1. Three subsamples with a size of 0.0225 m² are necessary to cover more than 80 % of the total number of species at sites with less than 20 species. Sites with more than 20 species require five subsamples of the same size to obtain a similar percentage.

2. The use of a deep penetrating box corer is necessary to obtain quantitative biomass values. The biomass dominating species are deep burying bivalves (*M. arenaria, M. balthica*) and polychaetes (*N. diversicolor, M. viridis*). Even a heavy Van Veen grab (70 kg) catches only about 70 % of the total biomass from shallow sandy banks.

3. A minimum of three subsamples with a size of 0.1 m² or five subsamples with a size of < 0.05 m² has to be taken to require biomass RCL values ≤ 50 %.

4. Abundance RCL values ≤ 50 % require only three subsamples with a size of 0.0225 m².

5. The use of a 0.5 mm sieve is recommended for the collection of small polychaete species, oligochaetes and first-year bivalves at any time of the year.

6. Mobile *Mytilus*-clumps and related epibenthic species can not be sampled precisely with less than ten grab subsamples. Dredging and video surveys should be additionally applied.

7. Multivariate analyses should be performed separately for in- and epifauna species.

8. Multivariate analyses are more sensitive than univariate statistics and require not more than three subsamples with a size of 0.0225 m² for a significant separation of sites.

9. Multivariate abundance analyses of data from different sieves should not be compared without considering biomass data.

10. The determination of oligochaetes to species level seems not to be essential for routine monitoring purposes in coastal habitats of the Baltic Sea.

3. Benthic macrofauna communities of the Pomeranian Bay and their variations in space and time
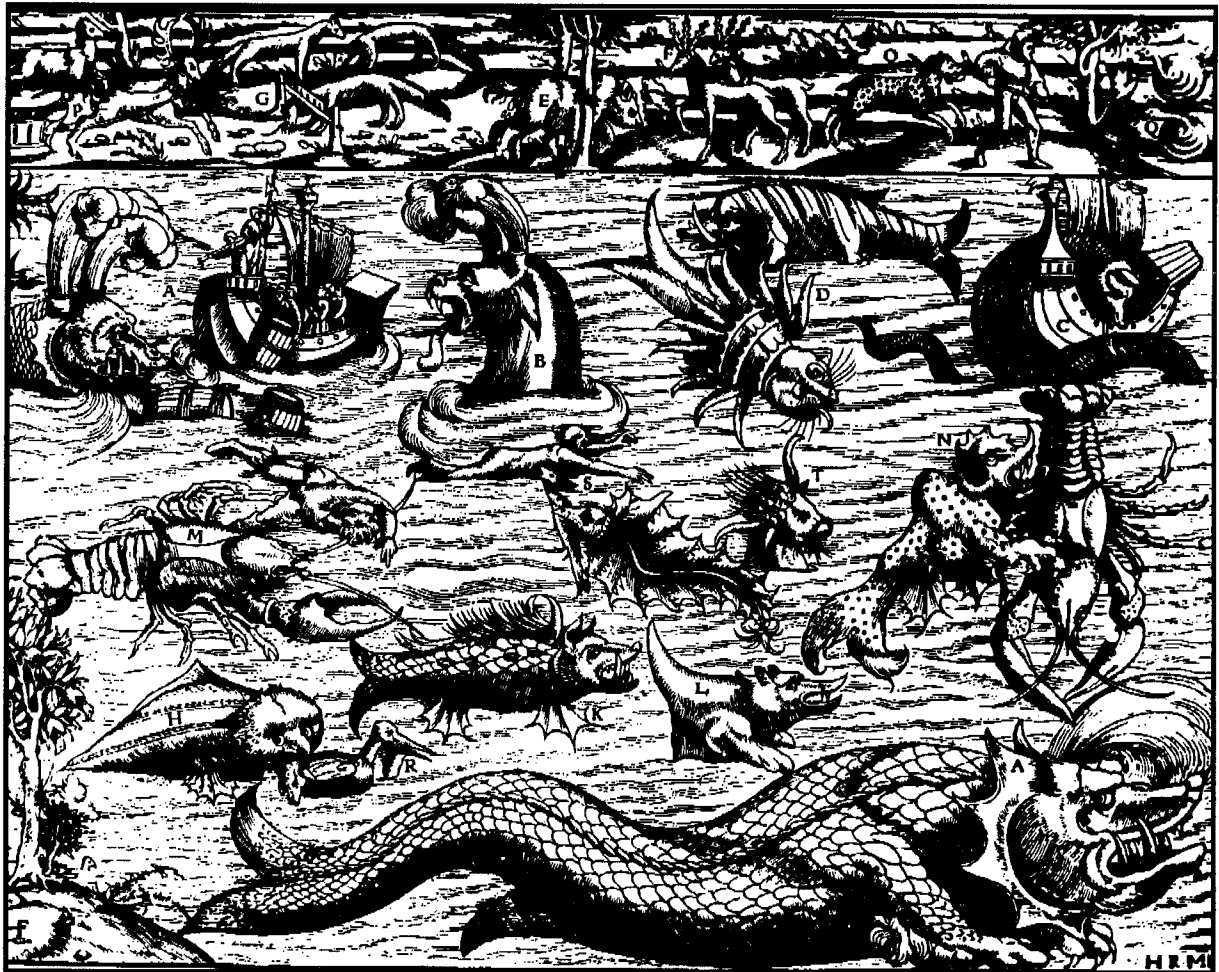
macrofauna of the middle ages; Münster, 1628

Coastal sublittoral sands in the southern Baltic Sea as a habitat for benthic fauna

Salinity is the key factor governing the physiology of the organisms to a large extent. The diversity decreases gradually as the marine nature of the biotope is lost, but increases again as limnetic waters are approached. The diversity minimum is found at salinities between 5-8 ‰ (Remane, 1940). In general, bottom fauna communities in the Baltic Sea are mainly influenced by a horizontal decrease in salinity from about 25 ‰ in the west to about 4 ‰ in the northern gulfs. A strong vertical salinity stratification, with little or no oxygen present below the primary halocline, leads to an oxygen-controlled vertical zonation of the fauna (Andersin et al., 1977; Elmgren, 1978).

Within any certain area or vertical stratum, salinity gradients have only minor effects. Substrate characteristics such as sediment structure, organic matter content, and the presence of macrophytes have a greater influence. There is an agreement on the hierarchy of abiotic and biotic factors controlling macrobenthic communities (e.g. Reise, 1985).

Gage (1974) concluded that in shallow water the faunal distribution is determined primarily by physical exposure together with salinity and temperature, whereas in sheltered waters sediment quality becomes more important. The stress on the benthic animals increases towards the shore due to a decreasing physical stability of the sediments and an increase in temperature varibility (Oertzen, 1973). Species richness is significantly higher at moderate exposed localities than at exposed localities (Persson & Olafsson, 1986). Zonation of species is due to their zoogeographical origin and the capacity to withstand exposure. Abundances are highest in the shallow littoral parts whereas biomass increases with depth due to the dominance of large bivalves (Kube, 1992; Persson, 1983).

Food availability was described to play an important role too (e.g. Beukema & Cadee, 1986; Josefson et al., 1993; Pearson & Rosenberg, 1978). Small-scale variations are often due to biological interactions (e.g. Brey, 1991; Reise, 1979).

Many of the species found during our investigation in the Pomeranian Bay can be characterised by a high tolerance against various environmental factors. They are typical euryhaline, estuarine species. The species composition of macrobenthic invertebrates of the Pomeranian Bay is characteristic for shallow and dynamic sandy parts of the western and southern Baltic Sea. Similar assemblages were described previously by Brey (1984), Blomquist & Bonsdorff (1986), Persson (1983), and Prena & Gosselck (1989).

The importance of hydrodynamic processes and food availability for the structure of macrofauna assemblages in the Pomeranian Bay (Southern Baltic Sea)

Jan Kube, Martin Powilleit & Jan Warzocha

Abstract: Macrofauna community structures were investigated in the Pomeranian Bay (Southern Baltic Sea) in relation to important prevailing abiotic and trophic factors. Quantitative grab samples were collected at 34 sites at depths between 6 and 30 m in 1993/94. 45 species were identified. *Mya arenaria*, *Macoma balthica* and *Marenzelleria viridis* are the most important species in respect to biomass. Mean total biomass values decreased from about 100 g AFDW·m^{-2} in the Southwest of the bay to only about 10 g AFDW·m^{-2} in the North. Multivariate analyses suggest distinct assemblages within the shallow bay and at the slope to the adjacent deeper zones. Loose structuring was found for communities of the shallow parts. They all are dominated by filter-feeders. Surface deposit-feeders are dominant at the northern boundary of the study area adjacent to the Arkona Basin. The small range of sediment variation could not explain distribution pattern of species with a large tolerance for sediment parameters. Physical disturbance and available food supply are proposed to be important in structuring the benthic community. The high biomass values in the southwest of the bay are thought to reflect the high anorganic and organic loads from the Oder River.

Introduction

Macrobenthic invertebrate assemblages of shallow sandy bottoms are an important part of coastal marine biotops. They are nurseries for fishes and feeding grounds for seaducks (e.g. Durinck et al., 1994; Persson & Olafsson, 1986; Pihl, 1982) and play a significant role in the turnover of organic and inorganic matter (e.g. Graf, 1992). Several studies have been published about spatial and temporal distribution pattern of macrofauna species of shallow sandy areas within the Baltic Sea (e.g. Blomquist & Bonsdorff, 1986; Rosenberg, 1984). Food supply was proposed to be one of the most important external factors for large-scale structuring of the communities (Brey, 1984). Fluctuating abiotic factors like physical disturbance, temperature and substratum were found to control species distribution too (Persson, 1983).

The benthic macrofauna of the Pomeranian Bay was studied intensively by Demel & Mulicki (1954) and Löwe (1963). Since then only a few quantitative data exist on the spatial composition of macro-zoobenthos assemblages and species distribution pattern (e.g. Gruszka, 1991a).

However, in the last decades the area has been influenced by increasing anthropogenic discharges (HELCOM, 1993a; 1993b). The excessive nutrient loads caused severe oxygen deficiency in bottom waters of the adjacent Arkona and Bornholm Basin and formed areas with hydrogen sulphide and with reduced diversity in the macrozoobenthos (HELCOM, 1990). A joint German and Polish investigation was started in 1993 to evaluate the impact of the riverine material on the ecosystem of the Pomeranian Bay. Benthic macrofauna studies were carried out in 1993/1994. The present paper describes the recent distribution of macrofauna assemblages in relation to the prevailing abiotic and trophic factors.

Methods

Study area

The Pomeranian Bay is located in the southern Baltic Sea, north of the Oder Estuary. The Oder Estuary, which is the largest estuary of the entire Baltic, is a transition area between the Oder River and the Baltic Poper and forms a system of shallow inner coastal water lagoons (Haffs and Bodden). Shallow sandy bottoms, between 0-20 m water depth, cover an area of more than 8.000 km^2. The

steep edge beyond the 20 m isobath is the northern boundary of the bay to the adjacent Arkona Basin and Bornholm Basin. A 30 m deep narrow channel separates the bay from the shallow Rønne Bank near Bornholm Island. From the southern coast the depths fall to 12 m quickly. The Oder Bank, a large shallow sandy bank of only 7-10 m depth, is located almost in the centre of the bay (Fig. 3.1).

The Oder and Peene Rivers transport about 20 km³/a freshwater into the Pomeranian Bay via several brackish coastal lagoons. 60-70 % of the freshwater input runs through the Swina Mouth in the South of the Bay. The input through the Dziwna in the East and the Peene via the neighbouring Greifswalder Bodden in the West is less important (Lampe, 1993; Siegel et al., 1994).

In general the sediment consists of fine sand, but at some places the sediment is mixed with coarse sand and gravel, especially in the Polish part. The Sassnitz Deep near the Isle of Rugia in the West is very muddy (Neumann & Bublitz, 1969). The salinity of the bottom water varies between 6-8 ‰ near the coast and between 8-10 ‰ in the Sassnitz Deep. A halocline was normally found at the slope to the Arkona Basin between 30-40 m depth and has been rising after a strong saltwater influx in winter 1993 to only 18-25 m depth (Majewski, 1972; Nehring, 1990; Nehring et al., 1994).
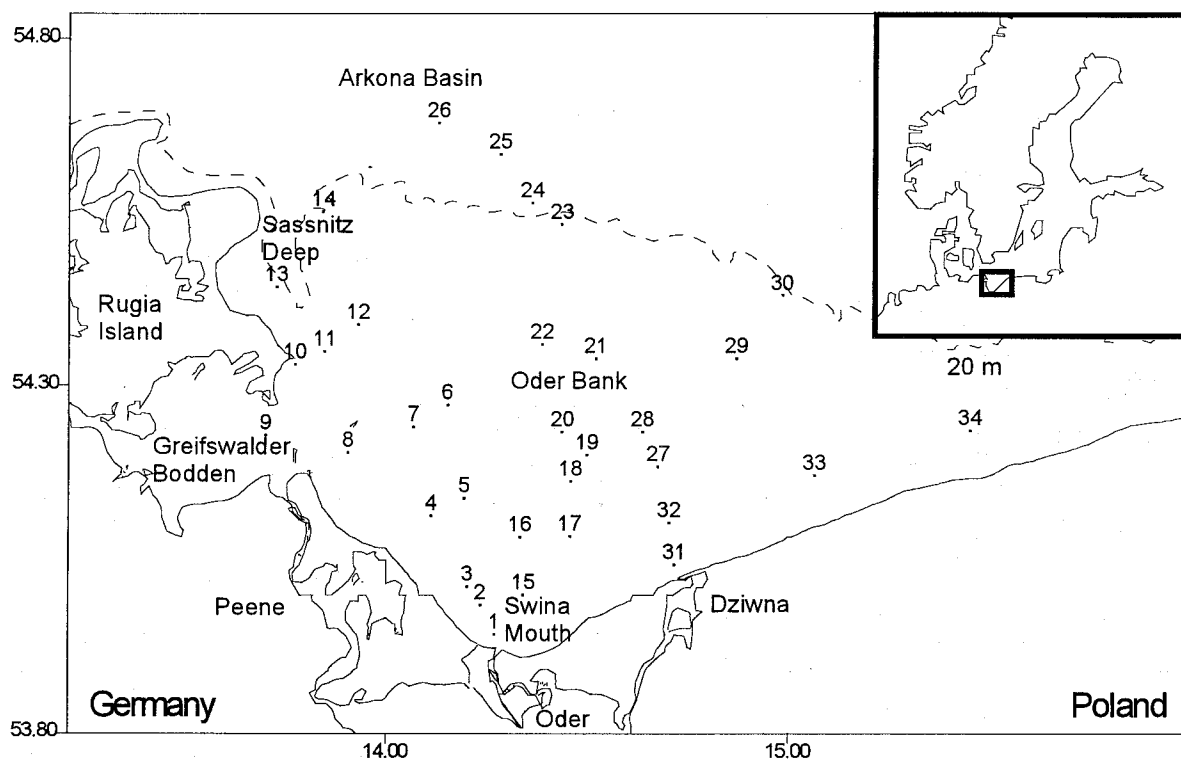

Fig. 3.1: Map of the investigation area and the location of sampling sites.

Sampling programme

Benthos surveys were carried out at 23 stations in late April and at 25 stations in early October 1993 (fig. 1). In total 31 sampling sites were placed randomly within the bay. Two additonal stations were located at the edge to the Arkona Basin and another one at the mouth of the Greifswalder Bodden in the Southwest. A minimum of three replicate samples was taken at each site. Samples were collected with a Van Veen grab (23kg and 70 kg, 0.1 m², 8-12 cm penetration depth) and a modified "Reineck box corer (0.0225 m², 15-25 cm penetration depth). Van Veen grab samples were sieved with a 1 mm sieve and box corer samples with a 0.5 mm sieve. An intercalibration between both sampling techniques was performed at nine sites in April and again at four sites in October (Powilleit et al., 1996).

Sediment cores of the upper 10 cm were taken at selected sites from additional box corer samples for the analysis of sediment parameters. All sediment data represent means of 3-5 samples per station collected between April 1993 and October 1994. Values differed only marginally between sampling cruises.

Sample processing and data analysis

Samples were preserved aboard ship with a 4 % neutral formalin/seawater solution. Organisms were extracted after three months of starvation and staining with Rose Bengal. They were identified to species level, except for oligochaetes, and counted. Oligochaetes were determined to species level in box corer samples only. Hydrozoans, bryozoans and barnacles were excluded from the data analyses. Wet weight and dry weight (after drying for 24 hours at 60 °C) were measured to the nearest 0.1 mg. Ash free dry weight was calculated from dry weight data by own conversion factors (incineration for 12 hour at 500 °C). The conversion factors were in the range of data given by Rumohr et al. (1987).

Several samples contained siphones of the soft-shell clam, *Mya arenaria*, cut by the buckets of the grabs. The width of such siphones was measured to the nearest mm and the size and weigth of the complete specimens were reconstructed from allometric correlation functions calculated for samples from stations 3 and 22 collected in April 1993.

Data of Van Veen grab and box corer samples were combined for the analysis of spatial distribution pattern. Between sampling methods conversion factors for density and biomass data were calculated for both sampling seasons. Estimates of density and biomass means were higher for box corer samples than for Van Veen grab samples in most cases. All small sized polychaete species found in Van Veen grab samples with estimated mean densities of less than 50 % of the estimated means of box corer samples (Powilleit et al., 1996) were excluded from multivariate analyses. The patchy distributed blue mussel, *Mytilus edulis*, and all associated mobile epifauna species (Powilleit et al., 1996) were also excluded. They were not sampled precisely within only three replicates. Because of the patchy distribution of mussel-clumps relative 95% confidence limits were greater than 100% of the mean values. 13 species could be used for multivariate statistics. $\sqrt{\sqrt{}}$-transformed abundances were used for cluster analyses and MDS ordination of stations. Abundance data were standardised for species MDS (Clarke & Warwick, 1994).

Plexiglas tubes of 10 cm inner diameter were used for sediment samplings. Horizontal sediment slices of 1 cm width were sectioned for determination of ATP- and chlorophyll content and for sediment analyses (organic content, median grain size, silt content).

Profiles of the redoxpotential were measured immediately after sampling at intact sediment cores using an Eh-electrode (Ingold, Pt-4800-M5). A value of +100 mV was defined as chemocline (Jørgensen & Fenchel, 1974).

ATP was extracted immediately from 1 cm³ sediment samples aboard ship with TRIS buffer. The extract was stored deep frozen until analysed in the laboratory. ATP was measured with the luciferin/luciferase enzyme system using a ATP-photometer (Graf, 1987; Pamatmat et al., 1981). The amount of ATP (ng·cm⁻³) of the upper 10 cm sediment was integrated for each single core per station and recalculated per one square meter. ATP-content was transformed into biomass (g AFDW·m⁻²) by conversion factors carbon content=200·ATP (Gerlach, 1978) and AFDW=2 carbon content (Van Der Tol & Scholten, 1993).

Samples for pigment and sediment analyses were stored deep frozen too. In the laboratory chlorophyll was analysed according to Edler (1979) adapted to sediments. Organic content was determined as weight loss on ignition at 550 °C after drying to constant weight at 105 °C. Grain size analyses were performed by wet sieving.

Results

Based on the densities of 13 species, three station groups and two single stations were separated using hierarchical clustering. Furthermore, station group 2 was divided into two subgroups a and b (Fig. 3.2). Plotting these groups on the original sampling sites (Fig. 3.3) shows that there is a clear gradient from the Southwest to the Northeast of the bay. The two single sites A/B are located in the Sassnitz Deep. Station groups 1 and 2 are located within the 20 m isobath. They are more similar to each other than to stations of group 3 and sites A and B, which are 20-30 m deep. This is shown also by the MDS analysis, based on the same Bray-Curtis similarity matrix and by superimposing station labels with water depths (Fig. 3.4a and b).
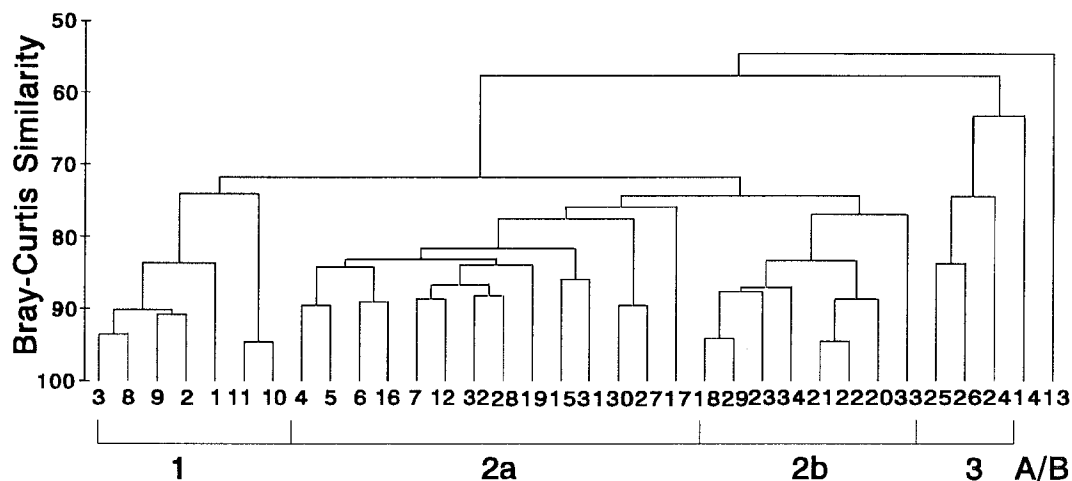
Fig. 3.2: Cluster dendrogram for 34 sites using group-average linking of Bray-Curtis similarities computed for √√-transformed species abundances. Numbers refer to sites (Fig. 3.1).
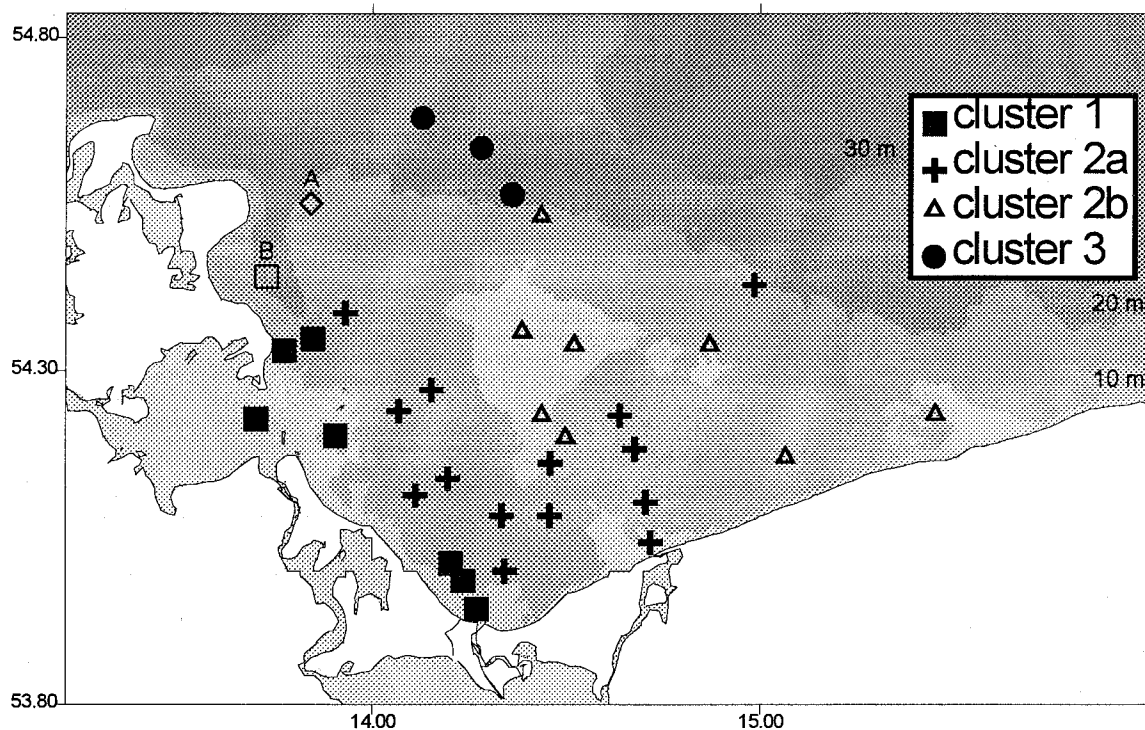

Fig. 3.3: Map showing the spatial pattern of different cluster groups.

The total number of species was highest for cluster group 1 and lowest at sites A/B. Although, 45 different species were found in total, the species composition is quite similar between sites. About 15-25 species were found per station of groups 1-3. Only 5-10 species were found per sample at sites A/B. Ten species show a presence of 100 % (Tab. 3.1). *Sphaeroma hookeri* and *Leptocheirus pilosus* were found only at cluster group 1. *Scoloplos armiger*, *Travisia forbesi* and *Diastylis rathkei* occurred mainly within group 3. This is shown also by the MDS ordination for species (Fig. 3.5). Species are spread along the horizontal axis according to an increasing water depth and along the vertical axis according to an increasing physical exposure. Common and widespread estuarine species are aggregated in the middle of the plot.
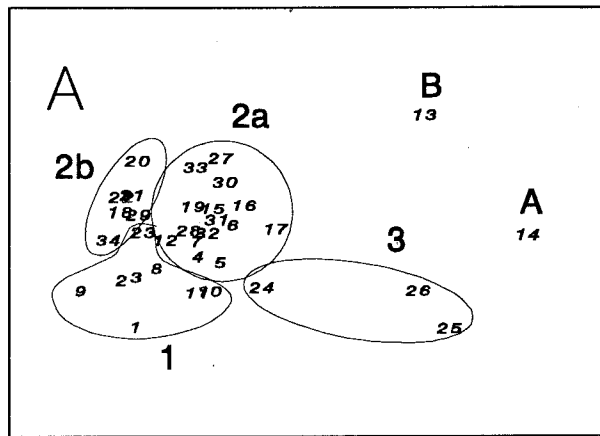
Fig. 3.4: A: MDS plot from Bray-Curtis similarities (stress = 0.15). Numbers refer to sites (Fig. 3.1) or to station groups separated at 72 % similarity level (Fig. 3.2). B: The same MDS with superimposed symbols representing the depth of the sampling locations.
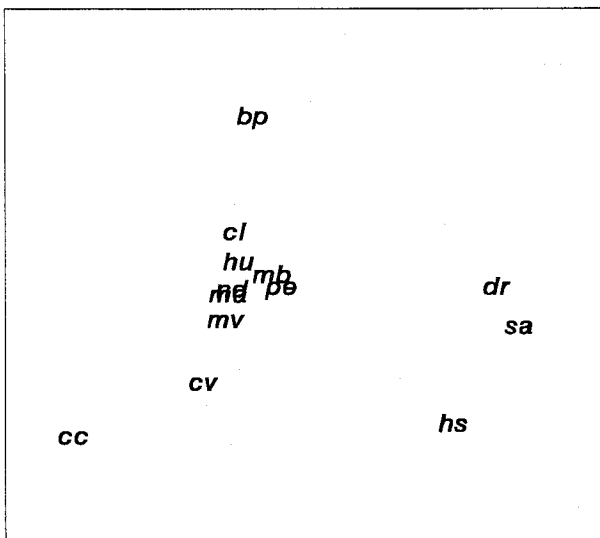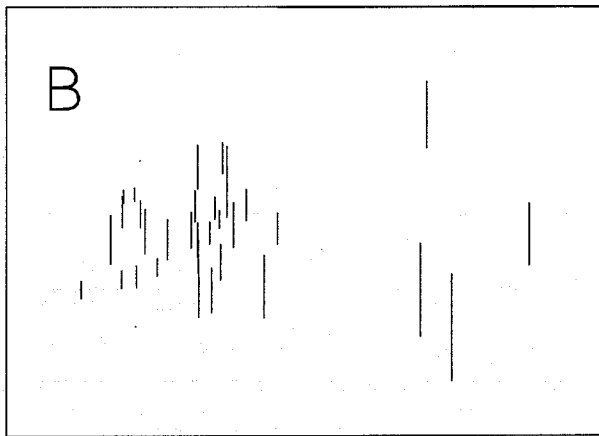
Fig. 3.5: Species MDS from standardised abundances (stress=0.04). Labels repre-sent the following species: hs - *Halicryptus spinulosus*, nd - *Nereis diversicolor*, sa - *Scoloplos armiger*, mv - *Marenzelleria viridis*, pe - *Pygospio elegans*, cc - *Cyathura carinata*, dr - *Diastylis rathkei*, bp - *Bathyporeia pilosa*, cv - *Corophium volutator*, hu - *Hydrobia ulvae*, cl - *Cerastoderma lamarcki*, mb - *Macoma balthica*, ma - *Mya arenaria*.

Tab. 3.1: Species list and presence of benthic macrofauna species in the Pomeranian Bight in 1993/1994 for station assemblages 1, 2a, 2b, 3, A/B separated by cluster analysis (* species rare, ** species common, *** species abundant).

species	presence				
	1	2a	2b	3	A/B
Priapulida					
Halicryptus spinulosus	*			**	*
Nemertini					
Lineus spec.		*	*		*
Prostoma obscurum	*	*	*		
Oligochaeta					
Enchytraeidae	**	**	***	*	
Nais elinguis	*	*	*		
Paranais litoralis	*	*	*		
Tubifex costatus	***	***	***	**	*
Tubificoides benedeni	**	***	*	***	***
Polychaeta					
Eteone longa		*		*	
Antionella sarsi		*	*	*	
Nereis diversicolor	***	***	***	***	*
Neanthes succinea	*				
Scoloplos armiger				**	*
Travisia forbesi				*	
Arenicola marina					*
Polydora ligni	*				
Pygospio elegans	***	***	***	***	***
Streblospio shrubsoli	***	***	**		
Marenzelleria viridis	***	**	**	*	
Fabricia sabella	*	**		**	
Manayunkia aestuarina	***	**			
Crustacea					
Mysis mixta				**	**
Praunus inermis				**	**
Hemimysis lamornae			*		
Neomysis integer	**	**			
Idotea chelipes	*				
Cyathura carinata	*				
Saduria entomon		*		*	
Sphaeroma hookeri	*				
Jaera albifrons	**	**		*	
Diastylis rathkei				***	
Amphithoe rubricata		*			
Leptocheirus pilosus	**				
Bathyporeia pilosa		*	***		
Bathyporeia pelagica (?)			*		
Gammarus oceanicus	*				
Gammarus salinus	***	***	**	***	*
Gammarus zaddachi	***	***	*	**	
Corophium volutator	***	**	*		
Crangon crangon	**	**	**	**	**
Mollusca					
Hydrobia ulvae	***	***	***	***	*
Cerastoderma lamarcki	***	*	***	*	
Mytilus edulis	***	***	**	***	***
Macoma balthica	***	***	***	***	***
Mya arenaria	***	***	***	*	*
Σ	31	29	24	25	15

Station groups were plotted against abiotic and biotic factors in order to find out which environmental variables are responsible for the clustering of stations (Fig. 3.6). Clusters were orde'red with increasing distance from the Swina mouth: 1, 2a, 2b, A/B, 3. Figure 3.6 also shows the results of the statistical comparisons between factor means of station groups (Mann-Withney U-test). A Kruskal-Wallis one-way analysis by ranks was run to select significant impacts of single factors (Tab. 3.2).
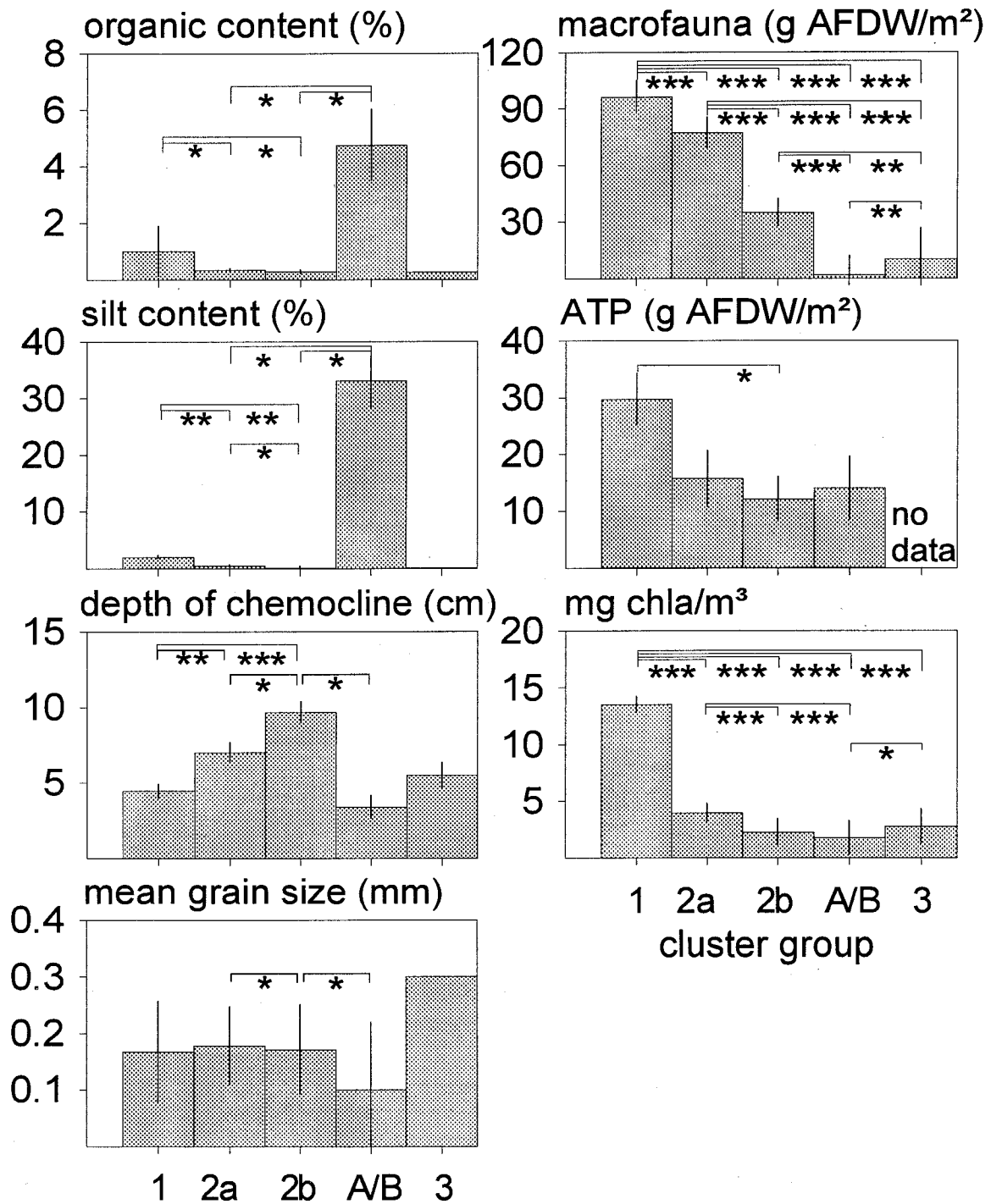

Fig. 3.6: Values of abiotic and biotic environmental factors (mean values ± se) per cluster groups 1, 2a, 2b, A/B, 3: organic content (expressed as % loss of ignition), silt content (% of the fraction < 63 μm), depth of the chemocline in the sediment (expressed as depth range of the +100 mV redoxcline) and median grain size (mm), total macrozoobenthos biomass (g AFDW), ATP-biomass (g AFDW) of the upper 10 cm sediment layer, Chla concentration ($mg\,m^{-3}$) of the overlaying water surface (summer means 1992-1994). Significant differences between means are indicated (Mann-Withney U-test; * p< 0.05, ** p<0.01, *** p< 0.001).

All tested variables showed significant effects. There were no differences between the sediments of groups 2a, 2b and 3. All sites were characterised by fine sand, very low organic contents and a deep penetrating chemocline. The muddy and less oxyginated sediment of sites A/B was clearly selected from all other clusters. Significant differences appeared also between the silt content and the depth of the chemocline between group 1 and groups 2a, 2b.

All measured biomass values decreased from the Southwest to the Northeast of the bay (R^2 of Person correlation coefficients 23.5-49.5 %, Tab. 3.2). Significantly highest mean summer concentrations of chlorophyll a in the water column of 10-20 mg Chl a·m⁻³ were observed at stations of group 1 compared to other groups. The mean summer value of group 2a was nearly twice as high as values of groups 2b, 3 and sites A/B. Mean values of groups 2b, 3 and sites A/B were ranging from 1-3 mg Chl a·m⁻³ and were very similar to each other. Comparable gradients were visible for the total macrobenthic biomass values and ATP-biomass values. ATP-biomass values ranged from 12.1 g AFDW·m⁻² on the Oder Bank to 29.7 g AFDW·m⁻² off the Swina Mouth. The total biomass was highest at the river mouths with almost 100 g AFDW·m⁻². About 60-85 % of the macrobenthic biomass of clusters 1, 2a and 2b belonged to soft-shell clams, *M. arenaria*. Plotted mean dominance values of *M. arenaria* decreased with distance from the river mouths and *Macoma balthica* dominance values increased from group 1 to group 3 (Fig. 3.7).
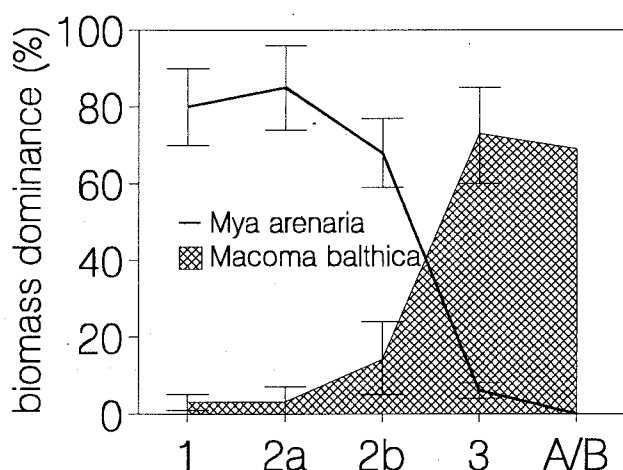

Fig. 3.7: Dominance values (means ± se) of *Mya arenaria* and *Macoma balthica* per cluster groups 1, 2a, 2b, A/B, 3.

Tab. 3.2: Results of a Kruskal-Wallis one-way analysis by ranks between cluster groups and environmental factors.

environmental factor	p	R^2	n
organic content	0.010	4.6	26
silt content	0.001	15.1	26
depth of chemocline	0.001	1.1	34
mean grain size	0.046	0	26
total macrofauna biomass	0.001	49.5	64
ATP biomass	0.081	23.5	23
summer chla concentration	0.001	24.7	204

Discussion

Macrobenthic communities and their structuring processes have been studied intensively during the last decades (e.g. Pearson & Rosenberg, 1987). Reise (1985) proposed a hierarchy of several biotic interactive levels following abiotic control in tidal flats. Although physical disturbance is known to play the key role in community development and succession, bioturbation is another important factor causing small-scale physical disturbances (Brey, 1991).

There are several references in which marine sub-tidal benthic fauna composition has been related to physical processes and food availability. Both, large-scale and small-scale pattern were studied (e.g.

Arntz et al., 1976; Duineveld et al., 1987; Rhoads & Young, 1970; Rosenberg, 1995). Our methods used to describe the structure of macrofauna and their relationship to environmental parameters can be used for the interpretation of large-scale differences only. They express the importance of depth for separating the community of the Pomeranian Bay from the assemblages of the Baltic Proper. The change of the water depth is combined with vertical changes of several abiotic variables like salinity, temperature, oxygen saturation and exposure. The concentration of organic matter in the water column attenuates with depth too. All these factors change rapidly beyond the northern slope of the Pomeranian Bay at the 20 m isobath (Nehring et al., 1994; Siegel et al., 1994).

Sediment characters like silt content and oxygen saturation are very important causes for the segregation of the community of stations A/B in the Sassnitz Deep. The depth range of the chemocline is very low. Number of species and total invertebrate densities and biomasses are very small at these sites. They are clear signs of irregular events of oxygen deficiencies (Heip, 1995; Pearson & Rosenberg, 1978).

Only loose structuring was found within the Pomeranian Bay community. Many of the occuring species have a large tolerance for sediment parameters, especially in relation to the small range found in the cluster groups 1, 2a, 2b (Remane, 1940). The presence and density of species is mainly determined by hydrodynamic conditions and the available food supply. The gradient of physical disturbance seems to be responsible for the presence or absence of a single species, as shown by the species MDS. Whereas the isopods *S. hookeri* and *Idotea chelipes* occurred only in the shelter inner coastal lagoon providing benthic macrophytes, the amphipod *Bathyporeia pilosa* was restricted to the exposed sandy Oder Bank.

Quality and quantity of the available food is likely to control species densities in shallow coastal waters (Beukema & Cadee, 1986; Brey, 1984; Meire et al., 1993). A direct coupling between pelagic primary production and consumption in the benthic system was proposed by Hargrave (1973). Biomass values of large filter feeding bivalves with a long life span present an average figure of the pelagic food supply. They integrate the effects of short-time and seasonal food pulses to the sea floor (Graf, 1992). In the Pomeranian Bay total invertebrate biomasses were highest nearshore closed to the river mouths (station group 1), where the transparency of the water column is low. The water carries a large amount of phytoplankton and other riverine loads (Bodungen et al., 1995). The bivalve *M. arenaria*, an obligatory filter-feeder, covers 80-90 % of the total invertebrate biomass, followed by facultative filter-feeding polychaetes *M. viridis* and *Nereis diversicolor*. Own qualitative observations on the food selection of *M. arenaria* showed a similar phytoplankton species composition for the stomachs of clams and the bottom near water layer. Hence, the benthic food chain of the Pomeranian Bay is mainly phytoplankton-based.

Local wind forces dominate the distribution pattern of the riverine pelagic constituents in the bay (Siegel et al., 1994). Distinct wind directions are producing characteristical phytoplankton distribution pattern. During the maximum freshwater outflow in spring after the snow melt the wind statistics is dominated by easterly directions. They guide the river water along the southwestern shorelines into the Arkona Basin. Westerly winds force the river water along the eastern shore during the rest of the year mainly (Siegel et al., 1994). However, there is usually a gradual decrease in phytoplankton concentration between the southwestern shore and the center of the bay. This gradient causes a corresponding gradient of decreasing biomass dominance values of *M. arenaria*. Hence, the decrease in phytoplankton concentration from station group 1 to group 2a is followed by a similar decrease in mean total invertebrate biomass. Both infauna clusters are dominated by filter-feeders. Biomasses of the epibenthic filter-feeding blue mussel *M. edulis* are highest at station groups 1 and 2a too (Powilleit et al., 1996). There is also a significant difference in the phytoplankton concentration between groups 2a and 2b and the mean total biomass of group 2a and group 2b.

An increasing dominance of the bivalve *M. balthica*, a facultative surface-deposit-feeder, indicates a change of the trophic structure of the community between cluster 2a and cluster 2b. Sampling sites of station group 2a were located mainly in the southwestern part of the Pomeranian Bay at 13-15 m water depth. The bottom zone is probably aphotic due to secchi depth of only 2-5 m. Sites of station group 2b were located mainly on the Oder Bank. The exposed sandy bank is very shallow (7-10 m depth). A high transparency of the water column presents an euphotic bottom biotop and allows the settlement of benthic diatoms. Chlorophyll a concentrations in the upper 3 cm of the sediment were found to be 1-2 $\mu g\,g^{-1}$ sediment DW at stations of group 2b instead of 0.3 $\mu g\,g^{-1}$ sediment DW at sites of groups 1 and 2a. Benthic diatoms present an extra food supply for macrobenthic invertebrates, especially *Pygospio elegans* and *B. pilosa*, and also for other benthic organisms. The high ATP-biomass values at stations of group 2b represent nucleotides of diatoms, bacteria, protozoans and

meiofauna (Graf, 1987). Thus, although the phytoplankton concentration is low on the Oder Bank, high benthic biomasses of heterotrophs occur because of the additional benthic primary production. The biomass portion of deposit-feeders is increasing from 5 % in groups 1 and 2a to 20 %.

The difference in phytoplankton is negligible between groups 2b, 3 and sites A/B. It is likely that other factors than phytoplankton concentration contribute to the absence of *M. arenaria* and the 80 % dominance of deposit feeders at sites A/B and group 3. Stations A/B and sites of the group 3 are much deeper than stations of group 2b. Lassig (1965) supposed that *M. arenaria* is restricted in the Baltic Sea to shallow waters above 20 m depth due to too low water temperatures near the sea floor during the growing season. However, this hypothesis can not fully explain the recent distribution pattern of *M. arenaria* in the Pomeranian Bay, because Löwe (1963) reported high clam densities north of Rugia Island down to 30 m depth. Lower bottom near oxygen saturations at the deeper sites during summer in recent years might be an important cause of the gradient change in the species composition. Otherwise, we suppose that particle fluxes at sites of cluster 3 are mainly dependent on vertical sedimentation and stochastic lateral transport events. Vertical mixing processes are more intensive in the shallow parts of the bay. The weaker currents and wave energy at the bottom near layer are, the stronger is the extent of depletion of POM by benthic filter-feeders (Frechette & Bourget, 1985). Wave induced current velocities at the sediment surface also cause resuspension events more regular at depths between 10-15 m than at depths between 20-30 m. Hence, short-time seasonal food pulses are probably longer available to filter-feeders at stations of group 1, 2a and 2b than at stations of group 3 and sites A/B (e.g. Graf, 1992). The enrichment of the benthic macrofauna of the Pomeranian Bay by the Oder River nutrients is considered to be restricted, therefore, to western and southern coastal areas.

Acknowledgements

Long-term changes in the benthic communities of the Pomeranian Bay (Southern Baltic Sea)

Jan Kube, Fritz Gosselck, Martin Powilleit & Jan Warzocha

Abstract: Long-term changes in the macrofauna of the Pomeranian Bay were studied by comparing survey data from the 1950s, 1980s and 1990s. The study area has undergone significant eutrophication. Riverine nitrogen loads were five times higher in the 1990s than in the 1960s. Phytoplankton and primary production have roughly doubled during the last 20 years. Accumulation of organic matter was observed in sediments only locally. Biomass of filter-feeding bivalves increased significantly. Spatial distribution patterns of the investigated species have changed. Strong decreases in species richness were caused by oxygen depletion at stations deeper than 15 m. *Saduria entomon, Monoporeia affinis* and *Pontoporeia femorata* vanished entirely between 1981 and 1993. Although a causal relationship between simultaneous increases of nutrient levels and macrobenthic biomass cannot be verified, eutrophication is proposed to be the major process affecting changes in macrofauna assemblages. In addition, changes in hydrography and climate increased frequency and severity of oxygen depletion events in the Pomeranian Bay since the mid 1980s.

Introduction

Several attempts have been made to explain long-term changes in the macrozoobenthos of the Baltic Sea. Severe biomass reductions or even macrofauna death were often observed below the halocline. A general change from bivalve-dominated towards polychaete-dominated communities was documented in the deeper parts of the southern Baltic (Andersin et al., 1978; HELCOM, 1990). The oxygen concentration of the deep water has started to decrease by the end of the 19th century and reached almost negligible concentrations in the early 1990s. This anoxia has been attributed to both man-made eutrophication and climatic changes (e.g. Fonselius, 1972; Gargas et al., 1978; Gerlach 1994).

Many authors described also a significant increase in macrofauna biomass above the halocline as a consequence of higher food supplies (Brey, 1986; Cederwall & Elmgren, 1980; Pearson & Rosenberg, 1978;). However, since 1980 oxygen depletions caused strong fluctuations of the benthic biomass also in several shallow bays during periods of strong stratification (Gosselck & Georgi, 1984; Weigelt & Rumohr, 1986). The observed remarkable changes in community composition were supposed to be caused by an increase in organic inputs to the sediment due to eutrophication and a change of hydrographic conditions (Prena, 1994; Weigelt, 1991).

This paper describes long-term changes in the macrozoobenthic communities of the Pomeranian Bay by comparing the 1950s with the 1980s and 1990s. The Pomeranian Bay is a shallow transition zone between the Oder Estuary and the deeper Arkona and Bornholm Basins (Fig. 3.8). Due to its topography and hydrography, recent macrofauna communities are influenced by both, an increase in organic riverine loads and severe oxygen depletions in the deeper basins. The aim of our study is to discuss the long-term changes in the macozoobenthos in relation to fluctuations and long-term trends in the environmental conditions.

Material and methods

The history of quantitative benthos research in the large shallow sandy bay north of the Oder Mouth extends over a period of 70 years. Hagmeier (1926; 1930) intensively sampled the area between 1924-1931. Unfortunately, his data were never published properly and got lost in 1944 (Rumohr, 1987). 20 years later, 13 Stations were sampled in the eastern part of the Pomeranian Bay by Demel & Mulicki in 1949 and 1951 (Demel & Mankowski, 1951; Demel & Mulicki, 1954). An intensive quantitative survey was carried out by Löwe (1963) in the western part between 1955 and 1958. Since then only a few quantitative data exist on the spatial composition of macrozoobenthos assem-

blages and species distribution patterns in nearshore regions (e.g. Gruszka, 1991a; Warzocha, 1995). Macrozoobenthos was investigated more recently in adjacent coastal and offshore parts of the Baltic (HELCOM, 1990). Gosselck (1985) studied the macrofauna of the southern Arkona Basin. Geisel & Messner (1989) presented an overview on invertebrate communities of the Greifswalder Bodden. The soft-bottom macrofauna of the Szczecin Lagoon was investigated by Maslowski (1992).
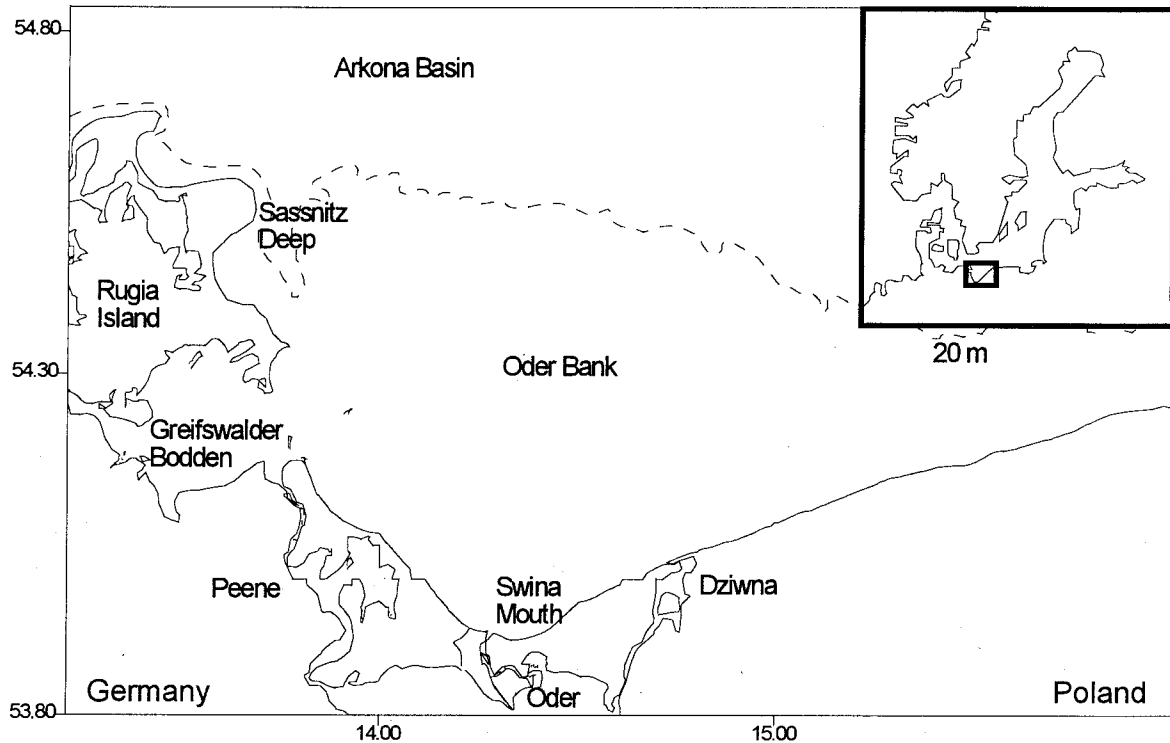

Fig. 3.8: Map of the area under investigation.

A joint Polish and German investigation was started in 1993 to evaluate the impact of the riverine material on the ecosystem of the Pomeranian Bay. Macrobenthic studies were carried out as a part of this investigation between 1993-1995 with three sampling cruises each year in spring, summer and fall.

We compared original data from four studies carried out from 1955 to 1958 (Löwe 1963), from 1980 to 1982 (Gosselck, 1985; Warzocha, 1995) and in 1993 (Powilleit et al., 1996). In all studies a heavy 0.1 m² Van Veen grab, a sieve with 1 mm mesh size and 4 % formalin for storage were used. All investigators collected three samples at each station and date. Samples were collected at depths between 6-30 m. The data sets compared here are based on 58 stations sampled by Löwe (1963), 23 stations sampled by Gosselck (1985) and Warzocha (1995) and 35 stations sampled by Powilleit et al. (1996). Sampling sites differed between investigation periods (Fig. 3.15). Samples were mainly collected in April/May and October/November. About 20 % of the samples were taken in July/August. We do not know how much grabs used during different periods of investigation differed regarding to penetration depth and the strength of shock wave.

