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Structure and dynamics of Baltic benthos communities, with particular reference to the relationship between macro- and meiofauna

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Abstract

The Baltic Sea is one of the largest brackish water areas in the world, and osmotic stress has severely reduced the number of species in its benthic macro- and meiofauna. This leads to an almost uniquely simple benthic ecosystem. – The benthic macrofauna shows a steep north to south increase in biomass, from mean values of about $1\,gm^{-2}$ wet weight in the Bothnian Bay, to over $100\,gm^{-2}$ above the halocline in the northern Baltic proper, and even higher values in the southwestern Baltic. Meiofauna biomass is much less variable, and increases only from about $2\,gm^{-2}$ wet weight to about $6\,gm^{-2}$ along the same gradient. There is also a north-south gradient in phytoplankton primary production, with an increase by a factor of about 3 to 6. Very low salinities (2–$3^0/_{00}$ S) exclude filter-feeding bivalves from most of the Bothnian Bay, explaining in part the extremely low biomasses in the north. When filter-feeders are substracted, the benthos-feeding macrofauna biomass still increases more from north to south than the primary production, while the meiofauna biomass, on the other hand' increases less. Calculations are presented which indicate that the total resource use by benthos-feeding macro + meiofauna increases roughly in proportion to the primary production. The observed shift in dominance from meiofauna to macrofauna is attributed to meiofauna being competitively superior in low food environments (Bothnian Bay), while in richer environments predation by macrofauna limits meiofauna populations (Bothnian Sea, Baltic proper). – Most of the Baltic shows strong salinity stratification, with little or no oxygen present below the primary halocline. This leads to an oxygen-dependent zonation of the fauna, with macrofauna disappearing at higher oxygen levels than some of the meiofauna. Nematodes in low numbers persist even in areas which have been anoxic for long periods. – The secondary productivity of the widely distributed *Pontoporeia* community is described, and it is concluded that te *Pontoporeia* populations are primarily food limited, and that the benthic system is intimately coupled to the pelagic system, and may respond to events in the plankton within weeks. – Attempts to estimate the energy flow through the benthos of the Askö-

Landort area (N. Baltic proper) indicate that $40 - 60\,\mathrm{gCm}$ to fuel the benthos. – Finally, direct interactions between macro- and meiofauna are discussed. The evidence for control of meiofauna populations by macrofauna predation is suggestive, but not yet conclusive. Examples are also given of more positive interactions between macro- and meiofauna, and it is proposed that a proper balance between different size classes of benthos may be necessary for efficient remineralization.

Zusammenfassung

Struktur und Dynamik baltischer Benthosgemeinschaften unter besonderer Berücksichtigung der Beziehung zwischen Makro- und Meiofauna