We excluded all small polychaetes and the mud snail *Hydrobia ulvae* from the data analyses to lower the impact of seasonal density variations. However, densities of all macrofauna species were observed in the early 1990s to vary strongly from one sampling cruise to the next, but seasonality could not explain any of these fluctuations convincingly (Fig. 3.9). According to the late spatfall and the slow growth rates, juvenile bivalves did not affect density estimates in fall. They usually passed through the 1 mm sieve even in November (Powilleit et al., 1996). All infaunal species, burying much deeper than 5 cm, were excluded from the analyses too. Square root-transformed abundances of 14 species were used for cluster analysis (group averaged Bray-Curtis similarities; Clarke & Warwick, 1994).
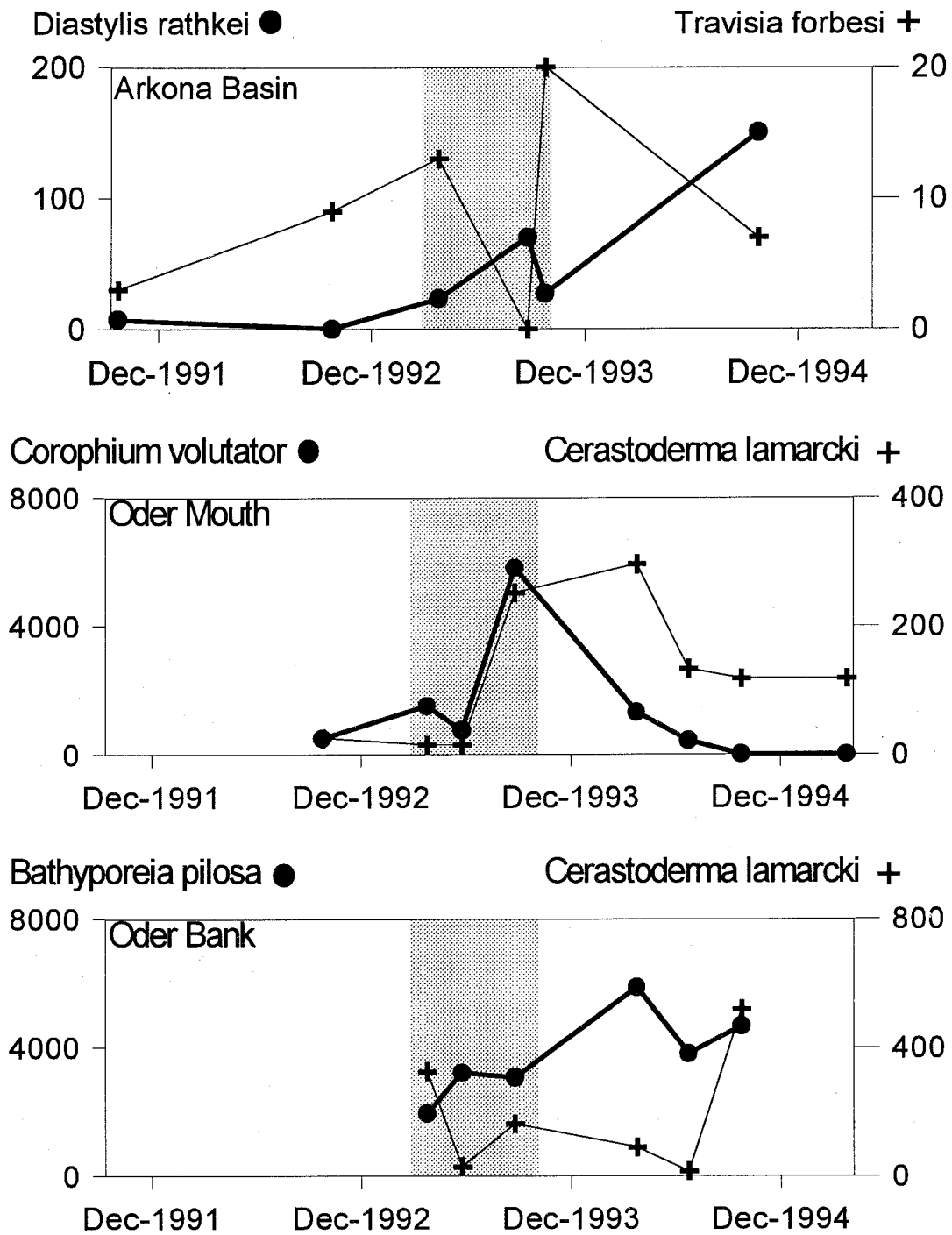
Fig. 3.9: Examples of density fluctuations (ind. m⁻²) of benthic invertebrates at three stations in different parts of the Pomeranian Bay in the early 1990s. Note, that trends in densities of *Cerastoderma lamarcki* differ remarkably between the Oder Bank and the Oder Mouth. The shaded bar indicates the sampling period of Powilleit et al. (1996).

The species that were used for the cluster analysis are representatives of all four major habitat types of the study area, i.e. the deeper parts at the slopes of the adjacent Arkona and Bornholm Basins, the exposed shallow sandy central parts, and the sheltered river mouth. This is shown by a cluster analysis for species based on the same data set (Fig. 3.10). Unfortunately, we are unable to quantify numerical changes in species densities, mainly due to the observed large short-term fluctuations in

abundances. Therefore, we used species distribution maps to show qualitative changes. The distribution maps were computed by kriging with WINSURF software package.
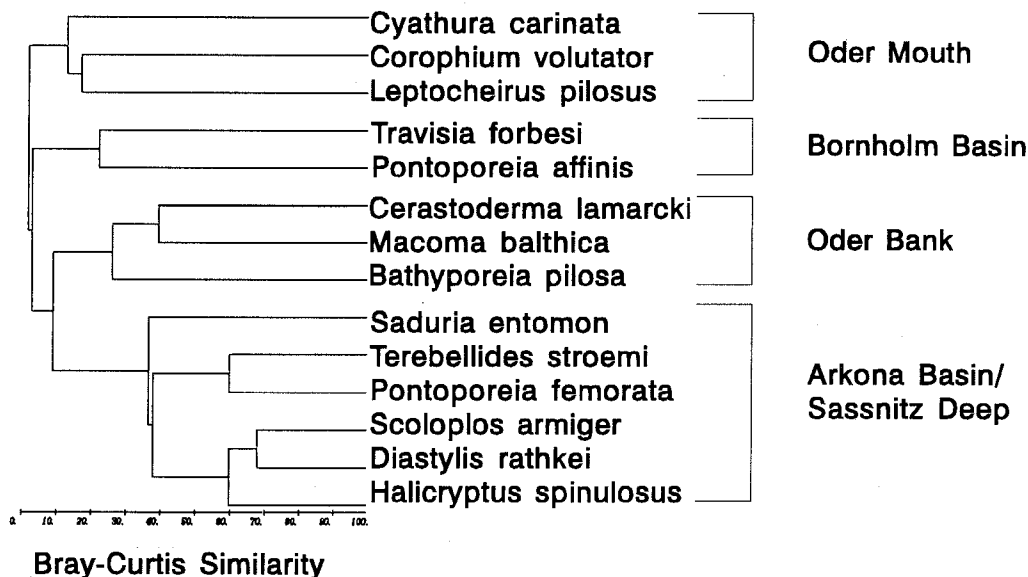

Bray-Curtis Similarity

Fig. 3.10: Dendrogram using group-average linking on Bray-Curtis species similarities from standardized abundance data. The four groups defined at arbitrary similarity level of 10 % reflect their core distribution areas (see also Figs 3.16-3.18).

Biomass comparisons were restricted to the bivalves *Mytilus edulis*, *Macoma balthica* and *Mya arenaria*. These species account for the largest share of the total zoobenthic biomass in the Pomeranian Bay. They are characterized by a longevity of more than ten years and a low P/B ratio.

Bivalve biomass data of Löwe (1963) were recalculated by allometric shell length-ash free dry weight (AFDW) relationships for samples taken in April 1993 (Kube & Skov, in prep). Biomass data of Gosselck (1985) and Warzocha (1995) were excluded from the analysis. These studies do not present length measurements in bivalves.

Results

Long-term variability of environmental factors

Oceanography: Both, salinity and oxygen conditions at the sea floor of the study area depend mainly on water mass transport and stratification processes. The water column in the Pomeranian Bay is usually well mixed down to a depth of about 15 m by wind forcing. As a consequence, fresh water supplied by the river runoff affects the entire water column (Trzosinska & Cyberska, 1992). There is a strong negative relationship between runoff data of the Oder River and annual salinity means (Fig. 3.11, r=-0.7, p< 0.05, n=41). Annual salinity means showed no trend within the last 40 years. Values fluctuated between 6-8 ‰ near the Oder Mouth and 7-9 ‰ on the Oder Bank (Cyberska, 1992; Cyberski, 1992; Nehring, 1990).
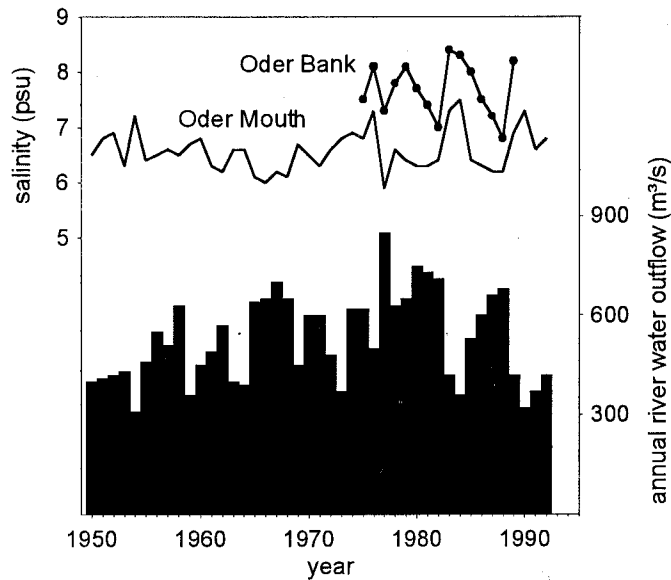
Fig. 3.11: Fluctuations in annual freshwater runoff and in mean annual salinity near the Oder Mouth and on the Oder Bank between 1950 and 1992 (redrawn from Cyberska, 1992; Cyberski, 1992; Nehring, 1990).

A strong vertical salinity gradient occurs at the steep northern edges of the bay, bordering with the adjacent Arkona and Bornholm Basins. The 10 ‰ halocline is known to fluctuate there between 15-35 m depth near the Arkona Basin and 40-60 m depth near the Bornholm Basin. Changes in halocline depth depend mainly on the frequency and intensity of the inflow of highly saline water from the Kattegat into the Baltic Sea (Matthäus & Lass, 1995; Nehring & Matthäus, 1991/92; Nehring et al., 1994). Occasionally, upwelling-like events are responsible for an uprising of the halocline in the southern part of the Arkona Basin. Upwelling occurs when easterly winds force coastal surface waters offshore. As a result, deep water from the Arkona Basin propagates into the bay via the Sassnitz Deep, a former part of the Oder River bed. Such upwelling events sometimes cause strong stratification in the western part of the Pomeranian Bay at depths between 10 and 15 m (Lass, pers. comm., own obs.).
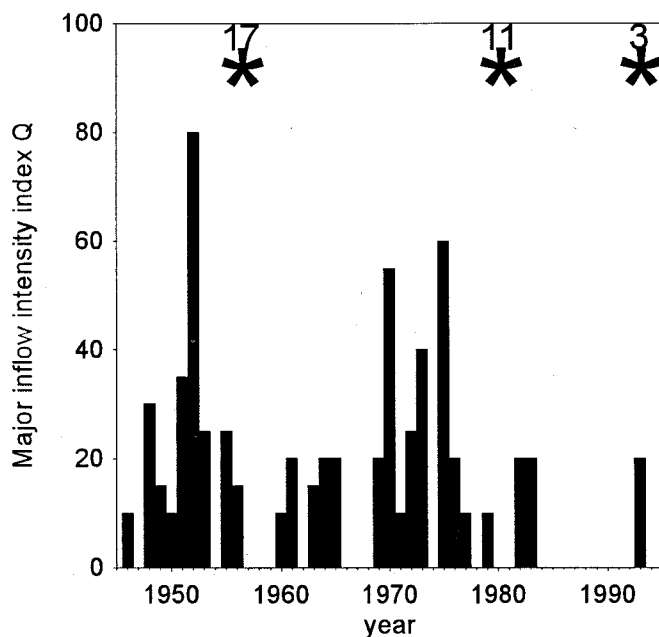

Fig. 3.12: Intensity index of inflows of highly saline water into the Baltic Sea (annual maximum) between 1946 and 1993 (redrawn from Frank & Matthäus, 1982, see Matthäus & Franck, 1992 for calculation of the index). Asterisks indicate benthos investigations. Values above the asterisks give the total number of major inflow events for the ten year periods preceding each benthos investigation.

The highly saline water inflowing from the North Sea during the winter is oxygen-rich. The oxygen of the highly saline deep water is depleted during periods of stagnation. Hence, the oxygen concentration of the deep water below the halocline depends both, on biological activity and on the frequency and intensity of major inflows. Until the 1970s major inflows were observed more or less regularly (Fig .3.12). They occurred usually in groups covering several years. Gaps between successive inflow events lasted up to four years. Seventeen major inflow events were observed within a period

of ten years preceding the investigations of Löwe (1963), and eleven inflows occured within the ten years before the studies carried out by Gosselck (1985) and Warzocha (1995). Since the mid 1970s, the frequency and intensity of major inflows have decreased. Only three events occurred within the ten years before the investigations of Powilleit et al. (1996). The long lasting stagnation period since 1983 resulted in extreme decreases of oxygen concentrations in the Bornholm Deep and, during summer, even in the Arkona Basin (Franck & Matthäus, 1992; Nehring, 1990; Nehring & Matthäus, 1991/92; Nehring et al., 1994). The stagnation period was interrupted in January 1993, only three months before the recent macrofauna investigations were carried out (Matthäus & Lass, 1995).

Temperature: Fluctuations of annual means of water temperature in the Pomeranian Bay are strongly related to the severity of the preceding winter season (Cyberska, 1992). Although the overall trend of the severness index of winter seasons was negative between 1946/47 and 1993/94 (r=-0.21, p>0.05, n=49), means of severness indices of a period of ten winter seasons before the beginn of an investigation did not differ significantly (Fig. 3.13). Large differences occurred in the course of the severness index over the three ten year periods. Whereas the investigations of Löwe (1963), Gosselck (1985), and Warzocha (1995) followed a period of cold winters preceded by a period of mild winters, opposite conditions predated the investigation of Powilleit et al. (1996).
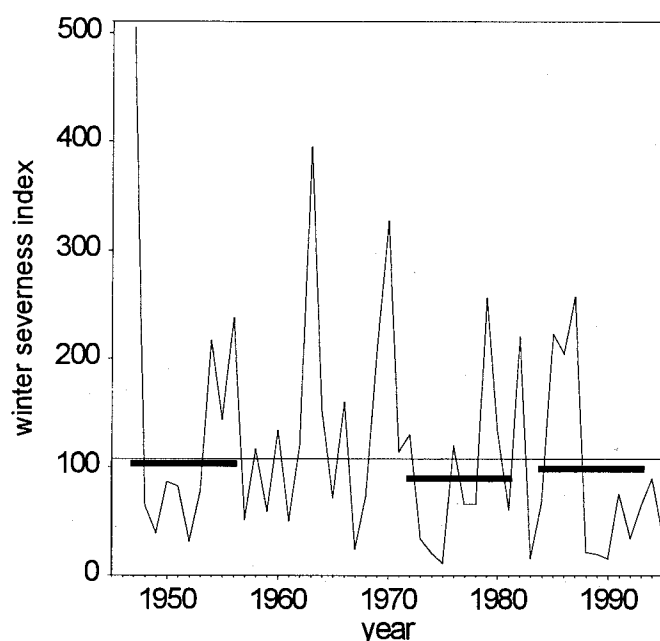

Fig. 3.13: Index of the severity of the winter season between 1946/47 and 1994/95 (sum of minus degrees (daily means) per winter season, data from the Meteorological Station Warnemünde, F.R.G.). Thin horizontal line shows the long-term average. Thick horizontal lines show the average for the ten year periods preceding each benthos investigation.

Food supply: The nitrogen input of the Oder River has increased from 10.000-20.000 t·a⁻¹ in the 1960s to 70.000-80.000 t·a⁻¹ in the 1990s (Cyberska et al., 1992; 1993; Lampe, 1993). This increase in nitrogen discharges was followed by an increase in phytoplankton biomass and primary production. Surface chlorophyll a concentrations have doubled in the Arkona Basin, in the Bornholm Basin, and in the Pomeranian Bay as well between 1970 and 1990 (Nakonieczny et al., 1991; Renk 1992; Schulz & Kaiser, 1986). The increase in phytoplankton biomass resulted in a decreasing water transparency and a heavy loss of macrophytobenthos in the adjacent Greifswalder Bodden (Messner & Oertzen, 1991).

Furthermore, an increasing accumulation of organic matter was observed in sediments of the sheltered Greifswalder Bodden and the deeper parts of the Sassnitz Deep. The redox potential at the sediment water interface decreased noticebly (Lampe, 1993; Leipe et al. 1995; own obs.). However, no accumulation of organic matter was found for sandy sediments of the Pomeranian Bay above the 15 m isobath (Koine, 1995; Neumann & Bublitz, 1969).

Long-term changes of the macrozoobenthos composition

Macrozoobenthic assemblages: Using hierarchical cluster analysis, based on densities of 14 macrobenthic species and 116 sampling locations, eight groups of stations were separated at a 50 % similarity threshhold and were computed to spatial distribution maps for all three investigation periods

(Figs 3.14 and 3.15). The first group combines stations showing a high species richness in the southern Arkona Basin. The second group covers locations with a high macrofauna biomass near the Oder Mouth and near the Greifswalder Bodden. Group three is separated into two main sub-groups 3a and 3b, representing exposed sandy stations on the shallow Oder Bank and ist deeper surroundings, respectively. The fourth group contains nearshore sites in the south of the bay with high bivalve biomasses. Group six represents stations in the Sassnitz Deep characterized by a high species richness. Group seven includes stations in the deeper northern part at the slope to the Bornholm Basin. Groups five and eight are separated due to heavily reduced species richness and densities.

The spatial distribution maps (Fig. 3.15) show clear changes in the areal extension of cluster groups from one investigation period to the next, especially in the western half of the bay. Cluster group one and six, representing diverse macrofauna assemblages in the southern Arkona Basin and in the Sassnitz Deep, almost disappeared between 1958 and 1993. The Oder Bank cluster group (3a) covered the largest part of the Pomeranian Bay in the 1950s. Since 1981 its extension has been restricted to the shallow central parts of the Oder Bank. The deeper sandy areas are now part of the cluster group 3b. Today, a wide range is also covered by cluster group four, as compared with the 1950s when it was restricted to deeper parts in the West near the Isle of Rugia in the 1950s. The cluster groups five and eight represent stations, more than 15 m deep, sampled in 1981 and 1993 in the Sassnitz Deep and along the former Oder River bed. These assemblages were absent during the investigation period of Löwe (1963).
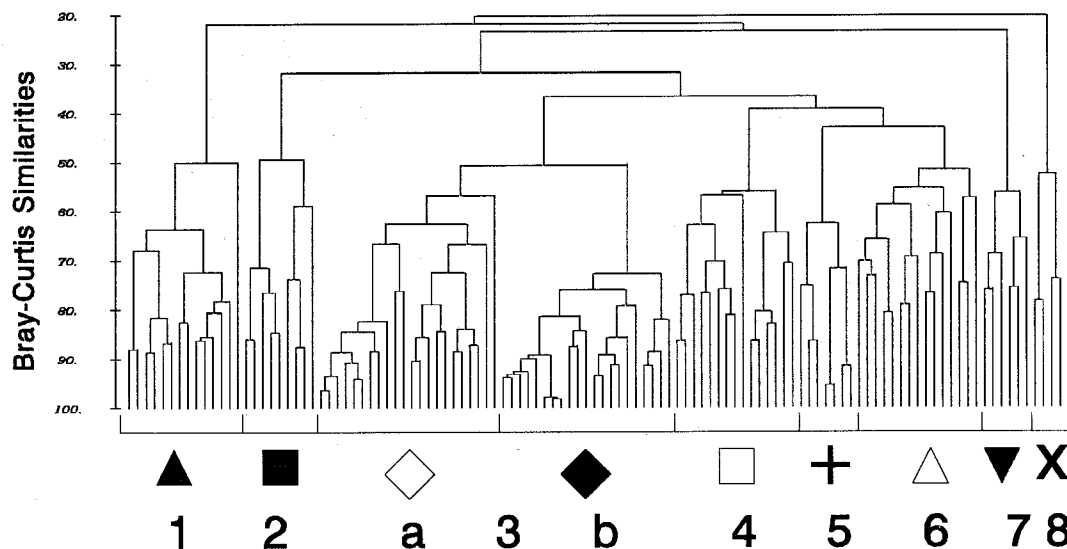

Fig. 3.14: Denrogram of the 116 stations using group-average clustering from Bray-Curtis similarities on square root-transformed abundances. The eight groups of stations separated at a 50 % threshhold are indicated (symbols and numbers). Additionally, the third station group was devided into the sub-groups 3a and 3b.

Changes in individual species: Distribution pattern of almost all 14 species under investigation have changed between 1958 and 1993. The crustaceans *Monoporeia affinis* and *Pontoporeia femorata* vanished entirely since 1981 (Fig. 3.16). Only a few single individuals of the isopod *Saduria entomon* were found since 1993. All other species, that were abundant in the southern part of the Arkona Basin and in the Sassnitz Deep between 1955 and 1980 were discovered to be very scarce in 1993. The cockle *Cerastoderma lamarcki* and the amphipod *Bathyporeia pilosa* disappeared from the Southwest of the study area. Their densities remained stable only on the Oder Bank (Fig. 3.17). The amphipod *Corophium volutator* has gradually declined in the Northwest of the bay since 1981. Its densities have probably increased near the Oder Mouth (Fig. 3.18). No dramatic changes were observed for the isopod *Cyathura carinata* and the amphipod *Leptocheirus pilosus*.
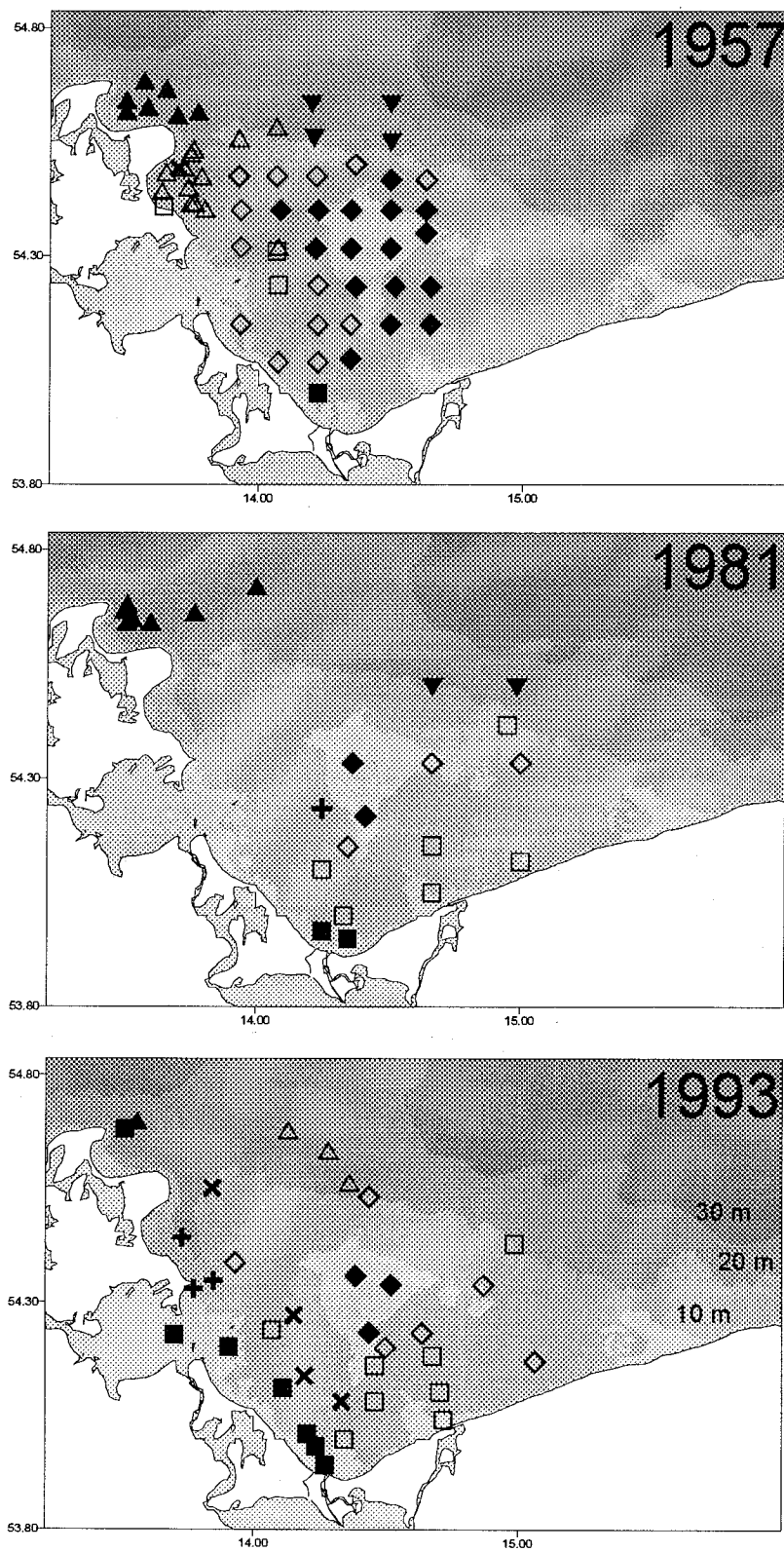
Fig. 3.15: Maps showing the spatial pattern of different cluster groups during the investigation periods of Löwe (1963), Gosselck (1985) and Warzocha (1995), Powilleit et al. (1996). Symbols are the same as in Fig. 3.14 See text for further explanations.

Monoporeia affinis

Pontoporeia femorata
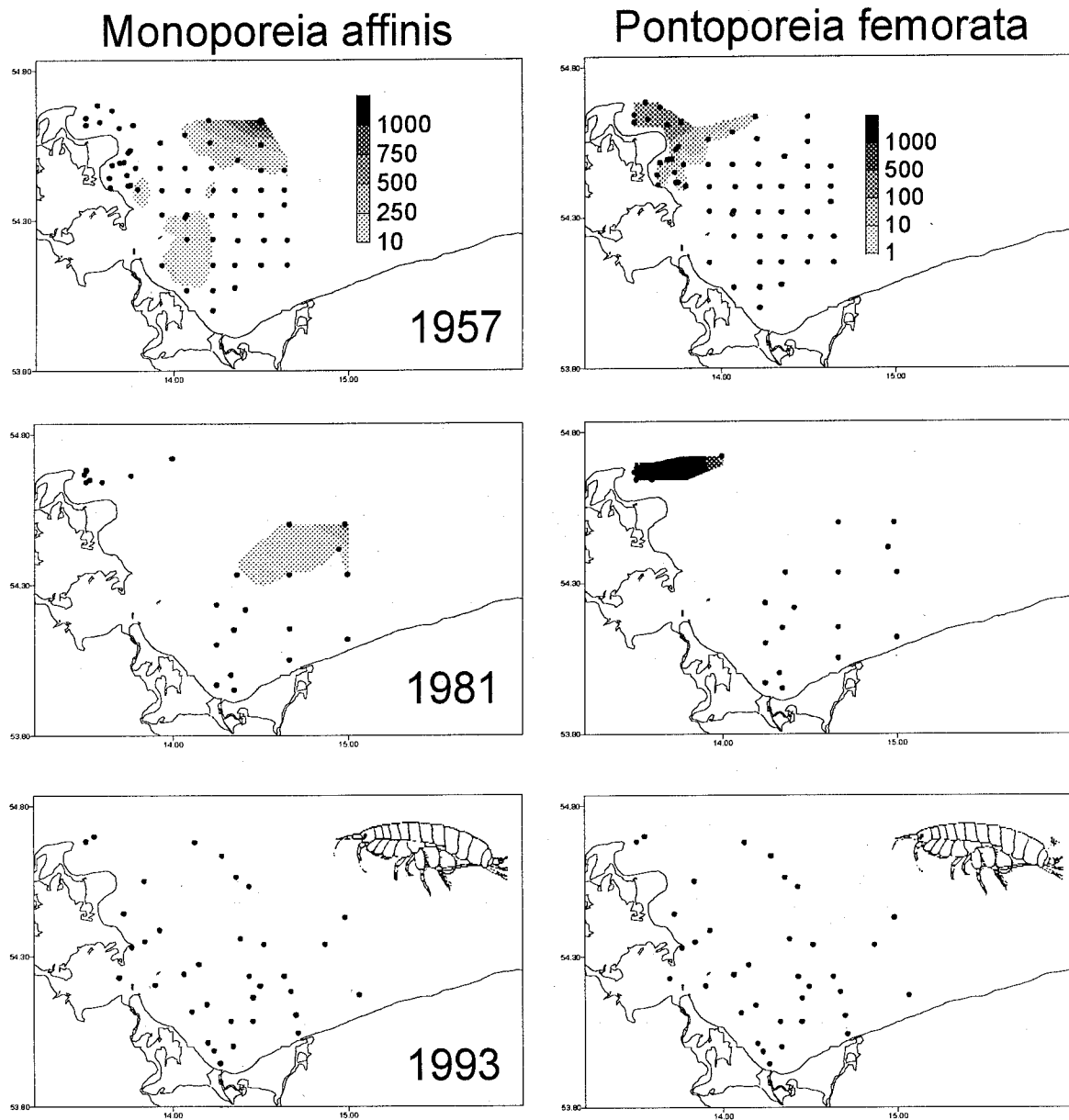
Fig. 3.16: Distribution of *Monoporeia affinis* and *Pontoporeia femorata* (ind. m^{-2}) during the investigation periods of Löwe (1963), Gosselck (1985) and Warzocha (1995), Powilleit et al. (1996).

Bathyporeia pilosa

Cerastoderma lamarcki

Fig. 3.17: Distribution of *Cerastoderma lamarcki* and *Bathyporeia pilosa* (ind. m⁻²) during the investigation periods of Löwe (1963), Gosselck (1985) and Warzocha (1995), Powilleit et al. (1996).

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Corophium volutator
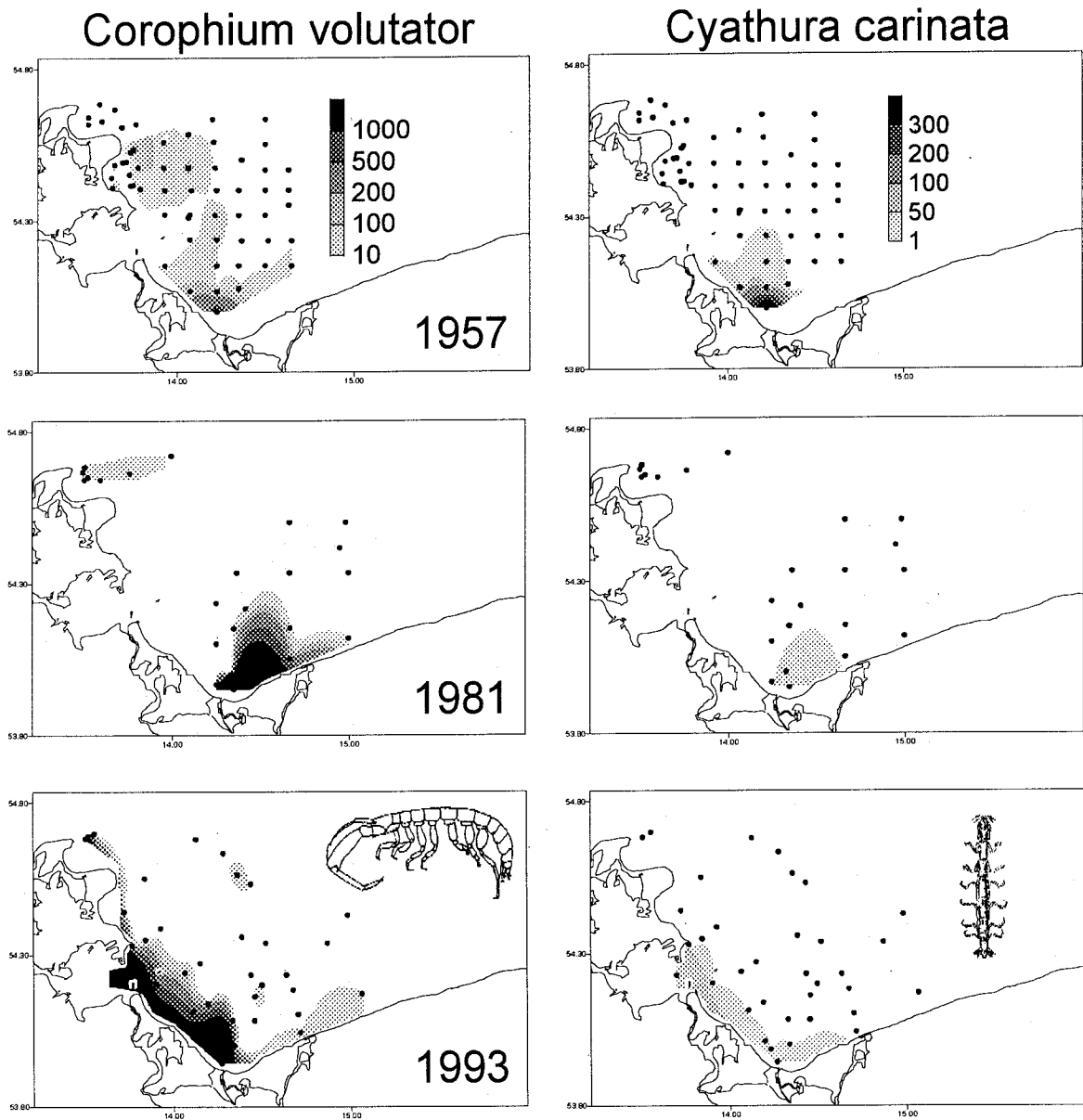
Cyathura carinata

Fig. 3.18: Distribution of *Corophium volutator* and *Cyathura carinata* (ind. m^{-2}) during the investigation periods of Löwe (1963), Gosselck (1985) and Warzocha (1995), Powilleit et al. (1996).
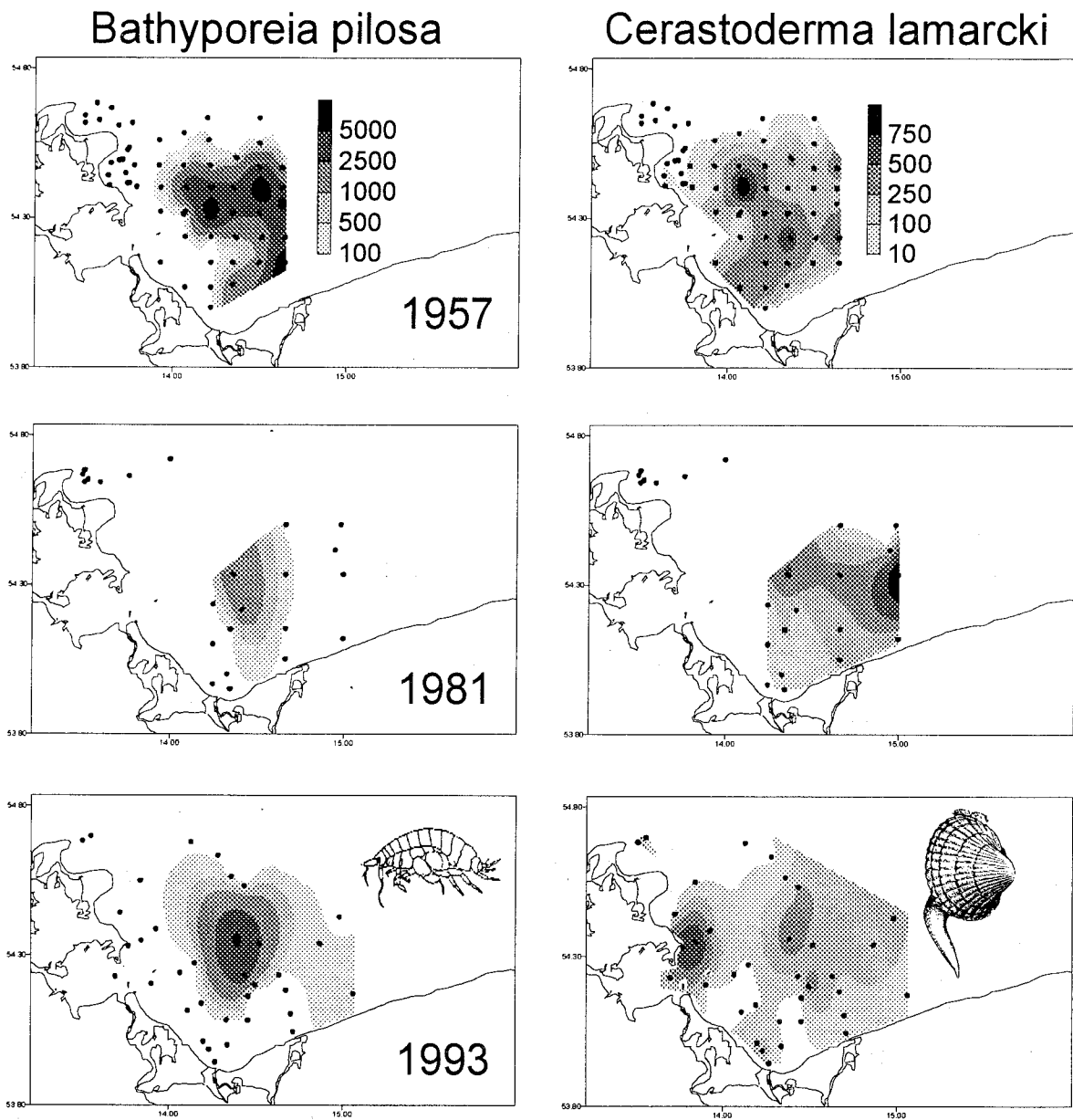
Macrozoobenthic biomass: Changes in the biomass distribution pattern between the 1950s and 1990s are shown for three bivalve species in Fig. 3.19. The distribution pattern of *M. edulis* and *M. arenaria* did not change within the last 35 years. The biomass distribution pattern of *M. balthica* in 1993 looked almost like an inversed picture of its 1950s distribution. Biomass values of *M. balthica* have decreased in the Southwest and increased north of the Oder Bank.

Mytilus edulis

Macoma balthica

Mya arenaria

Fig. 3.19: Distribution of *Mytilus edulis*, *Macoma balthica* and *Mya arenaria* (g Afdw) during the investigation periods of Löwe (1963) and Powilleit et al. (1996).

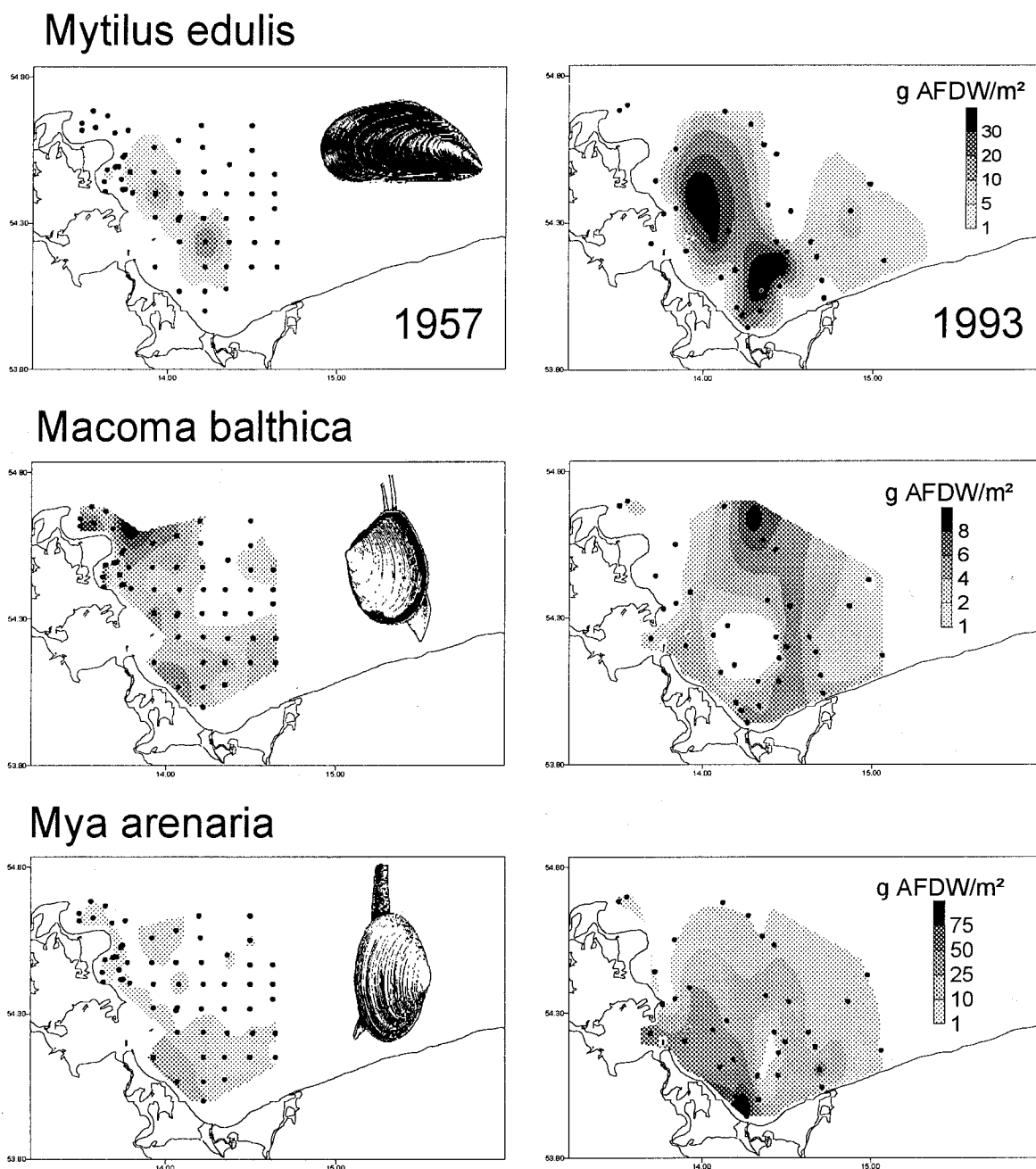The mean biomass of *M. edulis* and *M. arenaria* was about eight times higher in 1993 than in the 1950s. The increase is strongly significant. Mean biomass values of *M. balthica* showed no difference between the two investigation periods (Table 3.3).

To obtain a more detailed view, quantitative changes in bivalve biomasses were also calculated separately for cluster groups 3a, 3b, 4, and 6 (Table 3.3). Only four cluster groups provided a minimum of three samples per investigation period for a statistical comparison. Large differences occurred between the cluster groups. Whereas the biomass of *M. edulis* strongly increased in the Southwest, biomass values did not increase on the Oder Bank. The biomass of *M. arenaria* increased in all cluster groups, except for a decrease in cluster group 6. However, in all cases sample sizes were too small to obtain significant results.

Table 3.3: Changes in the biomass values (g AFDW m^{-2}) of *Mytilus edulis* (Me), *Macoma balthica* (Mb) and *Mya arenaria* (Ma) in the Pomeranian Bay. Asterisks denote statistical significant changes (*** p<0.001, Mann-Whitney U-test).

cluster group (n 1955-58/n 1993)	species	1955-58 (Löwe, 1963)		1993 (Powilleit et al., 1996)		factor of changes in the mean
		mean±se	median	mean±se	median	
3a	Me	3.4±1.9	0.4	11.5±7.3	5.32	3.4
(13/6)	Mb	2.5±0.4	2.2	3.1±0.9	2.1	1.2
	Ma	5.4±2.5	1.1	12.6±4.2	8.9	2.3
3b	Me	0.3±.01	0.2	0.3±0.2	0.1	0.8
(16/3)	Mb	1.2±0.2	1.1	2.5±1.5	2.3	2.0
	Ma	1.1±0.2	1.0	9.7±4.6	12.7	9.0
4	Me	1.9±1.7	0.3	14.5±8.1	2.0	7.8
(3/8)	Mb	1.4±0.6	1.8	2.2±0.6	1.9	1.6
	Ma	0.4±0.2	0.4	13.6±6.4	5.0	34.6
6	Me	0.8±0.4	0.0	2.1±1.2	2.1	2.6
(13/3)	Mb	3.6±0.5	4.0	6.1±2.0	6.9	1.7
	Ma	2.4±1.0	0.6	0.5±0.2	0.4	0.2
all samples	Me	1.1±0.5	0.2	9.7±2.9	2.0	8.5***
(58/33)	Mb	2.5±0.3	2.1	2.6±0.4	2.3	1.0
	Ma	2.4±0.7	1.0	19.7±5.0	8.6	8.1***

Discussion

Reliability of data

Comparing data that were gathered by different sampling methods is a general problem in evaluating past and present distribution patterns in the benthos (Reise et al., 1989). Unfortunately, long-term data series are often lacking for sublittoral marine areas, due to the enormous costs of shipboard sampling. As a consequence, almost all documentations of long-term changes in the macrofauna of the Baltic Sea are based on reinvestigations of areas that had been studied intensively several decades ago (Cederwall & Elmgren 1980; Brey, 1986; Rosenberg & Möller, 1979). For shallow waters in the western and southern Baltic Sea, we consider it unnecessary to resample exactly the same sites in the same season. The sediment structure is regularly disturbed during storms and the distribution of many species is very patchy. Repositioning the research vessel on exactly the same patch that had been sampled decades ago is impossible. Often, density variations can not be related to seasonal oscillations, provided by reproductive cycles. They are super-imposed by stochastic variations in hydrographic conditions (Arntz & Rumohr, 1986; Brey, 1986; Prena et al., in prep, this study). The sampling season has no strong effect on estimates of biomass values calculated from standardized length-weight relationships of bivalves with a high longevity and low P/B ratio.

Hence, it seems to us, that the total number of samples is more important for a statistical evaluation than seasonal acuracy. The total number of samples used in this study was much higher than the sample sizes of the investigations of Cederwall & Elmgren (1980) and Brey (1986). We also think, that differences in sampling gear were of minor importance for our data analyses. Although we suspect that the strength of the shock wave in front of the grab used in the 1990s was lower and sorting was more efficient due to the use of stain, abundances obtained for most crustaceans have been much higher in the 1950s than today. Estimates of changes in biomass of the burrying bivalves

M. balthica and *M. arenaria* might have been effected by a possibly lower penetration depth of the grab used by Löwe (1963). However, because values of the increase in biomass were similar for both filter-feeding bivalves *M. edulis* and *M. arenaria* penetration depths of the grabs used during the two investigations were presumably only marginally different.

Responses to eutrophication, and fluctuations in hydrography and climate

Eutrophication is usually defined as a complex of phenomenona triggered by an inrease of limiting nutrients. The increase in nutrients leads to increases in benthic abundance, biomass and number of species but also to anoxic conditions in sediments and massive die-off of benthic animals (Heip, 1995; Pearson & Rosenberg, 1978). Effects of eutrophication are difficult to measure and difficult to explain in a straightforward manner, because benthic communities usually respond in two ways: functionally by increasing their productivity and structurally by adapting their composition to the higher food supply (Beukema, 1991).

In the Balic Sea, rates of increase in bivalve biomass above the halocline varied between 5 and 47 % of the initial values per year (Table 3.4). We observed an annual rate of increase of about 20 % of the values estimated in the 1950s which fits well to the rates of increase in nitrogen input. However, large differences occurred between individual species. The biomasses of the filter-feeders *M. edulis* and *M. arenaria* increased by almost 25 %·a^{-1}. No increase was found for *C. lamarcki* and *M. balthica*, the biomass dominants of the benthic communities in the 1950s. These findings are in accordance with the results reported by Cederwall and Elmgren (1980), who also described that *M. balthica* was replaced by *M. edulis* as the dominant species. The change in dominances seems to be related to a larger complex of causes: competition for food and space, mechanical disturbance by drifting mussel clumps and shifts in the redox potential in summer due to the organic loading.

Table 3.4: Long-term increase in the biomass of molluscs in other shallow sublitoral waters of the Baltic Sea ([1] data from Cederwall & Elmgren, 1980; investigations 1920-23 and 1976/77 around the islands of Öland and Gotland, and [2] data from Brey, 1986; investigations 1961-65 and 1982-83 in Kiel Bay).

species	initial biomass (g AFDW·m^{-2})	later biomass (g AFDW·m^{-2})	mean increase (g AFDW·m^{-2}·a^{-1})	increase rate (%·a^{-1} of the initial biomass)
Mytilus edulis[1]	0.09	2.3	0.04	46.5
Cerastoderma spp.[1]	0.03	0.14	0.002	8.5
Macoma balthica[1]	0.61	1.96	0.025	5.84
Mya arenaria[1]	0.003	0.05	0.001	30.3
all Mollusca[2]	2.1	12.8	0.54	30.4

Spatial variations in the biomass increase of *M. edulis* demonstrate how strong limitations by other ecological factors can be. In the Pomeranian Bay, motile mussel-clumps lay attached to *Mya*-shells on the sandy sea floor. They have a mean diameter between 5 and 10 cm and drift over vast distances by strong bottom currents during storm events (video obs.). Depending on the current situation, single clumps can aggregate to patches of several square meters or disperse. Permanent erosion and strong bedload transports on the shallow Oder Bank prevent a successful settlement of mussel spat and encourage an accumulation of mussel-clumps in the deeper Southwest of the bay. As a consequence, distribution patterns of *M. edulis* have not changed considerably during the last 35 years.

Below 15 m, all stations showed a decrease in species richness in the 1990s. These changes were caused by an increase in oxygen depletion events in the Arkona Basin since 1983 and upwelling of deep water with lowered oxygen saturations from the Arkona Basin into the Pomeranian Bay via the Sassnitz Deep. Gosselck (1985) described a rate of increase in macrobenthic biomass of 16 %·a^{-1} between the 1950s and 1980s. *M. balthica* dominated macrobenthic biomass in 1980. Its biomass had increased annually by 53 % of the initial value. First signs of macrofauna death in the Arkona Basin were noticed in 1984 (HELCOM, 1990). A change in the *M. balthica* population from larger to smaller individuals was observed and its biomass decreased. The total number of species decreased from 40 to 20 between 1980 and 1986. The reduction in the numbers of the crustaceans *P. femorata* and *Diastylis rathkei* was particularly striking. Both, the southern Arkona Basin and the Sassnitz Deep were found to be almost devoid of macrofauna in 1992 (own obs.).

During the 1978-1988 period increasing oxygen deficiencies below the halocline had also been observed in the Bornholm Basin, affected areas being devoid of macrofauna too (HELCOM, 1990).

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Besides eutrophication, some of the observed phenomena seem also to be triggered by variations in oceanographic and climatic conditions. Although, changes due to eutrophication in the benthic communities of the Baltic Sea become more and more obvious, we are still unable to quantify the observed effects.

Events of oxygen depletion were found to increase since the 1980s (Frank & Matthäus, 1992; Weigelt, 1991). The large gap of important inflow events since 1983 might have been an impotant cause for the observed drastic changes in the oxygen regime of the Arkona Basin. Otherwise, the increase in benthic biomass until the 1980s might have accelerated the speed of oxygen depletion below the pycnocline during summer stratification. Actually, we observe a successful recolonisation at the northern slope of the Pomeranian Bay following the major inflow in January 1993 (see the example of *D. rathkei* in Fig. 3.9).

Results of the cluster analysis also suggest, that the increase in zoobenthic biomass leds to an increase in oxygen depletion events in the shallow parts of the Pomeranian Bay. Here, oxygen depletion events are governed by stochastic upwelling and stratification processes along the former Oder River bed (own obs. in 1994). Disturbances due to suboxic periods were obvious for all stations below 15 m depth in 1993. A strong and longlasting stratification period has led to anoxic conditions even below 11 m depth during the summer of 1994 and killed large parts of the macrofauna in the Southwest of the bay (data will be reported elsewhere).

Bivalves, the biomass dominants, show highly successful recruitment during summers following a cold winter (Beukema, 1982; Kube, 1996). This positive effect can establish extaordinary high biomasses after a series of severe winters due to the long life span of bivalves and, therefore, accelerates the speed of biomass increase (Beukema, 1989). Indeed, the population structure of *M. arenaria* differed strongly between the 1950s and the 1990s. Whereas smaller size classes prevailed during the late 1950s, the population was dominated by large specimens in 1993 (Kube, 1996). This observation agrees with differences in the time course of the winter severness index during the ten-year periods preceding both investigations.

Conclusions

Populations of macrofauna species in the Pomeranian Bay were found to follow one of two dominant patterns: either an increasing or decreasing trend. Basically, both patterns seem to be related to eutrophication impacts. The fauna responds by increasing its productivity due to a higher food supply and by decreasing biomass and diversity under strong oxygen limitation. Hydrographic and climatic factors act as additional accelerating or reversing factors. Details of the processes that affect water stratification and oxygen conditions in the Pomeranian Bay are not completely understood.

Changes in the species composition of the macrofauna of the Pomeranian Bay does not result in an increasing proportion of deposit-feeders, as reported previously by other investigators (Heip, 1995). Our analyses rather suggest an increase in the proportion of filter-feeders until 1993. A high rate of resuspension of phytoplankton and particulate organic matter in the shallow parts of the bay might be the cause for these findings. This hypothesis is supported by the fact that no organic matter was accumulated in the sediments. Furthermore, the North American polychaete *Marenzelleria viridis* successfully immigrated into the study area since the mid 1980s. This preferably filter-feeding worm contributed for up to 8 % of the total benthic biomass in the Southwest of the study area in 1993 (Kube et al., 1996).

Only little is known on the importance of species interactions during the eutrophication process. There is a clear need for investigations on the interspecific effects between the dominant bivalves and the process of recolonisation of a community which lacks typical opportunistic members.

Acknowledgements

4. Spatial and temporal variations in the population structure of benthic filter-feeders
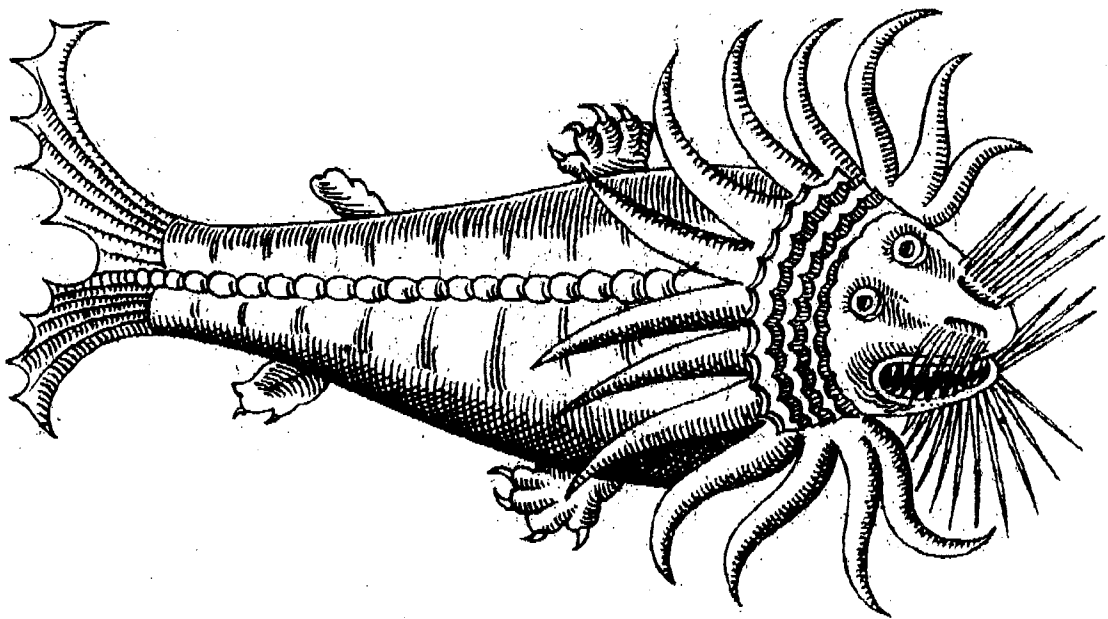
suspension-feeding whale; Gessner, 1583

Functional implications: the analysis of population structure and dynamics as a baseline study

The ecological importance of filter-feeding

The importance of the benthos for the overall carbon and energy flow in coastal marine areas has been recognized for a long time. Quantitative estimates of the coupling between pelagic and benthic components usually require measurements of various flux rates (e.g. filtration rate, respiration rate). However, crude estimates can be obtained also by assessing growth and production of the dominant species in combination with published data on their energetics.

The benthic infauna in the Pomeranian Bay is dominated by filter-feeders (*M. arenaria, M. viridis*). Biomasses of the epibenthic filter-feeding blue mussel are high too. Biomasses of all three species increased significantly during the last 35 years and perhaps reflect the high loads of discharges entering the system through the Oder River.

Herman & Scholten (1990) described a general energy-flow scheme for suspension-feeders (Fig. 4.1). The clearence rate is a Q_{10} function of temperature, a negative exponential function of seston concentration, and an allometric function of body weight. Respiration is an allometric function of body weight and a Q_{10} function of temperature. Filtration rate is a linear function of the food concentration, with slope equal to the clearence rate.
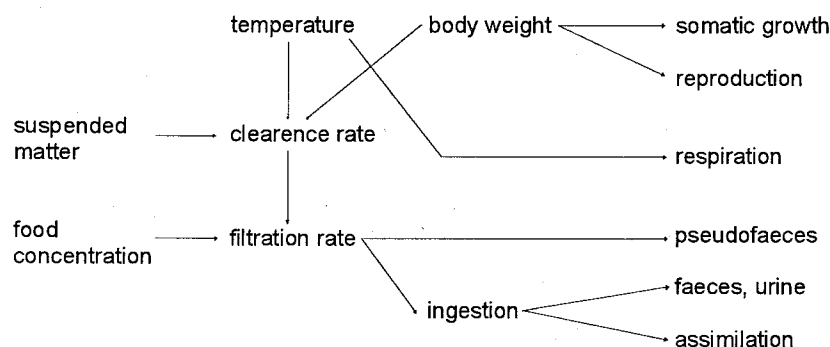

Fig. 4.1: General scheme of the suspension-feeder energetics. Arrows indicate that one variable or rate determines another (from Herman & Scholten, 1990).

The model shows that densities of suspension-feeding bivalves may substantially affect their environments. Such impact may manifest itself in (Emerson et al., 1988; Jørgensen, 1990):
- biodeposition
- control of phytoplankton growth
- oxygen depletion
- nutrient regeneration.

Suspension-feeding bivalves egest the ingested matter as true faeces and as pseudofaeces. Both faeces and pseudofaeces sediment more rapidly than does the suspended matter from which they originate. Thus the water processing activity of filter-feeding bivalves may enhance the rate of deposition of the seston (Jørgensen, 1990). However, these biodeposits are likely to become resuspended immediately by water currents as we usually observed only little organic matter accumulated on the sediment surface in the Pomeranian Bay.

Dense populations of filter-feeders may process the ambient water at such high rates that they affect and even control phytoplankton production. Calculations based on the biomass and size distribution of benthic suspension-feeding bivalves and rates of water filtration provided evidence that bivalves can filter a volume of water daily that exceeds the total volume of shallow waters (e.g. Officer et al., 1982).

Rates at which bivalves process the surrounding water can be estimated from the size frequency distribution and the relation between size and clearence rates. Attempts have been made to determine pump capacities and their relation to body size in about ten filter-feeding bivalve species. The similarities in rates of water processing suggest that such allometric relationships may be used to assess

the ecological importance of filter-feeding bivalves in general. Some caution is warranted as it still remains uncertain if these experimental data are applicable also to other species and biotops (Jørgensen, 1990). Allometric relationships, listed by Jørgensen (1990) provided mean constants of a = 5.85 and b = 0.74 for the function:

log (filtration rate ($l\cdot h^{-1}$)) = b·log (dry weight) + a,

measured at temperatures and salinities typical during the season of growth in boreal marine habitats.

In the following account I will give preliminary estimates of filtration rates of the soft-shell clam at some stations in the Pomeranian Bay. As described in paper 3, biomasses of *M. arenaria* are highest in the Southwest of the study area, especially near the Swina Mouth. Values there range from 50-100 g AFDW·m⁻². Much lower values of only 10-20 g AFDW·m⁻² were found on the Oder Bank in the centre of the bay. By using the formula given above for the calculation of filtration rates, the volumes filtered at the stations 2, 3, 7 and 8 can be estimated as 0.2-1 $m^3\cdot m^{-2}\cdot h^{-1}$ (Table 4.1; see Fig. 4.4 in paper 3 for the location of stations and the size-frequency distribution of clams). Actually, it is impossible to make any judgements on these values, since several related turnover rates of environmental variables in the Pomeranian Bay are not balanced yet (phytoplankton doubling time, benthic metabolism). These measures provide a feed-back control for the estimates of filtration rates.

Table 4.1: Estimates of rates of water processing by *Mya arenaria* in the Pomeranian Bay near the Swina mouth (station 2, 3) and on the Oder Bank (stations 7, 8).

station	mean biomass in April 1993 (g AFDW·m⁻²)	mean filtration rate in June-September ($m^3\cdot m^{-2}\cdot h^{-1}$)	water depth (m)	turnover rate for the whole water column (days)
2	83.4	0.979	6	0.25
3	91.4	0.879	11	0.5
7	15.1	0.313	8	1.05
8	12.7	0.237	9	1.55

Most likely, clearence rates were overestimated, because of a generally lowered metabolic activity of bivalves in brackish habitats (see also paper 4). Furthermore, it seems very unlikely that *M. arenaria* is able to maintain constant high filtration rates throughout the day. Experiments of Pedersen (1992) showed, that high activity lasted only for 31-61 % of his measured time intervals.

However, the estimated values are still much lower than the maximum rates of water processing by mussel beds of 6 - 12 $m^3\cdot m^{-2}\cdot h^{-1}$, published by Jørgensen (1990). These estimates were calculated for bivalve biomasses of about 500-1000 g AFDW·m⁻² (e.g. Dare, 1976).

Dense populations of bivalves depend not only upon the food in the water above the sediment. In the absence of currents the bottom near water is also rapidly depleted of oxygen. This phenomenon was already discussed in paper 2. Oxygen consumption depends on the metabolic activity. Direct measurements of metabolic activity are often unsuitable for modelling the ecosystem energy flow, because metabolic rates are known to be influenced by a variety of environmental factors and fluctuate strongly over time. Estimates of metabolism can also be obtained from growth measurements, as growth is an integral component of the matter and energy balance of an organism. Metabolism (M) is expressed as:

M = I-E-P

(I is ingestion, E is excretion, P is production).

The term E may be subdivided into faeces and urine. P+M constitute assimilation (A).

The common way to get information about growth and production of benthic macro-invertebrates is calculating the cohort-production from field data. Total annual somatic production is equal to the sum of annual cohort-productions (Crisp, 1984):

P = Σ ((N_t+N_{t+1})/2)·($w_{t+1}-w_t$)

(P is production over time, N is abundance, w is mean individual weight).

Using this method, two parameters must be determined as exactly as possible: abundance per cohort and mean individual weight per cohort. Especially the abundance value is often difficult to obtain if the animals show a patchy distribution. Furthermore, the age of each specimen must be determined individually.

Balancing the budget for *Mya arenaria*, the most important macrofauna species in the Pomeranian Bay

A detailed description of the population structure of *M. arenaria* in different parts of the study area is given in paper 3. As reported there, it was possible to ensure reliable age determinations for all specimens less than ten years old by counting of annual growth checks. The maximum age ever observed was 13 years. Spatial variations in mean annual growth rates are described in paper 4. Estimated means of the allometric relationship between shell length and weight of the soft part are given in paper 6.

On the Oder Bank, it was impossible to obtain any estimates of annual mortality due to a high intensity of bedload clam-transport. Annual mortality could be calculated for a more sheltered station in the southwest of the bay. Unfortunately, these estimates are not reliable. They are much to high for all cohorts older than three years and are perhaps caused by systematic errors in the sampling procedure (paper 3). Thus, mortality values were reestimated by assuming a size dependent exponential survival model derived from data published by Brousseau (1978b) (Table 4.2 and 4.3).

Based on this assumption, annual production was computed to be 30.3 g $AFDW \cdot m^{-2} \cdot a^{-1}$ equivalent th 16 g $C \cdot m^{-2} \cdot a^{-1}$ (which is only 10 % higher than the production estimate using our own mortality data). The estimate of an annual P/B ratio of 0.33 fits well to values of 0.27 and 0.34 predicted from empirical relationships between maximum age and annual P/B ratio in benthic invertebrate populations given by Etim & Brey (1994) and Hoenig (1983), respectively.
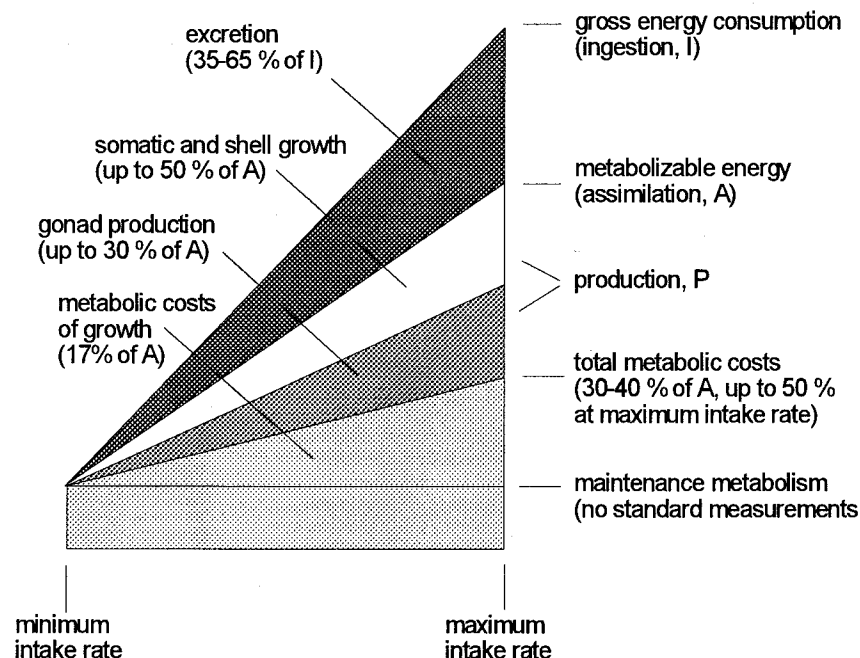

Fig. 2: 'Scope for growth'. The energy balance equation for suspension-feeding bivalves (after Bayne, 1976; Gosling, 1992; Jørgensen, 1990).

A first rough estimate of the annual energy intake rate of *M. arenaria* in the Pomeranian Bay can be obtained now by applying known relationships between rates of metabolism, reproduction and growth, which are available for a number of filter-feeding bivalves. Fig. 4.2 summarises the model of energy balance based on several literature sources. The model shows, that annual somatic growth represents only about 10-20 % of the total annual carbon consumption. Based on this assumption, it can be assumed that the dense beds of *M. arenaria* in the southwestern part of the study area turnover a minimum of about 100 g $C \cdot m^{-2} \cdot a^{-1}$, assuming a conversion factor from g AFDW to g C of 0.4348 (Van Der Tol & Scholten, 1993).

Table 2: Population model for *Mya arenaria* at station 3 (see Fig. 4.4 in paper 3 for the location). Hypothetical densities of single age groups in previous years were calculated based on own estimates of mean annual survival rates. Densities of first year specimens increase dramatically after five years. The model is becoming senseless.

age in years	observed density in April 1993	estimated survival rate until April 1994 (%)	calculated density of the same cohorts in April of previous years											
			1992	1991	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981
0	303	26												
1	136	31	514											
2	30	55	98	371										
3	28	59	51	166	625									
4	30	42	51	93	299	1128								
5	65	84	156	264	476	1535	5795							
6	63	74	·75	180	304	549	1770	6683						
7	61	69	83	98	237	399	720	2324	8774					
8	24	87	35	48	57	137	231	416	1343	5069				
9	14	59	16	24	32	38	92	155	279	900	3399			
10	12	35	21	24	34	46	55	133	223	403	1300	4909		
11	24	35	70	119	136	197	267	318	766	1290	2329	7512	28360	
12	8	0	23	68	114	131	190	257	306	737	1242	2242	7233	27307

Table 3: Hypothetical population model for *Mya arenaria* at the same station. Densities of single age groups in previous years were calculated based on Brousseau's (1978b) size dependent estimates of mean annual survival rates. Densities of first year specimens are always of the same magnitude as found during the investigation period April 1993-April 1995. The model is not not becoming senseless.

age in years	observed density in April 1993	estimated survival rate until April 1994 (%)	calculated density of the same cohorts in April of previous years											
			1992	1991	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981
0	303	25												
1	136	25	544											
2	30	92	122	487										
3	28	92	31	124	494									
4	30	92	33	36	144	576								
5	65	92	71	77	83	334	1335							
6	63	92	68	74	81	88	351	1406						
7	61	92	66	72	78	85	92	370	1479					
8	24	92	26	29	31	34	37	40	161	643				
9	14	92	15	17	18	20	22	23	25	102	408			
10	12	92	13	14	16	17	18	20	22	24	95	380		
11	24	92	26	29	31	34	37	40	44	47	52	206	826	
12	8	0	9	10	10	11	12	13	15	16	17	19	75	299

Spatial and temporal variations in the population structure of the soft-shell clam, *Mya arenaria*, in the Pomeranian Bay (Southern Baltic Sea)

Jan Kube

Abstract: The population structure of *Mya arenaria* has been investigated in the sublittoral zone of the Pomeranian Bay (southern Baltic Sea). Box core samples were collected during a 1.5-year period in 1993/94 to follow changes in the size and age structure of the clam populations in different parts of the study area. Large spatial differences in the population structure were found between the sheltered Southwest of the bay and the shallow and exposed Oder Bank in the centre. The clam stock of the Oder Bank was formed by two different clam types. A slow growing cohort was assumed to be autochtonous on the Oder Bank. A fast growing one was assumed to have been introduced from the surrounding area. Their contribution to the total density varied seasonally. Because of bedload transport of clams, the contribution to the reduction of the clam stock by wintering sea ducks could not be quantified. Erosion was of minor importance in the Southwest of the Pomeranian Bay. High mortality rates during the first two years of life were assumed to be caused by predation. Mortality rates of older cohorts remained stable until old age. Variations in the density of cohorts were related to interannual differences in the reproductive success. A mild winter presumably lowers the reproductive success in the subsequent summer. A severe oxygen depletion in summer 1994 caused a strong reduction in the clam stock at stations deeper than 10 m.

Introduction

The soft-shell clam, *Mya arenaria* L., is a brackish-water bivalve widely distributed over the northern hemisphere. Many comparative studies on different aspects of its biology and ecology have been conducted in intertidal areas of North America where this species is exploited by commercial fisheries (Appeldoorn, 1983; Brousseau, 1978a; 1978b; Manzi & Castagna, 1989).

During the 16th or the 17th century, the soft-shell clam has probably been transferred by man to Europe (Hessland, 1946). Today, the species forms dense beds on intertidal flats of the North Sea (e.g. Beukema, 1976; Zwarts & Wanink, 1993) and is also common subtidally in the Baltic Sea and Black Sea where it is found down to depths of about 30 m (Lassig, 1965; Muus, 1967; Savchuck, 1976). *M. arenaria* is one of the dominant species (by biomass) in many shallow coastal bays in the southwestern Baltic (Brey, 1984; Prena & Gosselck, 1989). It contributes up to about 80% of the total macrobenthic biomass in the Pomeranian Bay except for areas below the 20 m isobath (Powilleit et al., 1996).

Small soft-shell clams are one of the main food sources for shrimps, *Crangon crangon*, and flatfishes (Hertling, 1928; Pihl, 1982; Pihl & Rosenberg, 1984). Together with the blue mussel, *Mytilus edulis*, *M. arenaria* is also the main prey for sea ducks wintering in the Baltic proper. Especially long-tailed ducks, *Clangula hyemalis*, and common scoters, *Melanitta nigra*, feed on this bivalve (Leipe, 1985; Madsen, 1954; Meissner & Bräger, 1992). During mild winters, the extensive clam stocks of the Pomeranian Bay are fed upon by more than half a million long-tailed ducks and 100.000 to 200.000 common scoters from late October until early May. These numbers reflect about 15 % and 10 % of the total westpalaearctic flyway populations, respectively (Durinck et al., 1994).

It is not known how stable sublittoral prey stocks of species such as *M. arenaria* are. Few studies on the population dynamics of *M. arenaria* have been carried out in the sublittoral zone. Quantitative investigations were restricted to very shallow coastal waters in the western part of the Baltic Sea (Munch-Petersen, 1973; Möller & Rosenberg, 1983; Winther & Gray, 1985). Saavedra (1990) has studied the reproductive cycle of *M. arenaria* in the Greifswalder Bodden, a sheltered coastal lagoon which opens up to the Pomeranian Bay. Due to the cold climate, spawning takes place there in July, about three months later than in the Wadden Sea (Günther, 1992).
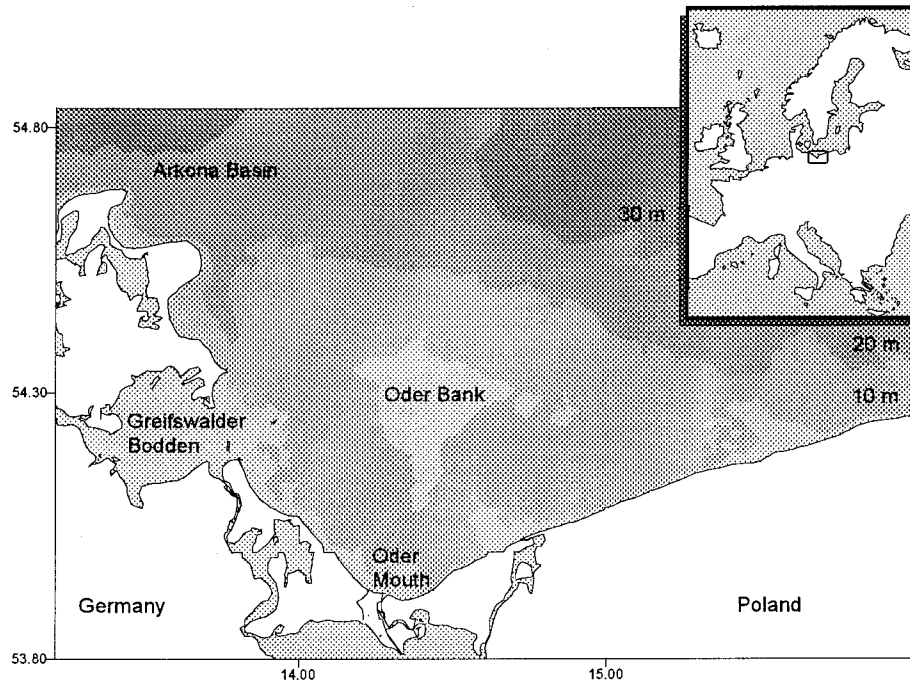
Fig. 4.3: Map of the area under investigation.

As shown for intertidal areas with similar faunas by Beukema (1993), Beukema et al. (1993) and Zwarts & Wanink (1993), the standing stock (or the available prey fraction) of burrying filter-feeding bivalves can fluctuate significantly seasonally and from year to year. Recently, *M. arenaria* in the Baltic Sea has been observed to increase in abundance particularly near source of organic enrichment (Brey, 1986, own obs.). The species can also disappear during periods of oxygen depletion when the organic loads have increased (Prena, 1994).

This study describes the seasonal and year-to-year variability in the population structure of *M. arenaria* in the Pomeranian Bay and gives insight into its population dynamics in relation to environmental factors.

Study area

The study area, the Pomeranian Bay, southern Baltic Sea, is a shallow bay situated north of the Oder Estuary between Germany and Poland. The northern border to the adjacent Arkona and Bornholm Basins is defined as the 20 m isobath. The Oder Bank with depths of only 7 to 9 m is located almost in the centre of the bay. There are several large lagoons behind the coastline (Fig. 4.3).

During the last decades, the whole area has been affected by increasing anthropogenic discharges. The Oder River drains an area of 119.000 km² in eastern Europe. The area is well industrialised and, hence, the freshwater contains high concentrations of dissolved and suspended organic and inorganic constituents (HELCOM, 1993a and b). After passing through the shallow coastal lagoons, a reduced amount of these loads finally enters the Pomeranian Bay and the southern Baltic Sea (Lampe, 1993).

A recent description of the macrofauna community was given by Powilleit et al. (1996).

Sampling design and laboratory procedures

Macrofauna sampling was carried out to analyse the structure of the benthic community of the Pomeranian Bay at 34 stations in April and October 1993 between 6 and 30 m water depth (Powilleit et al., 1996). Samples were collected with a modified 'Reineck' box corer (0.0225 m², 15-20 cm penetration depth) and rinsed over a 0.5 mm sieve. A minimum of three replicates was sampled at every station.
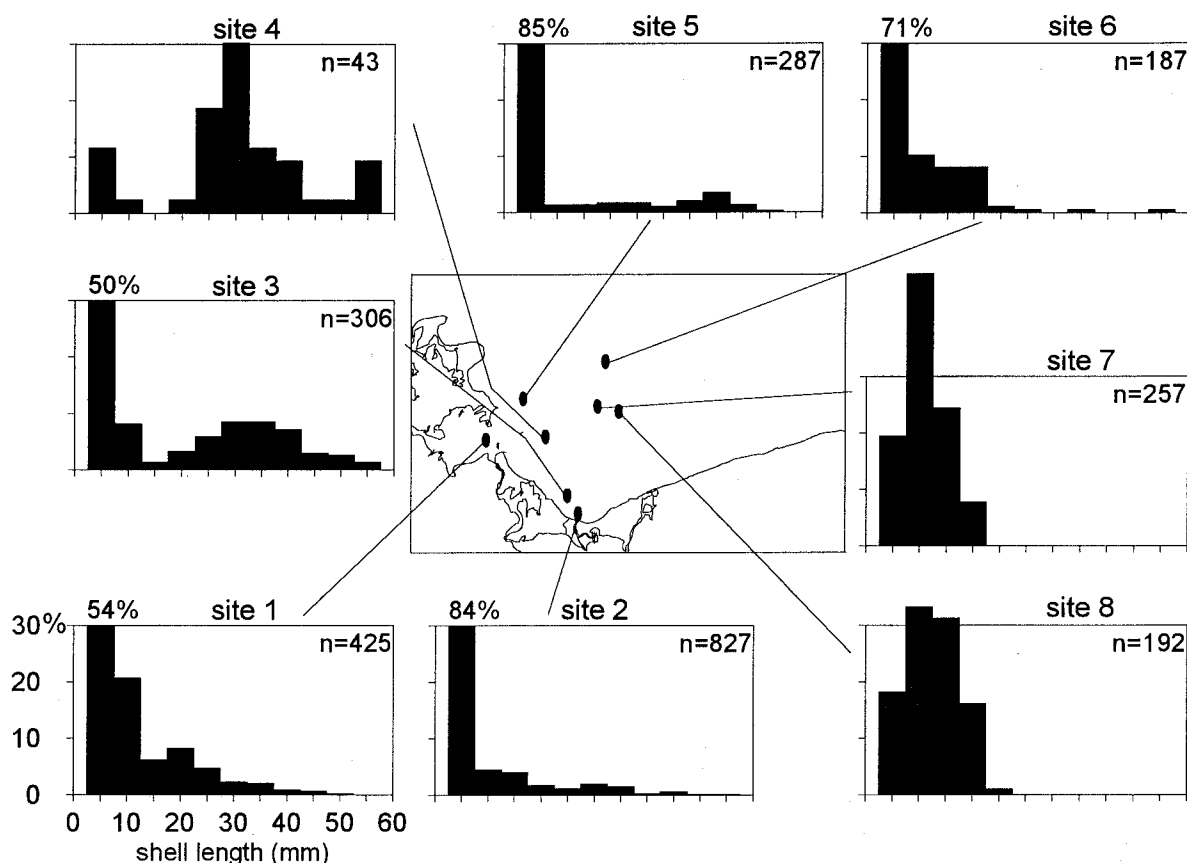
Fig. 4.4: Size-frequency histogrammes of *Mya arenaria* for eight stations in the Pomeranian Bay in April 1993 (all columns of each graph add up to 100 %, in some graphs high values for the cohort < 5mm are given by percentages written above the graphs).

Eight stations were selected for population studies on *M. arenaria* in the western half of the bay, where clams occure in high densities. They were sampled during a 1.5-year period. Sampling was carried out in 1993 in April, June and October and in 1994 in April, July and September. Observations on the formation of growth checks were also made in January 1994.

Sediment cores of the upper 15 cm were taken from additional box corer samples for the analyses of sediment parameters and the vertical distribution patterns of *M. arenaria*. The depth of clams was determined by cutting up the core in 1 cm thick slices, and measuring the distance between the upper edge of the shells and the sediment surface. Specimens were assigned to depth categories of 1 cm, starting at a minimum depth of 0.5 cm. The penetration depth of the box corer was deep enough to collect also the largest specimens. The greatest depth at which clams were found was 8 cm.

The selected stations represented all three main macrofauna assemblages of the Pomeranian Bay (Powilleit et al., 1996): the organically enriched Oder Mouth (stations 1, 2 and 3), the shallow and exposed Oder Bank (stations 6, 7 and 8) and an intermediate community of the deeper zone in between (stations 4 and 5). Stations near the Oder Mouth were 6-11 m deep. The sediment was sandy with an organic content of 1 %. The silt content was about 1 %. The median grain size was 160 μm. Stations on the Oder Bank were 9 m deep. The sediment was sandy with an organic content of only about 0.2 % and a silt content of 0.1 %. The median grain size was 165 μm. Stations 4 and 5 were located at 15 m depth. The sediment was sandy with an organic content of about 0.4 % and a silt content of 0.2 %. The median grain size was 175 μm. See Fig. 4.4 for the location of the stations.

Soft parts of the clams were removed from the shells for weight measurements after three months of preservation in a 4% buffered formalin/seawater solution.

The length of all shells was measured to the nearest mm. Aging was done by counting growth checks. I observed that clearly visible growth checks were formed in winter. The annual shell growth started in March or April. Growth rate was fast between late April and July and subsequently slowed
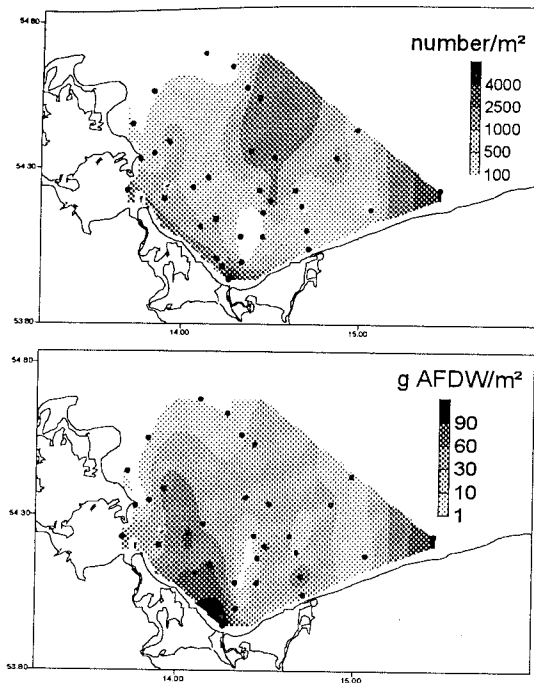
Fig. 4.5: Density (top) and biomass (bottom) distribution of *Mya arenaria* in the Pomeranian Bay (dots indicate sampling stations).
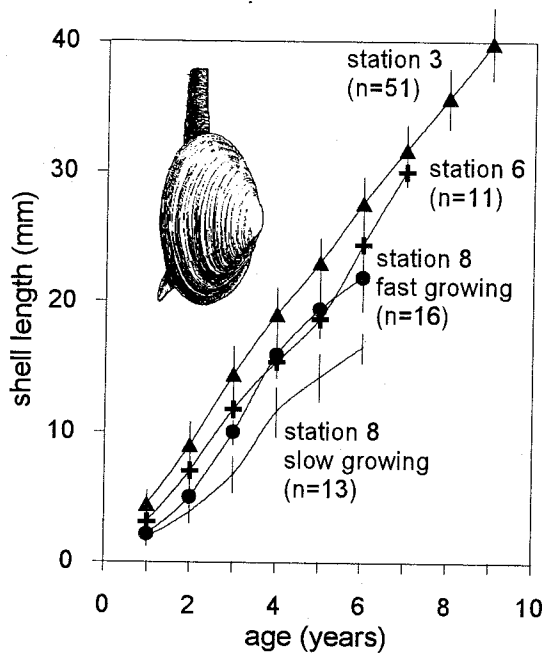

Fig. 4.6: Length-age relationships (means ± se) of *Mya arenaria* for stations in the Pomeranian Bay (see Fig. 4.4 for the location of stations).

down until October. According to earlier studies on the formation of growth checks in *M. arenaria* from the Baltic Sea, age determinations were exact within the first ten years of age (own obs.). Aging in older specimens was sometimes difficult, because earlier rings were worn away due to shell abrasion.

Results

Spatial variation in size and age structure

Although *M. arenaria* was found to form dense beds in most parts of the Pomeranian Bay, biomass values of more than 50 g AFDW·m^{-2} were restricted to the nearshore zone. About 116 g AFDW·m^{-2} were observed near the Oder Mouth, with densities of about 5.800 ind·m^{-2}. Densities of more than 1.000 ind·m^{-2} also occurred near the shores and on the Oder Bank (Fig. 4.5).

Fig. 4.4 shows the relative length-frequency histogrammes from the eight selected stations in April 1993. Size-frequency distribution patterns were highly different between stations 1-5 (with significant proportions of specimens > 20 mm) and stations 7 and 8 (with hardly any large specimens). Small, first year specimens comprised 50 % to 85 % of the total stock from stations 1-5, in the West, except for station 4. The cohorts of 25-40 mm in length (6+ to 8+ years of age, Fig. 4.6) were abundant at some of these stations too. The largest specimen ever collected in this part of the bay was 59 mm in length. This animal belonged to the 1981 cohort and had an age of 12+. Usually, specimens of this oldest age group do not exceed a length of 55-56 mm.

Soft-shell clams collected on the Oder Bank at stations 7 and 8 were never older than six years (Fig. 4.6). Their maximum size was about 25 mm in April 1993. There were no large variations among the densities of the cohorts 1+ to 4+ years of age. Older cohorts were found to be scarce. The size-frequency histogramme of station 6, north of the Oder Bank, was intermediate between the stations 3 and 8.

Temporal variation in size and age structure

Because of the similarities in the size and age structure within the two station groups 1-5 and 7-8, two representative stations, providing the largest sample sizes, were chosen for the following description of temporal variations, *viz.* station 3 (Oder Mouth) and station 8 (Oder Bank).

Near the Oder Mouth (station 3), there were no dramatic changes in the population structure between April 1993 and July 1994, though first-year specimens were more abundant in 1994 than in 1993 (Fig. 4.7). Among the older specimens, those born in 1985, 1986 and 1987 were always more abundant than other age groups (Fig. 4.11). The densities of the cohorts born in 1991 and 1992 continuously decreased during the study period. Cohorts, born earlier than in 1991 decreased by about 30 % between June and October 1993 and remained almost stable from October 1993 until July 1994 (Fig. 4.8). Estimated mortality rates between spring 1993 and spring 1994, given in Table 4.4, were about 70 % for animals during their first two years of life and about 30 % in older cohorts until 10+ years of age. The variation of mortality rates among the older cohorts may have been caused by the small sample sizes of these age groups.

Table 4.4: Mortality rates of *Mya arenaria* at station 3, measured between spring 1993 and spring 1994.

age in years	mortality (%)	n
1	74	168
2	69	77
3	45	19
4	41	18
5	58	18
6	16	45
7	26	42
8	31	40
9	13	27
10	41	9
11	65	7
12	65	13
13	100	4

The *M. arenaria* population near the Oder Mouth was strongly reduced by a local oxygen depletion extending to almost 20 days during July/August 1994. Only a few specimens of the age groups 4+ to 9+ had survived until late September (Fig. 4.8). Cohorts of the years 1985 to 1987 remained more abundant than other ones. Very high densities of spat were observed in September 1994.

A completely different temporal variation of the soft-shell clam population was observed on the Oder Bank (right hand part of Fig. 4.7). The clam stock on stations 7 and 8 consisted of two different groups of specimens. One group was characterised by a very small growth rate. The other group of clams was characterised by a more rigid growth rate (Fig. 4.6). Sometimes single specimens showed a faster growth rate within their first two or three years of life and a slower growth rate during later years. But usually, all specimens (except for spat) could be assigned to one of the two groups.

Total densities did not change very much on the Oder Bank between April 1993 and September 1994 (Fig. 4.9). Total biomass increased rapidly after April 1994. The biomass increase at station 7 was stronger than at station 8 (Fig. 4.9).

The size- (and age)-frequency distributions of the clam population changed dramatically on the Oder Bank from one sampling cruise to the next. The contribution of fast growing specimens varied heavily, too (Fig. 4.7). All younger age groups (1+ to 4+ years of age) of slow growing clams occurred in similar densities in April 1993. Almost all fast growing specimens belonged to the 1990 cohort. Only a few older slow growing specimens were found in June 1993. The size frequency histogramme had changed again in October. The new spat had started to settle in high densities. Older cohorts of slow growing clams had almost disappeared. Several cohorts of fast growing specimens occurred in low densities. The densities of all older cohorts of both groups of clams decreased between October 1993 and April 1994.
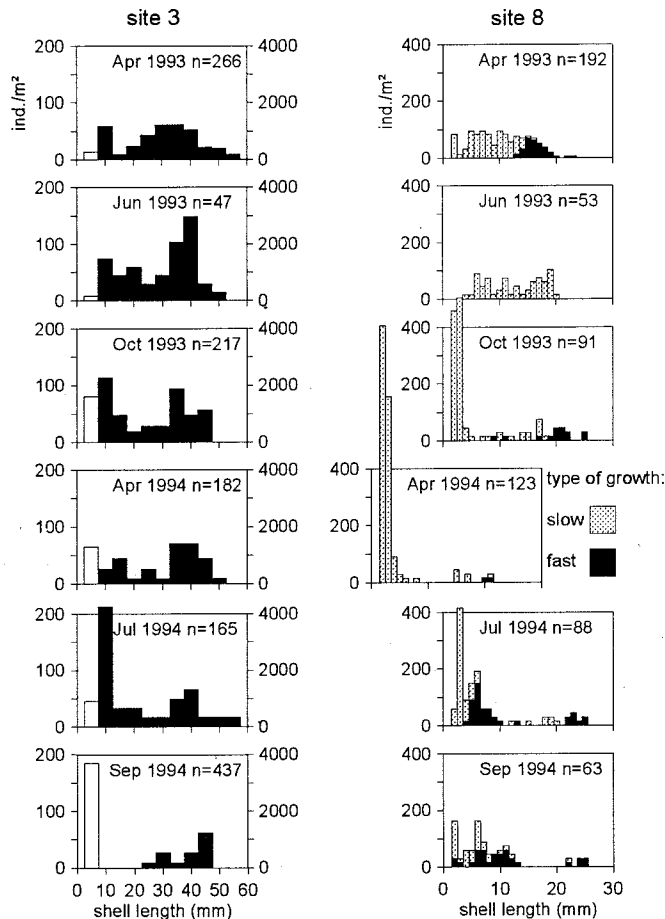

Fig. 4.7: Length-frequency histogrammes of *Mya arenaria* at stations 3 and 8 during the April 1993 to September 1994 period. At station 8, slow growing individuals included by shading, rapidly growing ones by black parts of columns.

All these changes were running parallel between stations 7 and 8 until April 1994. The population composition was differrent between these stations only during the last two cruises. In June and September 1994 older cohorts of fast growing specimens were found more numerous at station 7 than at station 8. The densities of slow growing clams remained low at both stations.

Discussion

M. arenaria exhibited tremendous spatial differences in its population dynamics in the Pomeranian Bay in 1993/94. The standing stock of the shallow and exposed Oder Bank must permanently have been influenced by immigration and emigration processes. Compared to the development at stations 7 and 8, the population structure remained relatively stable at stations in the Southwest of the bay at depths between 11 and 15 m (stations 1-5). The environmental forces responsible for the temporal variations in the age and size structure of the clam population presumably varied strongly within the study area. They will be discussed separately, therefore, for stations on the Oder Bank, and stations near the Oder Mouth.
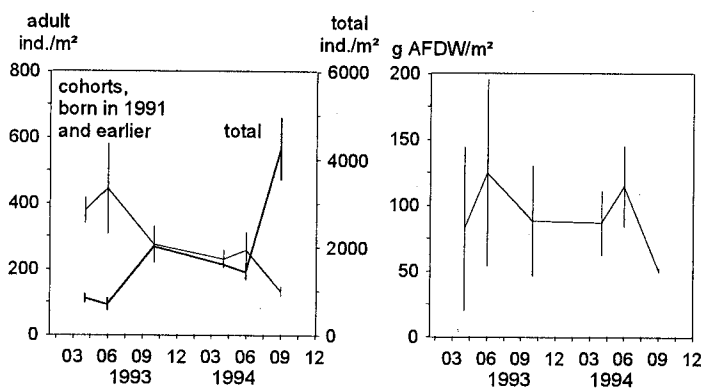
Fig. 4.8: Density (seperately for adult and all animals) and biomass (means ± se) of *Mya arenaria* at station 3 during the April 1993 to September 1994 period. Note difference of scale for adult (thin line, left hand axis) and all individuals (bold line, right hand axis).
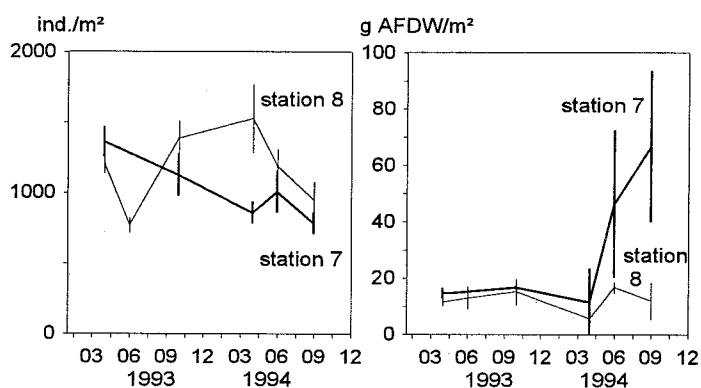

Fig. 4.9: Density (left) and biomass (right) (means ± se) of *Mya arenaria* at station 7 (thick line) and station 8 (thin line) during the April 1993 to September 1994 period.

Processes on the Oder Bank (at stations 7 and 8)

Physical forcing: An intensive transport of clams across the sediment surface is assumed to be the main reason for the occurrence of two different growth types and for the large fluctuations in clam density on the Oder Bank as well. However, the evidence for the exictance of passive mass transport of soft-shell clams is restricted to indirect observations.

The extremely slow growth rate of one of the two clam groups might be understood as a result of permanent removal and reburrowing of specimens that always lived on the Oder Bank. Clams belonging to the group with a faster growth rate are likely to have been introduced by strong bedload currents from the deeper surroundings. Their growth rates were comparable to those of clams from the north of the bay (Station 6, Fig. 4.6). The presence of specimens showing rapid growth during their first years of life and a slow growth during later years support this hypothesis. They were interpreted as examples of a successful establishment of imported clams on the Oder Bank. Emerson & Grant (1991) reported that clams, up to 28 mm long, could easily reburrow themselves. Zwarts & Wanink (1984) found that clams of even 103 mm were able to reburrow.

A negative influence of erosion on the growth of *M. arenaria* is assumed, because this bivalve is very sensitive to mechanical stimulation. When disturbed, the valve gape is reduced and the siphon and mantle edges are retracted, thereby reducing pumping and ingestion rate (Jørgensen & Riisgård, 1988). Otherwise, Emerson (1990) described a positive relationship between any degree of sediment disturbance and growth rate from experiments. Unfortunately, his experimental disturbances did not exceed a depth of more than 1 cm.

On the Oder Bank abrasion occurred probably down to depths of more than 5 cm. This is concluded from measurements of the vertical distribution of *M. arenaria* (Fig. 4.10). Clams of about 30 mm length were burrowed 6 cm deep on the Oder Bank. Such large specimens generally belonged to the fast growing group and were only occasionally found.

The differences in the changes of the population structure between stations 7 and 8 in summer 1994 after a oneyear period of synchroneous development also support the assumtion that changes in clam density on the Oder Bank were mainly caused by physical forcing. Strong bottom currents, transpor-

ting bivalves from the North to the South, are likely to introduce the same size spectrum of clams to both stations, because they were located at the same latitude. Strong bottom currents, running from the West to the East of the Oder Bank should deposit the larger specimens already at station 7 and transport only smaller specimens as far east as station 8.

Predation by sea ducks: common scoters, *M. nigra*, and long-tailed ducks, *C. hyemalis*, occure during winter on the Oder Bank in densities of up to 800 ind·km^{-2} (Durinck et al., 1994; own obs.). Common scoters feed on clams between 5 mm and 30 mm length, long-tailed ducks take clams up to 15 mm long (Kirchhoff, 1979, Leipe 1985; Stempniewicz, 1986). The decrease in the density of clams larger than 5 mm between October 1993 and April 1994 gives some circumstantial evidence for the assumption that sea duck predation is likely to cause severe reductions in the bivalve standing stock. However, quantification of the link between predation and the decline of the numbers of soft-shell clams is almost impossible because of the major importance of erosion processes and bedload sediment transport.
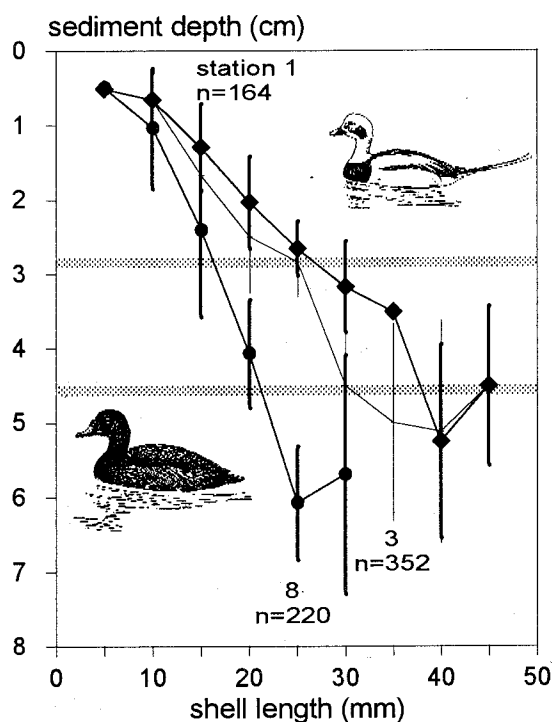

Fig. 4.10: Size dependend vertical distribution of *Mya arenaria* at three selected stations (means ± se, no seasonal variation was observed, see Fig. 4.4 for location of stations). The two shaded horizontal lines indicate the bill length of the long-tailed duck, *Clangula hyemalis*, and the common scoter, *Melanitta nigra*, respectively, to show the fraction accessible to sea duck predation.

Processes in the Southwest of the bay (at station 3)

Physical forcing: Wave-induced erosion processes seemed to be of minor importance for the population dynamics of soft-shell clams at the deeper stations in the Southwest of the area under investigation. This is concluded from the similarities in population structure between stations 1-5, the deeper habitats, the higher organic contents of the sediment and the more shallow burying depths of clams (Fig. 4.10). Imigration and emigration was assumed to be negligible for all age groups older than 1+ year.

Predation by fishes and sea ducks: *M. arenaria* is one of the main prey items of flatfish in the Pomeranian Bay. Flatfishes were observed to feed there on clams up to a length of 17 mm (Hertling, 1928). Because of the slow growth of *M. arenaria* in the study area, they can remove clams up to 3+ years. Predation by sea ducks can be almost ignored near the Oder Mouth. Their densities are much lower there than on the Oder Bank. The predation by fishes might be an important cause of the observed high mortality rates of clams within their first two or three years of life.

Mortality rates of older cohorts measured during this study were lower but rather erratic. Maybe this was caused by systematic errors in the sampling procedure (positioning of the research vessel was only possible with a precision of ±100 m).

A size or age dependend decrease of mortality was also described by Brousseau (1978b). She observed a fairly constant survivorship of clams after maturation in a North American intertidal mudflat. Mortality rates remained stable at very low rates for specimens larger than 30 mm in length. These results are in contrast to Munch-Petersen (1973) who assumed that *M. arenaria* show a constant mortality rate throughout their life.

If adult mortality rates are rather constant until very old age, the differences in density among the older cohorts (which were always encountered at station 3) must be explained by different initial densities, *i.e.* variability in recruitment.

Climate variations: annual variations in the reproductive success are likely to be the reason for the variation in densities of older cohorts. Variations in the reproductive success were reported for *Cerastoderma lamarcki, Macoma balthica* and *M. arenaria* from other parts of the Baltic Sea (Möller & Rosenberg, 1983; Mölsä et al., 1986; Segerstråle, 1960). Most of the investigations mentioned here, describe biological interactions (predation, interference, etc.) and pollution as causes for interannual differences in density and survival rate of larvae. The severety of the winter is related to the recruitment of bivalves in intertidal areas of the Wadden Sea and the shallow sublitoral of the western Baltic Sea. Recruitment of several species generally failed after extremely mild winters (Beukema, 1992; Beukema et al., 1993; Möller, 1986). Bivalves of temperate environments are generally loose weight in winter during periods of food shortage. Their stores of energy will be depleted especially at the higher temperatures during mild winters (Bayne & Newell, 1983; Zwarts, 1991), leaving less energy for gamete production. This may explain why recruitment is usually high after cold winters and low after mild winters (Bayne & Newell, 1983; Beukema, 1992).

The interannual difference in winter temperatures of the near bottom water of the Pomeranian Bay between cold and mild winters between 1980 and 1993 never exceeded 4°C. These differences were usually observed until May. In the Wadden Sea, a difference in the sea water temperature of only 1°C caused a significant increase in relative monthly weight losses of filter-feeding bivalves of about 5 % (Zwarts, 1991). It is supposed, therefore, that variations in the severeness of the winter season can have been an important cause of interannual differences in recruitment and agerelated densities of older cohorts of *M. arenaria* in the Pomeranian Bay. Densities of the 1985, 1986 and 1987 (cohorts at age 6+ to 8+) were much higher than densities of the 1988 and 1989 (cohorts at age 4+ and 5+). Winters of the years 1985, 1986 and 1987 were the coldest of the investigated time series. Winters of 1988 and 1989 were the mildest of the time series under investigation (Fig. 4.11).

Hence, prolonged periods of mild or cold winters may cause serious disturbances not only to intertidal environments (Beukema, 1992), but also to sublitoral coastal ecosystems of the Baltic Sea.
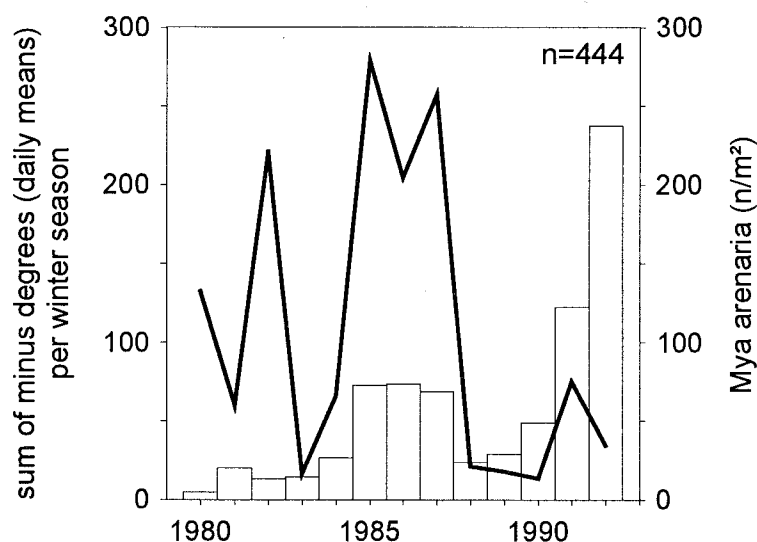

Fig. 4.11: Index of the severeness of the winter seasons from 1980-1993 (sum of minus degrees (daily means) per winter season) and age-frequency distribution of *Mya arenaria* at station 3 in spring 1993.

Oxygen depletion: the unusually strong decline of the clam density at stations 1-5 found in late September 1994 was a result of severe oxygen depletion during a three foregoing weeks period. Free hydrogensulphide was encountered in the near bottom water layer at water depths below 10 m in early August 1994. The sediment's chemocline rose at station 3 from almost 6 cm in July to only 2 cm in late September. The severe oxygen depletion in summer 1994 was caused by an unusual strong and prolonged stratification period (data will be reported elsewhere).

Acknowledgements

Spatial variation in growth of *Macoma balthica* and *Mya arenaria* (Mollusca: Bivalvia) in relation to environmental gradients in the Pomeranian Bay (Southern Baltic Sea)

Jan Kube, Christine Peters & Martin Powilleit

Abstract: This paper deals with spatial variations in individual growth rates of *Macoma balthica* L. and *Mya arenaria* L. in the shallow sublitoral zone of the southern Baltic Sea. Field sampling was carried out in the Pomeranian Bay between 6 and 30 m depth in 1993 and 1994. Growth of *M. balthica* and *M. arenaria* was studied by the analysis of annual growth checks. Compared to full marine environments, growth rates were considerably lower in this brackish area (salinity about 8‰). Growth of *M. balthica* correlated significantly with phytoplankton concentration. Growth of *M. arenaria* was assumed to be negatively effected by intensive physical disturbances. It is supposed that reduced salinities affect the growth of *M. arenaria* more than that of *M. balthica*.

Introduction

The growth of the baltic tellin, *Macoma balthica*, and the soft-shell clam, *Mya arenaria*, have been studied by many investigators, and much work has been done in assessing the importance of various environmental factors for the growth process. These factors include temperature, salinity, sediment characteristics, pollution, disturbance, and siphon cropping (e.g. Beukema et al., 1985; Brousseau, 1979; Emerson, 1990; Lammens, 1967; Newell & Hidu, 1982). Factors were studied individually and in relation to each other. The strongest relationship was found between latitude and growth rate (Appeldoorn, 1983; Beukema & Meehan, 1985). However, within a certain latitude, the relative importance of single factors varies among the different studies.

Although an overall trend could not be established, the available food supply was often considered to be of major importance in controlling growth rate of infaunal bivalvia (Beukema & Cadée, 1991; Nakaoka, 1992). *M. arenaria* is known to be an obligatory filter-feeder. Depending on the amount of food available in the water column, *M. balthica* is able to switch its feeding mode between surface deposit-feeding and filter-feeding. However, both species depend primarily on a pelagic food supply (Brey, 1989; Hummel, 1985; Jørgensen, 1990). They were found to grow more slowly with increasing exposure time on intertidal mudflats, but the magnitude of this effect appeared to be smaller in the deposit-feeder (Wanink & Zwarts, 1993). In sublitoral waters, food supply is mainly determined by the concentration of food particles in the water column and the current velocities near the bottom (Carlson et al., 1984; Fréchette & Bourget, 1985).

The aim of this study was to investigate several environmental factors contributing to growth rate variations in *M. balthica* and *M. arenaria*. Field work consisted mainly of taking sediment samples at various times of the year in 1993 and 1994 and measuring the shell growth, along with a description of hydrographic and biotic factors. Statistical analyses of the data yielded new information on the growth of both bivalves, especially in relation to spatial environmental gradients in the sublitoral zone of the brackish bay.

Study area

Field investigations were carried out in the Pomeranian Bay, southern Baltic Sea. This shallow bay is situated north of the Oder Mouth, bordering both the German and Polish coastline. The 20 m isobath was defined as the northern border to the adjacent Arkona and Bornholm Basins. The total area measures about 8.800 km². Almost in the centre of the bay, the Oder Bank is located with depths of only 7 to 9 m. Behind the coastline several large lagoons are situated (Fig. 4.12). A detailed description of the macrofauna was recently given by Powilleit et al. (1996).
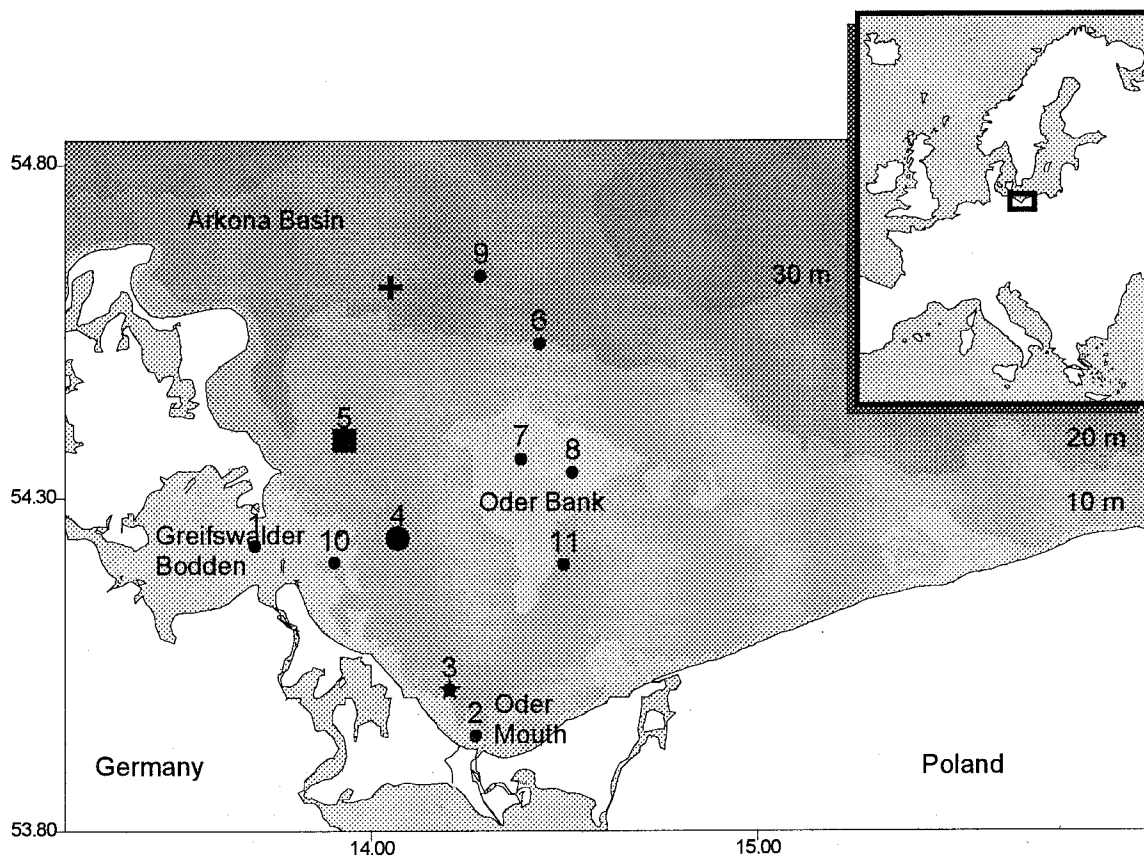
Fig. 4.12: Map of the study area and location of sampling stations (dots and numbers) and stations for the oceanographic monitoring (other symbols).