Die Ostsee ist eines der größten Brackwassergebiete der Welt, und die osmotische Belastung hat die Artenzahl ihrer benthischen Makro- und Meiofauna stark reduziert. Dies führt zu einem fast einzigartig einfachen benthischen Ökosystem. – Die benthische Makrofauna zeigt von Norden nach Süden einen steilen Anstieg in der Biomasse, von Mittelwerten von etwa $1\,\mathrm{g\,m^{-2}}$ Frischgewicht in der Bottenwiek bis über $100\,\mathrm{g\,m^{-2}}$ oberhalb der Sprungschicht in der inneren nördlichen Ostsee. Die Meiofauna-Biomasse weist weit weniger Schwankungen auf und steigt von nur etwa $2\,\mathrm{g\,m^{-2}}$ Naßgewicht bis etwa $6\,\mathrm{g\,m^{-2}}$ entlang desselben Gradienten. In der Phytoplankton-Primärproduktion ist ebenfalls ein Nord-Süd-Gradient mit einem Anstiegsfaktor von etwa 3 bis 6 vorhanden. Sehr niedrige Salzgehalte ($2–3^0/_{00}$ S) schließen filtrierende Bivalvier aus dem größten Bereich der Bottenwiek aus, was zum Teil die extrem geringe Biomasse im Norden erklärt. Auch wenn die Filtrierer ausgeklammert werden, steigt die benthosfressende Makrofauna-Biomasse immer noch stärker von Norden nach Süden an als die Primärproduktion, während andererseits die Meiofauna-Biomasse weniger anwächst. Berechnungen lassen erkennen, daß das von benthosfressender Makro- und Meiofauna genutzte Nahrungsangebot ungefähr im Verhältnis zur Primärproduktion ansteigt. Der beobachtete Wechsel der Dominanz von Meiofauna zur Makrofauna wird darauf zurückgeführt, daß die Meiofauna in Lebensräumen mit geringen Nahrungsmengen wettbewerbsmäßig überlegen ist (Bottenwiek), während in reicheren Lebensräumen die Makrofauna durch Wegfraß die Meiofaunapopulationen limitiert (Bottensee, eigentliche Ostsee). Der überwiegende Teil der Ostsee zeigt eine starke Salzgehaltsschichtung mit wenig oder ohne Sauerstoff unterhalb der primären Sprungschicht. Dies führt zu einer sauerstoffabhängigen Zonierung der Fauna, wobei die Makrofauna bereits bei höheren Sauerstoffgehalten verschwindet als ein Teil der Meiofauna. Eine geringe Zahl von Nematoden überlebt sogar in Gebieten, die schon seit langem anoxisch sind. – Die Sekundärproduktivität der weitverbreiteten *Pontoporeia*-Gemeinschaft wird beschrieben. Aus diesen Untersuchungen wird geschlossen, daß die *Pontoporeia*-Populationen in erster Linie nahrungslimitiert sind, daß das benthische System eng mit dem pelagischen verknüpft ist, und daß es auf Vorgänge im Plankton innerhalb von Wochen reagieren kann. – Versuche der Abschätzung des Energieflusses durch das Benthos des Askö-Landsort-Gebietes (nördlicher Teil der eigentlichen Ostsee) zeigen, daß $40 - 60\,\mathrm{g\,C\,m^{-2}}$ Jahr nötig sind, um das Benthos mit Energie zu versorgen. – Abschließend werden direkte Wechselwirkungen zwischen Makro- und Meiofauna diskutiert. Der Beweis für die Kontrolle der Meiofaunapopulationen aufgrund von Wegfraß durch die Makrofauna deutet sich an, ist aber noch nicht schlüssig. Auch Beispiele für positive Wechselbeziehungen zwischen Makro- und Meiofauna werden gegeben; und es könnte sein, daß ein ausgewogenes Gleichgewicht zwischen verschiedenen Größenklassen des Benthos für eine wirksame Remineralisierung erforderlich ist.

Introduction

The Baltic Sea is one of the largest brackish water areas in the world, and the largest with extensive areas of low but stable salinites, mostly within the ß-mesohaline range (5–10^0/oo S). There is a salinity gradient from north to south, from 2–3^0/oo S in the innermost Bothnian Bay, to about 15–20^0/oo S in Kiel Bay, where the salinity is much more variable than in most of the Baltic. There is also a gradient in climate, from almost arctic conditions and more than six months of ice cover in the coastal zone of the extreme north to a more maritime climate with an average of only about a month of coastal ice in the south.

Several excellent general reviews of the ecology of the Baltic Sea, partly or entirely concerned with the benthos, already exist. (REMANE 1934, 1940, 1958; SEGERSTRÅLE, 1957; ZENKEVITCH, 1963; JANSSON, 1972, in press). In the following I will therefore concentrate mainly on a few aspects of Baltic benthic ecology, that I personally have found particularly interesting. I will do this largely by summarizing some of the research done at the Askö Laboratory since 1971, when the project ,,Dynamics and Energy Flow in the Baltic Ecosystem'' was started. I will utilize data collected by many of the scientists at Askö. but special mention must be made of Sven Ankar and Hans Cederwall, my closest collaborators.

Askö is situated in the north-western Baltic proper (see map, Fig. 1.), and I have used results from the international cooperation within the ,,Joint macro- and meiofauna sampling programme for the whole Baltic'' to place the work at Askö in its wider Baltic setting. This international programme, initiated within the Baltic Marine Biologists, and carried out in 1974–75, involved 17 scientists from 6 countries, and only partial results are yet available. In the following I have used the results given in ELMGREN et al. (in press), plus results from the Baltic proper collected by the Askö Laboratory (ELMGREN, ANKAR and CEDERWALL, unpublished). I have also quoted a little of the historic background, and of the often highly relevant modern work from other areas of the Baltic, such as the work on benthos and demersal fish within the ,,Sonderfor-schungsbereich 95'' (Interaction Sea-Sea bottom) in Kiel, recently summarized by ARNTZ (in press; also ARNTZ and BRUNSWIG, 1975, 1976, in press). To avoid excessive overlap, I have, however, restricted myself mainly to the Baltic north of 56° N, and will mostly discuss somewhat deeper bottoms, where benthic photosynthesis is of minor importance.