Methods

Environmental variables

Long-term measurements of salinity, oxygen saturation, and water temperature were carried out 1 m above the seafloor at four sites five times per year between 1980 and 1994. Additional two stations were sampled at monthly intervals between 1990 and 1994 (Figs 4.12 and 4.14). At all stations, surface chlorophyll a concentrations were measured according to HELCOM (1988). Further data on hydrographic parameters and phytoplankton concentration were collected about ten times per year all over the bay in 1993 and 1994.

Sediment parameters (organic content: loss on ignition after 8 hours of incineration at 500°C; mud content: % dry weight of the sediment fraction < 63 μm) were measured at every macrofauna sampling station in April and October 1993 and 1994. Intensity of erosion processes at the sampling sites was estimated from water depths, sediment parameters, and video observations of seafloor topography. Erosion was classified into five levels (1-5): very low, low, moderate, high, very high.

Field sampling

Macrofauna samples were collected between April 1993 and October 1994 in the Pomeranian Bay using a Van Veen grab and a modified 'Reineck' box corer. Sampling was carried out in April, July and October (see Powilleit et al., 1996 for details). Additional observations on the formation of growth checks were made in January. Depending on an adequate minimum number of specimens per sample, growth rates of *M. balthica* and *M. arenaria* were investigated at ten stations per species (Fig. 4.12).

Aging bivalve shells and estimation of growth rates

The length of all bivalve specimens was measured to the nearest mm. Aging was performed by counting annual growth checks throughout the year. Surface growth rings on the shells of many bivalves are produced during periods of suspended shell growth, and may be associated with various environmental factors. Thus, the use of growth rings for aging is still controversial (e.g. Bayne, 1990; MacDonald & Thomas, 1980). From our observations in the study area, we assumed an annual origin of growth checks during the winter season. However, the formation of a nonannual growth check was observed in *M. balthica* during a three week period of oxygen depletion in summer 1994.

Counting of growth checks was easy in *M. arenaria*, even for older specimens up to about ten years of age. The age of specimens of *M. balthica* larger than 10 mm was often underestimated. Earlier rings were worn away due to shell abrasion. Moreover, growth rates decrease with increasing age. In specimens older than 7-8 years (11-13 mm shell length) rings at the posterior shell margin became closely packed and were difficult to resolve.

We restricted our calculations of the growth rates to an estimate of the mean annual length increments of specimens up to six years old. The mean annual length increment was defined as the slope (m) of the linear regression:

l=m·a+n (n=0)

between age (a) and length (l). The linear regression was used, because the growth of both species was almost linear within their first six years of age.
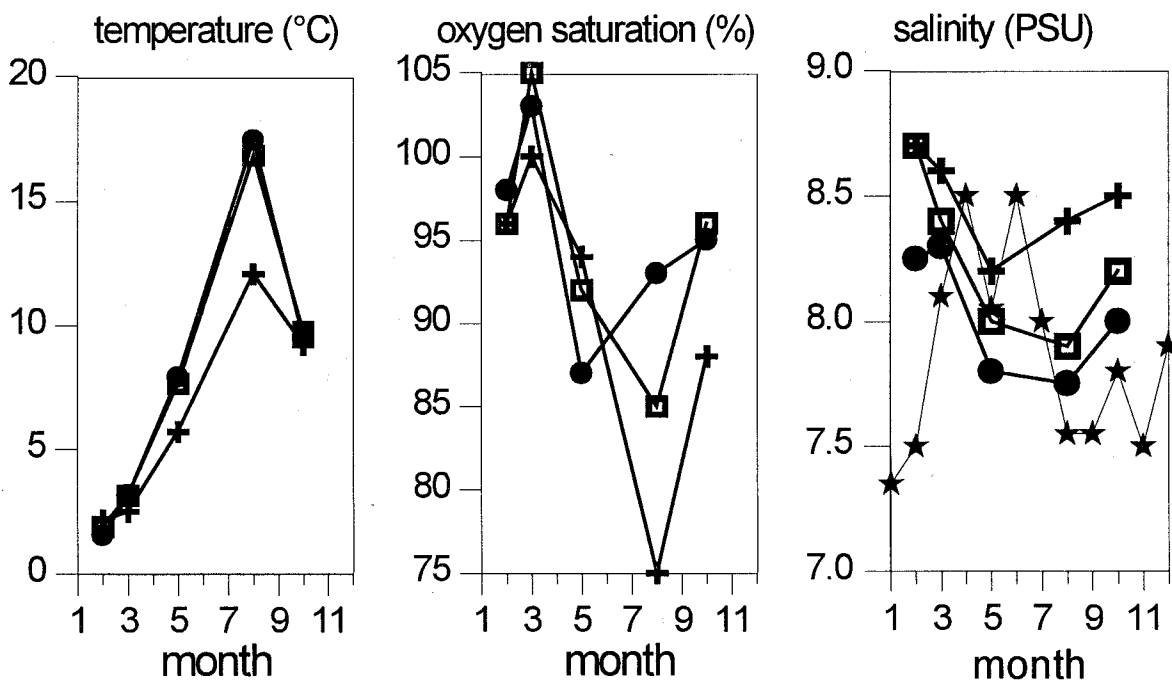
Fig. 4.13: Mean seasonal variation of environmental variables at different stations in the Pomeranian Bay (symbols indicate stations, shown in Fig. 4.12).

Results

Environmental variables

The means of environmental variables of the 11 stations chosen for shell growth measurements, are shown in Table 4.5. Several inter-correlations between environmental variables occurred. Water depth, salinity, and the intensity of erosion processes increased with distance offshore. Phytoplankton concentration and organic content of the sediment decreased with increasing distance from the shore. The organic content of the sediment increased with increasing silt content and phytoplankton concentration (Table 4.6).

The intra-annual variation of salinity, oxygen saturation, and water temperature of the near bottom zone is shown in Fig. 4.13. Salinity variations at any single station were larger than differences between stations. Reduced levels of oxygen saturation in summer occurred more regularly at the slope of the Arkona Basin than within the Pomeranian Bay. Mean summer temperatures were about 5°C higher within the bay than at the northern slope. On the other hand, mean winter values were about 1°C lower within the bay than at the northern slope.

Phytoplankton concentrations (annual means) of about 10-15 mg Chl a·m⁻³ occurred near the Oder Mouth and the Greifswalder Bodden. Values of only about 2 mg Chl a·m⁻³ were observed on the Oder Bank and at the slope of the Arkona Basin (Fig. 4.14).

Table 4.5: Mean values of environmental variables measured at 11 stations. See Fig. 4.12 and 4.14 for the location of stations. See methods for definition of variables.

station	distance from a river mouth (km)	water depth (m)	mg Chl a m⁻³	organic content (%)	silt content (%)	salinity (‰)	intensity of erosion
1	2	10	26.2	1.3	3	7.3	1
2	1	6	11.7	0.9	1.5	7	1
3	5	11	9.9	0.6	1	7.8	2
4	17	13	2.4	0.3	0.2	8	3
5	17	15	2.4	0.3	0.35	8.3	4
6	31	15	2.2	0.2	0.1	8.4	4
7	24	8	2	0.2	0.1	8.2	5
8	26	9	2	0.2	0.1	8.2	5
9	34	30	2.3	0.25	0.1	8.5	4
10	6	11	10	1.6	8	7.8	1
11	17	13	2.4	0.3	0.2	8	3

Table 4.6: Pearson correlation matrix amongst the environmental variables.

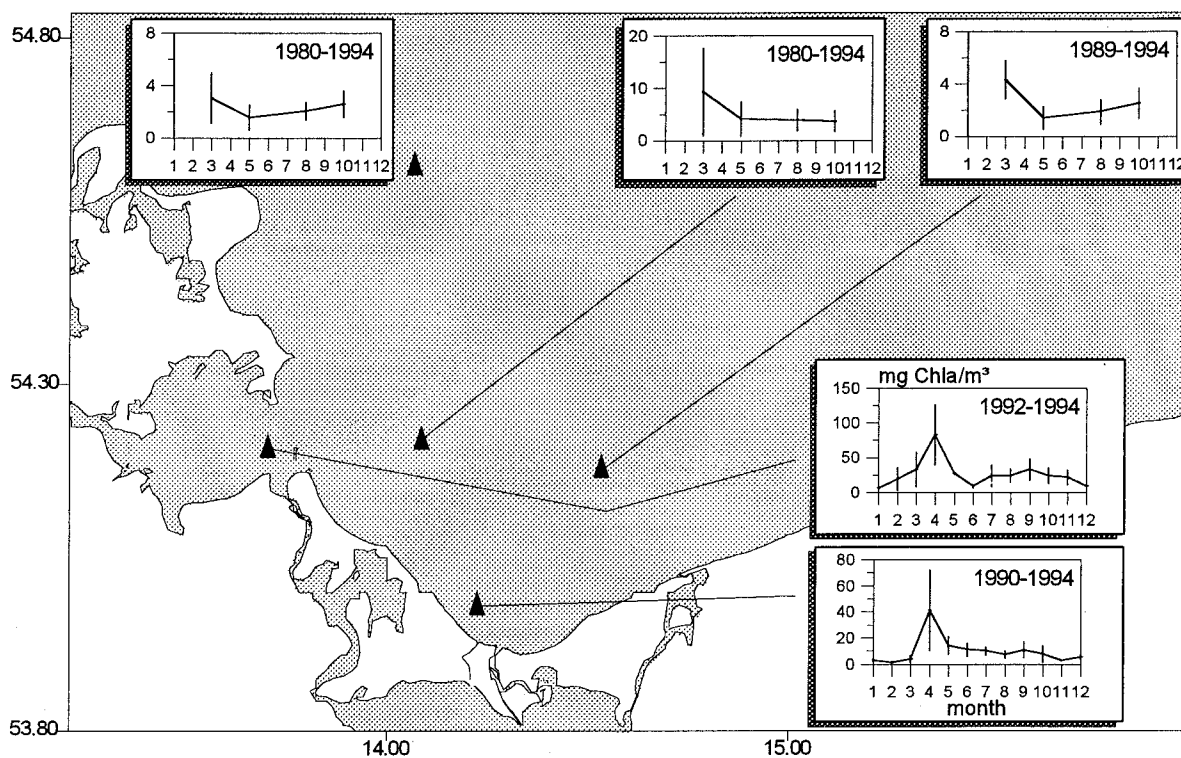|	distance from a river mouth (km)	water depth (m)	mg Chl a m⁻³	organic content (%)	silt content (%)	salinity (‰)
water depth (m)	0.61					
mg Chl a m⁻³	-0.76	-0.33				
organic content (%)	-0.78	-0.32	0.78			
silt content (%)	-0.56	-0.22	0.49	0.91		
salinity (‰)	0.90	0.61	-0.79	-0.71	-0.41	
intensity of erosion	0.88	-0.29	-0.79	-0.88	-0.69	0.84

Fig. 4.14: Seasonal variation (mean ± se) of the surface chlorophyll a concentration at different stations in the Pomeranian Bay.

Growth rates of Macoma balthica

At most stations, the mean annual growth of *M. balthica* was almost linear within the first six years of life (Fig. 4.15). Mean annual growth rates of *M. balthica* decreased with an increasing distance offshore (Table 4.7 and 4.8). Although the age of older specimens was frequently underestimated, it can be stated, that slow growing specimens from the North of the bay generally attained a higher age than fast growing specimens from the Southwest.

Significant negative correlations between growth and environmental factors were found for the variables salinity and intensity of erosion. Positive correlations were found for phytoplankton concentration and organic content of the sediment.

Growth rates of Mya arenaria

Major differences in the growth rates of clams were only found between the stations 7 and 8 on the Oder Bank, and a group of all other stations (Fig. 4.16, Table 4.7). Growth rates decreased almost significantly with increasing intensity of erosion. No other correlation was observed (Table 4.8). The growth of soft-shell clams was almost linear within their first ten years of life (Kube, 1996).

Table 4.7: Growth rates of *Macoma balthica* and *Mya arenaria* at stations in the Pomeranian Bay. Growth rate is expressed as the mean annual increment in length of specimens between 1-6 years old. The mean annual increment in length is expressed as the slope (m) of the linear regression: length=m·age+n, with n=0.

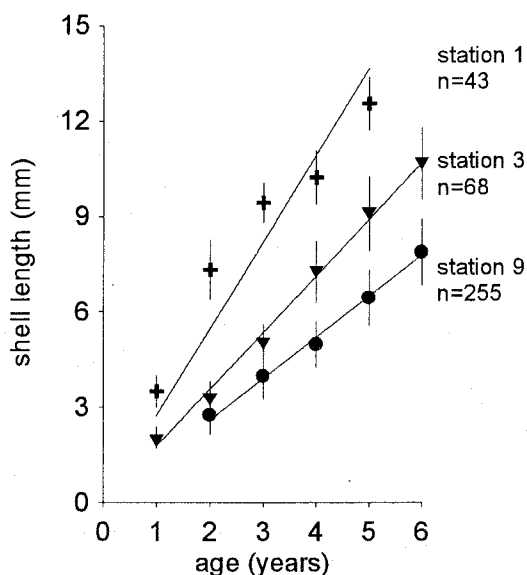| station	mean annual length increment in mm ± se (n)	
	Macoma balthica	*Mya arenaria*
1	2.67 ± 0.06 (44)	4.10 ± 0.04 (225)
2	1.98 ± 0.02 (74)	5.05 ± 0.09 (138)
3	1.77 ± 0.03 (68)	4.57 ± 0.04 (193)
4		5.05 ± 0.07 (59)
5	1.61 ± 0.03 (32)	4.44 ± 0.10 (39)
6	1.35 ± 0.03 (67)	3.97 ± 0.07 (50)
7	1.29 ± 0.03 (45)	2.43 ± 0.03 (237)
8	1.47 ± 0.03 (77)	2.68 ± 0.02 (232)
9	1.29 ± 0.01 (255)	
10	2.07 ± 0.05 (33)	3.71 ± 0.06 (71)
11	1.65 ± 0.04 (13)	4.44 ± 0.05 (53)

Fig. 4.15: Age-length relationship for *Macoma balthica* in the Pomeranian Bay (mean ± se). Station 1 and 9 representing the fastest and slowest growth rate, respectively. Station 3 gives an example of intermediate growth rates (see Fig. 4.12 for the location of stations).
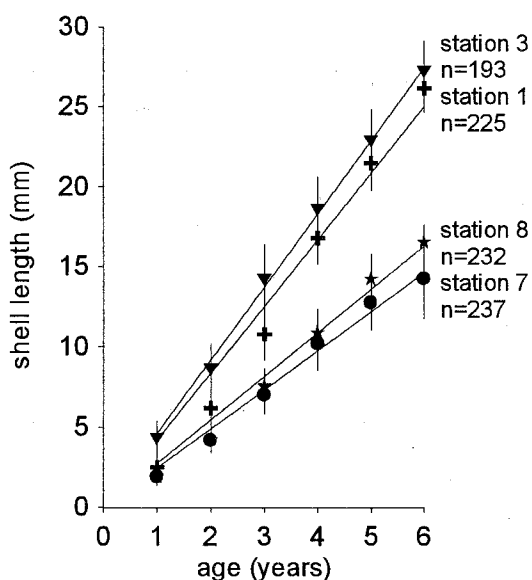

Fig. 4.16: Examples of age-length relationships for *Mya arenaria* in the Pomeranian Bay (mean ± se, see Fig. 4.12 for the location of stations).

Table 4.8: Pearson correlation coeffcents (r, p) between the growth rate of *Macoma balthica* and *Mya arenaria* and environmental variables.

environmental variable	*Macoma balthica* (n=10)		*Mya arenaria* (n=10)	
	r	p	r	p
distance from a river mouth (km)	-0.85	0.002	-0.50	0.14
water depth (m)	-0.40	0.25	0.30	0.40
mg Chl a m^{-3}	0.95	0.0001	0.20	0.59
organic content (%)	0.86	0.002	0.16	0.66
silt content (%)	0.61	0.06	-0.02	0.95
salinity (‰)	-0.81	0.04	-0.42	0.22
intensity of erosion	-0.85	0.02	-0.57	0.08

Discussion

In the present investigation, growth rates of *M. balthica* and *M. arenaria* were considered to be very low, as compared to investigations from more marine habitats (Appeldoorn, 1983; Bachelet, 1980; Bayne, 1990). They are even lower than growth rates reported from the western Baltic (Munch-Petersen, 1973; Möller & Rosenberg, 1983; Winther & Gray, 1985; Vogel, 1959). Growth rates of *M. balthica* are in accordance with values published for the Baltic Proper by Ankar (1980) and Segerstråle (1960).

A considerable amount of published data exists on the growth rates of filter-feeding bivalves from the North American and Europeans Seas. Many studies assessed the importance of various environmental factors in the growth process (Bayne, 1990; Gosling, 1992). Lowered salinity has an especially detrimental effect on growth (e.g. Essink & Bos, 1985). Salinity is the main factor reducing the growth rate and maximum size of bivalves in the Baltic Sea (Remane, 1940).

Mean annual growth rates of bivalves usually decrease during later years. However, in cases of strongly reduced annual growth rates bivalves are also known to show a linear growth performance throughout their life. For instance, Kautsky (1982) reported a very low and almost linear growth rate of *Mytilus edulis* between about 2-10 years of age. Growth rates of *M. arenaria*, observed during this study, were linear between about 1-10 years of age. Growth rates of *M. balthica* from the Pomeranian Bay were linear within the first 6 years of age. The same was observed by Segerstråle (1960) in Finish waters.

The climate is supposed to be of major importance for the growth rate of the stenothermic bivalve species, too. Bachelet (1980) described a positive correlation between growth and latitude. However, seasonal variations in food concentration and spawning conditions are known to modify the length of the growing season at different latitudes (Beukema & Meehan, 1985; Brousseau, 1978).

The growing season is relatively short in the southern Baltic Sea. Seasonal growth starts in early April and almost stops after spawning in June/July (Kautsky, 1982; Oertzen, 1972; Saavedra, 1990; own obs.). Spawning starts two or three months later than in the Wadden Sea (Günther, 1991; 1992; Zwarts, 1991), and about one month later than in the Skagerrak (Möller & Rosenberg, 1983). This is probably due to a temperature threshold of about 10-12 °C for spawning in *M. balthica* and *M. arenaria* (Heinonen, 1962; Nelson, 1928; Wilde, 1975).

Within a given salinity range and climatic zone, local variations in food supply and temperature are generally acknowledged as important factors causing spatial and temporal variations in growth (Beukema & Cadée, 1991; Beukema et al., 1977; Beukema et al., 1985). As already described by Segerstråle (1960) for Finish waters, growth rates of *M. balthica* were observed to decrease with increasing distance off shore and increasing water depth. This phenomenon most likely results from a decrease in water temperatures with increasing water depth. Furthermore, the food supply often decreases with both, increasing distance off shore and increasing depth, as it was also found during this study. The strong positive correlation between chlorophyll and growth is also likely to be the main reason for the observed negative relationship between salinity and growth. Salinity increases with increasing distance off shore in the Pomeranian Bay.

In *M. arenaria*, no significant trends were observed between environmental factors and growth. Growth rates showed little variation except for reduced values at the Oder Bank stations. The high

intensity of erosion and sediment disturbance on the Oder Bank is supposed to be responsible for this difference. Soft-shell clams of up to 40 mm length were commonly found to be transported across the sediment in this region (Kube, 1996). Although specimens of this size are able to reburrow themself into the sediment (Emerson & Grant, 1991), this intensive physical disturbance causes reductions of the growth rate (Emerson, 1990). A significant negative correlation between the intensity of erosion and growth was also observed for *M. balthica*.

Amongst the group of less disturbed stations, no large differences in growth rates of *M. arenaria* were found. It is assumed that possible effects of limited food supply or other environmental variables on *M. arenaria* growth rates were overruled by the strong impact of low salinities (7 to 9 ‰). This is in contrast to the above results for *M. balthica*. *M. balthica* has a greater tolerance for lowered salinities than *M. arenaria*. In the Baltic Sea, the baltic tellin is found regularly at salinities of only 2 ‰. For *M. arenaria*, the lowest reported mean salinity is 5 ‰ (Lassig, 1965).

Acknowledgements

Distribution of *Marenzelleria viridis* (Polychaeta: Spionidae) in the southwestern Baltic Sea in 1993/94 - ten years after introduction

Jan Kube, Michael L. Zettler, Fritz Gosselck, Susanne Ossig & Martin Powilleit

Abstract: *Marenzelleria viridis* (Verrill, 1873), a North American spionid polychaete, was first recorded in brackish water ecosystems of the Wadden Sea and Baltic Sea in the early 1980s. It has spread rapidly and is now a dominant element of the macrozoobenthos in meso- and oligohaline estuaries and coastal lagoons. The distribution and abundance of this polychaete was studied in the southwestern part of the Baltic Sea in 1993/94 in relation to environmental factors. All available macrozoobenthos samples from German Baltic waters were used to construct a general distribution map. Highest abundances and biomasses were found in semi-enclosed lagoons (39.000 ind. m^{-2} and 70 g AFDW m^{-2}). The western horizontal distribution border and the vertical distribution range were following the 15 ‰ isohaline. Neither a horizontal nor a vertical limit was found to the East. Dense settlement was restricted to sediments with an organic content of less than 5 % and a silt content of less than 10 %. Simultaneous population studies were carried out in the Oder Estuary and the Darss-Zingst Bodden from April 1993 to April 1994. Three different age groups were identified throughout the year. Settlement of larvae took place in autumn. Successful larval settlement was restricted to areas with a salinity above 5 ‰ and a winter phytoplankton concentration above 5 g Chl a m^{-3}. Benthic stages were found to be highly motile. Adults occurred up to 50 km away from recruitment areas. Potentially important causes of dispersal processes are discussed.

Introduction

The introduction of alien species to marine areas is an old phenomenon. Recently, unintentional introductions of coastal marine species to new environments have increased. Extensive man-induced changes of estuaries and the increasing size and speed of ships have augmented the risk of spreading species over seas. Ballast water and artificial waterways have been described to be the main causes of unintentional introductions (Carlton, 1985; Jansson, 1994).

The Baltic Sea is especially receptive to successful invadings. The history of coastal lagoons is short (2.000-6.000 years) and species assemblages have a low diversity. Many niches are unsaturated. About 30 animal species have been reported as introduced east of the Arkona Basin until 1984 (Leppäkoski, 1984). Among these, two macrobenthic bivalve species, *Dreissena polymorpha* (Pallas) and *Mya arenaria* (L.), make up the predominant biomass in some coastal areas (Leppäkoski, 1991).

A North American polychaete, *Marenzelleria viridis* (Verrill, 1873), was introduced to the Baltic during the 1980s. The first specimens in Europe were found in 1982 in the Forth Estuary, Scotland (McLusky et al., 1993) and in 1983 in the Ems estuary between The Netherlands and Germany (Essink & Kleef, 1988). It is assumed that larvae were transported across the Atlantic in the ballast water of ships. Since, it has spread rapidly around the North Sea (Essink & Kleef, 1993).

Bick & Burckhardt (1989) observed the first specimens of *M. viridis* in the Darss-Zingst Bodden, a coastal lagoon system of the southern Baltic Sea, in 1985. Densities of about 1.000 ind. m^{-2} were reported from the eastern part of the Darss-Zingst Bodden and all over the Oder Estuary already in 1988 (Arndt, 1994; Gruszka, 1991a; Saavedra, 1990). This spionid polychaete was probably imported by ballast water to one of the big harbours in the Oder Estuary around 1983/84. The polychaete dispersed eastward to Estonian inshore areas and to the south coasts of Sweden and Finland. The first specimens were found there in 1989 and in 1990 (Norkko et al., 1993; Persson, 1990; Zmudzinski et al., 1994). Today it is dominant in some Baltic coastal benthic communities at about 90 % (e.g. Zmudzinski, 1993; Zettler, 1994). West of the Oder Estuary it was reported only for the Wismar Bay by Prena & Gosselck (1989) and the Schlei Estuary (Schroeren pers. comm.). The North Sea and Baltic Sea populations are of different genetic origin (Bastrop et al., 1995). There is

no doubt, that these populations were introduced separately. They might even belong to different species (Bastrop & Röhner pers. comm.).

M. viridis has been studied intensively since it was discovered to become an important component of the coastal macrozoobenthos of the Baltic Sea. Field studies and laboratory investigations were carried out to analyse the life cycle (Bochert et al., 1994), the distribution and physiological capacities according to ecological factors (Bochert & Bick, 1995; Fritzsche & Oertzen, 1995; Zettler et al., 1995; Zmudzinski et al., 1994). This paper presents a descriptive picture of the recent distribution of *M. viridis* for the southwestern Baltic Sea. Comparable analyses of population dynamics were used simultaneously in several subareas of the Oder Estuary and the Darss-Zingst Bodden to describe its niche in the field in relation to various environmental factors.

Material and methods

Study area

Samples were collected in 1993/94 from the German part of the Baltic Sea and adjacent Polish waters (Fig. 4.18). The salinity ranged from 15-25 ‰ in the West (Kiel Bay) to less than 2 ‰ in the East (Oderhaff). Samples were taken in shallow coastal regions up to 0.5 m depth and down to 40 m deep offshore (Arkona Basin). A recent description of the hydrography of the southwestern part of the Baltic Sea is given by Nehring et al. (1994). Detailed hydrographic data are presented for the Oder Estuary and the Darss-Zingst Bodden by Lampe (1993) and Schlungbaum et al. (1994a; 1994b).
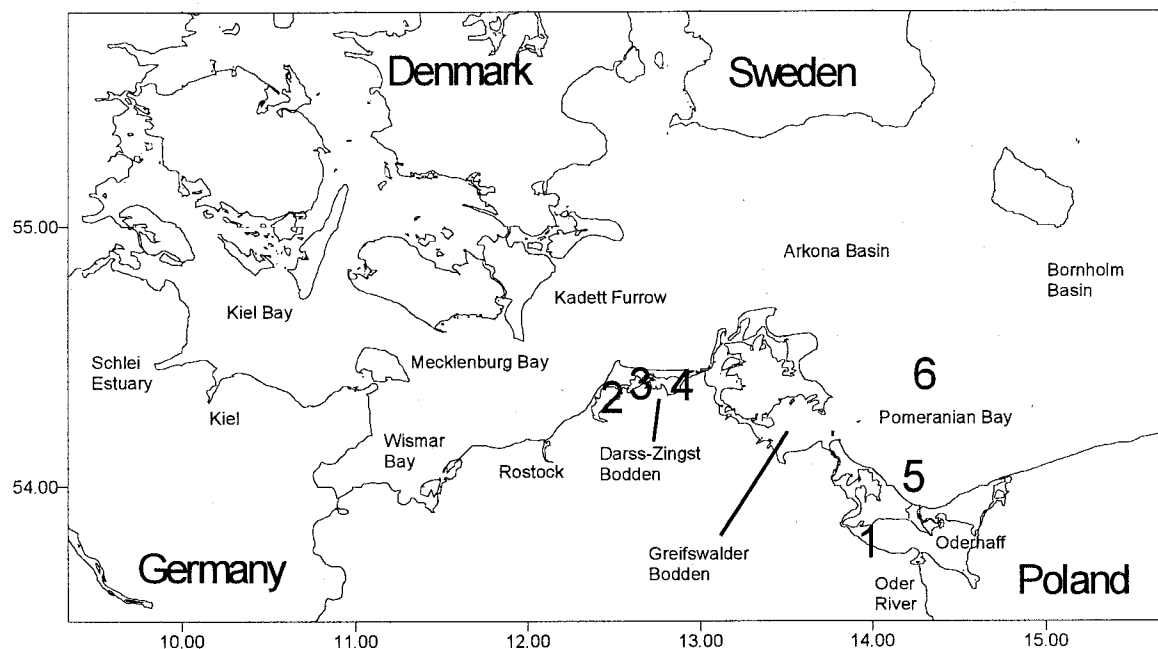

Fig. 4.18: Study area in the Baltic Sea. Labels indicate subareas mentioned in the text.

Sampling design and data analysis

Macrozoobenthos samples were collected in the Darss-Zingst Bodden (50 sampling sites), the Pomeranian Bay (35 sampling sites) and the Oderhaff (85 sampling sites) between April and September 1993 to compute detailed distribution maps. Density isolines were calculated by kriging with WINSURF software package.

The applied sampling methods were comparable for these areas. Reineck-Box corers (0.0225 m² and 0.006 m², penetration depth 15-20 cm) were used in the Pomeranian Bay and in the Oderhaff. Sampling was carried out by a hand-operated tube corer (0.0078 m², penetration depth 40 cm) in the Darss-Zingst Bodden. All samples were sieved with a 0.5 mm sieve. Ash free dry weight (AFDW)

was measured following the HELCOM-guidelines (HELCOM 1988) for samples collected in the Pomeranian Bay.

M. viridis is known to burrow up to 35 cm deep into the sediment. Only about 20-30 % of the large mature worms live in the upper 10 cm of the sediment. In the Darss-Zingst Bodden, occasionally, up to 45 % of the adults were found burrowed deeper than 20 cm (Zettler et al., 1994). However, the penetration depth of the box corer was deep enough to catch all worms in the Pomeranian Bay (burying deeper than about 10 cm was prevented there by a thick layer of bivalve shells). Perhaps, 10 % to 20 % of the worms were lost in samples from the Oderhaff. Unfortunately, an intercalibration with the deep penetrating hand-operated tube corer was technically impossible.

Detailed population studies were carried out in selected subareas between April 1993 and April 1994 at 1-3 sites (Fig. 1, not for subarea 4). Sites of subarea 1 were 2-4 m deep. Sites of subareas 2 and 3 were 0.5 m deep. Sites of subareas 5 and 6 were 9-10 m deep. All samples taken from these areas were collected in the same way as described above. Maximum width of all specimens was measured within the first 30 segments by only two persons to minimize systematic errors.

We also analyzed sediment parameter and phytoplankton concentration in all subareas. According to the small-scale spatial variability in the distribution of *M. viridis* (Zettler & Bick, 1996), relationships between sediment parameter and densitiy estimates were plotted only for macrofauna and sediment samples, simultaneously collected. Sediment samples were taken from the upper 5 cm. Median grain size, silt content (relative DW of the fraction < 63 µm after wet sieving) and organic content (loss on ignition after incineration at 500 °C) were measured. Samples taken before April and later than September were excluded from the analysis to minimize the impact of reproductive processes. Monthly measurements of water chlorophyll a concentration were obtained from 1-5 sites per subarea between 1992-1994. Chlorophyll a was analysed according to Jeffrey & Humphrey (1975). Data were splitted into summer months (June-September) and winter months (November-February). Spring bloom data from March-May and data from October (maximum of planctonic larvae) were excluded.

Salinity was measured for each samling site and date.

Furthermore, we computed a distribution map for the German part of the Baltic Sea. Several hundred macrozoobenthos samples were collected in this area in 1993/94, mainly for monitoring purposes. A large variety of sampling gear was applied due to the different scope of each investigation. The sampling methods applied in the Oder Estuary and in the Darss-Zingst Bodden were already described. An Ekman-Birge grab sampler (0.021 m², penetration depth 5-10 cm) was used in a few coastal inlets in the West. Van-Veen grab samples (0.1 m², penetration depth 8-12 cm) were taken in Kiel Bay, Mecklenburg Bay, Wismar Bay, and in the Arkona Basin. Al these samples were sieved with a 1 mm sieve (Table 4.8).

Table 4.8: Sampling methods, applied in different parts of the study area.

subarea	grab type	sampling area (m²)	penetration depth (cm)	sieve mesh size (mm)
Kiel Bay	Van Veen	0.1	10-12	1
Wismar Bay	Van Veen	0.1	8-10	1
	Ekman Birge	0.021	5-10	1
Mecklenburg Bay	Van Veen	0.1	10-12	1
Warnow Estuary	Van Veen	0.1	8-10	1
	Ekman Birge	0.021	5-10	1
Arkona Basin	Van Veen	0.1	10-12	1
Darß-Zingst Bodden	hand-operated tube corer	0.0078	40	0.5
Greifswalder Bodden	box corer	0.006	15-20	0.5
Pomeranian Bay	box corer	0.0225	15-20	0.5
Oderhaff	box corer	0.006	15-20	0.5

Hence, large differences in density estimates occurred according to the penetration depth of the grabs applied. A logarithmic scaling of density isolines was used, therefore, to compute a general distribution map. Density estimates obtained from Ekman-Birge grab samples for instance, presented only between 30 % and 50 % of the true values. An interclibration between box corer samples, sieved

with a 0.5 mm sieve, and Van Veen grab samples, sieved with a 1 mm sieve, was performed in the Pomeranian Bay in April and October 1993. Mean densities of *M. viridis* were about 50 % lower in Van Veen grab samples than in box corer samples (Powilleit et al., 1996). However, the impact of underestimations of densities onto the shape of density isolines was less important, since most of the grab samples were taken in the West, where no *M. viridis* occurred.

Differences in density estimates were caused also by differences in the sieve mesh sizes. Juveniles were observed passing completely through the meshes of the 1 mm sieve up to a size of less than 0.8 mm (Powilleit et al., 1996). Settlement of larvae takes place in the Darss-Zingst Bodden between October and January (Bochert et al., 1994). Juveniles from inner coastal lagoons reach a width of about 1 mm in March/April. Therefore, samples collected between October and March were excluded from the data analyses to minimize the impact of juvenile abundances. At least 200 samples could be used for computing a general distribution map with WINSURF software package (Fig. 4.19).
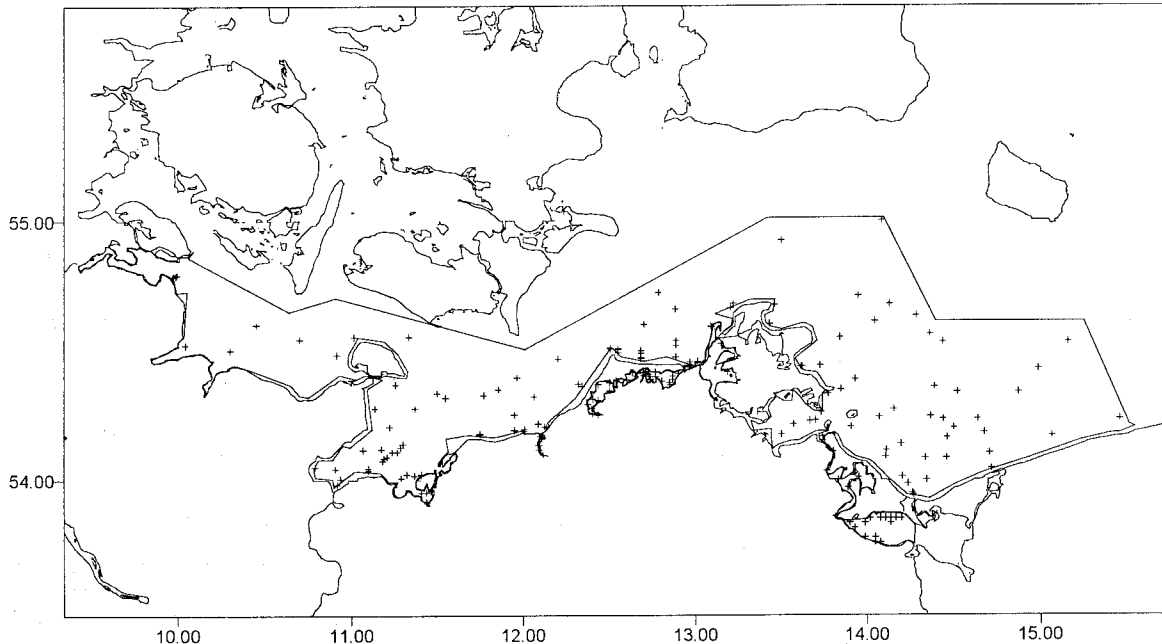

Fig. 4.19: Distribution of sampling sites used for plotting a distribution map.

Results

General distribution in the southwestern Baltic

M. viridis was found in all inner coastal waters east of Mecklenburg Bay (Fig. 4.20). Mean abundances ranged between 1.000-5.000 ind. m^{-2}. Maximum values were 39.000 ind. m^{-2} for the Darss-Zingst Bodden in May 1994 and 28.000 ind. m^{-2} for the Oderhaff in summer 1993. Much lower densities were observed in offshore waters. Densities in the Pomeranian Bay decreased rapidly about 5 miles off the Greifswalder Bodden from 3.000-4.000 ind. m^{-2} to 100-300 ind. m^{-2}. Densities at the southern slope of the Arkona Basin did not exceed 30 ind. m^{-2} at 30 m water depth. No specimens were found in the deeper central part of Arkona Basin. Low densities between 10-30 ind. m^{-2} were found at 30 m depth in the eastern part of the Kadett Furrow. The polychaete was not found in Mecklenburg Bay. Only single individuals occurred occasionally north of the Warnow Estuary near Rostock. Within this estuary densities ranged between 10-100 ind. m^{-2}. A single specimen was collected during extensive sampling in the innermost part of the Wismar Bay in 1993. No worms were found in Kiel Bay. The species was reported recently from the Schlei Estuary which enters Kiel Bay. Densities seem to be high there, but have not yet been estimated (Schroeren pers. comm.). These animals also belong to the Baltic Sea genotype of *M. viridis* (Bastrop & Röhner pers. comm.).
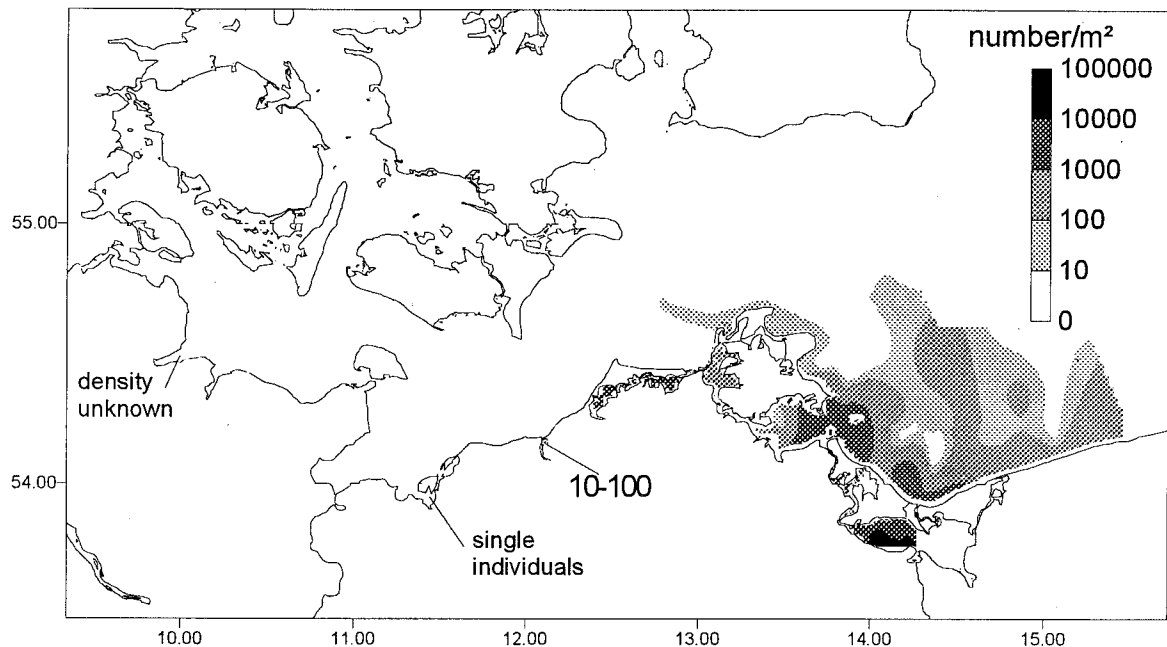
Fig. 4.20: Distribution and densities of *Marenzelleria viridis* in the southwestern Baltic Sea in 1993/1994.

Distribution in the Darss-Zingst Bodden and the Oder Estuary

Fig. 4.21 shows detailed distribution maps of *M. viridis* for the Darss-Zingst Bodden and the Oder Estuary in summer 1993. Maximum densities were revealed in the middle of the Darss-Zingst Bodden and in the south of the Oderhaff (10.000 and 28.000 ind. m^{-2}, respectively). High density values of inner coastal waters were restricted to sites near the coastline and less than 2 m depth. The species was often generally absent from the deeper central parts of the lagoons (3-5 m). Stations studied in the Pomeranian Bay ranged from 6 to 20 m depth. No relationship was observed between abundance and depth. High densities of about 3.500 ind. m^{-2} were found only in the Southwest of the bay, close to river mouths. Numbers decreased rapidly with increasing distances from the shore. Only single specimens were recovered at the northern edge to the adjacent Arkona Basin.

Comparable weight measurements were available for a few stations only. Highest biomass values of 8-9 g AFDW m^{-2} were found in the southwestern part of the Pomeranian Bay. Biomass values ranged from 0.2-1.3 g AFDW m^{-2} offshore. Wet weight measurements from the Darss-Zingst Bodden were transformed into AFDW by own conversion factors. Mean values ranged from 30-40 g AFDW m^{-2} (maximum 70 g AFDW m^{-2}).

Environmental factors

The relationship between abundance and sediment parameter is given for samples from the Pomeranian Bay, the Darss-Zingst Bodden and the Oderhaff collected during summer 1993 (Fig. 4.22). Adult *M. viridis* occurred in sediments with an organic content between 0.1-10 % and a silt content between 0-10 %. The median grain size of colonized sediments ranged from 0.05-0.35 mm. Large differences occurred between the subareas in the range of the sediment types investigated. Whereas sediments in the Pomeranian Bay were found to be almost sandy with an organic content below 1 % of sediment DW, a great variety of sandy and muddy sediments was encountered in inner coastal waters. Stations differed substantially in organic content and silt content of the substrate, but not in median grain size.

Salinities of the subareas ranged from 1.7-14 ‰ in 1993 and were lowest in the Oderhaff (subarea 1). Fig. 4.23 shows that highest values of more than 10 ‰ were measured in the eastern part of the Darss-Zingst Bodden (subarea 4) and in the Northwest of the Pomeranian Bay (subarea 6).
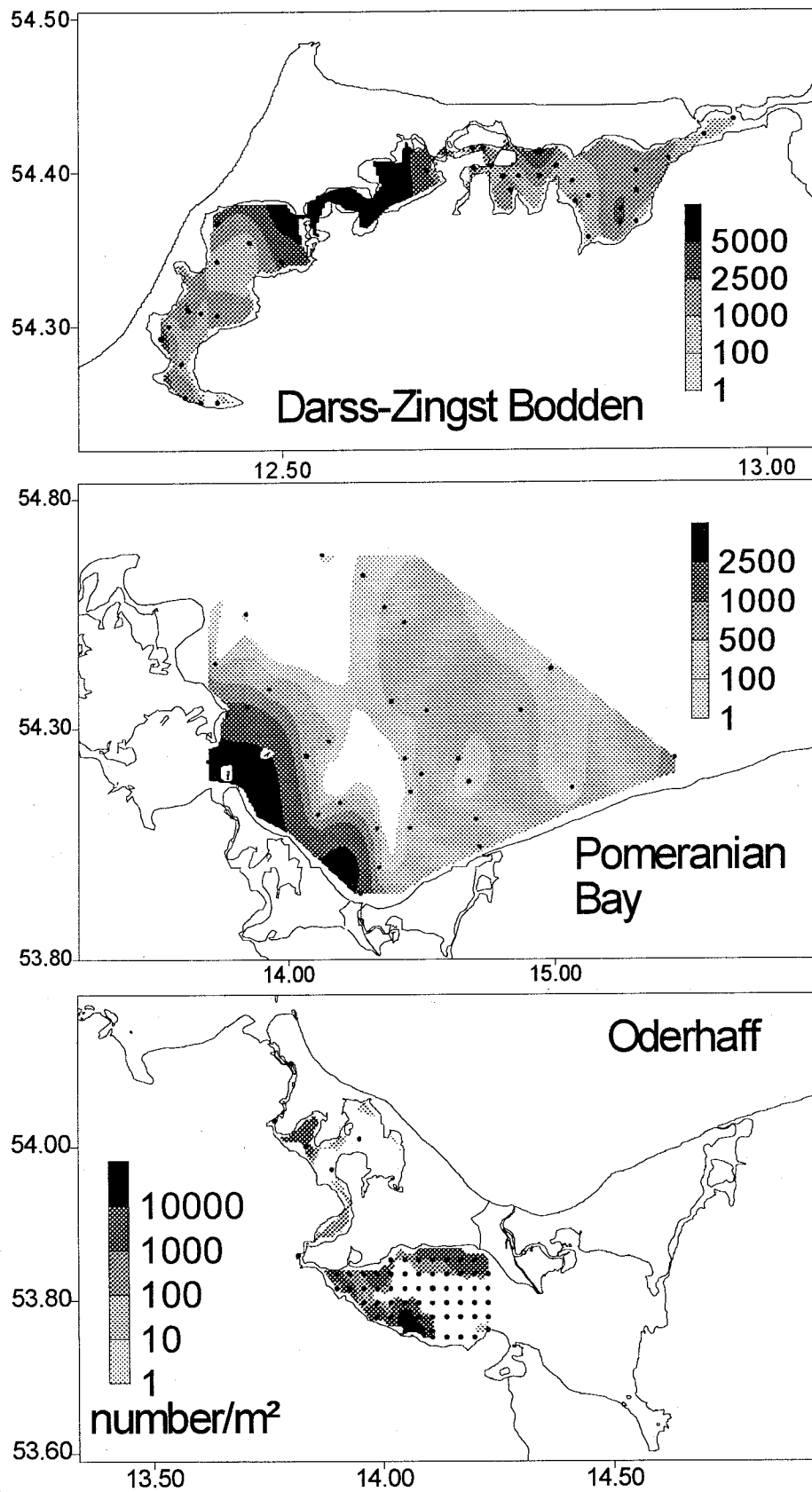
Fig. 4.21: Distribution and densities of *Marenzelleria viridis* in selected waters along the southern Baltic Sea. Dots indicate sampling sites. Note differences in density scaling between maps.

No intraanual cyclic variation was found for the chlorophyll a content of the shallow lagoons in the Darss-Zingst Bodden. Median values ranged from 25 to 105 mg Chl a m^{-3}. The chlorophyll concentration decreased from the West (subarea 2) to the East (subarea 4) of the Bodden chain. Similar high values were found in the Oderhaff (subarea 1) during summer, but concentrations decreased in winter. The median winter concentration of chlorophyll a was only 13 mg m^{-3}. The lowest chlorophyll concentrations were found in the Pomeranian Bay (subareas 5, 6). Median summer values were 11 and 2.3 mg Chl a m^{-3}, respectively. Winter values appeared to be even lower (4.3 and 1.8 mg Chl a m^{-3}, respectively).
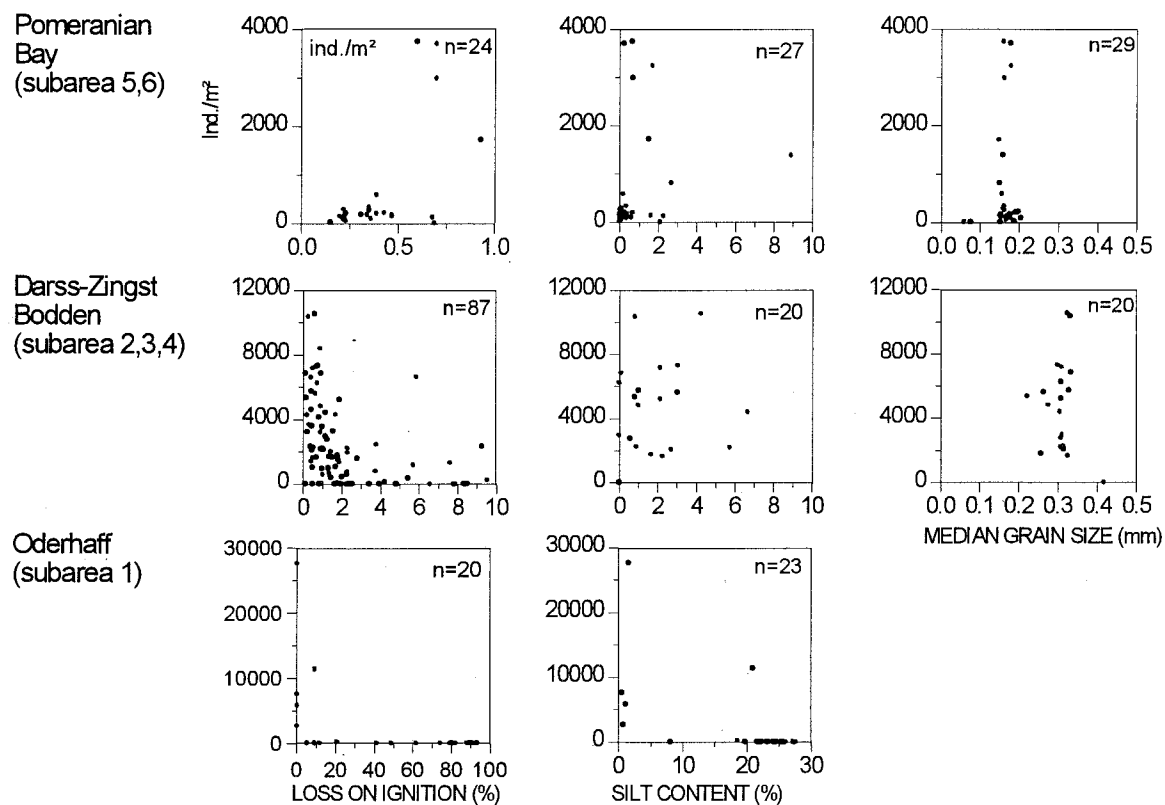
Fig. 4.22: Relationship between density of *Marenzelleria viridis* and sediment parameters in different subareas.

Population dynamics

Fig. 4.24 presents the dynamics of the total population density of six sites from April 1993 to October 1994. Only subarea 2 showed a clear increase in total density within the time period under investigation. Salinity increased in subarea 2 from about 2 ‰ in 1992 to about 5 ‰ in 1993. A successful recruitment of larvae in autumn 1993 caused the exponential increase in densities (see also Fig. 4.25). Only slight temporal variation of abundances was observed at all other sites.

Fig. 4.25 shows the details of the population dynamics of selected single sites from the same subareas. We selected sites with the largest n-values for presentation, because there was no difference in the population dynamics between sites within a certain subarea. Subarea 4 was not investigated.

A clear annual life cycle was observed in the Darss-Zingst Bodden in subareas 2 and 3. Settlement of larvae took place in late autumn. Juveniles were growing fast. They grew to a width of about 1.2

mm by April 1993 and up to about 1 mm by April 1994. They reached a mean width of about 2.1 mm in September and could not be distinguished from adult cohorts by width measurements in winter (about 2.5 mm mean width of adults). Two different adult cohorts were distinguished by a difference in the number of segments with large gills between one and two year old specimens. Whereas the large gills of one year old worms appeared only within the first 40-50 segments, large gills of two year old worms reached up to the 60thiest segment (Zettler own obs.). The maximum width of adults was 3.1 mm.

Only few first year worms were found in the Oderhaff in 1993/94 (subarea 1). Older cohorts occurred throughout the year and grew to a mean width of 2.5 mm (maximum 3.1 mm).
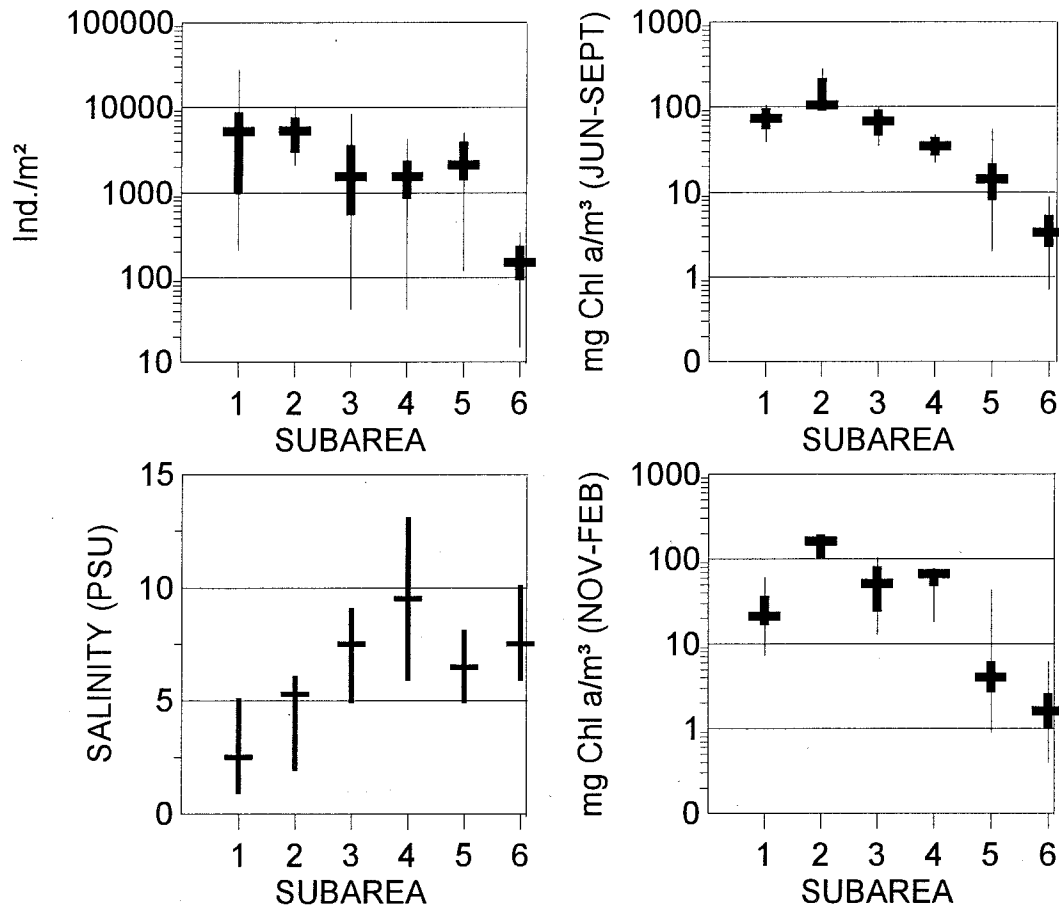

Fig. 4.23: Median densities of *Marenzelleria viridis* (zero values exculded), annual mean salinity, median summer concentration of chlorophyll a and median winter concentration of chlorophyll a in six subareas along the southern Baltic. Thick lines indicate quartiles, thin lines indicate minimum and maximum. Note logarithmic scaling of three Y-axes.

First year specimens were found occasionally in the offshore part of the Pomeranian Bay (subarea 6). Two year old specimens seemed to be dominant. The largest worm ever found was 2.6 mm in width. The mean width of adults was about 2.2 mm.

An inverse population structure with low numbers of first year worms and large numbers of adult worms was found at coastal sites in the Pomeranian Bay (subarea 5). 3 cohorts could be distinguished for all seasons. No other variation than a slight increase of adult cohorts in late summer was observed throughout the year. Juveniles grew only to a mean width of 1.1 mm within the first year of life. Adult worms usually did not exceed a mean width of 1.8 mm. The maximum width of adults was once 2.2 mm and 2.4 mm, respectively. Separation of adult cohorts was not investigated.
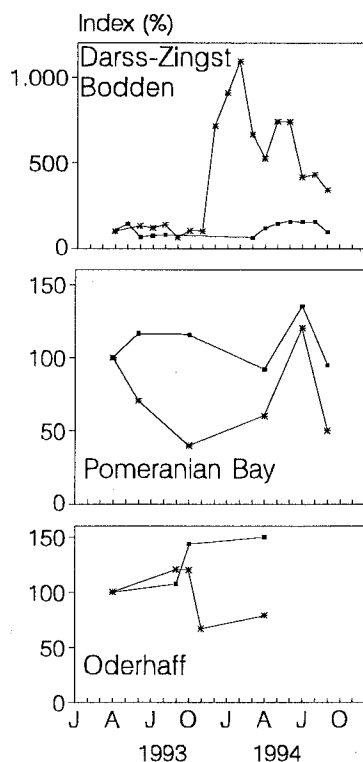
Fig. 4.24: Population trends of *Marenzelleria viridis* at two sampling sites from three different subareas along the southern Baltic. 100 % values of the population-index: Darss-Zingst Bodden: 5223 ind. m^{-2} - squares; 7176 ind. m^{-2} - asterisks, Pomeranian Bay: 148 ind. m^2 - squares, 3244 ind. m^{-2} - asterisks; Oderhaff: 2558 ind. m^{-2} - squares, 4226 ind. m^{-2} - asterisks.
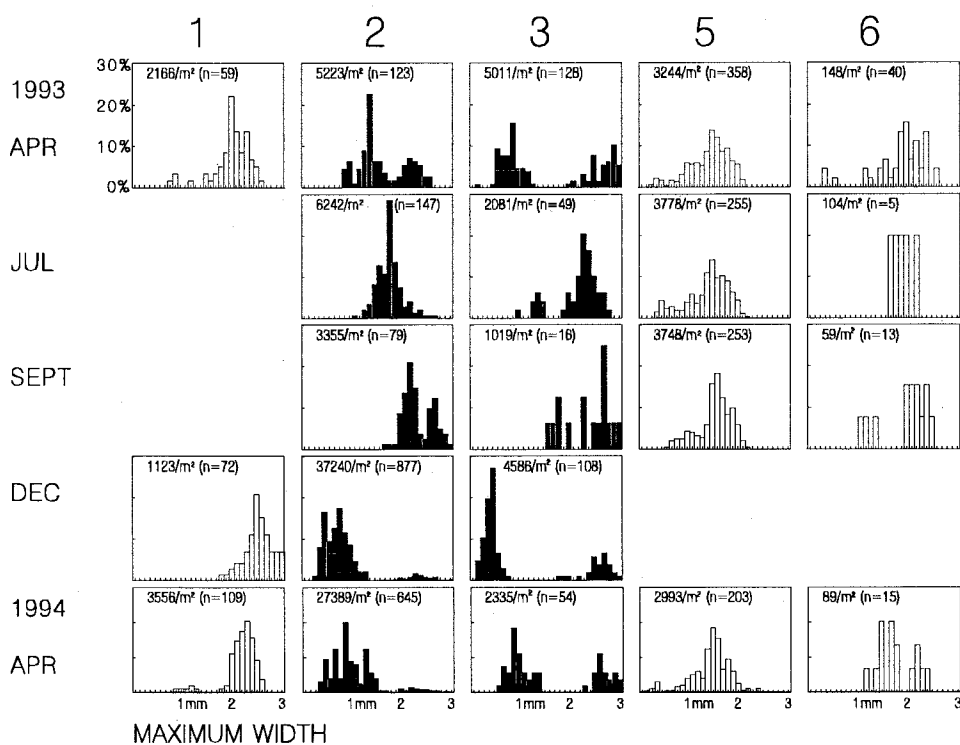
Fig. 4.25: Width-frequency histogramms of five selected subareas along the southern Baltic from April 1993 to April 1994. Filled bars indicate sites with successful larval settlement in the Darss-Zingst Bodden, open bars indicate a site at the mouth of Oder River with weak recruitment and sites in the Oderhaff and the offshore part of the Pomeranian Bay where recruitment has failed. Note also differences in maximum width between inshore and offshore waters.

Discussion

Species are known to be distributed along natural gradients of environmental factors. Gradients of several factors usually overlap each other. The importance of a single factor for the regulation of the density of a species follows an optimum curve or a saturation curve. The realized niche depends on the combination of all important factors. The character of the minimum factor changes spatially and temporally due to kind of overlap in many different environmental factors. Hence, the acceptable range of a single factor may change between areas and times in relation to the prevailing composition of other factors (Gray, 1984).

During our investigation we discovered *M. viridis* in a wide range of brackish habitats. It propagated in semi-enclosed shallow lagoons as well as in coastal zones and offshore bays. Thus, the species occurred in areas exhibiting also a wide range of environmental conditions. The following account will describe the realized pattern of optimum or saturation curves of environmental factors in the southwestern Baltic Sea in relation to data available from experimental studies.

Salinity

M. viridis was found during this study at salinities of almost 1 ‰ and up to almost 15 ‰. Abundances were highest at salinities of around 5-8 ‰ and decreased rapidly above 10 ‰. A low salinity range from 2-8 ‰ was reported also for the eastern Baltic Sea by Zmudzinski et al. (1993). Salinity of interstitial water at the Ems Estuary varied between 5-17 ‰ (Essink & Kleef, 1993). The species is most frequently found in areas of reduced salinities in North America. It is known to dominate the salinity range between 0.5-15 ‰ (Boesch, 1977; Doerjes & Howard, 1975).

Early larval stages are unable to develop at salinities of less than 5 ‰. The growth of older larvae ceases, according to Bochert & Bick (1995) and George (1966). These experimental studies were confirmed by our population studies in the Oderhaff at salinities between 1-4 ‰. Although, high densities of planktonic larvae were reported for the Oderhaff by Gruszka (1991b), no successful settlement of juveniles was observed. Most likely, the larvae were drifted occasionally into the Oderhaff by strong water influxes from the Pomeranian Bay during storms (Lampe, 1993). The absence of juveniles in the offshore part of the Pomeranian Bay can not be explained by this factor, because no significant differences were found between the salinities of all other subareas.

We are unable to explain why adult stages did not occurred in the southwestern Baltic Sea at salinities above 15 ‰. There are some indications from recent experimental studies that adult worms, adapted to the horohalinicum, avoid salinities above 15 ‰. Fritzsche (1995) reported hyperosmoregulation by this polychaete for a salinity range between 0-30 ‰. He also recorded a 50 % mortality rate of adult stages, adapted to salinities of 5 ‰, at a salinity of almost 30 ‰. From this it can be concluded that *M. viridis* is a typical genuine brackish water species, well adapted to the horohalinicum (Arndt, 1989; Kinne, 1971).

Water depth

At present, *M. viridis* inhabits depths between 0.2 and 30 m in the southwestern Baltic with a maximum nearshore at depths below 2 m. Zmudzinski et al. (1993) recorded the polychaete down to 50 m with a maximum of 20-30 m in the eastern part of the Baltic Sea. The deepest observations of single adult specimens from the Baltic ranged down to 90 m in the Bornholm Basin (own obs. in 1993). The lower depth range of the species in the southwestern Baltic Sea was probably caused by high salinity values of the bottom water at 20-25 ‰ after a massive salt water influx from the North Sea in January 1993 (Nehring et al., 1994).

Sediment type

Adult *M. viridis* inhabit vertical J-shaped, mucus-lined burrows with a mean diameter of about 2 mm. The depth of the burrow is governed mainly by sediment type: the more sandy or muddy the substrate, the smaller the depth (Dauer et al., 1981; Zettler et al., 1994). Tubes were generally deeper in sand than in mud (Hines & Comtois, 1985).

Water content and grain size of the substrate are important factors for burrowing polychaetes (e.g. Esselink & Zwarts, 1989). A high water content is likely to be unfavourable for the stability of the unbranched burrows of *M. viridis*. An increase in water content of the substrate is usually correlated with an increase in organic- and silt content (Schlungbaum et al., 1994b). Adult worms from the southwestern Baltic Sea were restricted to sediments with an organic content below 5 %. They never occurred in sediments with an organic content above 10 %. Similar values were found for the silt content. No lower limit was observed. Kinner et al. (1974) reported major occurrences in sediments of 0-25 % silt content from a North American Estuary.

Silty sediments with high organic contents were restricted to the central parts of the semi-enclosed lagoons under investigation. Due to the effects of eutrophication large oxygen amplitudes occured there during summer (Lampe, 1993, Schlungbaum et al., 1994b, own measurements). In contrast, nearshore areas of the lagoons were sandy and well oxyginated in most cases. As described above, *M. viridis* inhabited mainly shallow sandy nearshore parts of inner coastal waters and was often absent from the deeper central parts. The impact of temporal events of oxygen deficiency and formation of sulphide in the muddy central areas on densities of *M. viridis* is unclear. The spionide has remarkable adaptation strategies enabling it to live under such inhospitable conditions (Fritzsche & Oertzen, 1995). Oxygen demands of about 20 days were observed to reduce abundances in the Pomeranian Bay in summer 1994, especially of first year specimens.

Also, coarse gravel might cause negative effects on penetrability and stability of the substrate. The lower and upper value of the vulnerable grain size was not measured precisely during this study. No prefered grain size range was found between 0.15-0.35 mm median grain size. Only two sites with a median grain size below 0.1 and above 0.4 mm were studied. Single worms were found at these sites.

Food supply

Polychaetous annelids of the family *Spionidae* feed at the sediment-water interface with a single pair of tentaculate palps. They have been classified as selective surface deposit-feeders as well as suspension-feeders (Fauchald & Jumars, 1979; Hempel, 1957). Due to the available food supply, *M. viridis* can utilize particles both in suspension and from sediment surface (Dauer et al., 1981). If no suspended particles are available, both palps stay in contact with the sediment surface. Palps are lashing in the water column when suspended particles occur. Individuals from muddy sediments were observed to continue surface deposit-feeding even when suspended particles were available. The worms significantly increase the rate of defecation when suspended particles are present (Dauer et al. 1981, own laboratory obs.).
Qualitative and quantitative observations on the food composition of *M. viridis* from the southwestern Baltic Sea revealed mainly planktonic algae from all semi-enclosed lagoons. Fresh phytoplankton and resuspended organic material are the most important food sources. Sand gravel was a considerable part of the material found in intestines too. Specimens of the Pomeranian Bay mainly contained sand. A minor part of fresh phytoplankton was found only near river mouths (Burckhardt & Meyer-Harms pers. comm.; own obs.).

However, fresh phytoplankton is supposed to be the most important food source of *M. viridis*. Therefore, abundances of this spionid still can be related to the feeding biology. Water phytoplankton concentration can be used to describe the food supply, because the water column in shallow coastal waters is usually well mixed by wind forcing down to the bottom. Our observations indicate a clear positive relationship between distribution, abundances, population dynamics, and growth rate and the phytoplankton concentration of the water column. Abundances of adult stages were about ten times higher in inner coastal waters than in offshore parts of the Pomeranian Bay (10.000-20.000 ind. m^{-2} and 100-200 ind. m^{-2}, respectively). The same difference was found for the chlorophyll concentration (50-100 mg chl a m^{-3} and 3-5 mg chl a m^{-3}, respectively). Maximum widths and growth rates were much greater in the semi-enclosed lagoons than in the Pomeranian Bay too. No successful settlement of juveniles was found in offshore parts of the Pomeranian Bay with winter chlorophyll a contents below 5 mg m^{-3}.

Outlook for future dispersal of M. viridis

Since this North American polychaete was found in the Baltic Sea, it has proliferated very successfully. It has probably established itself permanently and has already become the dominating species in many horohaline coastal parts of the Baltic Proper. A similar process was observed in estuaries

around the North Sea. The rapid dispersal can be explained by several causes. First of all, the species propagates in a wide range of horohaline to oligohaline extreme biotopes with periods of hypoxic and anoxic conditions. There are not many other large benthic invertebrates living in such environments within the Baltic Sea. *Nereis diversicolor* (O.F. Müller) is the only polychaete inhabiting the same areas. Within the horohalinicum until today no negative interspecific interactions were detected with other macrobenthic invertebrates (Zettler, 1994; Zettler, & Bick, 1996).

Due to the effects of eutrophication, primary production is extra ordinary high in Baltic estuaries (e.g. Wasmund & Schiewer, 1994). No food shortage will limit the phytoplankton feeding spionide because of the absence of large filter-feeding bivalves in horohaline waters. Competition for food is likely to occur in oligohaline waters with mussel beds of *Dreissena polymorpha* and in coastal offshore parts with high densities of filter-feeding bivalves, *Mytilus edulis* (L.) and *Mya arenaria*. Bivalves are also known to reduce the recruitment rate of larvae (Hines et al., 1989).

The motility of older larval stages and benthic stages is important for the species success too. Adult stages were found in the southwestern Baltic up to 50 km away from successful recruitment areas. The phenology and causes of planktonic phases in the Baltic Sea have not been properly investigated yet. The life cycle of North American *M. viridis* involves three planktonic phases: a juvenile dispersal up the estuary, an adult dispersal down the estuary and a spawning phase (Dauer et al., 1982). Dauer et al. (1981) observed intensive movements of worms in relation to food supply.

The enormous production of larvae (Bochert et al., 1994) is probably the reason for the rapid speed of dispersal. The chance of the larvae to survive a ballast water ship transport to the receiving ecosystem is high. Transport distances are short within the Baltic. Most of the Baltics' harbours are horohaline brackish and eutrophicated. It is precisely in such areas, that alien species are numerous (Jansson, 1994; Leppäkoski, 1984).

Acknowledgements

5. The feeding ecology of wintering sea ducks
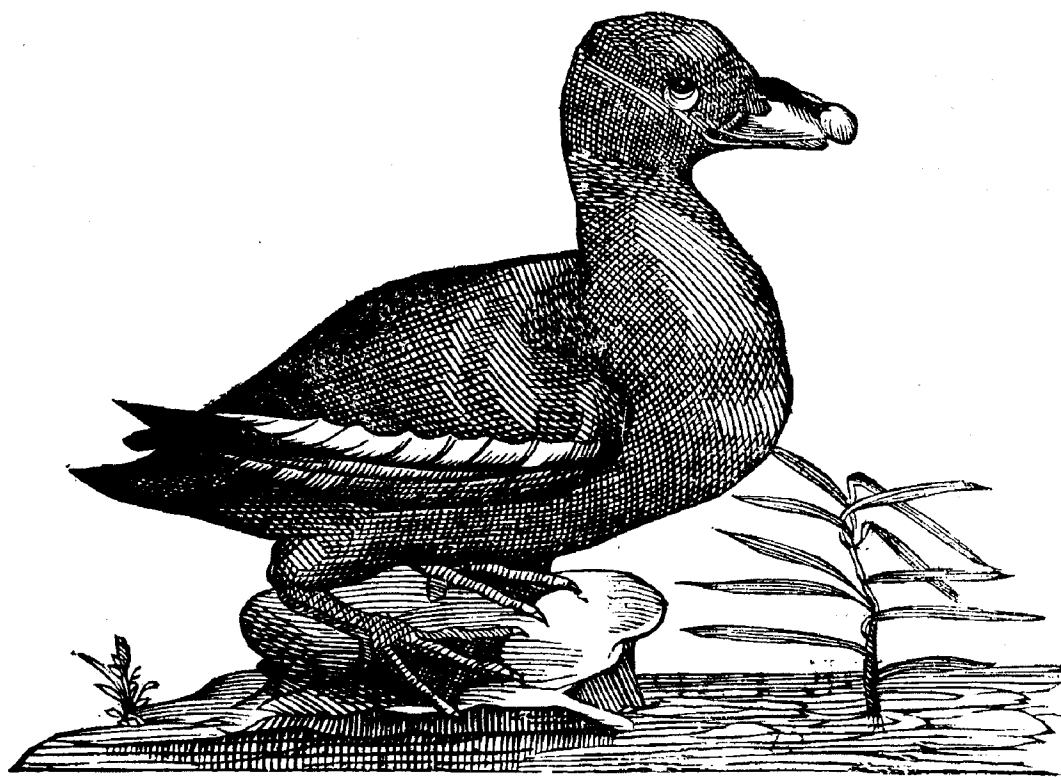
Aldrovandi, 1602

The importance of predation: trophic interactions between sea ducks and their invertebrate prey

The most important sea bird area in the Baltic Sea

An international team of ornithologists was formed in 1991 to provide basic knowledge on the Baltic Sea bird fauna. All potential wintering areas for sea birds in the Baltic Sea were surveyed by combined ship and aeroplane counts and all available data were compiled. The results were published by Durinck et al. (1994).

During the surveys from 1987 to 1993 an average of 9 Mio. sea birds occurred in the studied parts of the Baltic Sea each winter. The large number of birds recorded was far from evenly distributed. The birds showed a clear preference for certain areas and habitats. Coastal and off shore zones with water depths up to 50 m were prefered by sea ducks and several fish-eaters. Fish-eating species preying upon schools of pelagic fish showed no preference for a certain water depth. Herbivorous species feeding on macrophytobenthos prefered sheltered, shallow coastal lagoons (see the distribution atlas of Durinck et al., 1994 for more details).

The costal lagoons of the Oder estuary and the Pomeranian Bay were identified to be the most important wintering areas for a variety of sea birds in the entire Baltic Sea during mild winters. The Greifswalder Bodden and Szczecin Lagoon are very important wintering areas for grebes, swans, diving ducks, mergansers and coots. Very large numbers of sea ducks, divers, grebes, mergansers and auks spend the winter in the Pomeranian Bay. From 1988 to 1995, 18 species were recorded in numbers of international importance (number of international importance means $\geq$ 1 % of a westpalaearctic flyway population, Table 5.1).

Feeding ecology of sea ducks - an overview

Data in Table 5.1 show that sea ducks are by far the most important avian predators in the Pomeranian Bay during winter. They are mainly preying upon benthic invertebrates, especially molluscs (Madsen, 1954). Sea ducks ingest molluscs as a whole, a technique commonly found among various kinds of waterbirds (Piersma, 1994). It still remains unknown, how sea ducks perceive and handle their prey.

The shells of ingested molluscs are crushed in the muscular gizzard. Crushed shells are ejected via the intestine. Shell crushing necessitates a strong and muscular stomach (Fig. 5.1). The gizzard size and weight is related to the total body weight (Borkenhagen, 1976; Nehls, 1995). The muscular stomach does not retain its size when there are no hard shells to crush. Females show gizzard atrophy during the breeding season, resulting from a dietary shift towards small snails, arthropods and crustaceans (Cantin et al., 1974).

Mollusc digestion requires a high proportion of the ingested energy. Common eiders, *Somateria mollissima*, expend about 50-60 % of the ingested energy for diving, prey handling, prey heating, shell crushing and digestion (Nehls, 1995). This value probably also applies to other sea duck species. Since sea ducks have to devote half of the daily energy budget for foraging and digestion, their energy expenditure reaches four times the basal metabolic rate in winter (Nehls, 1995). Such a high value of daily energy expenditure is close to the limit of sustainable metabolic rate (Drent & Daan, 1980).

In contrast to the classic Bergmann's Rule (stating that among warm-blooded genera varying geographically in size, species tend to be larger towards higher latitudes) smaller sea duck species co-occur with larger species in winter. Bergmann' s Rule is based on the assumption that smaller birds have higher specific metabolic rates, store less energy per unit mass, are less efficient at insulating themselves from their external environment, and have higher heat conductance per unit of body mass (Calder, 1974). However, mid winter distribution patterns of sea ducks in the Baltic Sea demonstrate that species are able to evolve different adaptation strategies to survive under the same harsh environmental conditions. Large-sized eiders tend to use the most profitable part of benthic food recources. They forage on large-sized mussels. Their adaptation for consuming these large mussels requires an enlargement of the whole body mass and, perhaps, reduces their flight ability (Nehls, 1995). Due

to their large body size, eiders also require more food from their environment and, thus, food availability puts an eastern limit on winter distribution in the Baltic Sea. Mussels occurring east of Mecklenburg Bay are too small to provide profitable food resources for eiders (data will be reported elsewhere). Smaller species select smaller prey items. Like long-tailed ducks, they partly select diets yielding higher energy per unit mass (crustaceans, fish eggs) and spend more time feeding (Goudie & Ankney, 1986). Furthermore, they are generalists switching frequently between sources of suitable prey. They are more mobile and, therefore, may be able to exploit a wider range of potential food sources/habitats (paper 6).

Table 5.1: Sea bird species wintering in internationally important numbers in the Oder Estuary and in the Pomeranian Bay (modified after Durinck et al., 1994).

species	average number 1988-1995	habitat preference: coastal lagoons (L), Pomeranian Bay (PB)	percentage of NW-European winter population (%)
divers *Gavia stellata et arctica*	4.000	PB	3.3
great crested grebe *Podiceps cristatus*	5.000	PB	5.0
red-necked grebe *Podiceps griseigena*	1.250	PB	8.3
slavonian grebe *Podiceps auritus*	1.700	PB	34.0
mute swan *Cygnus olor*	15.000	L	8.3
pochard *Aythia ferina*	20.000	L	5.7
tufted duck *Aythia fuligula*	85.000	L	11.3
great scaup *Aythia marila*	70.000	L	22.6
common goldeneye *Bucephala clangula*	20.000	L	6.7
long-tailed duck *Clangula hyemalis*	800.000	PB	17
common scoter *Melanitta nigra*	100.000	PB	7.7
velvet scoter *Melanitta fusca*	357.000	PB	38.4
smew *Mergus albellus*	13.000	L	52
goosander *Mergus merganser*	30.000	L	20
red-breasted merganser *Mergus serrator*	15.000	L/PB	15
coot *Fulica atra*	30.000	L	2
black guillemot *Cepphus grylle*	6.000	PB	12

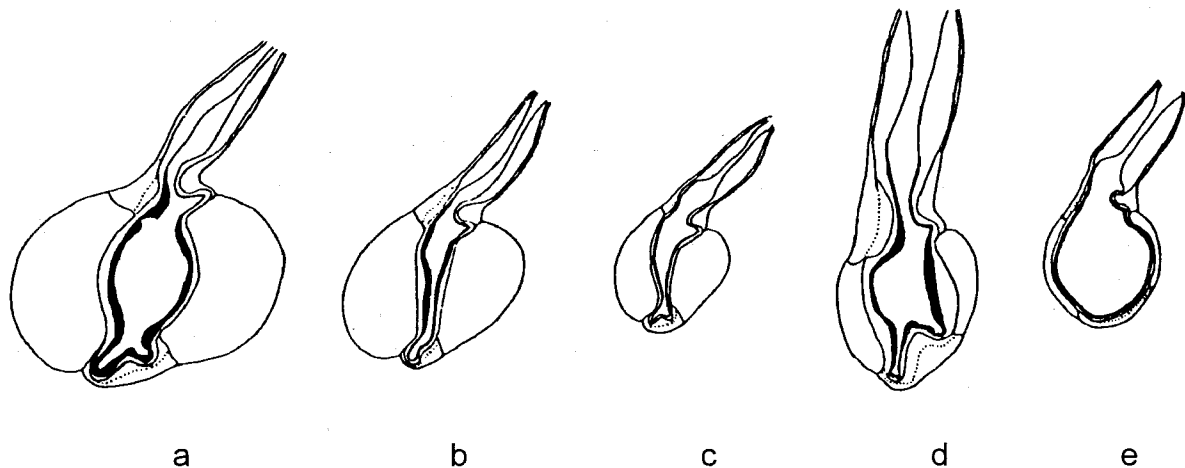

a   b   c   d   e

Fig. 5.1: Stomachs of mollusc-eating sea ducks (a: velvet scoter, *Melanitta fusca*, b: common scoter, *Melanitta nigra*; c: long-tailed duck, *Clangula hyemalis*) compared with stomachs of fish-eating mergansers (d: goosander, *Mergus merganser*; e: smew, *Mergus albellus*). Drawings from Borken-hagen (1976).

Distribution and migration phenology of sea ducks in the Pomeranian Bay during mild winters

Sea ducks use tundra habitats mainly of high Arctic location for breeding. They spend the winter predominantly off coasts. The North Sea and the Baltic Sea appear to be the most important winte-

ring areas in the western Palaearctic (Cramp & Simmons, 1977). Distribution patterns and migration phenology vary strongly among species.

Distribution patterns of **long-tailed ducks**, the most numerous species wintering in the Pomeranian Bay, are described in paper 6.

The **common scoter** is a 'specialist' feeding exclusively on molluscs, preferably on clams (*Spisula, Venus, Mya*) and cockles, but in some areas also on mussels (e.g. Goudie & Ryan, 1991; Offringa, 1991; Stempniewicz, 1986). Distribution patterns and seasonal density variations in the Pomeranian Bay are well known. Their occurrence is almost completely restricted to the shallow Oder Bank (Fig. 5.2).

Autumn migration starts already in late June. Male common scoters perform a considerable moult migration. More than hundred thousand birds pass the area in July-August (Nehls & Zöllick, 1990). Several thousand males are moulting in the Pomeranian Bay. It is difficult to give a secure estimate, because some thousand immature non-breeders may join the moult flocks. The birds are flightless between July and September. About 10.000-30.000 birds were estimated in total during summer. Peak autumn migration takes place in September-October. An estimated number of 100.000 common scoters was counted in the winter season (December-March, Durinck et al., 1994; this study).

As a rule, most common scoters wintering west of the study area pass the southern Baltic between mid March and mid April (Nehls, pers. comm.). Numbers in the Pomeranian Bay increase during this time. Up to 200.000 birds were estimated on the Oder Bank in late April. Migration continues in early May when more than 1 Mio. birds pass the Gulf of Finnland to fly overland to the breeding grounds in northern Siberia (Bergmann & Donner, 1964).

Common scoters might have removed substantial parts of the bivalve stocks on the Oder Bank between autumn 1992 and spring 1995. Locally, their predatory impact is assumed to be much more important than the impact of long-tailed ducks. This assumption is based on the facts that:
- winter and spring densities of common scoter on the Oder Bank were of the same magnitude as those of long-tailed ducks
- common scoters have to gain about twice as much energy per day as long-tailed ducks
- common scoters stay much longer in the Pomeranian Bay as long-tailed ducks
A detailed estimate of the consumption rate of common scoters will be given elsewhere.

Little is known about the distribution and migration of **velvet scoters**. Their prefered midwinter grounds are situated in Polish waters (Fig. 5.2). Postbreeding migration starts in September. A few thousand birds are present in the study area in early October. They appear mainly north of the Oder Bank in areas of 15 m water depth. Spring migration starts in March/April. About 50.000 velvet scoters are still present in late April. Highest densities were observed in spring along the northern edge of the Pomeranian Bay at the 20 m isobath. These birds leave in early May, when huge numbers of velvet scoters concentrate in the Gulf of Riga before they move overland to the breeding grounds (Durinck et al., 1993; Kontiokorpi & Parviainen 1995; Kontkanen, 1995) .

Only 500-1.000 **common eiders** are known to winter in the Pomeranian Bay. Their occurrence is restricted to the sublittoral sea grass beds southwest of Rugia Island in the Greifswalder Bodden. Birds arrive in autumn and leave in early May. Immature individuals may spend the breeding season in the Greifswalder Bodden too.

Possible implications of hard winters

It should be noted that all sea duck surveys from 1988 to 1995 were carried out in mild winters, with local ice-cover of shallow lagoons only. During hard winters, distribution should be somewhat different, as the birds are forced out of the coastal zones by ice.

In 1996, the Baltic Sea went through one of the hardest winters of this century. Large parts of the southern Baltic were covered by ice between late January and mid March. Unfortunately, we were unable to perform any large scale sea duck surveys during this time. However, some assumptions can be drawn from satellite photographs, showing the ice coverage in the southern Baltic during this time and from the analysis of victims found dead along the eastern shoreline of Rugia Island in mid March.

80

Fig. 5.2: Distribution of scoters *Melanitta nigra* and *M. fusca* in the Pomeranian Bay in fall, winter and spring.
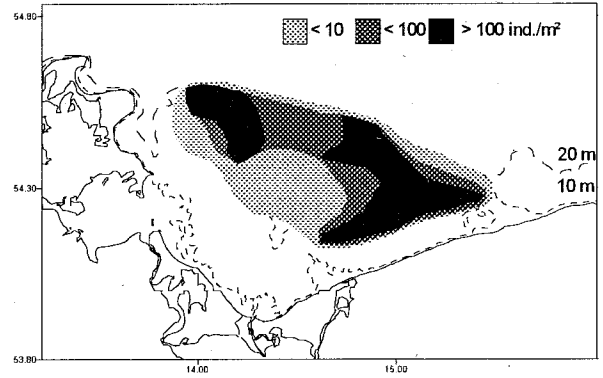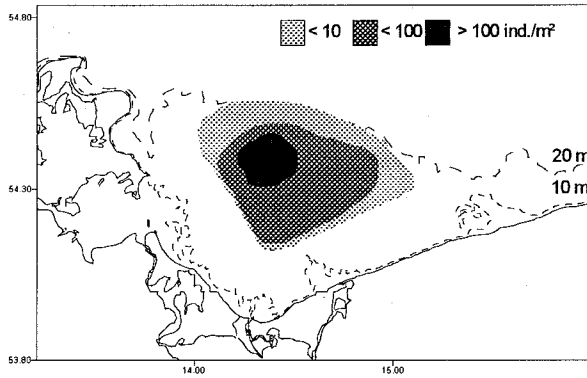
common scoter   velvet scoter

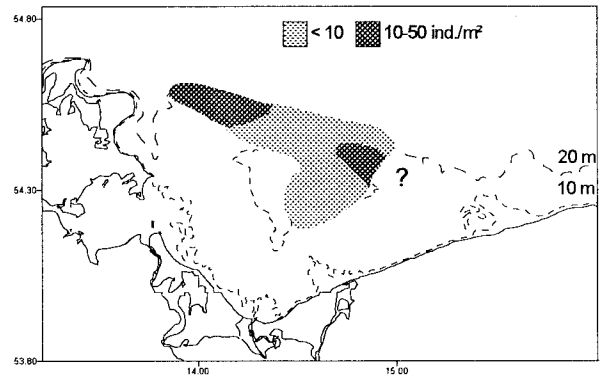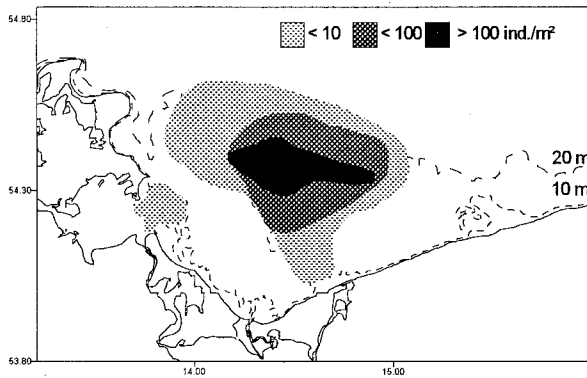September-October
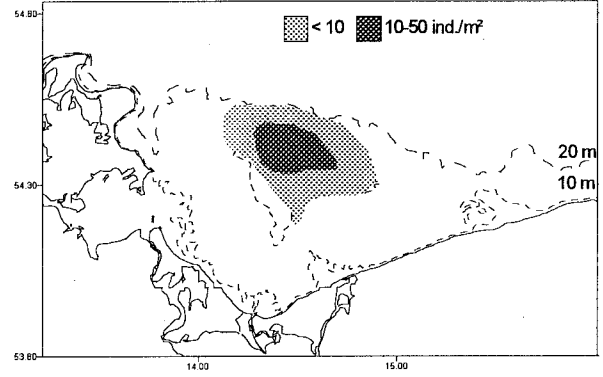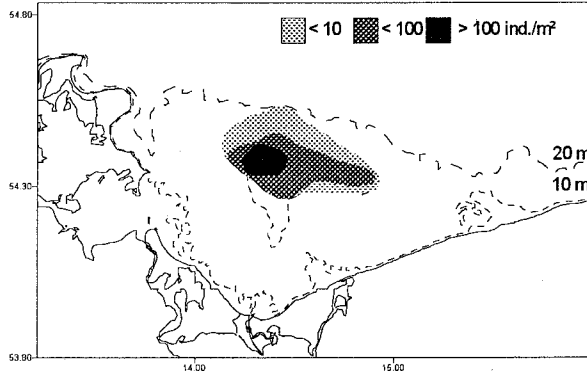
December-February

April

Fig. 5.3 shows the distribution and density of long-tailed ducks in the southern Baltic Sea in mild winters. It is supposed that this distribution pattern reflects the most profitable feeding grounds (paper 6). The Pomeranian Bay is by far the most important area. The Plantagenet Bank west of Rugia Island is another important wintering area. The Rønne Bank south of Bornholm Island is the third important area. Up to 100.000 birds were also estimated for the shallow waters around Fehmarn Island in the western Baltic Sea.

Fig. 5.4 shows the distribution of pack ice in the southern Baltic in February 1996. Temporal differences in distribution patterns are mainly due to wind forcing. Easterly winds caused upwelling events along the southern shoreline in early February and moved the ice to the North and to the West (09.02.1996). Westerly winds initiated opposite movements two weeks later (23.02.1996). A strong northward movement of the ice was observed during a period of southwesterly winds in late February, most the pack ice disappearing in early March (26.02.1996).

Satellite photographs show clearly that the largest part of the prefered feeding area was covered by ice in February and profitable benthic food stocks became unavailable for several days or even weeks. Almost 1 Mio. long-tailed ducks had to emigrate to less profitable but ice-free shallow areas along the Polish coast and around Bornholm Island. The Rønne Bank south of Bornholm Island was the only ice-free feeding area during this time. As described by Laursen et al. (1995) long-tailed ducks are especially numerous in that area in severe winters. However, high densities of long-tailed ducks were also discovered by anecdotal evidence during an oceanographic research cruise in areas between the 20 m and 30 m depth isobaths at the northern edge of the pack ice in the Pomeranian Bay in early February. Obviously, large numbers of birds tried to stay as close as possible to their prefered wintering areas.

The ducks returned to the Pomeranian Bay in early March. More than ten thousand long-tailed ducks were found dead within a few days along the eastern shoreline of Rugia Island. Although many of them were severely affected by an oil spill, tremendous body weight losses indicated heavy mortality caused by starvation too. The mean total body weight of the victims had decreased from 700-800 g (described for fit adults by Cramp & Simmons, 1977) to only 400-500 g (Schumm, pers. comm.).

Only a few dozen dead velvet scoters and almost no common scoters were found among thousands of dead long-tailed ducks. Perhaps, most of the scoters had moved to wintering areas in the northern Kattegat and in the North Sea.
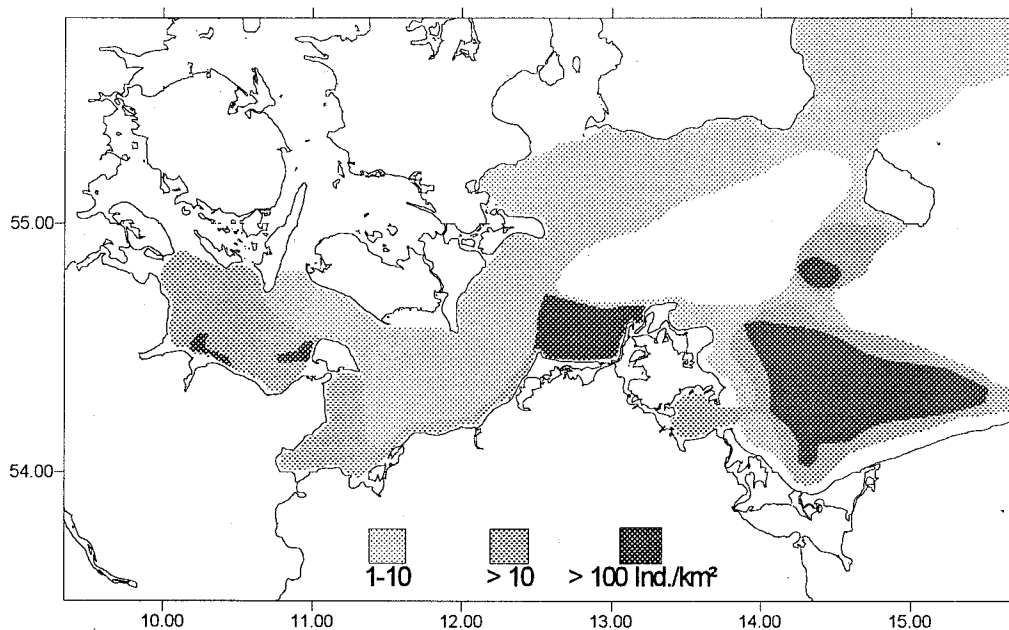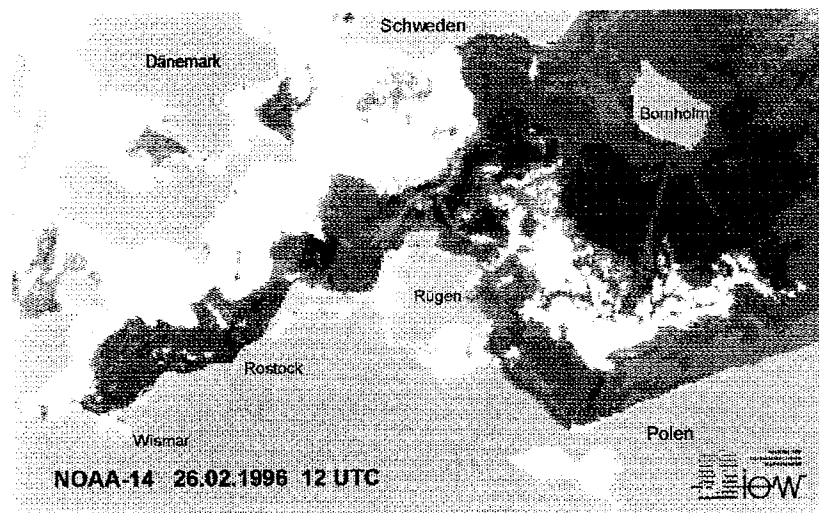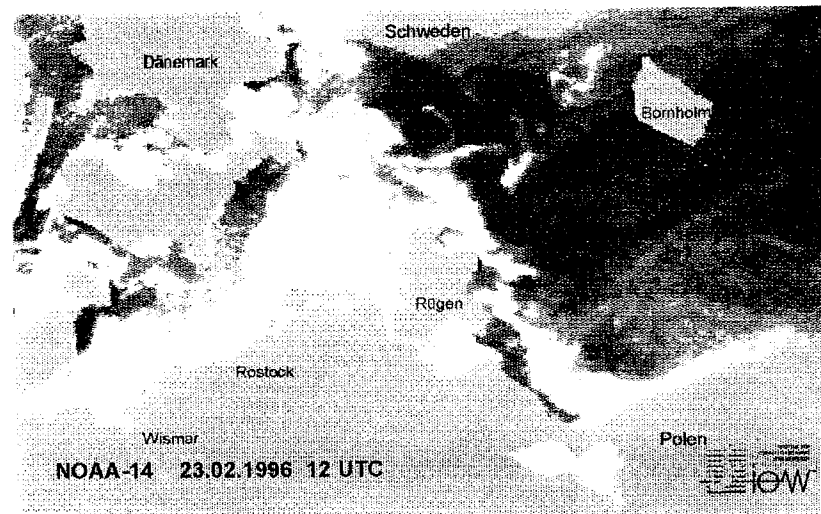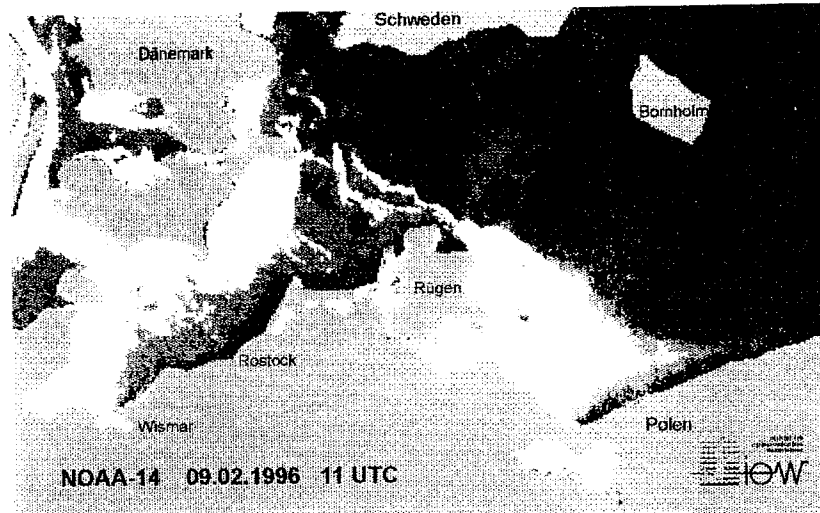

Fig. 5.3: Distribution and density of wintering long-tailed ducks, *Clangula hyemalis*, in the southern Baltic Sea, 1988-1995 (changed after Durinck et al., 1994).

Fig. 5.4: Distribution of pack ice in the southern Baltic Sea in February 1996 (data from 'Bundesamt für Seeschiffahrt und Hydrographie Hamburg', figures are prepared by Siegel & Gerth, unpubl.).

Habitat selection, feeding characteristics, and food consumption of long-tailed ducks, *Clangula hyemalis*, in the southern Baltic Sea

Jan Kube & Henrik Skov

Abstract: Between January 1992 and April 1995 the distribution and abundance of long-tailed ducks, *Clangula hyemalis*, were studied in the Pomeranian Bay in the southern Baltic Sea. We evaluate the extent to which these patterns can be explained by benthic food supply and disturbance by an international shipping lane. Long-tailed ducks arrive in the study area in late autumn and leave in early May. Maximum numbers of 800.000 birds were recorded in winter. About the half of these birds was still present in March-April. According to literature data are bivalves, *Mytilus edulis*, *Mya arenaria*, *Cerastoderma lamarcki* and *Macoma balthica* the preferred prey of long-tailed ducks. They select prey that are not to small to be profitable and prey that are not to large to be crushed in the muscular gizzard. All prey that is suitable in size was detectable by the birds in the study area, except for *Macoma balthica*. We assume the application of three different feeding techniques in long-tailed ducks. Birds have to apply both suction-feeding and digging for single prey items. Furthermore, a part of the birds feeds on herring spawn in spring due to its high profitability. The spatial distribution of long-tailed ducks was best explained by the harvestable biomass of prevalent prey species. Bird densities were highest in areas with a harvestable biomass > 10 g AFDW m^{-2}. Long-tailed ducks were more evenly distributed in the study area in winter than in spring. In spring, they seemed to be able to narrow the selection of feeding habitats to the most profitable patches and avoided areas providing a harvestable biomass < 5 g AFDW m^{-2} and disturbance by shipp traffic.

Introduction

Millions of arctic seaducks annually migrate in summer and autumn to central Europe to spend the cold winter season in shallow sublittoral offshore areas (Kistchinski, 1979; Rutschke, 1989). The main seaduck concentrations are restricted to a few concentration areas only (Durinck et al., 1994; Skov et al., 1995). Here they feed on benthic invertebrates, especially bivalves (e.g. Madsen, 1954). The reasons for the winter distribution patterns and the ecological impact of these large seaduck concentrations are still far from clear.

Food supply is known to be the most important factor controlling the distribution patterns and densities in animal ecology (Bernstein et al., 1991; Krebs, 1972). Seasonal and annual variations in the food supply of birds foraging on benthic invertebrates in intertidal habitats are easy to measure (Wanink & Zwarts, 1993; Zwarts & Wanink, 1993). Distribution patterns of non-breeding waders *Charadrii* have been explained by direct measurements of food selection and intake rates (e.g. Goss-Custard et al., 1982; Zwarts et al., 1992) or by indirect comparisons of patterns of food availability and shorebird densities (Piersma et al., 1993a ; Zwarts et al., 1990). Waders are known to remove a substantial part of the benthic biomass or production from the intertidal. Mean annual consumption rates usually range from 10-20 % of the total macrozoobenthos biomass but much higher values have been reported too (see review by Meire, 1993).

Comparable studies for seaducks are sparse (but see Nehls, 1995). Seaducks are difficult to count and to observe in their preferred feeding habitats offshore. Only nearshore areas which may be suboptimal feeding habitats for seaducks can be used for observations on their feeding behaviour (e.g. Leipe & Scabell, 1990; Nilsson, 1972). Food choices can be measured in the field only from stomach analysis and active diet selection processes and prey handling have so far mainly been studied by laboratory experiments (e.g. Ball, 1990; De Leeuw & Van Eerden, 1992; Draulans, 1982).

The development of more precise offshore counting methods has encouraged the frequency and quality of seabird counts at sea (Komdeur et al., 1992; Tasker et al., 1984). Extensive recent surveys revealed a much more detailed picture of seaduck winter distribution patterns in Europe

(Camphuysen & Leopold, 1994; Durinck et al., 1994; Meissner & Struwe, 1994; Nehls, 1994; Skov et al., 1994). The long-tailed duck is the most numerous seaduck species during winter in the Baltic Sea, and about 4 million individuals have been estimated to overwinter there. Six areas have been identified to be of major importance, one of these being the Pomeranian Bay in the southern Baltic Sea which harbours more than half a million long-tailed ducks (Durinck et al., 1994).

We attempt to describe the major components of the offshore winter habitat of the long-tailed duck *Clangula hyemalis* in the Pomeranian Bay and estimate the predatory impact that this most abundant of the seaducks wintering in European waters has on local prey stocks. During four successive winter seasons, 1992 to 1995, abundances and distribution patterns of long-tailed ducks were studied by ship and aerial surveys (first results in Durinck et al., 1993; 1994; Nehls, 1994). Data collected in the nearby Greifswalder Bodden by ground surveys from 1978-1982 were published by Leipe & Sellin (1983). The results of these surveys will be used to explain distribution patterns in relation to the available food supply.

Comparisons of the total benthic invertebrate stock and distribution patterns of seaducks in the Baltic Sea were described previously by Nehls (1989), Nilsson (1969), and Pehrsson (1976). Unfortunately, these studies did not distinguish between the total density of food items and their availability to the birds. If prey availability is not taken into account, wrong conclusions can be drawn about the amount of the food supply (Ens et al., 1994). Field observations on the feeding behaviour and stomach analyses of long-tailed ducks were carried out in the Pomeranian Bay by Gorski (1981) and Leipe (1982; 1985; 1989). The data of these authors were reanalysed in combination with other data on diet choices from adjacents parts of the southern Baltic Sea to define which part of the standing stock of benthic invertebrates is selected by long-tailed ducks. The available prey fraction was measured in the field by macrozoobenthos investigations in 1993/1994. Abundances, biomasses, size classes and vertical distributions of macrobenthic invertebrates were studied.

Study area

The Pomeranian Bay, one of the largest, shallow offshore areas in European waters, is part of the transition zone between the Oder River and the Baltic Proper. The Oder River enters the bay via a system of inner coastal lagoons (Szczecin Lagoon, Greifswalder Bodden). Extended sandy bottoms, between 0-20 m water depth, cover an area of more than 8.000 km². The 20 m depth line is the northern boundary of the bay to the adjacent Arkona and Bornholm Basins. The Oder Bank is located almost in the centre of the bay and is not deeper than 7-10 m (Fig. 5.6).
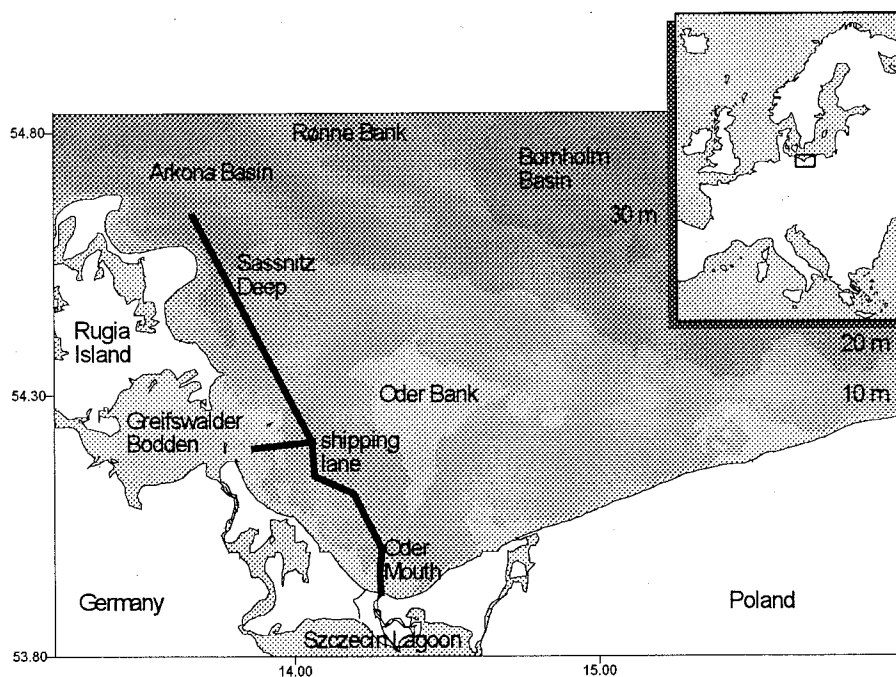

Fig. 5.6: Map of the study area. The thick line indicates the international shipping lane.

The fine sandy sediments are locally mixed with coarse sand and gravel, especially in the Polish part. Silty sediments occur off the Oder Mouth. The Sassnitz Deep, near the Isle of Rugia in the West, is muddy (Koine, 1995; Neumann & Bublitz, 1969). The water salinity varies between 6-8 ‰ near the coast and between 8-10 ‰ in the north of the bay (Nehring et al., 1994).

Fourtyfive benthic invertebrate species were recently found in the study area (Powilleit et al., 1996). In the western, coastal parts of the bay the soft-shelled clam *Mya arenaria* and the polychaete *Marenzelleria viridis* dominate the total biomass (ca. 85 %) whereas in the deeper northern part the Baltic tellin *Macoma balthica* is dominant with respect to biomass (69 to 73 %). Mean total biomass values ranged from 150 g AFDW m^{-2} in the coastal zone to 18 g AFDW m^{-2} on the Oder Bank and 1 g AFDW m^{-2} in the Sassnitz Deep. The high total biomass, especially in the western coastal region is thought to reflect the high anorganic and organic load from the Oder river which enters the system through the Oder estuary since the last decades (Kube et al., in prep).

During the study, disturbance effects on bird densities were observed in the western part of the Pomeranian Bay which is used intensively as an international shipping corridor to the harbours of Swinoujscie and Szczecin, Poland. The location of the shipping lane was therefore added to the description of the habitat preferences of the long-tailed duck.

Methods

Sampling of bird density in offshore waters

It is generally impossible to count all the long-tailed ducks occurring in a relatively large offshore area like the Pomeranian Bay. Information on the density of ducks is derived from survey tracks covering representative parts of the area. Normally either line transect surveys or strip census surveys are employed from aeroplanes or ships, both of which generate relative densities of birds for straight lines over variable distances depending on the speed of the observation platform and the length of the count units. The long-tailed duck is regarded as one of the most difficult seaduck species to count (Joensen, 1974). The birds are often observed in extensive aggregations extending tens of kilometres with dense and loose flocks alternating. In order to make an effective count of high density segments with dense flocks it is necessary to scan individual flocks repeatedly. A large proportion of ducks (often 50 %) associated with a flock may be submerged at the time when the flock is first recorded. This is due to a combination of feeding birds and birds reacting to the approaching ship or aeroplane. Due to this behaviour and the frequent occurrence of high densities (> 100 birds km^{-2}), it is deemed necessary to operate narrow survey tracks.

Table 5.2: Comparison of the results of offshore long-tailed duck surveys carried out using aeroplanes and ships during winter in 1992-1993 in the Pomeranian Bay. The comparison is based on mean densities obtained from strip censuses and line transects from aeroplane and ship. For the ship-based surveys, the observed mean density as well as the corrected density are shown (see text).

survey period	platform	method	density (birds km^{-2})	corrected density (birds km^{-2})
Jan/Feb 1992	Aeroplane	150-250 m strip census	70	-
Jan/Feb 1992	Ship	300 m line transect	138	187
Jan/Feb 1993	Aeroplane	150-250 m strip census	50	-
Jan/Feb 1993	Ship	300 m line transect	104	145
Early March 1993	Aeroplane	180 m strip transect	42	-
Dec 1993	Ship	300 m strip transect	70	125

Six comparative large-scale surveys for seaducks were undertaken from ships and aeroplanes in the Pomeranian Bay during the winter months in 1992 and 1993 (Table 5.2). Based on these surveys a comparison could be made on the estimated density of long-tailed ducks produced from aeroplane and ship. There seems to be a general underestimation of the observed density from the aerial surveys as compared to the ship-based surveys of the magnitude of approximately 50 %. This finding fits well with the general knowledge of the benefits and drawbacks of using ships and aeroplanes for surveying long-tailed ducks (Durinck et al., 1994, Laursen et al., 1995). Due to the small number of comparative surveys from aeroplane and ship, we regard it as premature to estimate the amount of correction needed to be able to use data from aerial surveys in quantitative judgements of long-tailed duck abundance. Accordingly, we had to limit the estimation of the density of long-tailed ducks to

the ship-based data (Fig. 5.7). Table 5.3 lists the nine ship-based surveys carried out in the Pomeranian Bay between January 1992 and April 1995.