Main structural features of the Baltic benthos

Diversity and species richness

Salinity is the ecological master factor in the Baltic Sea, as reviewed by REMANE (1934, 1940, 1958) and SEGERSTRÅLE (1957). It places the organisms in an osmotic environment, which allows only a limited number of euryhaline marine and freshwater organisms, and a few brackish water specialists to establish themselves in the inner Baltic. The classic generalized ,,Remane's curve'' (REMANE, 1934) shows a marked species minimum at 6–7^0/oo S, but the exact shape of the salinity-species richness curve will vary, depending on what groups or habitats are studied (DAHL, 1956; REMANE, 1958). Remane's curve is meant to show the total number of species from all taxonomic groups in all biotopes. As discussed by McARTHUR (1965), a reduction in total diversity is likely to show up first in between-habitat diversity, and only a greater total reduction can be expected to give reduced diversity also within each habitat. In the inner Baltic even within-habitat diversity is drastically reduced (Fig. 2, measured as no. of macrofauna taxa per van Veen grab sample). It reaches a minimum of 0–2 taxa per grab sample in the Bothnian Bay, at a salinity of 3–4^0/oo S, slightly lower than Remane's
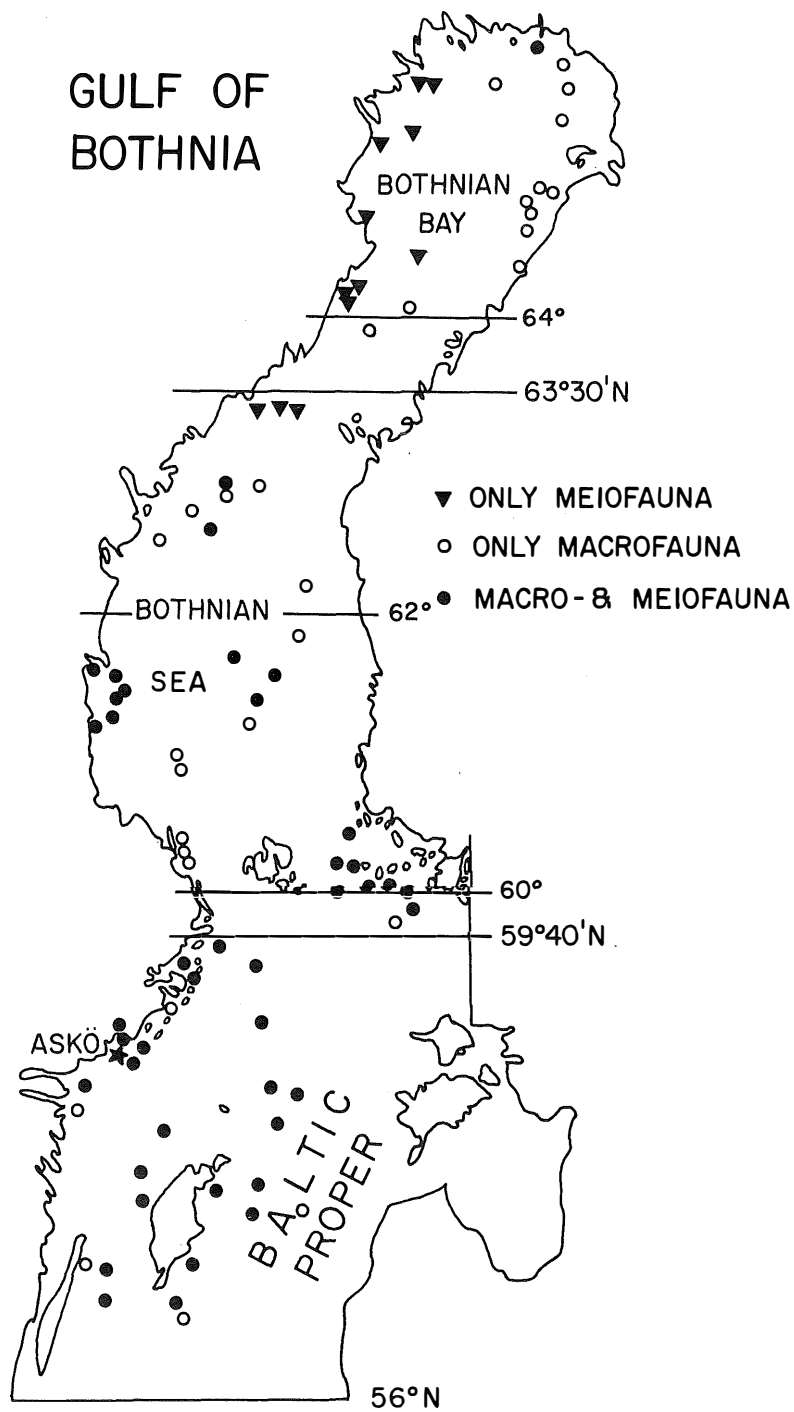
Figure 1