Table 5.3: Ship-based long-tailed duck surveys carried out in the Pomeranian Bay between January 1992 and April 1995.

| survey period	transect length (km)	observer	method
31/1 - 21/2 1992	302.6	P. Andell, J. Duinck, H. Skov	300 m line transect
29/1 - 9/3 1993	267.3	P. Andell, J. Duinck, H. Skov	300 m line transect
23/4 - 28/4 1993	253.3	J. Kube	500 m strip census
5/10 - 6/10 1993	112.6	J. Kube	500 m strip census
4/12 - 7/12 1993	187.1	J. Kube	300 m strip transect
22/4 - 27/4 1994	330.8	J. Kube	300 m strip transect
1/7 - 6/7 1994	168.9	J. Kube	300 m strip transect
10/9 - 24/9 1994	154.8	J. Kube	300 m strip transect
5/4 - 12/4 1995	239.3	J. Kube	300 m line transect
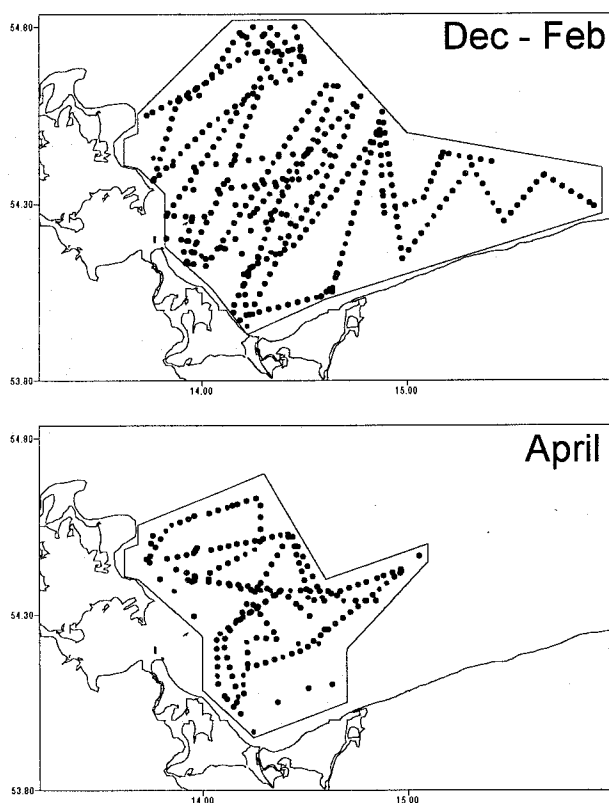
Fig. 5.7: Ship-based transects included in the data analyses for the winter and spring seasons. Dots indicate the position of bird density samples.

The counting methods used on the nine ship-based surveys are comparable, although some distinct differences should be noted. All surveys were made in relatively calm conditions (less than 10 m/sec wind speed) by experienced ornithologists working from an exposed platform on the roof of a medium-sized ship steaming with an average speed of 10-12 miles·h⁻¹. The probability of missing a bird within the counting strip increases with distance to the observer, and varies between observers, ship types and weather conditions. Line transect methods attempt to take account of the distance bias by stratifying observations within the counting strip by distance. A modified version of the standard line transect methodology for surveys of seabirds at sea as suggested by Tasker et al. (1984) was used during three surveys. Observations of long-tailed ducks within a 300 m perpendicular distance were grouped into three 100 m wide corridors assuming that all birds sitting on the water were detected in front of the ship close to the survey track (in the first observation corridor, from 0-100 m). To meet this assumption, binoculars were used continuously to detect birds that dive in response to the approaching ship. In order to record the perpendicular distances correctly, distance callipers were used

(Heinemann, 1981), and supplied with angle/distance correctors (Durinck et al., 1993) for birds alighting in front of the ship. The first two surveys were carried out by the same team of three observers. The following seven cruises were made by another single observer; only on the last cruise in April 1995 line transect methods were applied. However, since these cruises were made by one observer from the same ship during comparable conditions it was possible to use the results from the last line transect survey to establish correction factors for the strip census surveys carried out on the preceeding six surveys. Correction factors for birds missed within 300 m were calculated using the detection function to numbers of birds observed at different distances described in Skov et al. (1995). The correction factor calculated for the two cruises of the first team was 1.32 and 1.78 for the seven following cruises. In April and October 1993 birds were counted within a 500 m transect width. Thus, the corrected densities of long-tailed ducks calculated for these two cruises may be regarded as underestimates. One cruise carried out in summer 1994 and the two surveys in September and October showed that very few long-tailed ducks occur in the Pomeranian Bay during summer and autumn. Estimation of average densities and total numbers of long-tailed ducks in the study area were therefore made for the winter (December-February) and spring (March-April) seasons only. Distribution maps were produced with WINSURF software package applying ordinary kriging techniques to the corrected densities of long-tailed ducks obtained during the winter and spring cruises.

Total counts of birds in coastal waters

In general, only 10.000-20.000 long-tailed ducks stay in coastal waters of the Pomeranian Bay in mid-winter (Leipe & Sellin, 1983; Nehls, 1994; this study). But during March a change in the distribution of birds takes place in the coastal areas. Long-tailed ducks form dense flocks of several thousand birds on certain shallow sandy banks especially in the Greifswalder Bodden. Therefore, ship-based total counts were carried out in the Greifswalder Bodden in late April 1993 and 1994 by searching for flocks of more than 1.000 birds. The numbers of the larger flocks were estimated and totals were formed by adding up these estimates.

Sampling of macrozoobenthos

Thirtyfour stations were sampled in the Pomeranian Bay, on the slope of the Arkona Basin and in the Greifswalder Bodden. A minimum of three replicate grab samples was collected at each station in April and October 1993. Additional samples were taken at ten stations, three times per year (April, July, October), between April 1993 and April 1995. Samples were collected either with a Van Veen grab (23 kg or 70 kg, 0.1 m², 8-12 cm penetration depth), or with a modified 'Reineck' box corer (0.0225 m², 15-25 cm penetration depth). Van Veen grab samples were sieved with a 1 mm sieve and box corer samples rinsed over a 0.5 mm sieve. An intercalibration between both sampling techniques was performed at nine stations in April 1993. Fixation, sorting, species and biomass determination were carried out following the HELCOM-guidelines for soft bottom macrozoobenthos (HELCOM, 1988). The precision of bivalve density estimates was described by Powilleit et al. (1996).

The maximum shell length of bivalves was measured to the nearest mm using graph paper. The soft parts of *M. baltica*, *M. arenaria* and blue mussels, *Mytilus edulis*, collected in April 1993 were separated from the shell, and shells and meat of different-sized specimens from one station were weighed and incinerated. Allometric relationships between shell length and ash free dry weight (AFDW) of soft parts were calculated (Table 5.4). There was no significant difference for the allometric length-weight relationship between sites (analysis of covariance, p>0.05). Due to seasonal variations in body weight, slope and intercept of the correlation functions vary throughout the year. The seasonal effect was not tested by us. According to Kautsky (1982) and Zwarts (1991) we assumed, that biomass data from April and October reflect the same level of body condition index. Data for the mid winter season were not available and condition indices from July are not relevant for this study.

Sediment cores of the upper 10 cm were taken from additional box corer samples for the analyses of sediment parameters and the vertical distribution patterns of bivalves. The depth of bivalves was determined by cutting up the core horizontally into 1 cm thick slices, and measuring the distance between the upper edge of the shell and the sediment surface. Specimens were assigned to depth categories of 1 cm, starting at a minimum depth of 0.5 cm.

Table 5.4: AFDW (g) of soft parts of bivalves in relation to shell length (mm). a is intercept ($\pm$ SE), b is slope ($\pm$ SE) of the function $\ln y = b \cdot \ln x + a$. All specimens were fixed in a 4% formalin/seawater solution for 3 month.

	a	b	r	n
Mytilus edulis	-10.23±0.28	2.27±0.11	0.995	409
Macoma balthica	-10.67±0.38	2.56±0.16	0.928	45
Mya arenaria	-12.70±0.22	3.23±0.09	0.966	150

Habitat selection

The assessment of the association between the distribution of long-tailed ducks and macrozoobenthos could not be investigated by correlation techniques due to a poor fit of line transect and station data. This was especially the case with blue mussels which displayed a very patchy distribution in the bay (Powilleit et al., 1996). In order to properly test the hypothesis that long-tailed ducks used areas with high biomasses of suitable prey more than areas with low biomasses, we choose Bonferroni's inequality test. This test is a distribution-free z-test which is appropriate for handling skewed count data and which allows a robust indication of significant preferences/non-preferences of arbitrary categories of bivalve biomass by ducks (Neu et al., 1974). The test was based on individual comparisons of observed proportions to expected proportions of ducks observed within broad zones of different bivalve biomass. As we observed a negative impact of the international shipping lane (Fig. 5.6) on the density of long-tailed ducks, it was necessary to test whether this impact significantly altered the habitat preferences of the ducks. The zoobenthos station data were contoured into four bivalve biomass/disturbance categories using ordinary kriging techniques (Cressie, 1991):
1. low biomass (< 1 g AFDW$\cdot$m^{-2}), undisturbed and disturbed
2. medium biomass (1-9.99 g AFDW$\cdot$m^{-2}), mainly cockles, *Cerastoderma lamarcki*, and *M. arenaria*, undisturbed
3. high biomass (≥ 10 g AFDW$\cdot$m^{-2}), mainly blue mussels, disturbed
4. high biomass (≥ 10 g AFDW$\cdot$m^{-2}), mainly blue mussels, undisturbed.

The disturbed areas were defined as areas within a distance of 3 km from the shipping lane. Geographical Informations Systems (Microstation PC) were used to extract numbers of long-tailed ducks observed per count interval (1.8-5.3 nautical miles of cruising distance) within each biomass polygon area. Bird counts lying on the border between two polygons were allocated to both categories. The bird data were standardized due to the variations in the distances of count units. The following formula provided confidence limits on observed probabilities for each bivalve biomass category: $p \pm Z(\alpha/2k) \sqrt{(p(1-p)/n)}$, where p is observed proportion, $Z(\alpha/2k)$ is the upper standard normal table value corresponding to a probability tail area of $(0.05/2k)$ and k is the number of categories.

Estimation of the daily consumption rate

We were unable to calculate the natural daily energy expenditure (DEE) of wintering long-tailed ducks by direct measurements of the time-energy budget. According to Nehls (1995), who studied wintering eiders, *Somateria molissima*, in the Wadden Sea, we assumed a ratio of DEE/basal metabolic rate (BMR) = 4. This ratio is just below the upper limit to natural sustainable energy expenditure (Drent & Daan, 1980). Similar high values were described by Castro et al. (1992) and Wiersma & Piersma (1993) for waders wintering in the northern hemisphere.

BMR can be predicted from allometric equations between total body weight and BMR (Aschoff & Pohl, 1970; Daan et al., 1990; Lasiewski & Dawson, 1967). Male long-tailed ducks have a mean weight of 0.78 kg. Females have a mean weight of 0.7 kg (Cramp & Simmons, 1977). By using an average weight of 0.74 kg, calculated BMR values range from 247 to 302 kJ/day. The only measurement of BMR in long-tailed ducks revealed a value of about 260 kJ/day (Jenssen & Ekker, 1989). According to measurements of BMR in mallards, *Anas platyrhynchos*, of similar body weight (Daan et al., 1990; Miller & Reinecke, 1984), we used an average value of 275 kJ/day. Hence, the DEE of wintering long-tailed ducks can be estimated at 1.100 kJ.

Consumption rates calculated from DEE must also take the metabolizability of the food into account. In general, assimilation efficiency in carnivorous birds is about 75 % (Castro et al., 1989). Efficiencies of about 85 % were reported for birds preying upon crustaceans (Karasov, 1990). On average,

crustaceans accounted for only about 5-10 % of the food taken by long-tailed ducks in the study area. We simplified our estimate of the daily food intake by excluding the crustaceans and lowering the DEE value to only about 1.000 kJ. In order to meet this assumption, we calculated a daily energy intake for wintering long-tailed ducks of about 1.333 kJ.

To balance the mean annual food consumption in selected parts of our study area, we transferred kJ into ash free dry weight (AFDW). On average, invertebrates from the Baltic Sea contain 22 kJ/g AFDW (Bast & Oertzen, 1976; Kreuzberg & Oertzen, 1973; Rumohr et al., 1987). By dividing the estimated daily energy intake by 22, the daily food intake by long-tailed ducks in the Baltic was estimated to be 60 g AFDW of bivalves. Estimates of consumption rates were made separately for each of the four bivalve habitat areas by multiplying the daily energy intake by the number of bird days·m^{-2}.

Furthermore, we transferred AFDW of bivalves into total wet weight (WW) by multiplying it by 14.5 (Rumohr et al., 1987), to be able to compare our own estimate with earlier estimates. Our own estimate of the daily intake of bivalves of almost 860 g WW is about 30 % higher than the estimate of Leipe (1985) and about 25 % higher than the estimate of Böhme (1992).

Results

Spatial variation of long-tailed ducks

The average distribution of long-tailed ducks during winter and spring in the Pomeranian Bay is shown in Fig. 5.8. During the winter season long-tailed ducks were observed over the entire bay with densities above 100 birds·km^{-2} occurrring throughout the shallow offshore area to the limit of the bay at the 30 m depth contour where densities dropped sharply. The average density in the studied western section of the bay was 155.1 birds·km^{-2} or slightly below the average winter density estimated by Durinck et al. (1994) for the entire Pomeranian Bay (172.0 birds·km^{-2}). Mean winter densities were much lower in the adjacent Greifswalder Bodden, where only 10-50 birds·km^{-2} occurred (Nehls pers. comm., this study).

In spring the long-tailed ducks concentrated in two areas; the majority were still offshore, but mainly in the Oder Bank area and towards the east while dense flocks amounted to 60.000 - 80.000 birds in the Greifswalder Bodden. The average density in the studied section of the bay was 96.9 birds·km^{-2} or 37.5 % below the estimated winter density.

Suitable prey fraction

In this chapter, we will try to identify which prey are suitable for long-tailed ducks in the study area. The suitable prey of long-tailed ducks was never measured in the field. Hence, we assessed suitability indirectly by using informations on food selection, obtained from published stomach analyses.

Six data sets were available on the food compositon of long-tailed ducks from the southern Baltic. 469 birds were examined in total (Böhme, 1992; Gorski, 1981; Kirchhoff, 1979; Leipe, 1982; 1985; Madsen, 1954; Nilsson, 1972). 234 examined birds were collected in coastal parts of the Pomeranian Bay, 59 birds were available from the nearby Rønne Bank.

Taking all data into account, the diet of long-tailed ducks seems very diverse. Bivalves contributed the main portion of the food in all studies. Blue mussels have been by far the most prominent food, but the preferred bivalve species differred between the study areas. Whereas long-tailed ducks fed exclusively upon cockles, *Cerastoderma spp.*, in the Kiel Bay, they exploited mainly blue mussels in the Wismar Bay, on the Rønne Bank and in the eastern Pomeranian Bay. Soft-shell clams prevailed in the diet of birds from the Greifswalder Bodden. Baltic tellins were taken by only a few birds (Fig. 5.9).

Almost all birds had eaten crustaceans. Their quantities varied from single individuals to several hundreds in a single bird. On average, amphipods and isopods comprised about 5-10 % of the prey taken. Fishes (mainly *Pomatochistus spp.*) and ragworms, *Nereis diversicolor*, formed a regular, though not very important part of the diet too.

Fish eggs were observed by Leipe (1985) and Sellin (1990) to be an important prey of long-tailed ducks in the Pomeranian Bay during the spawning time of herring, *Clupea harengus*, in spring (March and April).
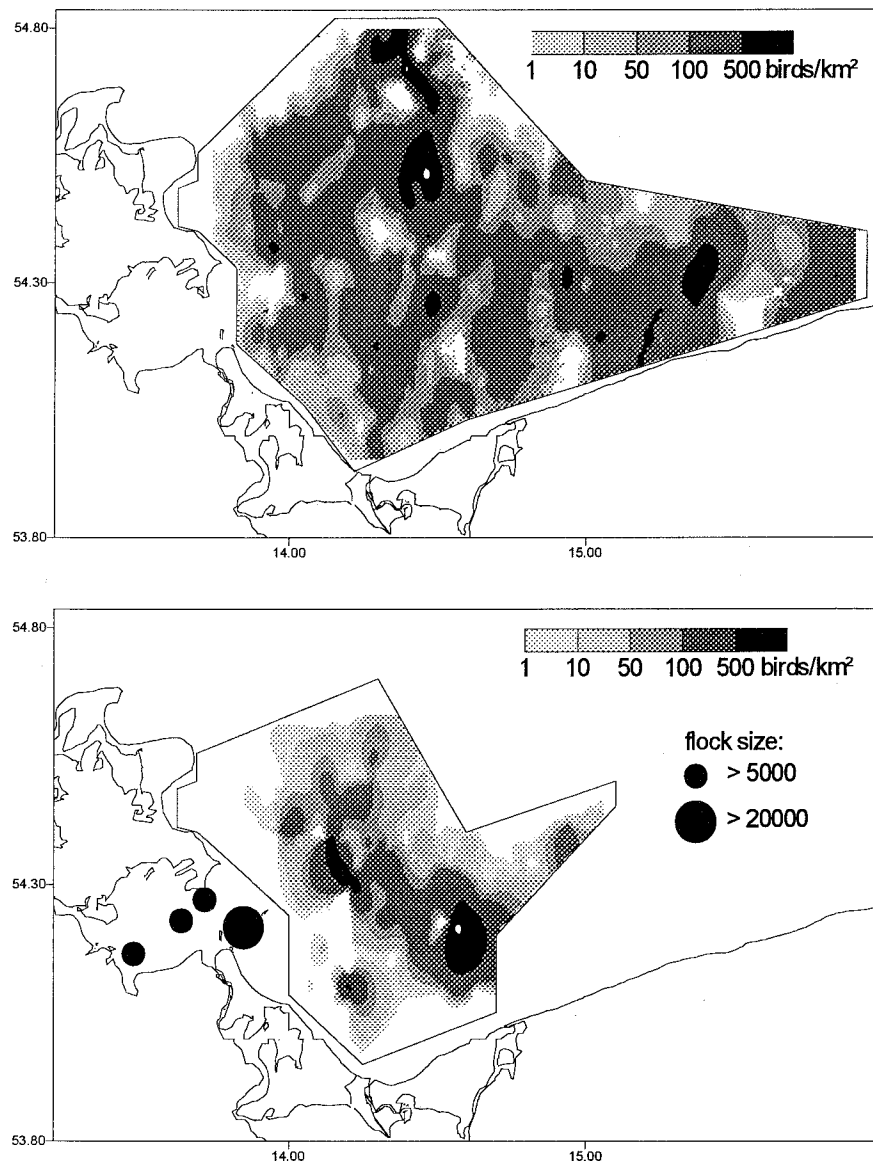

Fig. 5.8: Distribution maps of long-tailed ducks in the Pomeranian Bay in winter and spring between 1992 and 1994. The sizes of dense flocks in the Greifswalder Bodden fluctuate according to the spawning acctivities of herring. Between 60.000 and 80.000 long-tailed ducks were estimated in the Greifswalder Bodden during spring.

Although the size of the prey taken, can be easily measured for prey items from the oesophagus of dead birds, only two authors presented detailed data on prey size selection (Böhme, 1992; Kirchhoff, 1979). Unfortunately, both of them dissected only a few birds. Leipe (1982; 1985) and Madsen (1954) mentioned the minimum and the maximum size and a preferred size range for bivalves. No data on prey sizes were given by Gorski (1981) and Nilsson (1972). Hence, prey size selection could not be quantified by us. Therefore, by combining all available data, we were able to produce a rough general estimate of bivalve sizes taken, by distinguishing between the minimum and the maximum size and a preferred size range. Long-tailed ducks ingest mainly the smaller size classes of bivalves. They select preferably cockles, 4-8 mm in length, and soft-shell clams, 5-10 mm in length, and mussels, 1-10 mm in length. Bivalves longer than 15 mm are eaten only occasionally (Table 5.5). These size ranges formed the basis for the following estimations of the quantities of suitable prey.

Tab. 5.5: Lengths of bivalves, selected as prey by long-tailed ducks in the southern Baltic Sea.

species	minimum (mm)	maximum (mm)	preferred size range (mm)	references
Mytilus edulis	1	15 (20)	1-10	Böhme (1992) Madsen (1954)
Cerastoderma spp.	3	10	4-8	Kirchhoff (1979) Leipe (1982)
Macoma balthica	?	15	?	Leipe (1982) Madsen (1954)
Mya arenaria	4	15	5-10	Kirchhoff (1979) Leipe (1982) Madsen(1954)
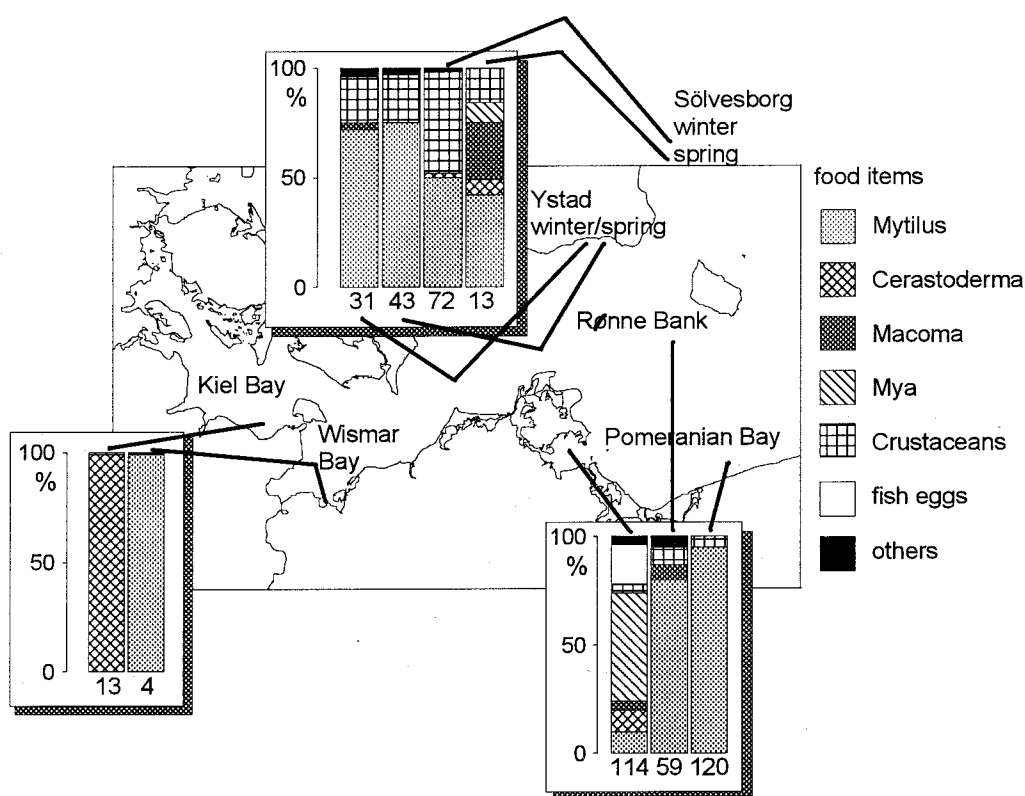
Fig. 5.9: Food composition of long-tailed ducks in the southern Baltic Sea (Böhme, 1992; Gorski, 1981; Kirchhoff, 1979; Leipe, 1982; 1985; Madsen, 1954; Nilsson, 1972). All values are given in weight percentages. Numbers below bars refer to number of examined birds.

Spatial variation of available food stock

All prey of sufficient profitability (prey that yield a sufficient energy gain per handling time unit), which is available, was defined by Zwarts et al. (1992) as the harvestable prey fraction for a shore-bird, feeding upon bivalves. Available are all prey that are both accessible/detectable (within the reach of the bill) and ingestible (small enough to be swallowed or digested).

We calculated the available prey fraction of long-tailed ducks in the Pomeranian Bay in 1993 and 1994. We present the spatial distribution of total biomasses and suitable biomasses (not too small, not too large, not too deep) of each bivalve species in 1993 (Fig. 5.10). To illustrate the spatial variability of suitably sized prey, length-frequency distributions from selected stations are shown too (Fig. 5.11-14). Since the great majority of *C. lamarcki* was of the right size to be eaten, we did not distinguish between the total and the available standing stock. The biomass of the available prey fraction of the other three species was calculated by the allometric equations given in Table 5.4.
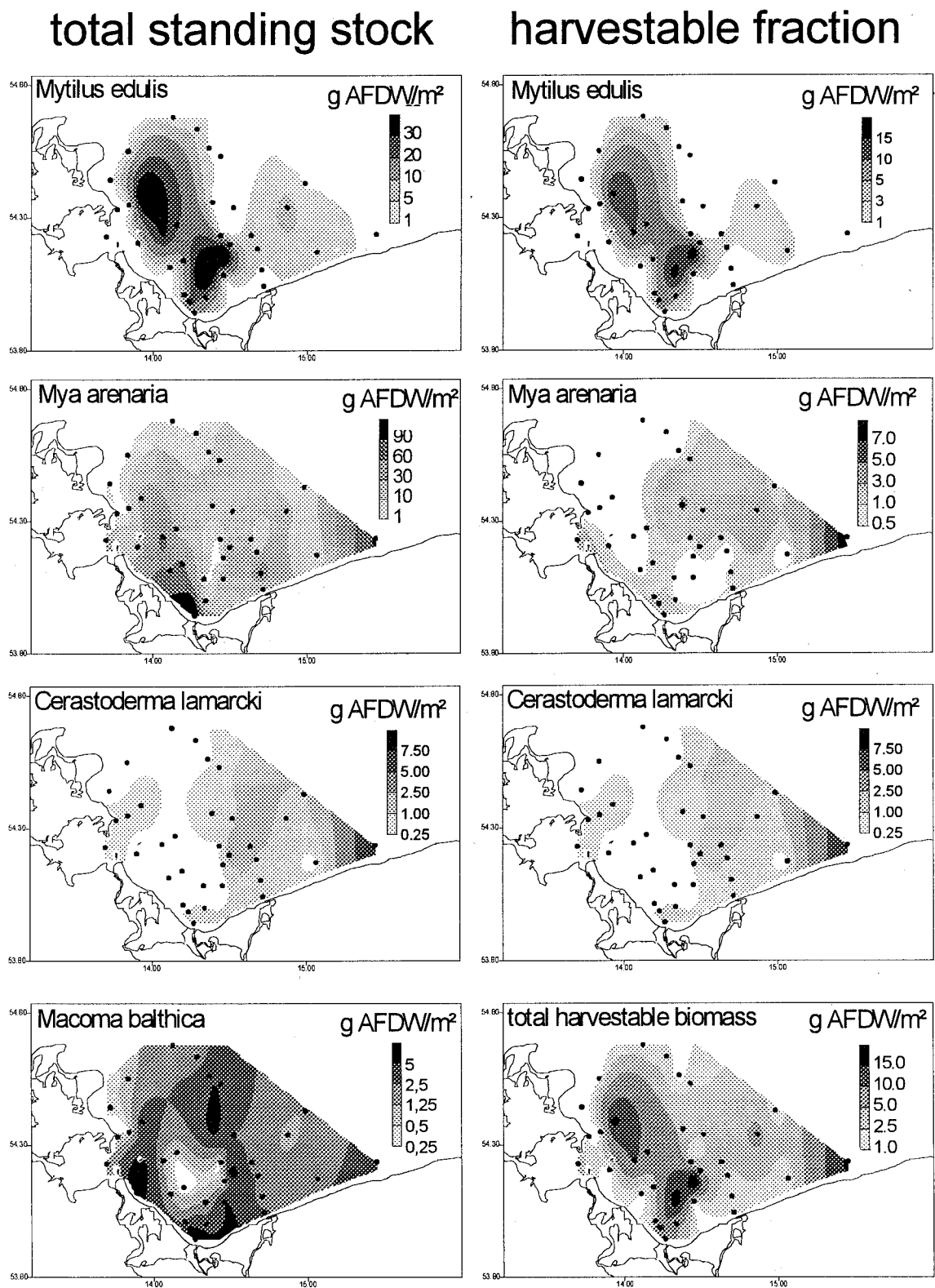
total standing stock   harvestable fraction

Fig. 5.10: Distribution maps of bivalve total biomasses in the Pomeranian Bay in 1993 and distribution maps of the fraction, harvestable by long-tailed ducks (not too small, not too large, not too deep, see text for explanation). Dots indicate sampling sites.
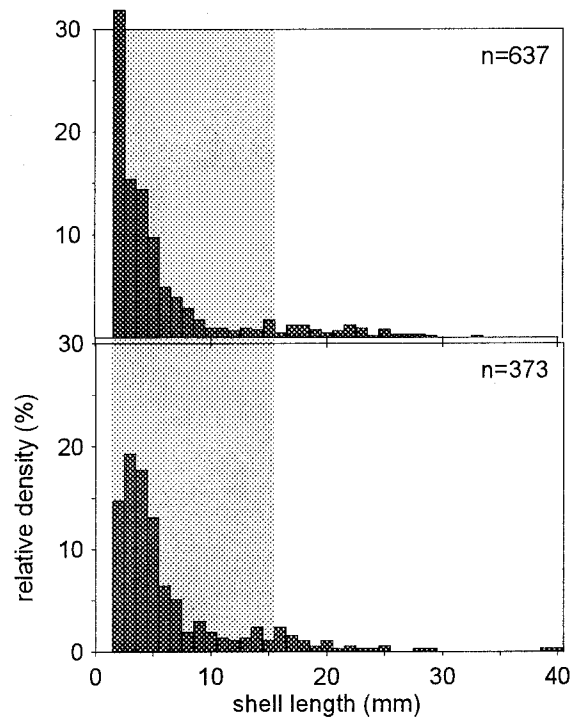
Fig. 5.11: Typical examples of relative size-frequency distributions of blue mussels, *Mytilus edulis*, from the western part of the Pomeranian Bay in 1993. The shaded bars indicate mussels which are suitable for long-tailed ducks.
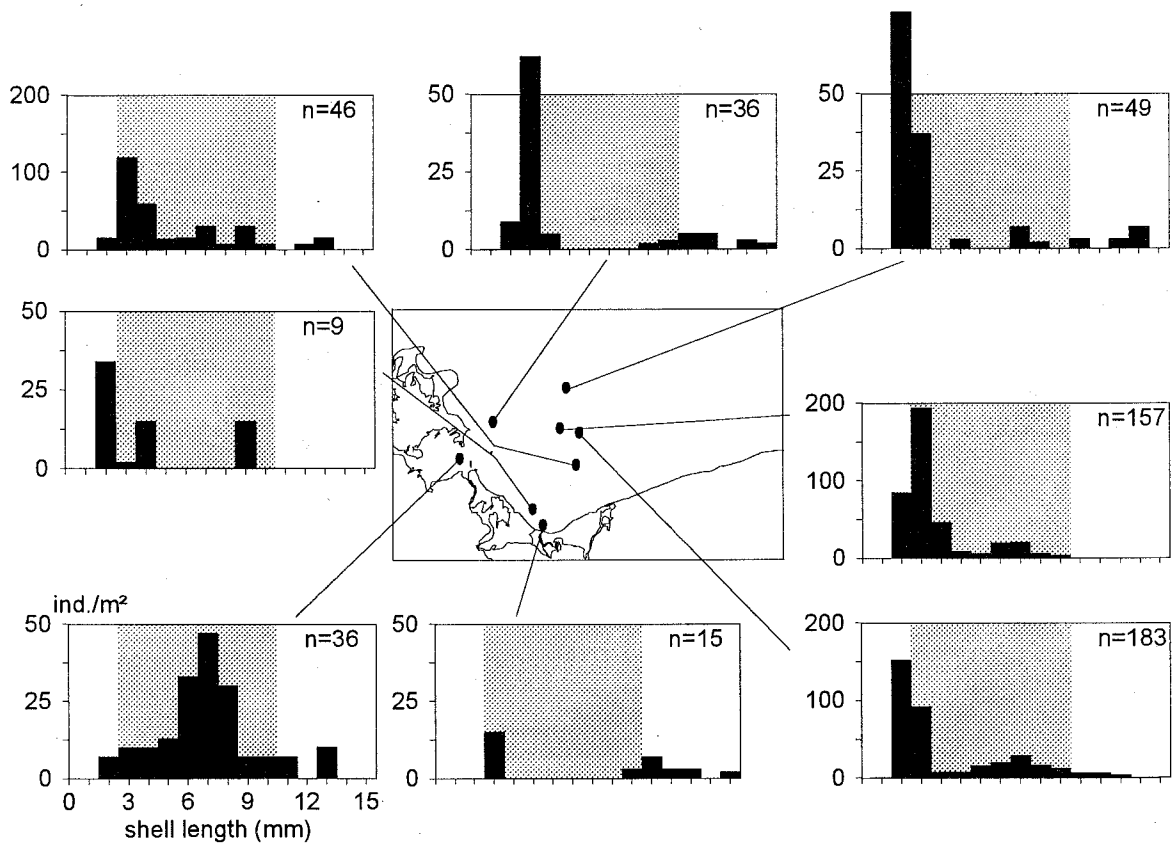

Fig. 5.12: Examples of the size-frequency distribution of cockles, *Cerastoderma lamarcki*, from the Pomeranian Bay in 1993. The shaded bars indicate cockles which are suitable for long-tailed ducks.
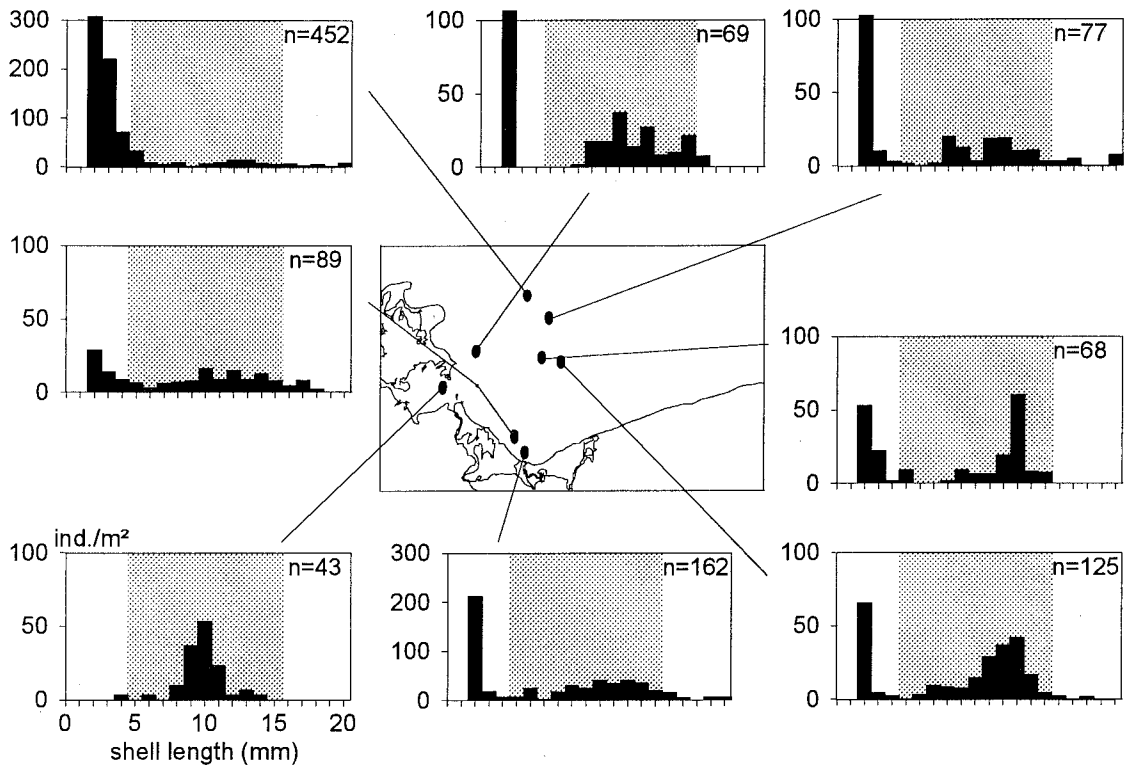
Fig. 5.13: Examples of the size-frequency distribution of Baltic tellins, *Macoma balthica*, from the Pomeranian Bay in 1993. The shaded bars indicate tellins which are perhaps suitable for long-tailed ducks.
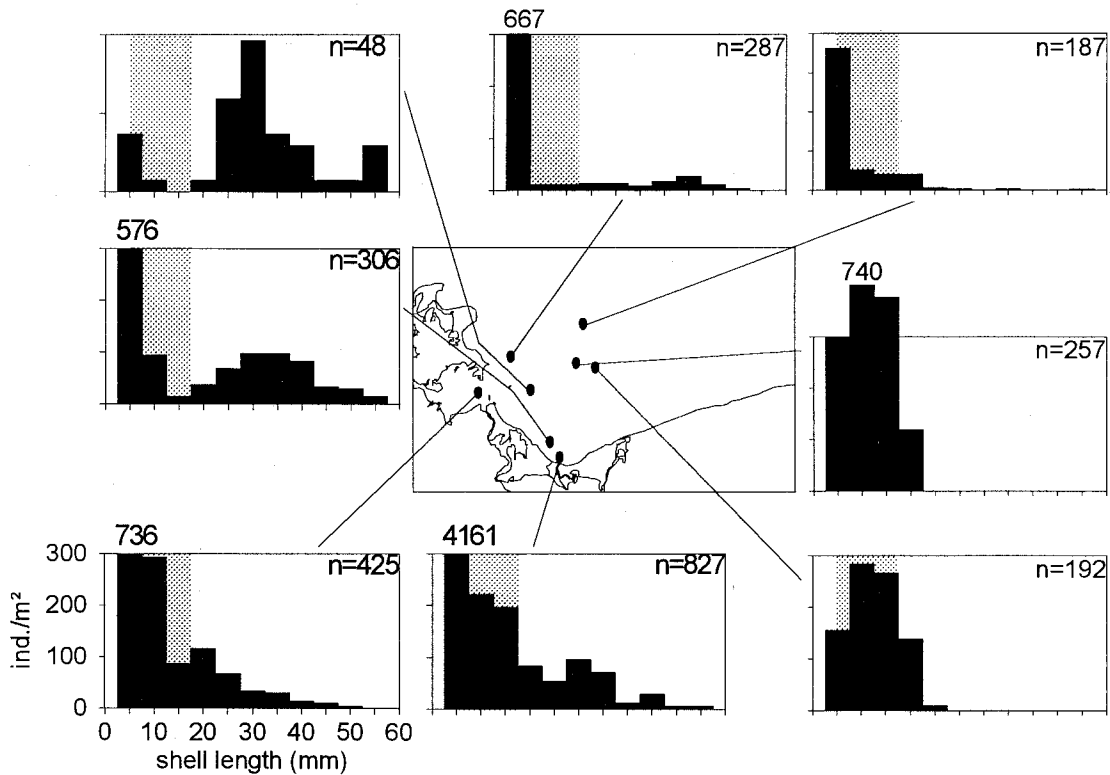

Fig. 5.14: Examples of relative size-frequency distributions of soft-shelled clams, *Mya arenaria*, from the Pomeranian Bay in 1993. The shaded bars indicate clams which are suitable for long-tailed ducks. Numbers above single bars denote higher density values.

Both *M. edulis* and *C. lamarcki* live close to the sediment surface. Cockles do not go deeper than 2 cm. Hence, they are always accessible to the birds. In contrast, specimens of *M. balthica* and *M. arenaria* bury themselves into the sediment. Their burying depth increases with size. No seasonal variation in burying depth was observed. Spatial variations in the vertical distribution in the Pomeranian Bay were related to sediment characteristics (Fig. 5.15).
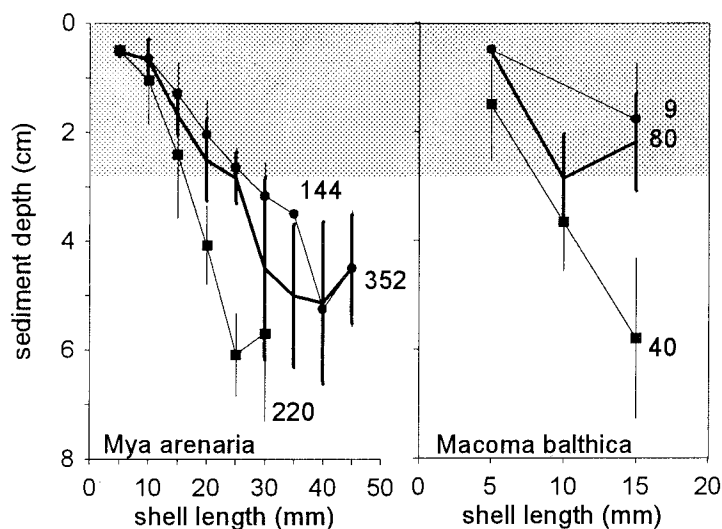

Fig. 5.15: Vertical distribution of *Mya arenaria* and *Macoma balthica* in the Pomeranian Bay. Different curves represent samples collected from sediments with different organic contents (data are combined for all seasons): thin line, squares: < 0.5 %; thick line: 0.5 -1 %; thin line, dots: > 1 %. The shaded part of the plot shows which size classes are within the reach of the bill of a long-tailed duck.

Suitably sized specimens of *M. balthica* were almost out of the reach of the bill of long-tailed ducks at most stations. Only four nearshore stations provided an organic content of the sediment of more than 0.5 %, which was necessary to lower the burying depth of larger *M. balthica* into the accessible depth range. Only one of these four stations, which was located in the Greifswalder Bodden, provided a suitable biomass of *M. balthica* of about 1 g AFDW·m^{-2}. Thus, we excluded *M. balthica* from the analysis.

The available fraction of the other three prey species showed large variations in their distribution and population structure. Whereas small sized *M. arenaria* were almost absent from the southwest, they dominated on the Oder Bank. Densities of *C. lamarcki* were usually highest in the east. *M. edulis* was dominant in the southwestern part of the Bay. No spatial variations in the population structure of this species were observed there.

Temporal changes in the biomass of suitably sized prey were measured between April 1993 and April 1995 at ten stations in the western half of the bay (see examples in Fig. 5.16). The available fraction of blue mussels was always about 30 % of the total standing stock until the occurrence of a prolonged period of oxygen depletion at depths below 10 m in summer 1994. This event reduced the suitable fraction by about 50 %. Densities of small sized *M. arenaria* decreased remarkably within the investigated time period on the Oder Bank. No changes were observed for this species in the southwest until summer 1994. Suitably sized soft-shell clams formed always a negligible portion of the total standing stock. Most of the small specimens were killed there during the period of oxygen depletion, but new clams were introduced immediately from more shallow parts of the bay by bed-load transport. Biomass of cockles remained constanly low in the western half of the bay during the whole observation period.

Habitat selection

The results of the Bonferronii's inequality tests (Table 5.6) clearly indicate that long-tailed ducks in the Pomeranian Bay select areas characterised by medium and high biomass of harvestable prey. Both, during the winter and spring seasons, the ducks avoided the area of low prey biomass in the impoverished zone associated with the German coast. In Figure 5.17 it is indicated that a lower density of ducks in the area of high biomass was affected by the international shipping route. However, the Bonferronii tests show that the avoidance of the disturbed high biomass zone by the long-tailed ducks was only statistically significant ($p<0.05$) during spring (Table 5.7). The tests further show that the ducks narrow their preference for the areas with the higher biomass during spring as indicated by the significant avoidance of areas with medium biomass.
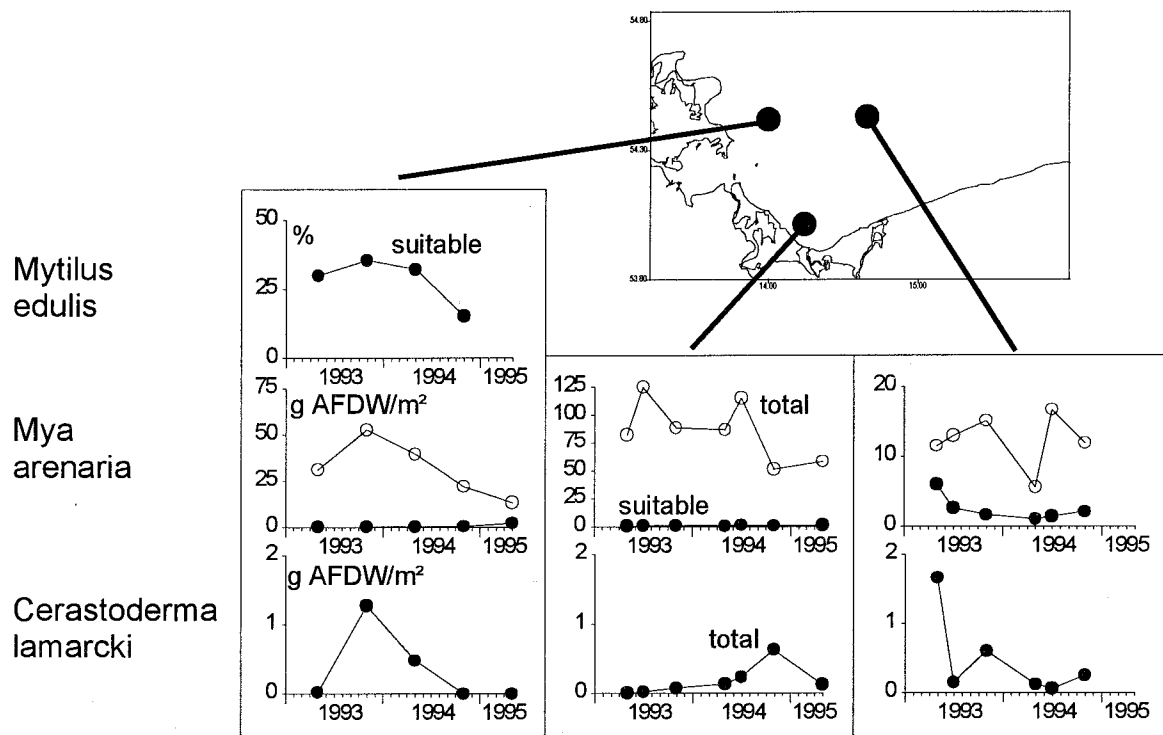
Fig. 5.16: Seasonal variation in the food stocks of long-tailed ducks at selected stations in the western half of the Pomeranian Bay between April 1993 and April 1995. The suitable portion (in %) of the total standing stock is shown for *Mytilus edulis*. Biomasses of the total standing stock (circles) and the suitable fraction (dots) are shown for *Mya arenaria*. For *Cerastoderma lamarcki* we assumed that both total standing stock and suitable fraction were almost identical.

Table 5.6: Differential use of long-tailed ducks of habitats in the Pomeranian Bay in winter defined by level of disturbance and bivalve biomass (see text for details). Occurrence of bivalves is defined as: low biomass: < 1 g $AFDW \cdot m^{-2}$, medium biomass: $1-9.99$ g $AFDW \cdot m^{-2}$ and high biomass: ≥ 10 g $AFDW \cdot m^{-2}$. The occurrence of ducks is indicated by the number of birds seen within 300 m perpendicular distance from the survey ship; n = 36.717 during the winter season and 18.012 during the spring seasons. Tests are based on individual comparisons of observed proportions (p_i) of ducks to expected proportions (p). [a] Significantly $(P < 0.05)$ lower than expected use, [b] Significantly $(P < 0.05)$ greater than expected use.

habitat	effort ratio	ratio of observed ducks	95% confidence interval on observed proportion of occurrence (p)
low biomass	0.231	0.118	$0.113 \leq p \leq 0.123_a$
medium biomass	0.403	0.673	$0.666 \leq p \leq 0.680_b$
high biomass, disturbed	0.172	0.209	$0.203 \leq p \leq 0.215_b$
high biomass, undisturbed	0.193	0.342	$0.335 \leq p \leq 0.349_b$

Table 5.7: Differential use of long-tailed ducks of habitats in the Pomeranian Bay in spring defined by level of disturbance and bivalve biomass (see Table 5.6 for explanation).

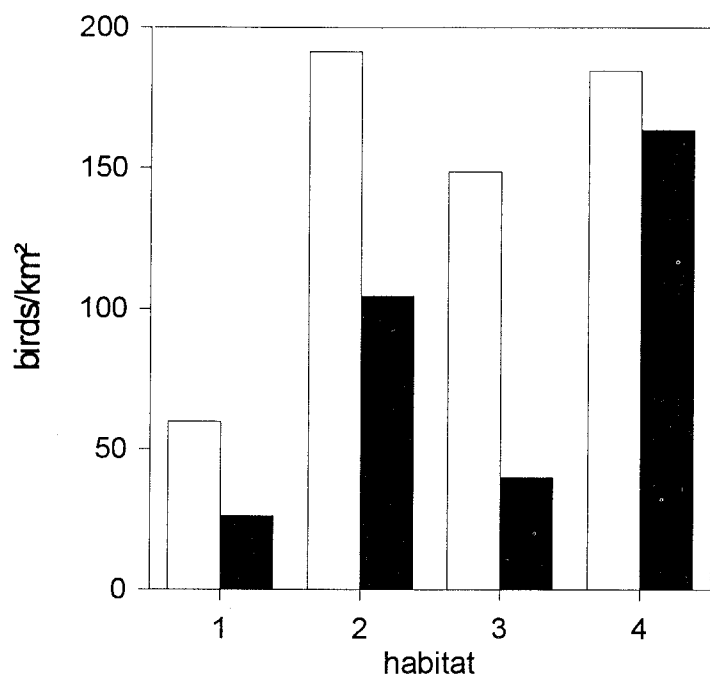| habitat	effort ratio	ratio of observed ducks	95% confidence interval on observed proportion of occurrence (p)
low biomass	0.162	0.027	$0.023 \leq p \leq 0.031_a$
medium biomass	0.487	0.344	$0.332 \leq p \leq 0.355_a$
high biomass, disturbed	0.130	0.031	$0.027 \leq p \leq 0.036_a$
high biomass, undisturbed	0.222	0.257	$0.246 \leq p \leq 0.267_b$

Fig. 5.17: Average densities (birds km^{-2}) of long-tailed ducks during the winter (white bars) and spring seasons (black bars) in areas defined by different habitat categories (see methods for details).

Consumption rate

Mean annual consumption was calculated for each of the four habitats, using the total number of bird days per habitat as a basis (Table 5.8). All our estimates of the mean annual food consumption were based on two assumptions: 1) food intake rates of the birds counted are identical for all four habitat types in winter and spring, and 2) all birds feed exclusively on bivalves.

These assumptions are certainly wrong for areas providing low biomasses of harvestable food. An estimate of the predation pressure for areas with less than 1 g AFDW m^{-2} of harvestable prey, which was found to be 96 %, seems to be not very probable.

Long-tailed ducks removed 10 % of the harvestable food supply in areas with more than 10 g AFDW m^{-2} of *M. edulis*. About 40 % were taken in areas with 1-10 g AFDW m^{-2} of harvestable *M. arenaria* and *C. lamarcki*. Estimated values of the mean annual food consumption were of the same magnitude for undisturbed habitats providing more than 1 g AFDW m^{-2} of suitable prey and about one third lower in the disturbed area.

Tab. 5.8: Estimates of the annual food consumption of long-tailed ducks for different habitats of the Pomeranian Bay in relation to the harvestable food supply. Consumption was calculated by adding mean bird densities m^{-2} in winter x 105 days x DEE with mean bird densities m^{-2} in spring x 45 days x DEE. DEE (daily energy expenditure) was estimated at 60 g AFDW. The percentage of harvestable biomass removed by long-tailed ducks is given in brackets.

habitat	mean total biomass of bivalves (g AFDW m^{-2})	mean biomass of the suitable fraction (g AFDW m^{-2})	mean annual food consumption of long-tailed ducks (g AFDW m^{-2} a^{-1})
low biomass	1.09	0.47	0.45 (96 %)
medium biomass	21.10	3.68	1.49 (40 %)
high biomass, disturbed	107.04	10.71	1.05 (10 %)
high biomass, undisturbed	61.77	15.25	1.61 (11 %)

Discussion

Prey size selection and feeding techniques

Feeding by diving is energetically very expensive. The metabolic rate is about 3.5 times BMR (Woakes & Butler, 1983; 1986). Birds feeding by diving must also regularly interrupt the food intake at the seafloor for breathing and digesting at the water surface. Often, times spent diving are shorter than one minute (Kooyman, 1989; Nehls, 1995; Ydenberg & Guillemette, 1991). Hence, prey choices have to be made very quickly, to minimize the time and energy costs for recognizing and grasping food items.

Based on the results of the analyses of prey and habitat selection and on the knowledge of zoo-benthos communities in the bay , we assume the application of three different feeding techniques in long-tailed ducks.

1) **Digging for single prey items:** We suppose a search by tactile cues for bivalve species, buryied in the sediment (*M. balthica* and *M. arenaria*). Digging for single prey items, distributed randomly within the upper horizon of the sediment, was described by Ball (1990) for canvasback ducks, *Aythya valisineria*, and for pochards, *Aythya ferina*, by Suter (1982). Furthermore, Ball (1990) supposed that prey items are recognized only when they are grasped by the bill.

Large single prey items are generally taken to the water surface and handled there (Ball, 1990; De Leeuw & Van Eerden, 1992; Nehls, 1995). The upper size threshold of bivalves eaten in this way, was assumed to be determined by a strong reduction in the intake rake with increasing size, caused by an increase in handling time (Draulans, 1982). Draulans (1984) also suggested, that the birds try to avoid the risk of taking prey that is too large to be swallowed.

In our opinion, the preference for smaller items is a consequence of the habit of digestion. All bivalves are swallowed whole and crushed in the muscular gizzard. The energetic costs for crushing shells increase with increasing shell length (Nehls, 1995; Piersma et al., 1993b). Hence, the size and the power of the gizzard muscles, as well as the digestive costs are likely to be responsible for the upper size threshold of the prey eaten. This hypothesis was already put forward by Goudie & Ankney (1986). These authors compared the morphology of the bills and digestive organs of five sea duck species. Among these species, they found only negligible differences in bill shape, but large differences in gizzard weights. The gizzard weight of seaducks correlates with total body weight and never exceeds more than 3.5 % of the total body weight (Borkenhagen, 1976; Nehls, 1995).

2) **Suction-feeding:** Blue mussels comprised the largest part of the food of long-tailed ducks in the southern Baltic. Mussels are attached in motile clumps which lay on the sediment surface. Mussel sizes are unequally distributed in these clumps. Both Böhme (1992) and Madsen (1954) described a non-selective ingestion of mussels between 1 mm and 12 mm in length and a negative selection of specimens, larger than 15 mm. De Leeuw & Van Eerden (1992) could show for tufted ducks, *Aythya fuligula*, that the preference for very small mussels can be explained by a high profitability of small prey items, when obtained by suction-feeding. Mussels less than 16 mm in length were stained from a waterflow generated in the bill. In this way, tufted ducks selected mussel sizes by indifferently accepting all specimens smaller than a certain threshold size. Thus, less profitable mussels were also sucked into the bill. De Leeuw & Van Eerden (1992) also supposed, that suction-feeding is widespread among diving ducks.

We believe, that suction-feeding is extensively used by long-tailed ducks in the study area. Small mussels inhabit the sandy bay in high densities, due to their extremely slow growth in the Baltic Sea east of Kiel Bay (e.g. Kautsky, 1982). The application of this technique by long-tailed ducks can be assumed also from the frequent occurrence of crustaceans, fishes and ragworms as prey items (Gorski, 1981; Leipe, 1985). Amphipods and isopods of the genera *Gammarus spp.* and *Idotea spp.*, which were described as common prey items, live in the sublitoral zone exclusively within mussel patches (Powilleit et al., 1996). Dredge samples in the Pomeranian Bay revealed small fishes (*Pomatochistus spp.*) and shrimps (*Crangon crangon, Mysis spp.*) as typical members of the epifaunal community of mussel patches, too.

Digging and suction-feeding are likely to be applied alternatively by the birds during one feeding bout and even within a certain feeding area. The dark mussel patches are highly visible on greyish sand during day light (own video obs.). Perhaps, decisions on which prey to take and which handling technique to apply are made already in relation to the density of visible mussel clumps.

3) Grazing on fish eggs: Flocks of long-tailed ducks feeding on fish eggs were observed not only in the Pomeranian Bay (Gjøsæter & Sætre, 1974). The ducks often feed at fish spawn beds. The eggs are attached to the substrate or to rocks and macrophytes. The handling technique applied while preying upon fish eggs was never observed.

Variation in spatial distribution and habitat preferences

The distribution patterns and prey selections found underline that the long-tailed ducks during their stay in the southern Baltic Sea should be regarded as food generalists switching frequently between different kinds of suitable prey. The midwinter distributions reflect the availability of extensive areas with biomasses of suitable-sized prey exceeding 1 g $AFDW \cdot m^{-2}$ and adaptions for both, feeding on single prey items and suction feeding. These feeding techniques have to be applied exclusively in the offshore Pomeranian Bay, as no mussels occur in the Greifswalder Bodden and on the Oder Bank in areas with a water depth less than 10 m and no cockles and clams of suitable size occur in areas with a water depth exceeding 10 m.

The huge total number of long-tailed ducks in the Pomeranian Bay during mild winters might be an important cause for the observed high bird densities even in sub-optimal feeding areas. Food intake rates of predatory birds usually tend to decrease, as bird densities in an area increase, because predators interfere with each other's ability to capture prey. As a consequence, birds will have to move to other feeding areas when densities are too high to provide a minimum food intake rate as required to balance the daily energy budget. Birds that move may, in addition, change their diet (Goss-Custard, 1980). The decreasing reliance of long-tailed ducks on areas with medium biomasses of harvestable prey (1-9.99 g $AFDW \cdot m^{-2}$) in spring, when the total number of birds was about 50 % lower than in mid winter, gives some evidence for interference during the winter season. In spring, long-tailed ducks seem to narrow the selection of feeding habitats to the two most profitable patches: the zone with high biomasses of harvestable *M. edulis* far from the international shipping lane and the herring spawn area in the Greifswalder Bodden.

Herring eggs provide a particularly profitable food source for long-tailed ducks in spring. The spawn is usually found on pebbles and macrophytes at depths of 3-5 m (Scabell & Jönsson, 1989). Hence, diving costs are lower in the Greifswalder Bodden than in the deeper offshore bay. Digestive costs are much lower for fish spawn than for bivalves too. Diving ducks do require up to 14 % of the ingested energy for shell crushing when feeding on bivalves (Nehls, 1995). Furthermore, herring eggs contain 15 % more energy per weight unit than benthic invertebrates (Klinkhardt & Nicolaus, 1984). The sufficient quality of fish spawn can probably also explain differences in intraspecific behaviour between long-tailed ducks in the offshore bay and in the Greifswalder Bodden. Whereas birds are more or less equally distributed when feeding on bivalves in offshore waters, they usually form dense flocks when feeding on herring eggs in the Greifswalder Bodden. Perhaps, the daily energy budget can be balanced easier and faster by feeding on herring spawn and, therefore, the birds might tolerate then closer nearest neighbours. Otherwise, flocking seems to enable the ducks to investigate the unpredictable and clumped spawn resources in a highly efficient way (Leipe & Scabell, 1990).

Consumption of benthos

Although methods used to calculate the amount of food removed are different, our estimates are with some caution comparable to those of other studies. The data from Table 7 show that long-tailed ducks removed only 1-2 % of the total benthic biomass in the Pomeranian Bay during mild minters. Similar low consumption rates were reported for sea ducks previously (Leipe, 1985; Nehls, 1989; Böhme, 1992; Meire 1993). Consumption in relation to the harvestable food resources was calculated at 12.5 % by Nehls (1989) and at 17 % by Leipe (1985). Comparable consumption rates of 10 % of the harvestable food supply were estimated by us for long-tailed ducks feeding on dense mussel beds. These low values imply, that long-tailed ducks have only a minor impact on mussel populations in the Pomeranian Bay, as mussel consumption is much lower than mussel production (4-6 g $AFDW \cdot m^{-2} \cdot a^{-1}$, own unpubl. estimate).

Much higher consumption rates were found for oystercatchers, *Haematopus ostralegus*, feeding on mussels in intertidal areas. Meire (1993) and Zwarts & Drent (1981) estimated their predation pressure at 30-40 % of the harvestable food supply. Under such circumstances, birds often consume

more than can be replaced by production and, therefore, oystercatchers are able to deplete their food resources completely within a few years.

A high predation pressure of 40 % was estimated by us for long-tailed ducks feeding on the Oder Bank at stations providing medium biomasses of *M. arenaria* and *C. lamarcki*. Unfortunately, we are unable to assess if long-tailed ducks are able to reduce their benthic food stocks there, because of an intensive bedload transport of clams and cockles throughout the year (Kube, 1996).

Anthropogenic alterations of distribution patterns

Our studies gave indirect evidence to both indirect as well as direct anthropogenic alterations of the preferred habitats of the long-tailed ducks in the Pomeranian Bay. The international shipping lane affected the observed density of ducks in the nearby areas. The negative effect from disturbance was most obvious during the spring season when the birds avoided the entire zone associated with dense traffic of large ships. This avoidance pattern can be probably explained by the reaction of the species towards approaching ships; during the passing of a ship birds will either flush or dive leaving no birds adjacent to the ship. Even though a part of the area associated with the shipping lane is characterized by high biomasses of harvestable prey, the energetic costs related to feeding under such conditions might be regarded as unfavourable.

Eutrophication processes, initiated by increasing riverine nutrient loads, have caused a significant increase in macrofauna biomass in the entire bay (Kube et al., in prep). The highest biomass increase was observed for filter-feeding bivalves. Blue mussels and soft-shelled clams, the most important food species for long-tailed ducks, increased in biomass by about eight times since 1958 (Kube et al., in prep). Thus, providing enormous amounts of harvestable food over large parts of the study area, the increase in zoobenthic biomass leads also to an increase in oxygen depletion events in the deeper parts of the Pomeranian Bay. Oxygen depletion events are connected with stochastic upwelling and stratification processes along the Sassnitz Deep in the northwest of the bay (own obs. in 1994). Reductions in macrofauna biomass caused by suboxic periods were already obvious for all stations below 15 m depth in April 1993. An unusual strong and longlasting stratification period has led to even anoxic conditions below 11 m depth in summer 1994 and killed large parts of the macrofauna in the southwest of the bay. As a result, only very few long-tailed ducks were observed in this part of the study area in spring 1995 (data will be reported elsewhere).

Acknowledgements

6. Conclusions

Münster, 1628

Benthic filter-feeding: a natural eutrophication control in the Pomeranian Bay ?

Evaluation of the approach

Coasts and shallow waters close to the shore are intensive contact zones between man and the sea. The exploitation of benthic and demersal resources is economically important. Especially in semi-enclosed seas with a high ratio of coastal areas to total area it is of interest to understand how benthic and pelagic ecosystem compartments interact and which role the benthos may play in the overall system behaviour. Therefore, the analysis of changes in benthic community structure has become one of the mainstays for detecting and monitoring effects of marine pollution.

The macrozoobenthos of the Pomeranian Bay provided a good opportunity to study the local effects of environmental changes, especially eutrophication. The advantages are:
1. The community consists only of 45 different species which are moderately easy to determine. Most of them are randomly distributed. Hence, sampling and laboratory work are not very time consuming.
2. There is an enormous dominance of a few filter-feeders with a high longevity. These bivalves are relatively non-mobile and are useful for studying spatial effects of eutrophication and pollutants on the level of species.

Despite this, there are also several disadvantages:
1. Planktonic stages, settlement and recruitment of bivalve spat are very erratic, and as a result dramatic changes in abundances may occur from year to year, resulting in natural temporal changes in population and community structures.
2. Mobile mussel-clumps and associated epibenthic species cannot be sampled precisely without time consuming and expensive sampling techniques.
3. There is little knowledge on the population dynamics of several of the dominant species in mesohaline sublittoral environments.
4. There is no extensive literature available on the applicability of established statistical methods in the interpretation of communities with low diversity.

Since different kinds of organisms or ecosystem components may respond to the same impact differently we examined several response levels in our studies. Each chapter of this thesis deals with a single question, that emerged during the investigations. In this epilogue I will try to develop an overall interpretation of the observed response of the macrozoobenthos to the eutrophication process in the study area.

Many of the species found during the investigation can be characterised by a high tolerance towards various environmental factors. They are typical euryhaline, estuarine species. Their physiological capacities for fluctuations in abiotic factors are much greater than the real niches occupied in the system (Arndt, 1973; 1989). All benthic communities of the Pomeranian Bay are dominated by filter-feeders. Surface deposit-feeders are only dominant along the northern boundary adjacent to the Arkona and Bornholm Basins. Physical disturbance and available food supply are assumed to be important in structuring the benthic community. The high macrofauna biomass, especially in the group of coastal stations is thought to reflect the high anorganic and organic load from the Oder River which has entered the system through the Oder Estuary during the last three decades (paper 1).

The biomass of filter-feeding bivalves increased significantly since the 1950s (paper 2). A predominantly filter-feeding polychaete, *M. viridis*, successfully invaded the southwestern part of the study area (paper 5). Several crustaceans vanished completely between 1981 and 1993, especially in the deeper parts (paper 2).

Growth rates of bivalves are remarkably low in the mesohaline environment. The growth of *M. balthica* correlated significantly with phytoplankton concentration (paper 4).

Though a causal relationship between simultaneous increases of nutrient levels in space and time and secondary production cannot be tested, eutrophication is supposed to be the major process affecting changes in macrofauna assemblages (paper 2). Variations in climatic and hydrographic factors as well as sea duck predation during mild winters cause to some extent fluctuations in the macrozoo-

benthic populations (paper 3 and 6). Sediment characteristics explain only a part of the observed variability (paper 1, 4 and 6).

Due to the "snap-shot"-character of this study it is difficult to draw any conclusions about the presence or absence of food limitations in the bay. However, a comparison of the dominance values of bivalve biomasses from the Pomeranian Bay with other investigations in shallow sandy parts of the western and southern Baltic Sea, carried out with comparable sampling methods, suggests a high level of organic enrichment in the Pomeranian Bay (Table 6.1). *Cerastoderma edule, M. arenaria* and *M. balthica* were found to be the dominant species in the Kiel Bay and total biomass values were low (Brey, 1984). But also extremely high biomasses of *M. edulis* were observed in Kiel Bay locally by Meissner (1992) during a later study. *M. edulis* and *M. arenaria* were dominant in the Wismar Bay and biomasses were very high. According to Prena & Gosselck (1989), the Wismar Bay is one of the most productive shallow bays in the Baltic Sea. Bivalve biomass values and the dominance proportions in the Pomeranian Bay are similar to those described for the Wismar Bay, but some caution is warrented by comparing the macrofauna assemblages between these bays, because of the huge differences in salinity (25 ‰ in Kiel Bay, 12‰ in Wismar Bay, 8‰ in Pommeranian Bay).

Table 6.1: Mean biomass and dominance values of bivalve species of shallow sandy bottoms of Kiel Bay (10 stations, mean depth 7 m, Brey, 1984), Wismar Bay (19 stations, mean depth 4,5 m, Prena & Gosselck, 1989, WW converted into AFDW after Rumohr et al., 1987), and Pomeranian Bay (8 stations, mean depth 10 m). All samples were collected with a heavy Van Veen grab ($0{,}1$ m^2) and rinsed over a 1 mm sieve. Biomass data of *M. arenaria* derived from Van Veen grab samples without computing the total individual weight from cutted siphones represent only about 60 % of biomass values found in box corer samples (own intercalibrations). AFDW of *M. edulis*, given in brackets, show biomass ranges within mussel beds (* after Meissner, 1992, ** Prena pers. comm.).

species	mean biomass (g AFDW m^{-2})			mean dominance (%)		
	Kiel Bay	Wismar Bay	Pomeranian Bay	Kiel Bay	Wismar Bay	Pomeranian Bay
Cerastoderma lamarcki		5.2	0.6		8.6	1.8
Cerastoderma edule	2.4			22.2		
Macoma balthica	2.8	3.0	3.5	25.9	8.6	10.3
Scrobicularia plana		0.8			1.4	
Mya arenaria	5.6	25.3	27.7	51.9	42.0	81.2
Mytilus edulis		25.7	2.3		42.8	6.7
	(300-500*)	(100-300**)	(20-80)			

An evaluation of the Pearson & Rosenberg's model of the eutrophication process

Whilst there are now some very detailed descriptions of community changes in relation to local controls, rather little attention has been paid to assessing the comparative severity of eutrophication incidents against each other on a regional or global scale (Warwick & Clarke, 1993). Only a few such attempts have been made since Pearson & Rosenberg (1978) published their model of effects of increased organic matter load on benthic communities (see introduction).

Gray (1992) suggested a general scenario of response for the benthos fauna of northern Europe based on the severity of reduction in bottom-near oxygen concentration, which has been detected as a typical sign of eutrophication in many effect studies (Fig. 6.1). A similar model was proposed by Rumohr (1993) for the Baltic Sea. His model is based on the process of uprising of the sediment redoxcline, a typical effect of severe oxygen reductions (Fig. 6.2). Both models describe qualitative and quantitative changes in the community.

Warwick & Clarke (1993) described a change in the phyletic composition of communities. They could show that generally annelids are more toletant to perturbations in comparison to molluscs or even echinoderms and crustaceans. Their model also describes the response of the community to reduced oxygen saturations, because different phyla often differ generally in their physiological and ecological abilities to withstand hypoxia or anoxia (e.g. Theede, 1984).

All three models were based on data from the deeper sublittoral (13-300 m deep) of the European shelf. Therefore, the applicability of these models to very shallow and intertidal regions still remains

to be investigated, because not all shallow areas that have increased anthropogenic nutrient supply suffer from lack of oxygen (Gray, 1992; HELCOM, 1987; Warwick & Clarke, 1993).

Vollenweider (1976) has developed a model for freshwater lake eutrophication which has been widely and successfully applied to many freshwater ecosystems. Briefly, his model is based on the empirical finding that there is a negative correlation between the sedimentation rate of phosphorus and the mean depth of the lake. This model was never applied to marine environments because nitrogen is the primary limiting nutrient for primary production in the marine environment. The depth component was ignored because marine coastal environments encompass a wide range of different hydrodynamic regimes (Gray, 1992). However, exactly these different hydrodynamic regimes are likely to be an important reason for the observed variety of responses of benthic communities to eutrophication.

Fig. 6.1: Model of effects of reduced oxygen saturation on benthos fauna of northern Europe (from Gray, 1992).
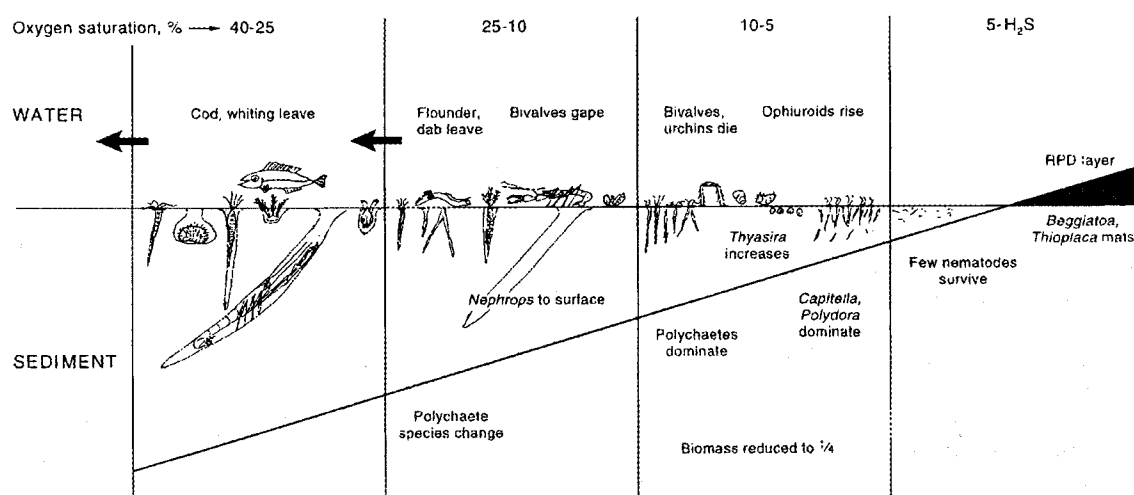
Fig. 6.2: Baltic Sea eutrophication model. The dotted line indicates the redoxcline depth (from Rumohr, 1993).
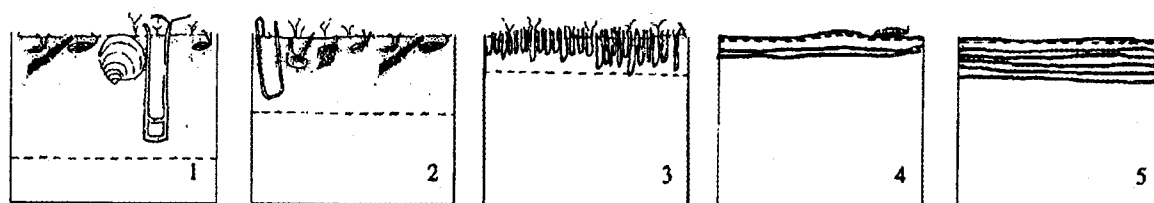
In the following, I will examine the role of hydrodynamic processes for the food and oxygen supply and for the development of the benthos community in three types of simplified situations, representing the main hydrographic regimes of the European seas, namely:
1. the shelf areas of intermediate depth which are characterised by a strong pycnocline and areas more than 50 m deep,
2. the shallow water areas which are characterised by permanent mixing of the water column down to the sea floor except during periods of strong stratification,
3. windflats and intertidal areas.

Deep water column: In the eeper parts, products of primary production are largely consumed in the water column. The particle flux to the sediments depends on vertical sedimentation and lateral advection. An erratic food supply to the benthos causes seasonal imbalances. Most of the time the quantity of organic material arriving at the bottom is low. In a boreal system, the sedimentation pattern creates pulses of food supply especially during spring and sometimes during autumn. In summer, short-term hypoxic conditions are common due to the sedimentation and degradation of marine

snow, the occurence of strong pycnoclines and due to the increased respiration rates at higher temperatures (Graf, 1992; Ott, 1992). The biomass of long-lived filter-feeders is low because of an unpredictable supply of suspended food particles. Filter-feeders, which can either ingest fairly large particles or switch to deposit-feeding, predominate (e.g. Andersin et al., 1977; Warzocha, 1995).

Increased quantities of organic matter can be buffered by an increasing biomass of benthic animals, especially deposit-feeders, only for a limited period of time. The increasing respiration rate of all kinds of benthic organisms can reduce the oxygen concentration in the bottom water in summer far below hypoxia. Local anoxic conditions may cause severe benthic mortality. The time of the onset as well as the strength of the anoxia are responsible for overall system behaviour. At the end of fall, water mixing and cooling reestablishes oxic conditions and the macrozoobenthos grows again (Arntz & Rumohr, 1982; 1986).

A series of episodic anoxia events leds to a decrease of species, which tend towards k-selection and are sensitive to organic pollution. Species, which tend towards r-selection, recolonize azoic sediments faster and may increase. A change from bigger to smaller individuals occurs (e.g. HELCOM, 1990; Rosenberg et al., 1987; Weigelt, 1991).

The accumulation rate of organic matter increases (Leipe et al., 1995) and if enrichment continues, finally all macrofauna disappears (Gray, 1992; Pearson & Rosenberg, 1978; Rumohr, 1993).

Shallow water column: Mixing of the water column always reaches the sea floor except during occasional periods of strong stratification. Much of the production reaches the bottom as high quality, living phyto- and zooplankton (Smetacek, 1984). The benthos, therefore, mainly consists of endo- and epibenthic filter-feeders and may reach very high biomasses (Brey, 1984; Fedra et al., 1976; Prena & Gosselck, 1989; this study). The benthos can potentially control primary production (Cohen et al., 1984; Officer et al., 1982; Ott & Fedra, 1977).

Particulate organic matter is not accumulated in sediments under well mixed conditions though net inputs may increase. Lateral near-bottom currents constantly resuspend deposited particles. On slopes, resuspension, lateral advection, and the influence of gravity cause an export to deeper areas (Graf, 1992, Leipe et al., 1995). The increased amounts of organic material are assimilated mainly by filter-feeders. Their biomass increases, whereas the biomass of deposit-feeders tends to remain stable. The stable pattern of deposit-feeders could be a consequence of competition for food and space with large-sized filter-feeders. Actually, it is difficult to decide whether the individual mean size of the animals increases or decreases (Brey, 1986; Cederwall & Elmgren, 1980; this study).

Strong stratification events can cause anoxic conditions even in shallow waters and may interrupt the biomass increase (Ott, 1992; Prena, 1994; Weigelt & Rumohr, 1986; this study). At the end of the stratification period the macrozoobenthos recolonizes the area and the cycle begins again. R-strategists, mainly polychaetes, colonize the azoic area more rapidly than filter-feeders with a high longevity (Fig. 6.3).

Fig. 6.3: Biomass values of the dominant bivalve species, *Mya arenaria* (thin line, squares), the dominant polychaete species, *Marenzelleria viridis* (thick line, crosses), and the dominant crustacean species, *Corophium volutator* (thick line, dots), at a station in the southwestern part of the Pomeranian Bay before and after a strong oxygen depletion event in August 1994. The event is indicated by a shaded bar.
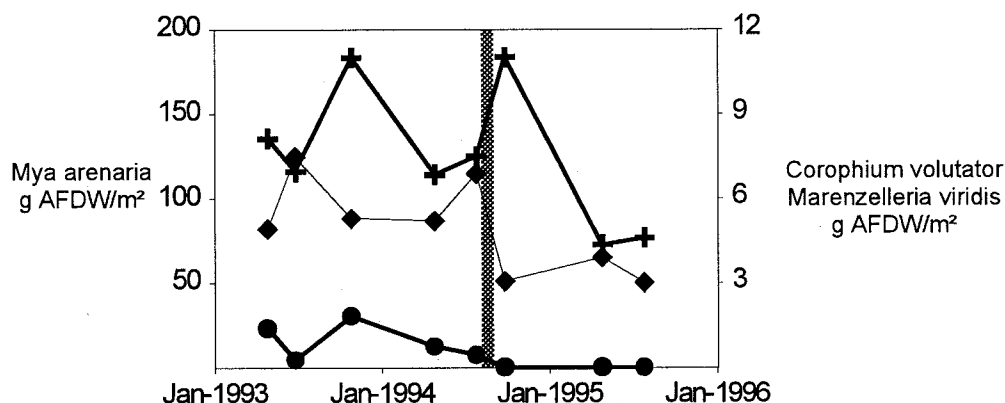
Windflats and intertidal areas: Tidal currents and winds cause an intensive mixing of the water column during high tide. Tidal variations appear to preclude prolonged periods with low oxygen concentrations. There is usually a constant food supply which can be consumed by the herbivorous macrozoobenthos. Variations in food availability are set by the tidal rhythm and, in boreal zones, by seasonal climatic variations. The structure of the benthic community depends mainly on exposure time and other hydrographic factors (Dankers & Beukema, 1983; Reise, 1985). Episodic events, especially cold winters, exert a profound effect on the macrofauna and cause strong year-to-year fluctuations in both, abundance and biomass (Beukema, 1989).

Eutrophication in intertidal areas first of all means an enhanced food supply for the herbivorous macrofauna, because both, pelagic and benthic primary production increase (Beukema & Cadée, 1986, Jonge & Essink, 1991). As a result, numerical densities of all non-carnivorous animals increase. The strongest increase was observed for deposit-feeders (Beukema, 1991; Reise, 1982; Reise et. al., 1989). As numerical densities increase more rapid than biomass, mean individual weigths are declining. This change is probably caused by a faster increase in numbers of small-sized species compared to large-sized species. The total number of species shows heavy fluctuations, but does not shows any trend (Beukema, 1991). The large increase of some small polychaetes (deposit-feeders, r-strategists) might be caused by their low sensitivity to cold winters. Cold winters can cause interruptions in the accumulation of biomass in k-strategists, and reproduction of filter-feeding bivalves fails after mild winters (Beukema, 1990). Otherwise, the polychaetes may benefit from their ability to feed during high tide as well as during low tide, whereas the food intake of obligatory filter-feeding animals is restricted to the immersion time periods.

Usually, models of system evolution are using averages of forcing functions. In practice, however, temporal changes are caused by a combination of long-term deterministic and stochastic processes. Especially, episodic events with extreme values of parameters (storms, anoxia, severe winters, etc.) play an important role (Fig. 6.5). Communities undergo cyclic and erratic changes, rather than reaching a stable equilibrium (Remmert, 1991). Therefore, Reise (1991) reviewed the model of Pearson & Rosenberg in the light of cyclic succession (Fig. 6.4). Up to now there is little empirical knowledge on such cycles in benthic communities. The mosaic-cycle concept for the modelling of possible trends caused by anthropogenic eutrophication may help to develop a more quantitative approach.
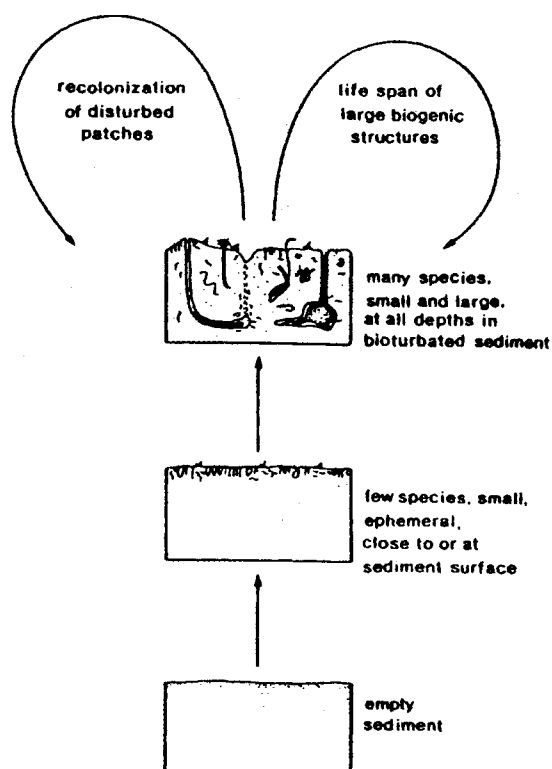

Fig. 6.4: Progressive and cyclic changes of the macrofauna in marine sediments (from Reise, 1991).

Fig. 6.5: Specification of Pearson & Rosenberg's model of effects of increased organic matter load on benthic communities. The effects of eutrophication depend on the accumulation rate of organic matter, the intensity of stratification events (anoxia is indicated by ^) and the intensity of climatic impacts (severe winters are indicated by *).

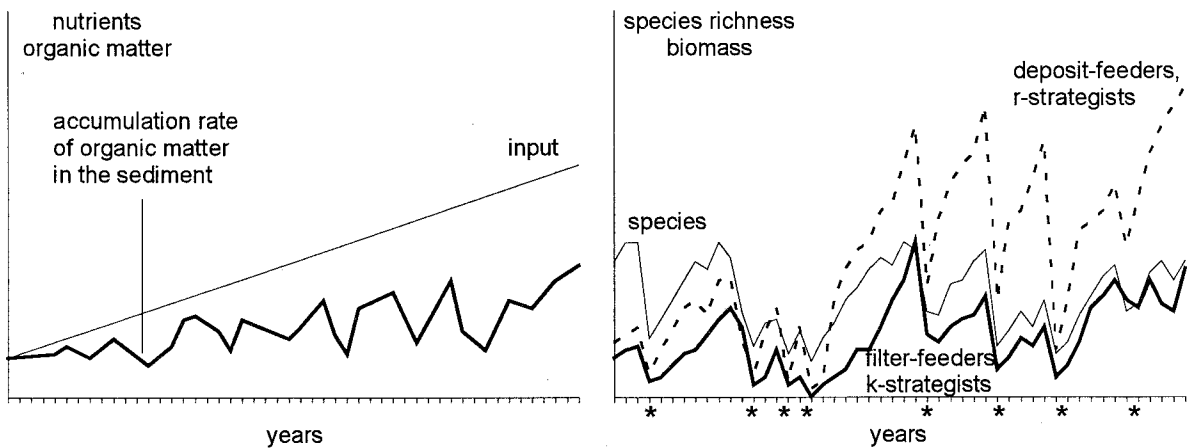deep water, never exposed to wave action
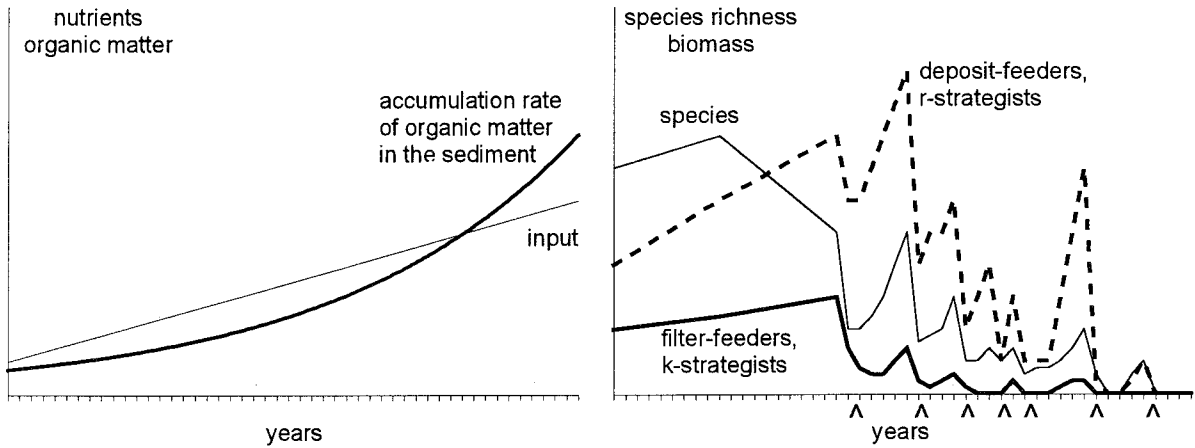
shallow water, permanently exposed to wave action
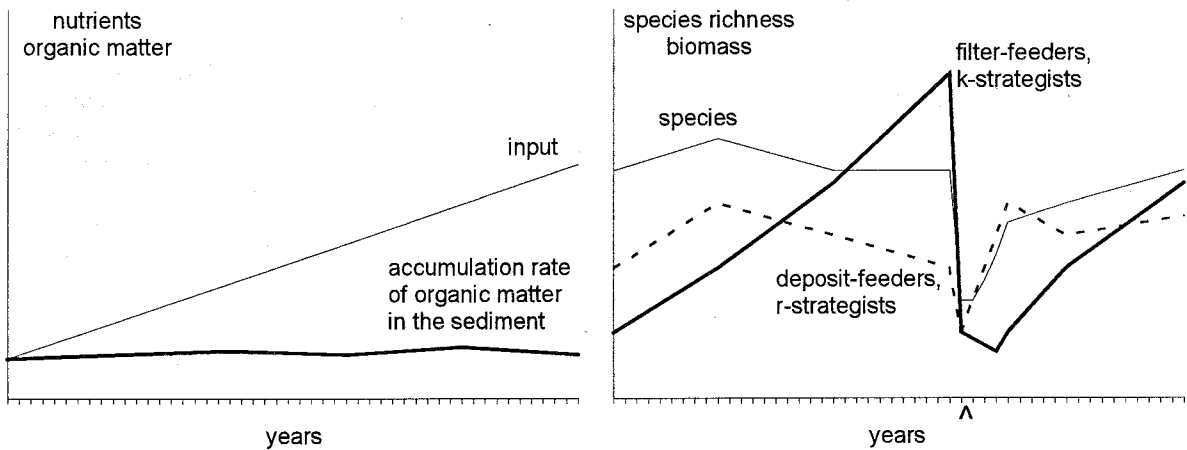
intertidal

Furthermore, the model, given in Fig. 6.5, can not be applied to certain areas by considering simply water depth. There are many shallow waters, especially semi-enclosed coastal lagoons, that behave on one hand like shallow waters due to a permanent mixing of the water column, and on the other hand like deep water areas, because they constantly trap large amounts of particulate organic matter (Schlungbaum et al., 1994a, b). Also, the process of accumulation of particulate organic matter in intermediate depth areas can be interrupted by strong mixing events which periodically export part of the deposits.

Benthic eutrophication control in the Pomeranian Bay: limits set by the environmental variability

Dense populations of filter-feeding bivalves, especially clams and mussels, can process the ambient water at such high rates that they may affect phytoplankton production (see introduction and chapter 2). The quantitative model of Herman & Scholten (1990) for the Osterschelde Delta in the Netherlands shows, for instance, that suspension-feeders can effectively control pelagic production and buffer external nutrient inputs. The long-term model, given in Fig. 4, also supports the assumption that benthic filter-feeders can stabilize overall ecosystem behaviour in shallow waters.

Officer et al. (1982) have searched the literature for marine areas in which benthic filter-feeding animals may be important for phytoplankton populations. The important criteria for identification were:
- shallow water depths in the range of 2-10 m,
- large and widespread benthic filter-feeding populations, dominated by small-sized animals,
- abundant nutrient supplies,
- constant low phytoplankton levels,
- semi-enclosed regions with relatively poor hydrodynamic exchange characteristics with adjacent water bodies.

Potential estimates of removal rates of pelagic biomass ranged from one to three days in waters not exceeding 10 m depth (Loo & Rosenberg, 1989; Officer et al., 1982). Own estimates of clearence rates for the Pomeranian Bay are in the same order of magnitude and, indeed, surface phytoplankton concentration often decreases rapidly beetwen the Swina mouth or the Greifswalder Bodden and the Oder Bank (paper 1, chapter 2). However, since the environmental conditions which are favourable for a control of the pelagic production, described by Officer et al. (1982), it is unlikely that the benthos of the Pomeranian Bay may effectively control phytoplankton and nutrient levels throughout the year. Perhaps, it may be important during part of the annual cycle. The environmental constraints of the study area set several limits to a benthic control.

1) Large amounts of the phytoplankton and organic matter is transported through the Pomeranian Bay without becoming available to filter-feeders, especially during westerly winds. The inputs of phytoplankton and particulate organic matter into the Pomeranian Bay via the river mouths fluctuate heavily from day to day and from place to place. This variability is caused by local winds. The local wind in the Pomeranian Bay is characterized by strong variations with time scales of a few hours to a few days. Winds of distinct directions enforce or interrupt the riverine outflow via the Swina mouth (Majewski, 1972). Winds of distinct directions also produce typical spatial distribution patterns of the riverine load within the bay (Siegel et al., 1994).

Though the dominant filter-feeding bivalves experience a continuous erratic renewal of food produced in the coastal lagoons and transported by currents into all near-shore zones, their distribution patterns are highly aggregated (paper 1, 2). Thus the spatial clustering of filter-feeding bivalves in the southwestern part of the study area is not only caused by the amount of food. This aggregation reflects also the ability for successful settlement of both, the pelagic larvae and older benthic stages on certain sediments (paper 2, 3; Beukema et al., 1983).

2) Phytoplankton concentrations show a strong annual cycle. Primary production is highest in March and April, during the spring bloom (paper 4). The rapid algal growth provides much more organic matter than can be consumed by filter-feeding bivalves. The largest portion of the spring bloom reaches the sediments (own obs.). Although this material is often resuspended, bedload-currents seem to transport most of it into the Sassnitz Deep and the adjacent Arkona Basin (Leipe et al., 1995).

3) In boreal systems, growth of filter-feeding bivalves is only rapid during spring and summer and slight or absent in winter. Though low temperature is unlikely to be the sole controlling factor, the

importance of the gametogenic cycle and the reduced availability of food in the winter are uncertain. However, temperature has been widely acknowledged as an important factor in controlling growth with an optimum between 10 and 20° C (Bayne, 1976).

Gilfillan et al. (1976) determined the carbon flux for a population of *M. arenaria* on a monthly basis. They found that filtration and respiration were low in winter. In the spring warming period, filtration increased to higher values, but assimilation ratios declined to near zero values. The result was a very large loss in carbon during this period. The large losses of carbon were pressumably a reflection of stress imposed by adaptation to warmer temperatures. During summer, filtration rates were generally high, and appeared to correlate with water temperature. During this time, assimilation ratios were high too. Respiration and assimilation ratios declined towards winter values during fall (Fig. 6.6).

Both, the mean annual water temperature cycle and the annual cycle of chlorophyll a concentration in the Pomeranian Bay are similar to the cycles described by Gilfillan et al. (1976) for their study area in Maine, USA. A comparable seasonal variation in filtration and assimilation can be assumed, therefore, for *M. arenaria* in the Pomeranian Bay. In conclusion, it seems unlikely that filter-feeding by bivalves can exert control to phytoplankton growth except for the summer months June-September.

Fig. 6.6: Annual cycle of water temperature, water chlorophyll a concentration, filtration rate and carbon flux in soft-shelled clams, *Mya arenaria*, 20-30 mm long, in Casco Bay, Maine, USA (after Gilfillan et al., 1976).
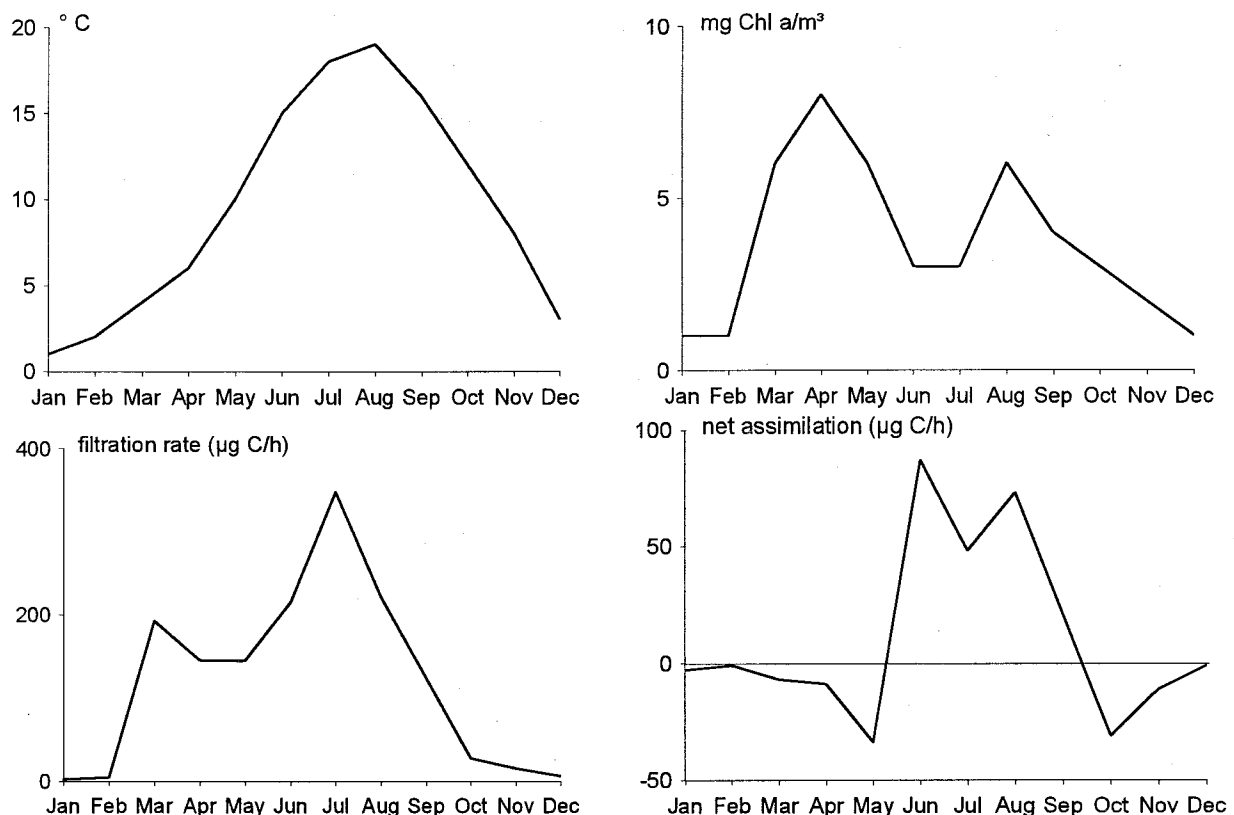
Epilogue

Based on the above discussion, it becomes obvious that many of the results presented in this thesis provide only tentative answers about the effects of eutrophication on the macrozoobenthos. The limited amount of data that could be collected during our study is the main reason for this restriction. As most of the local ecology of common species was unknown several important aspects became only apparent during the work. Many of the variables that had to be determined in detail, are not influenced by anthropogenic changes. However, the results give important information concerning the recent distribution, numbers and biomass of the bottom fauna and sea ducks in the coastal waters of the southern Baltic. Previously, incomplete data were available for the Pomeranian Bay. The methodological approach provided a useful guideline for future impact studies in coastal brackish waters. Apart from the descriptive part, the study also provided some new insight into spatial and temporal variations of sublittoral populations of common and widespread estuarine invertebrates. Furthermore, the study showed that methods developed for the measurement and evaluation of intertidal benthic food recources for waders preying upon bivalves (Piersma, 1994; Zwarts & Blomert, 1992; Zwarts et al., 1992) are also applicable to the sublittoral prey stocks of wintering sea ducks. In the near future, some additional results will be obtained on the effects of chemical pollutants. No obvious impact could be detected so far (Schneider, pers. comm.).

I am well aware that there are a lot more human activities which may have an impact on the macrozoobenthos. However, only very few reliable data were available on fish stocks and their exploitation, harbour construction works, sea traffic, oil pollution and gravel mining. For the scope of this thesis these activities were considered to be of minor importance.

Despite all the remaining uncertainities of the results, we detected enough obvious negative effects of anthropogenic impacts. This requires immediate action programmes to stop this development and to protect this marine area. I hope that the governments of the nine Baltic Sea States will take their responsibility to protect one of the most important areas for migrating and wintering sea birds of the entire Palaearctic.

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Acknowledgements

For a true naturalist as myself, there is no higher goal in work than studying a biotop which is untouched by man. The fascination exerted on me by pure nature is still unbroken. Consequently, I am indebted to my supervisor, the distinguished Bodo von Bodungen, for having guided me to and through this thesis. The cruises into the Pomeranian Bay gave me manyfold opportunities for thrilling observations of nature. The sight of thousands of sea ducks on the smooth surface of the sea on a qiet warm morning in April, the resting flock of exhausted small birds on deck on foggy days in autumn or the view of the sea floor using a video camera were both, a reward and a motivation, for the seemingly endless hours on the microscope and the computer.

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References

Andersin, A.B., Lassig, J., Parkkonen, L. & Sandler, H., 1978: The decline of macrrofauna in the deeper parts of the Baltic proper and the Gulf of Finland. – Kieler Meeresforsch., Sonderheft **4**, 23-52.

Andersin, A.B., Lassig, J. & Sandler, H., 1977: Community structures of soft-bottom macrofauna in different parts of the Baltic. In: Biology of benthic organisms. Ed. by B.F. Keegan, P.O. Ceigigh & P.J.S. Boaden. 11th European Symposium of Marine Biology, Galway, October 1976, Pergamon Press Oxford, 7-20.

Ankar, S., 1980: Growth and production of *Macoma balthica* (L.) in a northern Baltic soft bottom. – Ophelia, Suppl. **1**, 31-48.

Appeldoorn, R.S., 1983: Variation in the growth rate of *Mya arenaria* and its relationship to the environment as analyzed through principal component analysis and the ω parameter of the von Bertalanffy equation. – Fish. Bull. **81**, 75-84.

Arndt, E.A., 1973: Ecophysiological and adaptational problems confronting animals living in brakkish water. – Oikos (Suppl.) **15**, 239-245.

Arndt, E.A., 1989: Ecological, physiological and historical aspects of brackish water fauna distribution. In: Reproduction, genetics and distribution of marine organisms. Ed. by J.S. Ryland & P.A. Taylor. 23rd European Marine Biology Symposium. Olsen &Olsen, Fredensborg, 327-337.

Arndt, E.A., 1994: Struktur und Dynamik des Makrozoobenthos in der Darss-Zingster Boddenkette im Laufe der letzten 25 Jahre unter besonderer Berücksichtigung der Makrozoobenthos-Entwicklung im Saaler Bodden von 1986-1990. – Rostocker Meeresbiol. Beitr. **2**, 93-120.

Arntz, W.E., Brunswig, D. & Sarntheim, M., 1976: Zonierung von Mollusken und Schill im Rinnensystem der Kieler Bucht (Westliche Ostsee). – Senckenb. mar. **8**, 198-269.

Arntz, W.E. & Rumohr, H., 1982: An experimental study of macrobenthic colonization and succession, and the importance of seasonal variation in temperate latitudes. – J. Exp. Mar. Biol. Ecol. **64**, 17-45.

Arntz, W.E. & Rumohr, H., 1986: Fluctuations of benthic macrofauna during succession and in an established community. – Meeresforschung **31**, 97-114.

Aschoff, J. & Pohl, H., 1970: Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. – J. Orn. **111**, 38-47.

Bachelet, G., 1980: Growth and recruitment of the tellinid bivalve *Macoma balthica* at the southern limit of its geographical distribution, the Gironde Estuary (SW France). – Mar. Biol. **59**, 105-117.

Baker, J.M. & Wolff, W.J., (eds.), 1987: Biological surveys of estuaries and coasts. Cambridge University Press, Cambridge, 449 pp.

Ball, J.P., 1990: Active diet selection or passive reflection of changing food availability: the underwater foraging behaviour of canvasback ducks. In: Behavioural mechanisms of food selection. Ed. by R.N. Hughes. Springer-Verlag, Berlin-Heidelberg, 95-109.

Bartholomew, G., 1986: The role of natural history in contemporary biology. – BioScience **36**, 324-329.

Bast, H.-D. & Oertzen, J.-A. von, 1976: Zusammenstellung von Energieäquivalenten aquatischer Organismen unter besonderer Berücksichtigung der Ostsee. Teil 2. – Wiss. Zeitschr. Univ. Rostock **25**, Mat.-Nat. Reihe, H. **3**, 295-304.

Bastrop, R., Röhner, M. & Jürss, K., 1995: Are there two species of the polychaete genus *Marenzelleria* in Europe ? – Mar. Biol. **121**, 509-516.

Bayne, B.L. (ed.), 1976: Marine mussels: their ecology and physiology. International Biological Programme 10, Cambridge University Press, Cambridge, 411 pp.

Bayne, B.L., Clarke, K.R. & Gray, J.S. (eds.), 1988: Biological effects of pollutants: results of a practical workshop. – Mar. Ecol. Prog. Ser. **46**, 1-278.

Bayne, B.L., Livingstone, D.R., Moore, M.N., Stebbing, A.R.D. & Widdows, J., 1980: Ecological monitoring. – Mar. Pollut. Bull. 11, 238.

Bayne, I. & R.C. Newell, 1983: Physiological energetics of marine molluscs. In: The mollusca, Volume 4, Pysiology, Part 1. Ed. by A.S.M. Saleuddin & K.M. Wilbur. Academic Press, New York, 407-515.

Bayne, I. (ed), 1990: Marine mussels: their ecology and physiology. International Biological Programme 10, Cambridge University Press, Cambridge, 498 pp.

Berndt, R.K. & Busche, G. (ed.), 1993: Vogelwelt Schleswig-Holsteins. Band: 4: Entenvögel II (Kolbenente-Ruderente). Karl Wachholtz Verlag, Neumünster, 228 pp.

Bernstein, C., Kacelnik, A. & Krebs, J.R., 1991: Individual decisions and the distribution of predators in a patchy environment II: The influence of travel costs and structure of the environment. – J. Anim. Ecol. **60**, 205-226.

Bergmann, G. & Donner, K.O., 1964: An analysis of the spring migration of the common scoter and the long-tailed duck in southern Finland. Acta Zool. Fenn. **105**, 1-59.

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

Beukema, J.J., 1982: Annual variation in reproductive success and biomass of the major macrozoobenthic species living in a tidal flat area of the Wadden Sea. – Neth. J. Sea Res. **16**, 37-45.

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

Beukema, J.J., 1990: Expected effects of changes in winter temperatures on benthic animals living in soft sediments in coastal North Sea areas. In: Expected effects of climatic change in marine coastal ecosystems. Ed. by J.J. Beukema et al.. Kluwer Acad. Pub., Dordrecht, 83-92.

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

Beukema, J.J., 1992: Expected changes in the Wadden Sea benthos in a warmer world: lessons from periods with mild winters. – Neth. J. Sea Res. **30**, 73-79.

Beukema, J.J., 1993: Increased mortality in alternative bivalve prey during a period when the tidal flats of the Dutch Wadden Sea were devoid of mussels. – Neth. J. Sea Res. **31**, 395-406.

Beukema, J.J. & Cadée, G.C., 1986: Zoobenthos responses to eutrophication of the Dutch Wadden Sea. – Ophelia **26**, 66-76.

Beukema, J.J. & Cadée, G.C., 1991: Growth rates of the bivalve *Macoma balthica* in the Wadden Sea during a period of eutrophication: relationships with concentrations of pelagic diatoms and flagellates. – Mar. Ecol. Prog. Ser. **68**, 249-256.

Beukema, J.J., Cadée, G.C. & Hummel, H., 1983: Differential variability in time and space of numbers in suspension and deposit feeding benthic species in a tidal flat area. – Oceanol. Acta, Proceedings 17th European Marine Biology Symposium, 21-26.

Beukema, J.J., Cadée, G.C. & Jansen, J.J.M., 1977: Variability of growth rate of *Macoma balthica* (L.) in the Wadden Sea in relation to availability of food. In: Biology of benthic organisms. Ed. by B.F. Keegan, P.O. Ceidigh & P.J.S. Boaden. Pergamon Press, Oxford, 69-77.

Beukema, J.J., Essink, K., Michaelis, H. & Zwarts, L., 1993: Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden sea: How predictible is this food source for birds ? – Neth. J. Sea Res. **31**, 319-330.

Beukema, J.J., Knol, E., & Cadée, G.C., 1985: Effects of temperature on the length of the annual growing season in the tellinid bivalve *Macoma balthica* (L.) living on tidal flats in the dutch wadden Sea. – J. Exp. Mar. Biol. Ecol. **90**, 129-144.

Beukema, J.J. & Meehan, B.W., 1985: Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. – Mar. Biol. **90**, 27-33.

Bick, A. & Burckardt, R., 1989: Erstnachweis von *Marenzelleria viridis* (Polychaeta, Spionidae) für den Ostseeraum, mit einem Bestimmungsschlüssel der Spioniden der Ostsee. – Mitt. Zool. Mus. Berlin **65**, 237-247.

Blomquist, E.M. & Bonsdorff, E., 1986: Spatial and temporal variations of benthic macrofauna in a sandbottom area on Åland, northern Baltic Sea. – Ophelia, Suppl. **4**, 27-36.

Bochert, R. & Bick, A., 1995: Der Einfluß von Salzgehalt und Temperatur auf die Larvalentwicklung von *Marenzelleria viridis* (Polychaeta: Spionidae). – Verh. der Deutschen Zool. Gesellschaft **88**, 21.

Bochert, R., Bick, A., Zettler, M.L. & Arndt, E.A., 1993: *Marenzelleria viridis* (Verrill, 1873) (Polychaeta, Spionidae) an invader in the benthic community in Baltic coastal inlets - investigations of the reproduction. Proceedings of the 13. BMB-Symposium, Riga, Latvia, in press.

Bodungen, B. von, Graeve, M., Kube, J., Lass, H.U., Meyer-Harms, B., Mumm, N., Nagel, K., Pollehne, F., Powilleit, M., Reckermann, M., Sattler, C., Siegel, H. & Wodarg, D., 1995: Stoff-Flüsse am Grenzfluß - Transport und Umsatz-Prozesse im Übergangsbereich zwischen Oderästuar und Pommerscher Bucht (TRUMP). – Geowissenschaften **13**, 479-485.

Boesch, D.F., 1977: A new look at the zonation of benthos along the estuarine gradient. In: Ecology of marine benthos. Ed. by B.C. Coull. University of South Carolina Press, Columbia, 245-266.

Böhme, D., 1992: Zur Nahrungsökologie überwinternder Tauchenten in der Wohlenberger Wiek/Wismarbucht. – Beitr. Vogelkd. **39**, 257-284.

Borkenhagen, P., 1976: Vergleichende Untersuchungen am Verdauungssystem europäischer Entenvögel (Anatidae). – Beitr. Vogelkd. **22**, 301-366.