Map of the Baltic Sea north of 56° N, showing the location of the Askö Laboratory and of the stations from the ,,Joint macro- and meiofauna sampling programme for the whole Baltic'' from which data are presented in this paper. Results in the Gulf of Bothnia (Bothnian Bay and Bothnian Sea) from ELMGREN et al. (in press), in the Baltic proper from ANKAR and CEDERWALL (macrofauna, unpublished) and ELMGREN (meiofauna, unpublished). Filled circles: both macro- and meiofauna samples obtained; open circles: only macrofauna, triangles: only meiofauna.
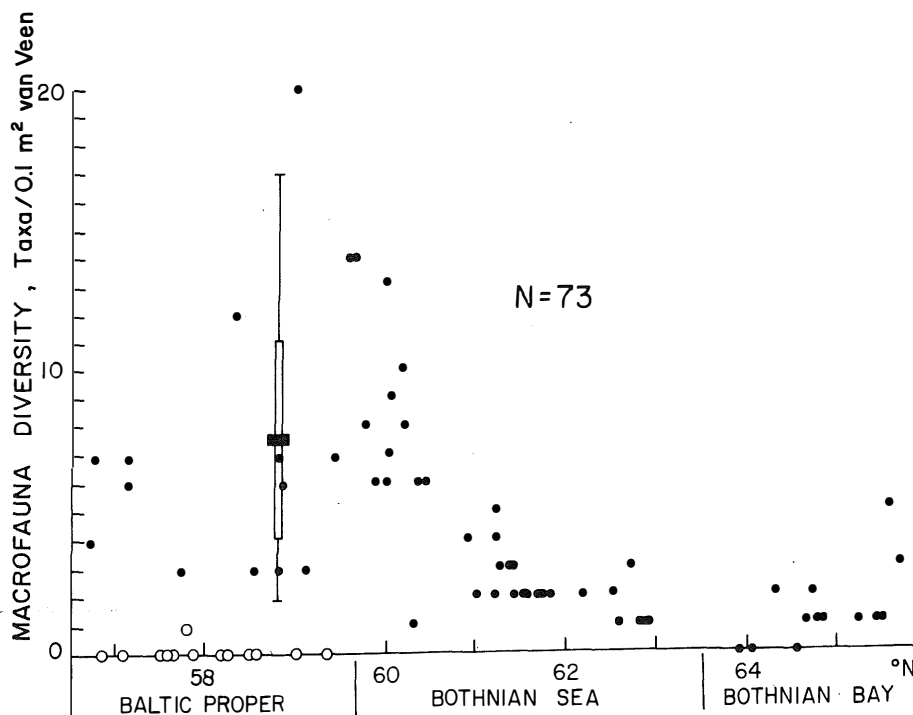
Figure 2

Baltic macrofauna diversity, measured as number of taxa per $0.1\,m^2$ van Veen grab (Oligochaeta, Chironomidae and Hydrobiidae counted as single taxa, others determined to species). Data from the ,,Joint macro- and meiofauna sampling programme für the whole Baltic'' (N = 73) shown as circles, where open circles denote samples from below 80 m depth in the Baltic proper (i.e. from the oxygen poor zone below the halocline). Data from the Askö-Landsort area (ANKAR and ELMGREN, 1976, N = 38), shown as single line (range), double line (standard deviation) and crossbar (mean).