Brey, T., 1984: Gemeinschaftsstrukturen, Abundanz, Biomasse und Produktion des Makrozoobenthos sandiger Böden der Kieler Bucht in 5-15 m Wassertiefe. – Ber. Inst. Meeresk. Kiel **123**, 1-124.

Brey, T., 1986: Increase in macrozoobenthos above the halocline in Kiel Bay comparing the 1960s with the 1980s. – Mar. Ecol. Prog. Ser. **28**, 299-302.

Brey, T., 1989: Der Einfluß physikalischer und biologischer Faktoren auf Struktur und Dynamik der sublitoralen Macoma-Gemeinschaft der Kieler Bucht. – Ber. Inst. Meereskunde Kiel, Nr. **186**, 1-248.

Brey, T., 1991: The relative significance of biological and physical disturbance: an example from intertidal and subtidal sandy bottom communities. – Estuarine Coast. Shelf Sci. **33**, 339-360.

Brousseau, D.J., 1978a: Spawnig cycle, fecundity, and recruitment in a population of soft-shell clam, *Mya arenaria*, from Cape Ann, Massachusetts. – Fish. Bull. **76**, 155-166.

Brousseau, D.J., 1978b: Population dynamics of the soft-shell clam *Mya arenaria*. – Mar. Biol. **50**, 63-71.

Brousseau, D.J., 1979: Analysis of growth rate in *Mya arenaria* using the von Bertalanffy Equation. – Mar. Biol. **51**, 221-227.

Calder, W.A., 1974: The consequences of body size for avian energetics. In: Avian energetics. Ed. by R.A. Paynter. Nuttall Ornithological Club 15, Cambridge, Massachusetts, USA, 86-151.

Camphuysen, C.J. & M.F. Leopold, 1994: Atlas for seabirds in the southern North Sea. IBN Research Report 94/6, NIOZ-Report 1994-8, Texel, 126 pp.

Cantin, M., Bédard, J. & Milne, H., 1974: The food and feeding of common eiders in the St. Lawrence estuary in summer. – Can. J. Zool. **52**, 319-334.

Carlson, D.J., Townshend, D.W., Hilyards, A.L. & Eaton, J.F., 1984: Effect of an intertidal mudflat on plankton of the overlaying water column. – Can. J. Fish. Aquat. Sci. **41**, 1523-1528.

Carlton, J.T., 1985: Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanogr. – Mar. Biol. Ann. Rev. **23**, 313-371.

Castro, G., Myers, J.P. & Ricklefs, R.E., 1992: Ecology and energetics of sanderlings migrating to four different latitudes. – Ecology **73**, 833-844.

Castro, G., Stoyan, N. & Myers, J.P., 1989: Assimilation efficiency in birds: A function of taxon or food type? – Comp. Biochem. Physiol. **92A**, 271-278.

Cederwall, H. & Elmgren, R., 1980: Biomass increase of benthic macrofauna demonstrates eutrophication of the Baltic Sea. – Ophelia, Suppl. **1**, 287-304.

Clarke, K.R. & Warwick, R.M., 1994: Changes in marine communities: an approach to statistical analysis and interpretation. Natural Environmental Research Council, Plymouth, U.K., 144 pp.

Cohen, R.R.H., Dresler, P.V., Phillips, E.J.P. & Cory, R.L., 1984: The effect of the asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. – Limnol. and Oceanogr. **26**, 170-180.

Cramp, S. & Simmons, K.E.L., 1977: Handbook of the birds of Europe and the Middle East. Volume 1. Oxford University Press, Oxford.

Cressie, N.A.C., 1991: Statistics for Spatial Data. John Wiley and Sons, Inc., New York, 900 pp.

Crisp, D.J., 1984: Energy flow measurements. In: Methods for the study of marine benthos. Ed. by N.A. Holme & A.D. McIntyre. IBP Handbook No. **16**, 284-372.

Cyberska, B., 1992: Thermohaline conditions. In: Marine pollution (2). An assessment of the effects of pollution in the Polish coastal area of the Baltic Sea. Ed. by A. Trzosinska. – Polish Academy of Sciences, National Scientific Comitee on Oceanic Research, Studia i materialy oceanologiczne **61**, 73-92.

Cyberska, B., Lauer, Z. & Trzosinska, A., 1992: Environmental conditions in the Polish zone of the southern Baltic Sea during 1991. Institute of Meterology and Water Management, Maritime Branch Materials, 257 pp.

Cyberska, B., Lauer, Z. & Trzosinska, A., 1993: Environmental conditions in the Polish zone of the southern Baltic Sea during 1992. Institute of Meterology and Water Management, Maritime Branch Materials, 256 pp.

Cyberski, J., 1992: River outflow from Poland. In: Marine pollution (2). An assessment of the effects of pollution in the Polish coastal area of the Baltic Sea. Ed. by A. Trzosinska. – Polish Academy of Sciences, National Scientific Comitee on Oceanic Research, Studia i materialy oceanologiczne **61**, 53-66.

Daan, S., Masman, D. & Gronewold, A., 1990: Avian basal metabolic rates: their association with body composition and energy expenditure in nature. – Am. J. Physiol. **259**, R333-R340.

Dankers, N. & Beukema, J.J., 1983: Distributional patterns of macrozoobenthic species in relation to some environmental factors. In: Ecology of the Wadden Sea. Vol. 1, Part 4. Ed. by W.J. Wolff. Balkema, Rotterdam, 69-103.

Dare, P.J., 1976: Settlement, growth, and production of the mussel, *Mytilus edulis* L., in Morecambe Bay, England. Fishery Investigation Series II, 28, No.1, 25 pp.

Dauer, D.M., Ewing, R.M., Sourbeer, J.W., Harlan, W.T. & Stokes, T.L., 1982: Nocturnal movements of the macrozoobenthos of the Lafayette River, Virginia. – Intern. Revue ges. Hydrobiol. **67**, 761-775.

Dauer, D.M., Maybury, C.A. & Ewing, R.M., 1981: Feeding behaviour and general ecology of several spionid polychaetes from the Chesapeake Bay. – J. Exp. Mar. Biol. Ecol. **54**, 21-38.

De Leeuw, J.J. & Van Eerden, M.R., 1992: Size selection in diving tufted ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*. – Ardea **80**, 353-362.

Demel, K. & Manikowski, W., 1951: Quantitative investigations on the bottom fauna in the southern Baltic (in Polish). – Pr. Mar. Inst. Ryb., Gdynia **6**, 58-82.

Demel, K. & Mulicki, Z., 1954: Quantitative investigations on the biological bottom fauna in the Southern Baltic (in Polish). – Pr. Mar. Inst. Ryb., Gdynia **6**, 57-82.

Dörjes, J. & Howard, J.D., 1975: Estuaries of the Georgia coast, USA: Sedimentology and biology. IV. Fluvial-marine transition indicators in an estuarine environment, Ogeechee River-Ossabaw Sound. - Senkenb. mar. **7**, 137-179.

Draulans, D., 1982: Foraging and size selection of mussels by the tufted duck, *Aythya fuligula*. – J. Anim. Ecol. **51**, 943-956.

Draulans, D., 1984: Suboptimal mussel selection by tufted ducks *Aythya fuligula*: test of a hypothesis. – Anim. Behav. **32**, 1192-1196.

Drent, R. & Daan, S., 1980: The prudent parent: energetic adjustment to avian breeding. – Ardea **68**, 225-252.

Duineveld, G.C.A., Künitzer, A. & Heyman, R.P., 1987: *Amphiura filiformis* (Ophiuridea: Echinodermata) in the North Sea. Distribution, present and former abundance and size composition. Neth. – J. Sea Res. **21**, 317-329.

Durinck, J., Petersen, I.K. & Pihl, S., 1993: Internationally important staging areas for waterfowl in the Gulf of Pärnu in early May. – IWRB Seaduck Research Group Bull. **3**, 11-26.

Durinck, J., Skov, H. & Andell, P., 1993: Seabird distribution and numbers in selected offshore parts of the Baltic Sea, winter 1992. – Ornis Svecia **3**, 11-26.

Durinck, J., Skov, H., Jensen, F.P. & Pihl, S., 1994: Important marine areas for wintering birds in the Baltic Sea. EU DG XI research contract no. 2242/90-09-01, Ornis Consult report, 110 pp.

Edler, L., 1979: Recommendations on methods for marine biological studies in the Balthic Sea. Phytoplankton and chlorophyll. – Baltic Marine Biologists, Publ. No. **5**, 1-38.

Elliott, J.M. & Drake, C.M., 1981: A comparative study of seven grabs used for benthic macroinvertebrates in rivers. – Freshwater Biology **11**, 99-120.

Elmgren, R., 1978: Structure and dynamics of Baltic benthos communities, with particular reference to the relationship betwen macro- and meiofauna. – Kieler Meeresforsch., Sonderheft **4**, 1-22.

Emerson, C.W., 1990: Influence of sediment disturbance and water flow on the growth of the sofshell clam, *Mya arenaria* L. – Can. J. Fish. Aquat.Sci. **47**, 1655-1663.

Emerson, C.W. & Grant, J., 1991: The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. – Limnol. Oceanogr. **36**, 1288-1300.

Emerson, C.W., Minchinton, T.E. & Grant, J., 1988: Population structure, biomass, and respiration of *Mya arenaria* L. on temperate sandflat. – J. Exp. Mar. Biol. Ecol. **115**, 99-111.

Ens, B, Piersma, T. & Drent, R., 1994: The dependence of waders and waterfowl migrating along the east atlantic flyway on their coastal food supplies: what is the most profitable research programm? – Ophelia, Suppl. **6**, 127-151.

Esselink, P. & Zwarts, L., 1989: Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. – Mar. Ecol. Prog. Ser. **56**, 243-254.

Essink, K. & Bos, A.H., 1985: Growth of three bivalve molluscs transplanted along the axis of the Ems Estuary. – Neth. J. Sea Res. **19**, 45-51.

Essink, K. & Kleef, H.L., 1988: *Marenzelleria viridis* (Verrill, 1873) (Polychaeta: Spionidae): a new record from the Ems Estuary (The Netherlands/Federal Republic of Germany). – Zoologische Bijdragen (Leiden) **38**, 31-43.

Essink, K. & Kleef, H.L., 1993: Distribution and life cycle of the north american spionid polychaete *Marenzelleria viridis* (Verrill, 1873) in the Ems estuary. – Neth. J.Aquat. Ecol. **27 (2-4)**, 237-246.

Etim, L. & Brey, T., 1994: Growth, productivity, and significance for fishery of the bivalve *Egeria radiata* (Donacidae) in the Cross River, Nigeria. – Arch. Fish. Mar. Res. **42**, 63-75.

Fauchald, K. & Jumars, P.A., 1979: The diet of worms: a study of polychaete feeding guilds. – Oceanogr. Mar. Biol. Ann. Rev. **17**, 193-284.

Fedra, K., Ölscher, E.M., Scherübel, C., Stachowitsch, M. & Wurzian, R.S., 1976: On the ecology of a North Adriatic benthic community: distribution, standing crop and the composition of the macrozoobenthos. – Mar. Biol. **38**, 129-145.

Fonselius, S.H., 1972: On eutrophication and pollution in the Baltic Sea. In: Marine pollution and sea life. Ed. by M. Ruivo. Fishing News Books Ltd., London, 23-28.

Franck, H. & Matthäus, W., 1992: The absence of effective major inflows and the present changes in the hydrographic conditions of the central Baltic deep water. Proceedings of the 12th Baltic Marine Biologists Symposium, Helsingør, Denmark, 25-30 August 1991, 53-60.

Frechette, M. & Bourget, E., 1985: Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. – Can. J. Fish. Aquat. Sci. **42**, 1158-1165.

Fritzsche, D., 1995: Leistungsanalytische und resistenzökologische Untersuchungen zur Emanzipation des Polychaeten *Marenzelleria viridis* (VERRILL 1873) gegenüber den Faktoren Salinität und Sauerstoffpartialdruck. phd-thesis, University of Rostock, Rostock, 106 pp.

Fritzsche, D., & Oertzen, J.A. von, 1995: Metabolic response to changing environmental conditions in the brackish water polychaetes *Marenzelleria viridis* and *Hediste diversicolor*. – Mar. Biol. **121**, 693-699.

Gargas, E., Dahl-Madsen, K.I., Schrøder, H. & Rasmussen, J., 1978: Dynamics of Baltic ecosystems and causes of their variability. – Kieler Meeresforsch., Sonderheft **4**, 210-232.

Gage, J., 1974: Shallow-water zonation of sea-loch benthos and its relation to hydrographic and other physical features. – J. Mar. Biol. Ass. U.K. **54**, 223-253.

Geisel, T. & Messner, U., 1989: Flora und Fauna des Bodens im Greifswalder Bodden. – Meer und Museum **5**, 44-51.

George, J.D., 1966: Reproduction and early development of the spionid polychaete, *Scolelepis viridis* (Verrill). – Biol. Bull. **139**, 76-93.

Gerlach, S.A., 1978: Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. – Oecologia **33**, 55-70.

Gerlach, S.A., 1994: Oxygen conditions improve when the salinity in the Baltic Sea decreases. – Mar. Poll. Bull. **28**, 413-416.

Gilfillan, E.S., Mayo, D., Hanson, S., Donovan, D. & Jiang, L.C., 1976: Reduction in carbon ·flux in *Mya arenaria* caused by a spill of No. 6 fuel oil. – Mar. Biol. **37**, 115-123.

Gjøsæter, J. & Sætre, R., 1974: Predation of eggs of capelin (*Mallotus villosus*) by diving ducks. – Astarte **7**, 83-89.

Gorski, W., 1981: Wintering of water birds in the western and middle parts of the Polish coast of the Baltic Sea in 1969-1972 (in Polish). – Acta zool. Cracov. **25**, 103-137.

Gosling, E. (ed.), 1992: The mussel *Mytilus*: ecology, physiology, genetics and culture. Developments in Aquaculture and Fisheries Science, 25, Elsevier, Amsterdam-London-New York-Tokyo, 590 pp.

Goss-Custard, J.D., 1980: Competition for food and interference among waders. – Ardea **68**, 31-52.

Goss-Custard, J.D., Durell, S.E.A. Le V. dit, McGrorty, S. & Reading, C.J., 1982: Use of mussel *Mytilus edulis* beds by oystercatchers *Haematopus ostralegus* according to age and population size. – J. Anim. Ecol. **51**, 543-554.

Gosselck, F., 1985: Untersuchungen am Makrozoobenthos des Arkonabeckens (südliche Ostsee). – Fischerei-Forschung 23, 28-32.

Gosselck, F. & Georgi, F., 1984: Benthic recolonization of the Lübeck Bay (Western Baltic) in 1980/81. – Limnologica **15**, 407-414.

Goudie, R.I. & Ankney, C.D., 1986: Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. – Ecology **67**, 1475-1482.

Goudie, R.I. & Ankney, C.D., 1988: Patterns of habitat use by seaducks wintering in southeastern Newfoundland. – Ornis Scand. **19**, 249-256.

Goudie, R.I. & Ryan, P.C., 1991: Diets and morphology of digestive organs of five species of sea ducks wintering in Newfoundland. – J. Yamashina Inst. Ornithol. **22**, 1-8.

Graf, G., 1987: Benthic energy flow during a simulated autumn bloom sedimentation. – Mar. Ecol. Prog. Ser. **39**, 23-29.

Graf, G., 1992: Benthic-pelagic coupling: a benthic view. – Oceanogr. Mar. Biol. Ann. Rev. **30**, 149-190.

Gray, J., 1984: Ökologie Mariner Sedimente. Springer-Verlag, Berlin-Heidelberg-New York-Tokio, 193 pp.

Gray, J.S., 1992: Eutrophication in the marine environment. In: Marine Eutrophication and Population dynamics. Ed. by G. Colombo, I. Ferrari, V.U. Ceccherelli & R. Rossi. 25th European Marine Biology Symposium, Olsen & Olsen, Fredensborg, 3-15.

Gruszka, P., 1991a: *Marenzelleria viridis* (Verrill, 1873) (Polychaeta: Spionidae) - a new component of shallow water benthic community in the southern Baltic. – Acta Ichtyol. Piscatoria **21** (Suppl.), 57-65.

Gruszka, P., 1991b. *Marenzelleria viridis* keeps conquering the Baltic Sea. 12th Baltic Marine Biologists Symposium. August 23-30, 1991, Helsingør, Denmark. Abstracts of poster, 14.

Günther, C.P., 1991: Settlement of *Macoma balthica* on an intertidal sandflat in the Wadden Sea. – Mar. Ecol. Prog. Ser. **76**, 73-79.

Günther, C.-P., 1992: Settlement and recruitment of *Mya arenaria* L., in the Wadden Sea. – J. Exp. Mar. Biol. Ecol. **159**, 203-215.

Hagmeier, A., 1926: Die Arbeiten mit dem Petersenschen Bodengreifer auf der Ostseefahrt April 1925. – Vorl. Mitteilung. Ber. D.W.K. Meeresforsch. N.F. Bd. 2, H. 4, 304-307.

Hagmeier, A., 1930: Die Bodenfauna der Ostsee im April 1929 nebst einigen Vergleichen mit April 1925 und Juni 1926. – Vorl. Mitteilung. Ber. D.W.K. Meeresforsch. N.F. Bd. 5, H. 3, 156-173.

Hargrave, B.T., 1973: Coupling carbon flow through some pelagic and benthic communities. – J. Fish. Res. Board Can. **30**, 1317-1326.

Heinemann, D., 1981: A range finder for pelagic bird censusing. – J. Wildl. Management **45**, 489-493.

Heinonen, A., 1962: Reproduction of *Mytilus edulis* in the Finish S.W. archipelago in summer 1960. – Suomalaisen elain-ja kasvitieteelisen seuran vanomen julkaisuja **16**, 137-143.

Heip, C., 1995: Eutrophication and zoobenthos dynamics. – Ophelia **41**, 113-136.

HELCOM, 1987: First periodic assessment of the state of the marine environment of the Baltic Sea area. Background Dokument. – Baltic Sea Environ. Proc. **17 B**, 351 pp.

HELCOM, 1988: Guidelines for the Baltic Monitoring Programme for the third stage. Part D. Biological Determinants. – Baltic Sea Environ. Proc. **27 D**, 161 pp.

HELCOM, 1990: Second periodic assesment of the state of the marine environment of the Baltic Sea area 1984-1988. Background Dokument. – Baltic Sea Environ. Proc. No. **35 B**, 432 pp.

HELCOM, 1993a: Second Baltic Sea pollution load compilation. – Baltic Sea Environ. Proc. No. **45**, 161 pp.

HELCOM, 1993b: Summaries of the pre-feasability studies. – Baltic Sea Environ. Proc. No. **46**, 163 pp.

Hempel, C., 1957: Über den Röhrenbau und die Nahrungsaufnahme einiger Spioniden (Polychaeta, Sedentaria) der deutschen Küsten. – Helgoländer wiss. Meeresunters. **6**, 100-135.

Herman, P.M.J. & Scholten, H., 1990: Can suspension-feeders stabilise estuarine ecosystems ? In: Trophic relationships in the marine environment. Ed. by M. Barnes & R.N. Gibson. Aberdeen University Press, Aberdeen, 104-116.

Hertling, H., 1928: Untersuchungen über die Ernährung von Meeresfischen I. Quantitative Nahrungsuntersuchungen an Pleuronectiden und einigen anderen Fischen der Ostsee. – Vorl. Mitteilung. Ber. D.W.K. Meeresforsch. N.F. Bd. 4, H. 2, 25-124.

Hessland, I., 1946: On the quaternary *Mya* period in Europe. – Arkiv for Zoologi. Bd. **37(A)** 8, 1-51.

Hines, A.H. & Comtois, K.L., 1985: Vertical distribution of infauna in sediments of a subestuary of central Chesapeake Bay. – Estuaries **8**, 296-304.

Hines, A.H., Posey, M.H. & Haddon, 1989: Effects of adult suspension-feeding bivalves on recruitment of estuarine infauna. – The Veliger **32**, 109-119.

Hoenig, J.M., 1983: Empirical use of longevity data to estimate mortality rates. – Fish. Bull. **82**, 898-903.

Holme, N.A. & McIntyre, A.D. (eds.), 1984: Methods for the study of marine benthos. IBP Handbook No. 16 (2nd ed). Blackwall Scientific Publications, Oxford, 387 pp.

Hummel, H., 1985: Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. – Neth. J. Sea Res. 19, 52-76.

Huston, M., 1979: A general hypothesis of species diversity. – Am. Nat. 113, 81-101.

Jansson, K. 1994. Alien Species in the marine environment - introductions to the Baltic Sea and the Swedish west coast. Swedish Environmental Protection Agency, Report 4357, Solna, 68 pp.

Jeffrey, S.W. & Humphrey, G.F., 1975: New spectrophotometric equations for determining chlorophylls a, b, c_1 and c_2, in higher plants, algae and natural phytoplankton. – Biochem. Physiologie der Pflanzen 167, 191-194.

Jensen, K., 1981: Comparison of two bottom samplers for benthos monitoring. – Environmental Technol. Letters 2, 81-84.

Jenssen, B.M. & Ekker, M., 1989: Thermoregulatory adaptations to cold in winter-acclimatized Long-tailed ducks (*Clangula hyemalis*). In: Physiology of cold adaptation in birds. Ed. by Bech, C. & R.E. Reinertsen. Plenum Press, New York, 147-152.

Joensen, A.H., 1974: Waterfowl populations in Denmark 1965-1973. – Dan. Rev. Game. Biol. **(9)1**, 1-209.

Jonge, V.N. de & Essink, K., 1991: Long-term changes in nutrient loads and primary and secondary producers in the Dutch Wadden Sea. In: Estuaries and coasts: spatial and temporal intercomparisons. Ed. by M. Elliot & J.P. Ducrotoy. ECSA 19 Symposium. Olsen & Olsen, Caen, 307-316.

Jørgensen, B.B. & Fenchel, T., 1974: The sulfur cycle of a marine sediment model system. – Mar. Biol. 24, 189-201.

Jørgensen, C.B., 1990: Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen & Olsen, Fredensborg, 140 pp.

Jørgensen, C.B. & Riisgård, H.U., 1988: Gill pump characteristics of the soft clam *Mya arenaria*. – Mar. Biol. 99, 107-109.

Josefson, A.B., Jensen, J.N. & Ærtebjerg, G., 1993: The benthos community structure anomaly in the late 1970s and early 1980s - a result of a major food pulse? – J. Exp. Mar. Biol. Ecol. 172, 31-45.

Kautsky, N., 1982: Growth and size structure in a Baltic *Mytilus edulis* population. – Mar. Biol. **68**, 117-133.

Karasov, W.H., 1990: Digestion in birds: chemical and physiological determinants and ecological implications. – Stud. Avian Biol. 13, 391-415.

Kinne, O., 1971: 4. Salinity, 4.3 Animals, 4.31 Invertebrates. In: Marine ecology 1,2. Ed. by O. Kinne. Hamburg, Biologische Anstalt Helgoland. 683-1244.

Kinner, P., Mauer, D. & Leathem, W., 1974: Benthic invertebrates in Delaware Bay: animal sediment associations of the dominant species. – Intern. Revue ges. Hydrobiol. 59, 685-701.

Kirchhoff, K., 1979: Nahrungsökologische Untersuchungen an benthosfressenden Enten in der Hohwachter Bucht. Diplom-thesis, University of Kiel (unpubl.), 99 pp.

Kirchhoff, K., 1981: Zur Verbreitung überwinternder Meeresenten auf der offenen Kieler und Lübecker Bucht (westliche Ostsee). – Corax 8, 197-207.

Kistchinski, A.A., 1979: Migrations of birds of Eastern Europe and Northern Asia. Ciconiiformes-Anseriformes. Nauka, Moscow, 247 pp.

Klinkhardt, M. & Nicolaus, G., 1984: Untersuchungen zur Veränderung der Trockenmasse und des Energiegehaltes sich entwickelnder Eier des Rügenschen Frühjahrsherings. – Wiss. Zeitschrift Univ. Rostock, Naturwiss. Reihe 33, H. 6, 64-67.

Koine, B., 1995: Sedimentuntersuchungen in der Pommerschen Bucht. Diplom thesis, Technische Fachhochschule Berlin (unpubl.), 50 pp.

Komdeur, J., Bertelsen, J. & Cracknell, G., 1992: Manual for aeroplane and ship surveys of waterfowl and seabirds. IWRB Special Publ. No. 19, Slimbridge, 37 pp.

Kontkanen, H., 1995: Visual observations of the spring migration of arctic waterfowl along the western coast of Estonia in 1993. – IWRB Seaduck Research Group Bull. 5, 19-24.

Kontiokorpi, J. & Parviainen, A., 1995: Spring migration of arctic waterfowl from Vyborg and Repino (Russia) in spring 1993. – IWRB Seaduck Research Group Bull. 5, 25-29.

Kooyman, G.L., 1989: Diverse divers, physiology and behaviour. Springer, Berlin, Heidelberg, New York.

Krebs, C.J., 1972: Ecology: the experimental analysis of distribution and abundance. Harper & Row, New York.

Kreuzberg, M. & Oertzen, J.-A. von, 1973: Zusammenstellung von Energieäquivalenten aquatischer Organismen unter besonderer Berücksichtigung der Ostsee. – Wiss. Zeitschr. Univ. Rostock 22, Mat.-Nat. Reihe, H. 10, 1153-1158.

Kube, J., 1992: Das Makrozoobenthos des Windwatts am Bock - Szenario des Jahres 1991. Diplomthesis, Univ. Rostock, (unpubl.), 152 pp.

Kube, J. & Skov, H., in prep: Habitat selection, feeding characteristics, and food consumption of long-tailed ducks, Clangula hyemalis, in the southern Baltic Sea.

Kube, J., 1996: Spatial and temporal variations in the population structure of the soft-shell clam, Mya arenaria, in the Pomeranian Bay (Southern Baltic Sea). – J. Sea Res. 35, 335-344.

Kube, J., Zettler, M.L., Gosselck, F., Ossig, S. & Powilleit, M., 1996: Distribution of Marenzelleria viridis (Polychaeta: Spionidae) in the Southwestern Baltic Sea in 1993/94 - ten years after introduction. – Sarsia 81, 131-142.

Lammens, J.J., 1967: Growth and reproduction in a tidal flat population of Macoma balthica (L.). – Neth. J. Sea Res. 3, 315-382.

Lampe, R., 1993: Environmental state and material flux in the western part of the Oder river estuary - results and consequences. – Petermanns Geogr. Mit. 137, 275-282.

Lasiewski, R.C. & Dawson, W.R., 1967: A re-examination of the relation between standard metabolic rate and body weight in birds. – Condor 69, 13-23.

Lassig. J., 1965: The distribution of marine and brackishwater lamellibranchs in the Baltic area. – Comment. biol. 28 (5), 1-41.

Laursen, K., Pihl, S., Skov, H., Durinck, J., Danielsen, F., Frikke, J. & Hansen, M., 1995: The numbers and distribution of waterfowl in Denmark 1987-1989. – Dan. Rev. Game Biol., in press.

Leipe, T., 1982: Ergebnisse von Magenuntersuchungen an Eisenten im Greifswalder Bodden. – Falke 29, 377-378.

Leipe, T., 1985: Zur Nahrungsökologie der Eisente (Clangula hyemalis) im Greifswalder Bodden. – Beitr. Vogelkd. 31, 121-140.

Leipe, T., 1989: Eutrophe Brackwasser-Ökosysteme und deren Bedeutung für Durchzug und Rast von Tauchenten im Nordosten der DDR. – Beitr. Vogelkd. 35, 24-35.

Leipe, T., Neumann, T. & Emeis, K.C., 1995: Schwermetallverteilung in holozänen Ostseesedimenten. – Geowissenschaften 13, 470-478.

Leipe, T. & Scabell, J., 1990: Die "Eisentenwalze" oder eine effektive Strategie der kollektiven Nahrungssuche am Meeresboden durch *Clangula hyemalis*. – Vogelwelt **111**, 224-229.

Leipe, T. & Sellin, D., 1983: Zum Vorkommen von Berg- und Eisenten auf dem Greifswalder Bodden. – Orn. Rundbr. Meckl. N.F. **26**, 34-47.

Leppäkoski, E., 1984: Introduced species in the Baltic Sea and its coastal ecosystems. – Ophelia, Suppl. **3**, 123-135.

Leppäkoski, E., 1991: Introduced species - recource or threat in brackish-water areas ? Examples from the Baltic and the Black Sea. – Mar. Poll. Bull. **23**, 219-223.

Loo, L.O. & Rosenberg, R., 1989: Bivalve suspension-feeding dynamics and benthic pelagic coupling in an eutrophicated marine bay. – J. Exp. Mar. Biol. Ecol. **130**, 253-276.

Löwe, F.-K., 1963: Quantitative Benthosuntersuchungen in der Arkonasee. – Mitt. Zool. Mus. Berlin **39**, 247-349.

MacDonald, B.A. & Thomas, M.L.H., 1980: Age determination of the soft-shell clam *Mya arenaria* using shell internal growth lines. – Mar. Biol. **58**, 105-109.

Madsen, F.J., 1954: On the food habits of the diving ducks in Denmark. – Danish Rev. Game Biol. **2**, 157-266.

Majewski, A., 1972: Hydrological characteristic of the Polish coast estuarine waters. (in Polish) – Prace PIHM **105**, 3-40.

Manzi, J.J. & Castagna, M. (eds.), 1989: Clam mariculture in North America. – Developments in Aquaculture and Fisheries Science **19**, 1-461.

Matthäus, W. & Franck, H., 1992: Characteristics of major Baltic inflows-a statistical analysis. – Continental Shelf Res. **12**, 1375-1400.

Matthäus, W. & Lass, H.U., 1995: The recent salt inflow into the Baltic Sea. – J. Phys. Oceanogr. **25**, 280-286.

McLusky, D.S., Hull, S.C. & Elliott, M., 1993: Variations in the intertidal and subtidal macrofauna and sediments along a salinity gradient in the upper Forth Estuary. – Neth. J. Aquat. Ecol. **27**, 101-109.

Meire, P., 1993: Wader populations and macrozoobenthos in a changing estuary: the Osterschelde (The Netherlands). phd-thesis, University of Gent, Institute of Nature Conservation, Hasselt, Report nr. 93.05, 311 pp.

Meire, P.M., Seys, J., Buys, J. & Coosen, J., 1993: Spatial and temporal patterns of intertidal macrobenthic populations in the Oosterschelde: are they influenced by the construction of the surge barrier ? – Hydrobiologia **282/283**, 157-182.

Meissner, J., 1992: Untersuchungen zum Vorkommen überwinternder Meeresenten in Abhängigkeit von Nahrungsangebot in der Kieler Bucht. Diplomarbeit Universität Kiel (unpubl.), 111 pp.

Meissner, J. & Bräger, S., 1987: Die Bedeutung der Schleswig-Holsteinischen Ostsee-Flachgründe für überwinternde Meeresenten. – Corax **12**, 234-254.

Meissner, J. & Struwe, B., 1994: Results of the midwinter count in 1993 on the Baltic coast of Schleswig-Holstein, Germany. – IWRB Seaduck Research Group Bull. **4**, 36-38.

Messner, U. & Oertzen, J.A. von, 1991: Long-term changes in the vertical distribution of macrophytobenthic communities in the Greifswalder Bodden. – Acta Ichtyol. Piscatoria **21**, Suppl., 135-144.

Miljøministeriet, Skov- og Naturstyrelsen, 1993: Fuglene i de danske farvande - Resultaterne af landsdækende optællinger 1987-91. Skov- og Naturstyrelsen, Copenhagen, 220 pp.

Miller, M.R. & Reinecke, K.J., 1984: Proper expression of metabolizable energy in avian energetics. – Condor **86**, 396-400.

Möller, P., 1986: Physical factors and biological interactions regulating infauna in shallow boreal areas. – Mar. Ecol. Prog. Ser. **30**, 33-47.

Möller, P. & Rosenberg, R., 1983: Recruitment, abundance and production of *Mya arenaria* and *Cardium edule* in marine shallow waters, western Sweden. – Ophelia **22**, 33-55.

Mölsä, H., Häkkila, S. & Puhakka, M., 1986: Reproductive success of *Macoma balthica* in relation to environmental stability. – Ophelia, Suppl. **4**, 167-177.

Munch-Petersen, S., 1973: An investigation of a population of the soft shell clam (*Mya arenaria* L.) in a Danish estuary. – Meddr. Danm. Fisk. og Havunders. N.S. 7, 47-73.

Muus, B.J., 1967: The fauna of danish estuaries and lagoons, distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. – Meddr. Danm. Fisk. og Havunders. N.S. **5**, 1-316.

Nakaoka, M., 1992: Spatial and seasonal variation in growth rate and secondary production of *Yoldia notabilis* in Otsuchi Bay, Japan, with reference to the influence of food supply from the water column. – Mar. Ecol. Prog. Ser. **88**, 215-223.

Nakonieczny, J., Ochocki, S., & Renk, H., 1991: Long-term changes in primary production and chlorophyll concentrations in the Southern Baltic. – Acta Ichtyol. Piscatoria **21**, Suppl., 145-152.

Nehls, G., 1989: Occurrence and food consumption of the common eider, *Somateria molissima*, in the Wadden Sea of Schleswig-Holstein. – Helgoländer Meeresunters. **43**, 385-393.

Nehls, G., 1995: Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologie der Eiderente (*Somateria mollissima*)(L., 1758). – Berichte, Forsch.- u. Technologiezentrum Westküste d. Univ. Kiel **10**, 1-177.

Nehls, H.W., 1994: Results of the midwinter waterfowl counts on the Baltic coast of Mecklenburg-Western Pomerania in January 1992 and 1993. – IWRB Seaduck Research Group Bulletin 4: 31-35.

Nehls, H.W. & Zöllick, H., 1990: The moult migration of the common scoter (*Melaitta nigra*) off the coast of the GDR. In: Baltic Birds 5, Vol. 2. Ed. by J. Viksne & I. Vilks. Proceedings of the fifth conference of the study and conservation of migratory birds of the Baltic basin, Riga, October 5-10, 1987, 36-46.

Nehring, D., 1990: Die hydrographisch-chemischen Bedingungen in der westlichen und zentralen Ostsee im Jahre 1989. – Fischerei-Forschung **28**, 35-45.

Nehring, D. & Matthäus, W., 1991/92: Die hydrographisch-chemischen Bedingungen in der westlichen und zentralen Ostsee im Jahre 1991. – Dt. Hydrogr.Z. **44**, 217-238.

Nehring, D., Matthäus, W., Lass, H.U. & Nausch, G., 1994: Hydrographisch-chemische Zustandseinschätzung der Ostsee 1993. – Meereswiss. Ber. No. 7, 1-68.

Nelson, T.C., 1928: On the distribution of critical temperatures for spawning and for ciliary activity in bivalve molluscs. Science (Wash., D.C.) **67**, 220-221.

Neu, C.W., Byers, C.R. & Peek, J.M.,1974: A technique for analysis of utilisation - availability data. – J. Wild. Mgmt. **38**, 541-545.

Neumann, G. & Bublitz, G., 1969: Seegrunduntersuchungen im westlichen Teil der Oder-Bucht. – Beitr. Meeresk. **24/25**, 81-109.

Newell, C.R. & Hidu, H., 1982: The effects of sediment type on growth rate and shell allometry in the soft shelled clam *Mya arenaria* L.. – J. Exp. Mar. Biol. Ecol. **65**, 285-295.

Nilsson, L., 1969: Food consumption of diving ducks wintering at the coast of south Sweden in relation to food resources. – Oikos **20**, 128-135.

Nilsson, L., 1972: Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season. – Ornis Scand. **3**, 55-78.

Norkko, A., Bonsdorff, E. & Boström, C., 1993: Observations of the polychaete *Marenzelleria viridis* (Verrill) on a shallow sandy bottom on the south coast of Finland. – Memoranda Societa Fauna Flora Fennica **69**, 112-113.

Oertzen, J.A. von, 1972: Cycles and rates of reproduction of six Baltic Sea bivalves of different zoogeographical origin. – Mar. Biol. **14**, 143-149.

Oertzen, J.A. von, 1973: Bemerkungen zur Hydrographie der westlichen Ostsee unter benthosökologischem Gesichtspunkt. – Beitr. Meereskd. **32**, 89-104.

Officer, C.B., Smayda, T.J. & Mann, R., 1982: Benthic filter feeding: a natural eutrophication control. – Mar. Ecol. Prog. Ser. **9**, 203-210.

Offringa, H., 1991: Verspreiding in voedseloecologie van de zwarte zeeënte (*Melanitta nigra*) in Nederland. NIOZ-rapport 1991-13, Den Burg, 39 pp.

Ott, J.A., 1992: The Adriatic Benthos: problems and perspectives. In: Marine Eutrophication and Population dynamics. Ed. by G. Colombo, I. Ferrari, V.U. Ceccherelli & R. Rossi. 25th European Marine Biology Symposium, Olsen & Olsen, Fredensborg, 367-378.

Ott, J.A. & Fedra, K., 1977: Stabilizing properties of a high-biomass benthic community in a fluctuating ecosystem. – Helgoländer wiss. Meeresunters. **30**, 485-494.

Pamatmat, M.M., Graf, G., Bengtsson, W. & Novak, C.S., 1981: Heat production, ATP concentration and electron transport activity of marine sediments. – Mar. Ecol. Prog. Ser. **4**, 135-143.

Pearson, T.H. & Rosenberg, R., 1978: Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. – Oceanogr. Mar. Biol. Ann. Rev. **16**, 229-311.

Pearson, T.H. & Rosenberg, R., 1987: Feast and famine: Structuring factors in marine benthic communities. In: Organization of communities, past and present. Ed. by J.H.R. Gee & P.S. Giller. Blackweel. Sci. Publ., Oxford, 373-395.

Pedersen, T.F., 1992: Temporal variations in heat dissipation and oxygen uptake of the soft shell clam *Mya arenaria* L. (Bivalvia). – Ophelia **36**, 203-216.

Pehrsson, O., 1976: Esturine production of waterfowl food on the Swedish west coast. In: Fresh water on the Sea. Ed. by S. Skrelet, R. Leinebø, J.B.L. Matthews & E. Sakshaug. Proceedings from a symposium on the influence of fresh-water outflow on biological processes in fjords and coastal waters, April 1974. Geilo, Norway, 22-25.

Persson, L.E., 1983: Temporal and spatial variation in coastal macrobenthic community structure, Hanö Bay (southern Baltic). – J. Exp. Mar. Biol. Ecol. **68**, 277-293.

Persson, L.E., 1990: The national Swedish environmental monitoring programme (PMK): soft macrofauna monitoring off the south coast of Sweden-Annual Report 1990. Naturvardsverket Rapport 3937, 5-12.

Persson L.E. & Olafsson, E.B., 1986: Distribution and abundance of mobile epifauna and macrozoobenthos in south Swedish shallow marine areas. – Ophelia, Suppl. **4**, 201-210.

Pihl, L., 1982: Food intake of young cod and flounder in a shallow bay of the Swedish west coast. – Neth. J. Sea Res. **15**, 419-432.

Pihl, L. & Rosenberg, R., 1984: Food selection and consumtion of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. – Mar. Ecol. Prog. Ser. **15**, 139-168.

Piersma, T., 1994: Close to the edge: energetic bottlenecks and the evolution of migratory pathways in knots. phd-thesis, University of Groningen, Uitgeverij Het Open Boek, Ben Burg, 366 pp.

Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P. & Wiersma, P. 1993: Scale and intensity of intertidal habitat use by knots Calidris canutus in the western Wadden Sea in relation to food, friends and foes. – Neth. J. Sea Res. **31**, 331-357.

Piersma, T., Koolhaas, A. & Dekinga, A. 1993: Interactions between stomach structure and diet choice in shorebirds. – Auk **110**, 552-564.

Powilleit, M., Kube, J., Maslowski, J. & Warzocha, J., 1996: Distribution of macrobenthic invertebrates in the Pomeranian Bay (Southern Baltic Sea) in 1993/94. – Bulletin of the Sea Fisheries Institute, Gdynia-Poland **3**, 75-87.

Prena, J., 1994: Oxygen depletion in Wismar Bay (Western Baltic Sea) 1988. – Arch. Fish. Mar. Res. **42**, 77-87.

Prena, J. & Gosselck, F., 1989: Das Makrozoobenthos eines hocheutrophierten Küstengewässers - Eine Bonitierung der Wismarer Bucht (westliche Ostsee). – Fischerei-Forschung **27**, 51-56.

Prena, J., Gosselck, F., Schroeren, V. & Voss, J., in prep: Periodic and episodic benthos recruitment in Southwest Mecklenburg Bay (Western Baltic Sea).

Rees, H.L., Heip, C., Vincx, M. & Parker, M.M., 1991: Benthic communities: use in monitoring point-source discharges. – Techniques in marine environmental sciences No. **16**, 1-70.

Reineck, H.E., 1963: Der Kastengreifer. – Natur und Museum **93**, 102-108.

Reise, K., 1979: Spatial configurations generated by motile benthic polychaezes. – Helgoländer wiss. Meeresunters. **32**, 55-72.

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

Reise, K., 1985: Tidal flat ecology: an experimental approach to species interactions. Springer-Verlag, Berlin, 191 pp.

Reise, K., 1991: Mosaic cycles in the marine benthos. In: The mosaic-cycle concept of ecosystems. Ed. by H. Remmert. Springer Verlag, Berlin-Heidelberg-New York, 61-82.

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

Remane, A., 1940: Einführung in die zoologische Ökologie der Nord- und Ostsee. In: Tierwelt der Nord- und Ostsee, **1a**. Ed. by Grimpe, G. & E. Wagler. Akad. Verlags-Gesell., Leipzig, 1-238.

Remmert, H. (ed.), 1991: The mosaic-cycle concept of ecosystems. Springer Verlag, Berlin-Heidelberg-New York.

Renk, H., 1992: Primary production and the concentration of chlorophyll a. In: Marine pollution (2). An assessment of the effects of pollution in the Polish coastal area of the Baltic Sea. Ed. by A. Trzosinska. Polish Academy of Sciences, National Scientific Comitee on Oceanic Research, Studia i materialy oceanologiczne **61**, 167-180.

Rhoads, D.C. & Young, D.K., 1970: The influence of deposit-feeding organisms on sediment stability and community trophic structure: A new protocol. – Hydrobiol. **142**, 291-308.

Rosenberg, R. (ed.), 1984: Biological assesment of Swedish shallow marine areas. Fish and bottom fauna. Statens Naturvårdsverk PM 1911 (in Swedish), 384 pp.

Rosenberg, R., 1995: Benthic marine fauna structured by hydrodynamic processes and food availability. – Neth. J. Sea Res. **34**, 303-317.

Rosenberg, R., Gray, J.S., Josefson, A.B. & Pearson, T.H., 1987: Peterson's benthic stations revisited II. Is the Oslofjord and eastern Skagerak enriched ? – J. Exp. Mar. Biol. Ecol. **105**, 219-251.

Rosenberg, R. & Möller, P., 1979: Salinity stratificated benthic macrofaunal communities and long-term monitoring along the west coast of Sweden. – J. Exp. Mar. Biol. Ecol. **37**, 175-203.

Rumohr, H., 1987: Der Beitrag A. Hagmeiers zur Kentniss des Benthos der Ostsee. – Mitt. aus dem Zool. Mus. Univ. Kiel II, Heft **5**, 1-32.

Rumohr, H., 1990: Soft-bottom macrofauna: collection and treatment of samples. – Techniques in marine environmental sciences No. **8**, 1-18.

Rumohr, H., 1993: Erfahrungen und Ergebnisse aus 7 Jahren Benthosmonitoring in der südlichen Ostsee. In: Das biologische Monitoring der Ostsee im Institut für Meereskunde Kiel 1985-1992. Ed. by J.C. Duinker. – Ber. Inst. Meereskunde Kiel, Nr. **248**, 90-109.

Rumohr, H., Brey, T. & Ankar, S., 1987: A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. – Baltic Marine Biologists, Publ. No. **9**, 1-56.

Rutschke, E., 1989: Die Wildenten Europas. Deutscher Landwirtschaftsverlag, Berlin 368 pp.

Saavedra, M.P., 1990: Bonitierung des Makrozoobenthos im Greifswalder Bodden. Diplom-thesis, University of Rostock (unpubl.), 99 pp.

Savchuck, M.Y., 1976: Acclimatization of the bivalve mollusc *Mya arenaria* in the Black Sea. – Sov. J. mar. Biol. **2**, 376-383.

Scabell, J. & Jönsson, N., 1989: Spawning behaviour of Rügen spring herring. – Rapp. P.-v. Réun. Cons. int. Explor. Mer. **190**, 113-116.

Schlungbaum, G., Baudler, H. & Nausch, G., 1994a: Die Darss-Zingster Boddenkette - ein typisches Flachwasserästuar an der südlichen Ostseeküste. – Rostocker Meeresbiol. Beitr. **2**, 5-26.

Schlungbaum, G., Baudler, H. & Nausch, G., 1994b: Sedimentstruktur und Sedimentdynamik in den Darss-Zingster Boddengewässern. – Rostocker Meeresbiol. Beitr. **2**, 27-40.

Schulz, S. & Kaiser, W., 1986: Increasing trends in plankton variables in the Baltic Sea - a further sign of eutrophication ? – Ophelia, Suppl. **4**, 249-257.

Segerstråle, S.G., 1960: Investigations on Baltic populations of the bivalve *Macoma baltica* (L.). Part I. Introduction. Studies on recruitment and its relation to depth in Finish coastal waters during the period 1922-1959. Age and growth. – Commentat. biol. **32**, 1-72.

Sellin, D., 1990: Fischlaich als Nahrung von Vögeln. – Vogelwelt **111**, 217-224.

Siegel, H., Gerth, M., Hoell, A. & Schmidt, T., 1994: Typical distribution pattern in the Pommeranian Bight derived from satellite data. Proceedings of 19th Conference of the Baltic Oceanographers, Gdansk, Poland, 268-277.

Skov, H., Durinck, J., Leopold, M.F. & Tasker, M.L., 1995: Important bird areas for seabirds in the North Sea. BirdLife International, Cambridge, 156 pp.

Smetacek, V., 1984: The supply of food to the benthos. In: Flows of energy and materials in marine ecosystems: theory and practice. Ed. by M.J. Fasham. Plenum Press, New York, 517-548.

Stempniewicz, L., 1991: The food intake of two scoters *Melanitta fusca* and *M. nigra* wintering in the Gulf of Gdansk, Polish Baltic coast. – Var. Fågelv. Suppl. **11**, 211-214.

Suter, W., 1982: Vergleichende Nahrungsökologie von überwinternden Tauchenten *Bucephala*, *Aythya* und Bläßhuhn *Fulica atra* am Untersee-Ende/Hochrhein (Bodensee). – Orn. Beob. **79**, 225-254.

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Tasker, M.L., Jones, P.H., Dixon, T.J. & Blake, B.F., 1984: Counting seabirds at sea from ship: a review of methods employed and a suggestion for a standardised approach. – Auk 101, 567-577.

Theede, H., 1984: Physiological approaches to environmental problems of the Baltic. – Limnologica 15, 443-458.

Trzosinska, A. (ed.), 1992: Marine pollution (2). An assessment of the effects of pollution in the Polish coastal area of the Baltic Sea. – Polish Academy of Sciences, National Scientific Comitee on Oceanic Research, Studia i materialy oceanologiczne 61, 1-226.

Trzosinska, A. & Cyberska, B., 1992: Oxygen and hydrogen sulphide. In: Marine pollution (2). An assessment of the effects of pollution in the Polish coastal area of the Baltic Sea. Ed. by A. Trzosinska. – Polish Academy of Sciences, National Scientific Comitee on Oceanic Research, Studia i materialy oceanologiczne 61, 93-100.

Van Der Tol, M.W. & Scholten, H., 1993: Response of the Eastern Scheldt ecosystem to a changing environment: functional or adaptive ? – Neth. J. Sea. Res. 30, 175-190.

Vogel, K., 1959: Wachstumsberechnungen bei Lamellibranchiaten und Brachiopoden. Ein Beitrag zur Beurteilung fossiler Kleinfaunen und zur Frage "Bio- oder Thanatocoenose". – N. Jahrb. Geol. Paläontol., Abhandl. B 109, 109-129.

Vollenweider, R.A., 1976: Advances in defining critical loading levels for phosphorus in lake eutrophication. – Mem. Ist. It. Idrobiol. 33, 53-84.

Wanink, J.H. & Zwarts, L., 1993: Environmental effects on the growth rate of intertidal invertebrates and some implications for foraging waders. – Neth. J. Sea Res. 31, 407-418.

Warwick, R.M., 1986: A new method for detecting pollution effects on marine macrobenthic communities. – Mar. Pollut. Bull. 92, 557-562.

Warwick, R.M., 1993: Environmental impact studies on marine communities: pragmatical considerations. – Aust. J. Ecol. 18, 63-80.

Warwick, R.M. & Clarke, K.R., 1993: Increased variability as asymptom of stress in marine communities. – J. Exp. Mar. Biol. Ecol. 172, 215-226.

Warwick, R.M. & Clarke, K.R., 1994: Reearning the ABC: taxonomic changes and abundance/biomass relationships in disturbed benthic communities. – Mar. Biol. 118, 739-744.

Warzocha, J., 1995: Classification and structure of macrofaunal communities in the southern Baltic. – Arch. Fish. Mar. Res. 42, 225-237.

Wasmund, N. & Schiewer, U., 1994: Überblick zur Ökologie und Produktionsbiologie des Phytoplanktons der Darss-Zingster Boddenkette (südliche Ostsee). – Rostocker Meeresbiol. Beitr. 2, 41-60.

Weber, E., 1980: Grundriss der biologischen Statistik. Gustav Fischer Verlag, Jena, 652 pp.

Weigelt, M., 1991: Short- and long-term changes in the benthic community of the deeper parts of Kiel Bay (Western Baltic) due tu oxygen depletion and eutrophication. – Meeresforsch. 33, 297-311.

Weigelt, M. & Rumohr, H., 1986: Effects of wide-range oxygen depletion on benthic fauna and demersal fish in Kiel Bay 1981-1983. – Meeresforsch. 31, 124-136.

Weinberg, S., 1978: The minimal area problem in invertebrate communities of mediterranean rocky substrata. – Mar. Biol. 49, 33-40.

Widdows, J. & Johnson, D., 1988: Physiological energetics of Mytilus edulis: scope for growth. – Mar. Ecol. Prog. Ser. 46, 113-121.

Wiersma, P. & Piersma, T., 1994: Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of knots. – Condor 96, 257-279.

Wilde, P.A.W.J. de, 1975: Influence of temperature on behaviour, energy metabolism, and growth of *Macoma balthica* (L.). In: Proc. 9th Europ. mar. Biol. Symp. Aberdeen. Ed. by H. Barnes. Aberdeen University Press, 239-256.

Winther, U. & Gray, J.S., 1985: The biology of *Mya arenaria* (Bivalvia) in the eutrophic inner Oslofjord. – Sarsia **70**, 1-9.

Woakes, A.J. & Butler, P.J., 1983: Swimming and diving in tufted ducks *Aythya fuligula* with particular reference to heart rate and gas exchange. – J. exp. Biol. **107**, 311-329.

Woakes, A.J. & Butler, P.J., 1986: Respiratory, circulatory and metabolic adjustments during swimming in the tufted duck, *Aythya fuligula*. – J. exp. Biol. **120**, 215-231.

Word, J.Q., 1980: Classification of benthic invertebrates into infaunal trophic index feeding groups. In: Southern California Coastal Water Research Project, Biennial Report 1979-1980. Ed. by Bascom, W.. El Segundo, California, 103-121.

Ydenberg, R. & Guillemette, M., 1991: Diving and foraging in the common eider. – Orn. Scand. **22**, 349-352.

Zettler, M.L., 1994: Immigration und Ausbreitung eines nordamerikanischen Polychaeten in ein inneres Küstengewässer der südlichen Ostsee und Auswirkungen auf das autochtone Makrozoobenthos. – Erweiterte Zusammenfassung der Jahrestagung der Deutschen Gesellschaft für Limnologie e.V., Hamburg, Bd. **2**, 659-699.

Zettler, M.L. & Bick, A., 1996: The analysis of small- and mesoscale dispersion patterns of *Marenzelleria viridis* (Polychaeta: Spionidae) in a coastal water area of the southern Baltic. – Helgoländer Meeresunters. **50**, 265-286.

Zettler, M.L., Bochert, R. & Bick, A., 1994: Röhrenbau und Vertikalverteilung von *Marenzelleria viridis* (Polychaeta: Spionidae) in einem inneren Küstengewässer der südlichen Ostsee. – Rostock. Meeresbiolog. Beitr. **2**, 215-226.

Zmudzinski, L., 1993: Long-term changes in macrozoobenthos of the Vistula lagoon. 2. Estuary Symposium; Estuarine environments and biology of estuarine species, Gdansk, Poland, October 18-22, 1993, Abstract of poster.

Zmudzinski, L., Chubarova, S., Dobrowolski, Z., Gruszka, P., Fall, I., Olenin, S. & Wolnomiejski, N., 1994: Expansion of the spionid polychaete *Marenzelleria viridis* in the southern part of the Baltic Sea. Proceedings of the 13. BMB-Symposium, Riga, Latvia, in press.

Zwarts, L., 1991: Seasonal variation in body weigth of the bivalves *Macoma balthica, Scrobicularia plana, Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden Sea. – Neth. J. Sea Res. **28**, 231-245.

Zwarts, L. & Blomert, A.M., 1992: Why knot *Calidris canutus* take medium-sized *Macoma balthica* when sic prey species are available. – Mar. Ecol. Prog. Ser. **83**, 113-128.

Zwarts, L., Blomert, A.M., Ens, B.J., Hupkes, R. & Van Spanje, T.M., 1990: Why do waders reach high feeding densities on the intertidal flats of the Banc d'Arguin, Mauretania ? – Ardea **78**, 39-52.

Zwarts, L., Blomert, A.M. & Wanink, J.H., 1992: Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer. – Mar. Ecol. Prog. Ser. **83**, 129-139.

Zwarts, L. & Drent, R.H. 1981: Prey depletion and the regulation of predator density: Oystercatchers feeding on Mussels (*Mytilus edulis*). In: Feeding and survival strategies of estuarine organisms. Ed. by Jones, N.V. & W.J. Wolff. Plenum Publ. Corporation, 193-216.

Zwarts, L. & Wanink, J.H., 1984: How oystercatchers and curlews successively deplete clams. In: Coastal waders and wildfowl in winter. Ed. by P.R. Evans, J.D. Goss-Custard & W.G. Hale. Cambridge University Press, 69-83.

Zwarts, L. & Wanink, J.H., 1993: How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. – Neth. J. Sea Res. **31**, 441-476.

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