overall minimum (disregarding in this connection stations below the halocline in the Baltic proper, where the almost total lack of macrofauna is due to oxygen deficiency). Within each subarea of the Baltic there is a fairly wide range in macrofauna diversity, showing the influence of both sediment type and water depth, with sandy sediments most and muddy least diverse (e.g. ANKAR and ELMGREN, 1976), and diversity decreasing with increasing depth for each sediment type (ROSENBERG et al., 1975; ANKAR and ELMGREN, 1976). This is probably related both to the complexity of the habitat and to the diversity of feeding niches available. Sandy sediments often contain pockets of finer sediments, and are thus more complex (ANKAR, 1977), and the presence of macrophyte fragments may increase the diversity of shallow water macrofauna (LAPPALAINEN and KANGAS, 1975). Sandy sediments in shallow water can offer food for herbivores and suspension feeders, as well as deposit feeders and carnivores, whereas only the two latter feeding types are common on deep soft bottoms.

Where the Baltic meiofauna is concerned, it is as yet impossible to construct any graphs showing the diversity of the total fauna (such as Fig. 2 for the macrofauna)

Numerous studies of restricted taxonomic groups have, however, shown much reduced diversity in the inner Baltic, when compared to fully marine areas (GERLACH, 1953, for nematodes; NOODT, 1970, for harpacticoids). For most groups only the southern Baltic, especially Kiel Bay, have been well investigated, and here salinity and diversity are still much higher than in the rest of the Baltic (eg. GERLACH, 1958, for nematodes; NOODT, 1957; BECKER, 1970, for harpacticoids). In spite of this paucity of information, it is clear that the meiofauna of the Baltic, while much less diverse than in fully marine areas, still has much higher diversity than Baltic macrofauna. As an example a soft bottom at 44 m depth in the Askö area (dominated by the amphipod *Pontoporeia*) may be mentioned. Here a single meiofauna sub-sample of less than 1 cm² contained 19 species of meiofauna (ELMGREEN, 1976) whereas a whole square metre, 10 van Veen grabs, normally yields only 5 or 6 macrofauna species at this station (CEDERWALL, pers. comm.).

The salinity-induced reduction in species richness in the Baltic Sea thus leads to an almost uniquely simple benthic ecosystem, with just a few dominant species, both in the macro- and the meiofauna. In many cases these are common estuarine or freshwater species, which have already been studied in great detail.

Benthic communities

The most important step in the description of the benthos of an area of the sea, has traditionally been a quantitative study, giving abundance and usually biomass, and culminating in the recognition and description of a number of benthos communities. This world-wide tradition originated in the wider Baltic area with the pioneer work of C.G.J. Petersen (PETERSEN and BOYSEN-JENSEN, 1911; PETERSEN, 1913). He designated almost the whole Baltic as a *Macoma* community, with *Macoma baltica* as its most characteristic member. Later workers have added several communities (see eg. ZENKEVITCH, 1963; LUKSENAS, 1969), but their number is still comparatively low, and they tend to show high coefficients of similarity (LUKSENAS, 1969). In the Kiel Bay, REMANE (1933, 1940) was the first to use meiofauna species to delineate benthic communities, and one of these, the *Cyprideis-Manayunkia* community, can be recognized as far north as at Askö, in an impoverished form. For most of the Baltic it is, however, still too early to discuss the species composition of meiofauna communities.

A recent re-evaluation of Petersen's classic paper of 1913 by STEPHENSON, WILLIAMS and COOK (1972), using modern, more objective computer-based statistical techniques, has confirmed the existence of recurring species groups in his data. But the communities found differed greatly from Petersen's, and quite different results were obtained, depending on whether presence-absence, abundance or biomass data were used for the analysis. This emphasizes the subjective nature of Petersen's communities, and today it is generally believed that the majority of species are distributed individually, in an overlapping manner, forming continua along environmental gradients, not as groups of interdependent species, which form discrete ecological entities (GRAY, 1974). Today the community concept is therefore used in a much more pragmatic sense, stripped of superorganismal overtones (MILLS, 1969). This neither detracts from its usefulness, nor denies the possibility of strong biological interactions between of the members of any given community (cf. CHRISTIANSEN and FENCHEL, 1977: 129–134).

The invalidity of the idea of the community as an integrated ecological unit, a "superorganism", should be especially clear in the Baltic, where the benthic communities are made up of a mixture of organisms of very different zoogeographical origin (SEGERSTRÅLE, 1957; LUKSENAS, 1967), which have only been living together

under salinity conditions similar to those of today since the beginning of the *Limnaea* sea, about 2000–2500 years ago (cf. ALHONEN, 1971). Since many of the important benthic invertebrates of the Baltic have generation times of 2 or more years, they have only been influencing each others evolution for about a thousand generations – enough certainly for some coadaptation, but hardly for major coevolution.

Biomass of benthos in the Baltic

The quantitative distribution of benthic macrofauna in the Baltic Sea has been know in its main outlines since the work of PETERSEN and BOYSEN JENSEN (1911) PETERSEN (1913), THULIN (1922), HESSLE (1924), HAGMEIER (1930), SEGERSTRALE (1933) and DEMEL and MULICKI (1954). Due to the differences in methods it is, however, always difficult to piece together a reliable view of the whole from several studies, each of which covers only a part. Only recently have two efforts been made to cover the whole Baltic, using the same methods throughout. ANDERSIN et al. (1977) gave an excellent synoptic survey of the macrobenthos of the whole Baltic in the summer of 1967, based on transects through all the major basis. Their paper provides the clearest illustration yet of the large areas totally or almost totally devoid of macrofauna in the deeper, oxygen-deficient parts of the Baltic proper. It also contrasts with the very low biomasses of the Bothnian Bay in the north with the high biomass to be found in the mollusc-dominated communities of the Arkona Basin in the south. The other such study is the ,,Joint macro- and meiofauna sampling programme for the whole Baltic" (already
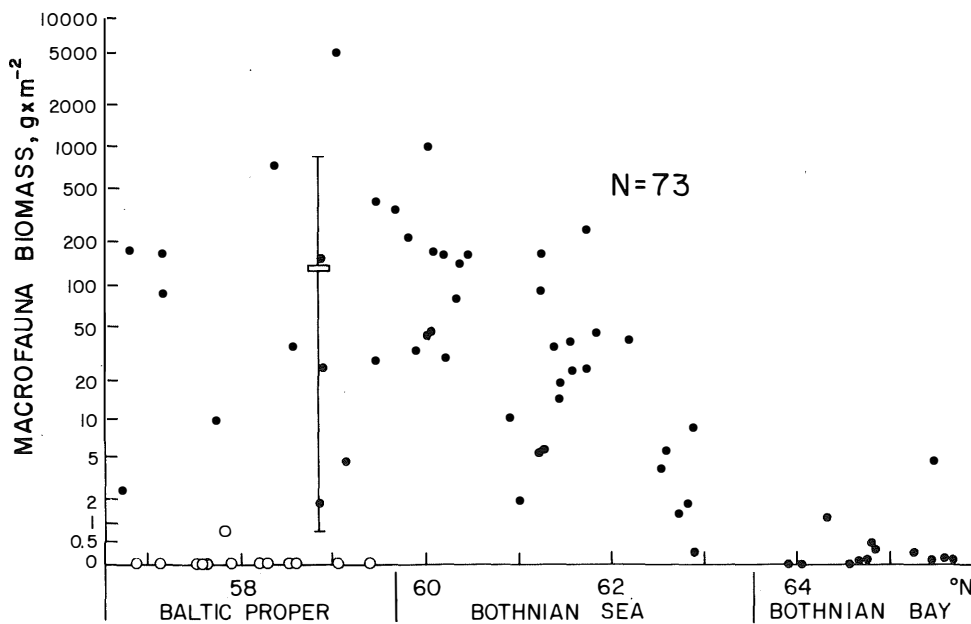

Figure 3

Baltic macrofauna wet weight biomass (includes shells). Data from the ,,Joint macro- and meiofauna sampling programme for the whole Baltic) (N = 73) shown as circles, where open circles denote samples from below 80 m depth in the Baltic proper (i.e. from the oxygen-poor zone below the halocline). Data from the Askö-Landsort area (ANKAR and ELMGREN, 1976, N = 38) shown as single line (range) and crossbar (mean). Note logarithmic biomass scale = $\log_{10}[1 +$ (biomass in g)]. Each point 0.1m² van Veen grab. Sieve mesh 1 mm.

referred to), which was different in using stratified random allocation of sampling stations, and unique in including meiofauna in the sampling programme. This is the reason why I will base the following discussion mainly on the latter study, even though only partial results are yet available, and the large number of scientists involved unavoidably means lowered comparability between individual macrofauna samples.

This study, carried out in 1974–75, also shows (Fig. 3) the area devoid of macrofauna below the primary halocline in the Baltic proper and the low biomass in the Bothnian Bay, but furthermore indicates that the southward biomass increase is a gradual process, continuing at least into the northern Baltic proper (excluding the impoverished zone below the halocline). The total increase is substantial, from about $1\,gm^{-2}$ to over $100\,gm^{-2}$ (wet weight, including shells), that is by a factor of over 100, and when areas further south are compared, there seems to be even further increase, through the Arkona Basin (ANDERSIN et al., op cit) into Kiel Bay, where mean values as high as $600\,gm^{-2}$ have been reported (ARNTZ, 1971). As with diversity, biomass is normally higher in shallower water, and on sandy bottoms, (e.g. ANKAR and ELMGREN, 1976) but since a variety of depth zones has been sampled within each area, this can explain part of the scatter, but not the general trend in the diagram (Fig. 3) (ELMGREN et al., in press, discuss this further).
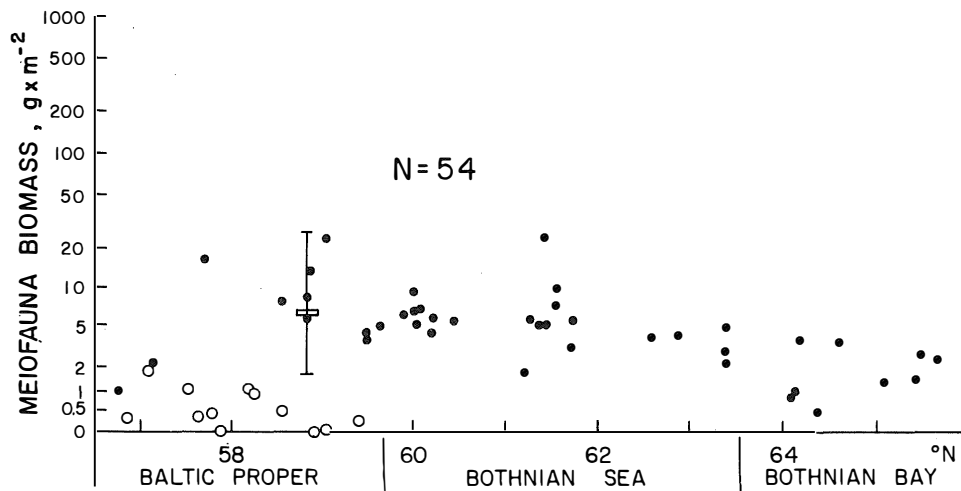

Figure 4

Baltic meiofauna wet weight biomass. Data from the ,,Joint macro- and meiofauna sampling programme for the whole Baltic'' (N = 54) shown as circles, where open circles denote samples from below 80 m depth in the Baltic proper (i.e. from the oxygen-poor zone below the halocline). Data from the Askö-Landsort area (ANKAR and ELMGREN, 1976, N = 36) shown as single line (range) and crossbar (mean). Note logarithmic biomass scale = $\log_{10}$ [1 + (biomass in g)]. Each point represents one 3.9cm² core sample. Animals passing 1 mm, but retained on 37 or 40 μm sieve.

By comparison, the meiofauna biomass (Fig. 4) shows much less variability, both within and between areas (for methods see ELMGREN et al., in press). The mean meiofauna biomass is almost $2\,gm^{-2}$ (wet weight) in the Bothnian Bay, i.e. higher than the macrofauna biomass, but increases only by a factor of 3 or 4 to the northern Baltic

proper (again disregarding values below the halocline). The few values available from the southern Baltic (ELMGREN, unpubl.) and Kiel Bay (SCHEIBEL, 1976, for metazoa; WEFER and LUTZE, 1976, for foraminifera) indicate no further increase.
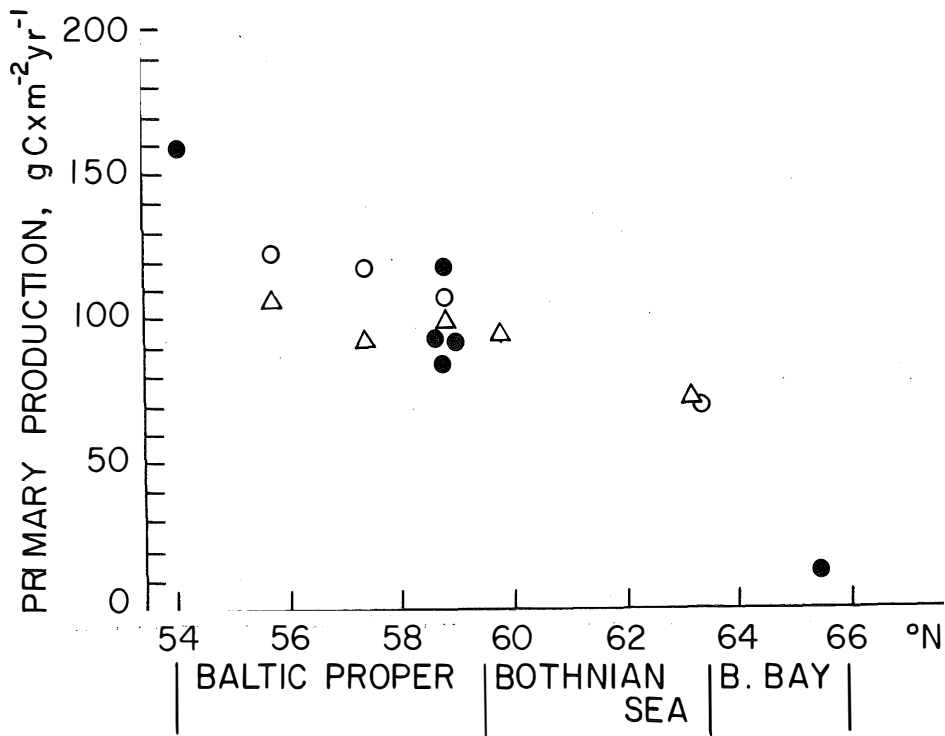

Figure 5

Phytoplanton primary production in the Baltic. Open triangles 1973, open circles 1974, filled circles other years. Sources: see text.

Since both macro- and meiofauna biomass increase from north to south, it is natural to expect a corresponding north-south gradient in primary productivity. From a multitude of literature values, hard to reconcile and compare, I have selected (Fig. 5) some measurement made by Swedish scientists with similar methods (Based on ACKE-FORS et al., 1976; WULFF et al., 1977; and unpublished Askö Laboratory reports), and also added an estimate for Kiel Bay (von BODUNGEN, 1975, quoted in ARNTZ, in press). The extremely low value in the extreme north is from the Luleå archipelago (WULFF et al., 1977), but Finnish measurements in the open Bothnian Bay indicate higher values, of at least $25\,\mathrm{gm^{-2}} \times$ year (for 1971 and 72, MESKUS, 1976). Using this as more representative and taking into account that Finnish measurements (24h incubation) generally seem to give lower values than the Swedish method (4h incubation), we can roughly estimate an increase in productivity by a factor of 3 to 6 from north to south in the Baltic. This is clearly not enough to explain, in itself, a hundredfold increase in the macrofauna biomass. ELMGREN et al. (in press) sought an explanation by pointing out that both the bivalves *Mytilus edulis* and *Macoma baltica* are excluded from most of the Bothnian Bay by the low salinity, and that this means that

in this area there are no filter-feeding benthic animals, which can directly utilize the phytoplankton primary production. This leads to longer, and therefore less efficient food chains, before the macrofauna is reached.

The absence of filter feeders is, however, only a partial explanation of the low macrofauna biomasses in the Bothnian Bay, since even with the filter-feeders subtracted, there is still 15–20 times more macrofauna in the Bothnian Sea and the northern Baltic proper (Table 1). Since the meiofauna increases less towards the south, we may try to roughly estimate the differences in total resource use by the benthic fauna in the three areas. Meiofauna has been suggested to have a metabolic rate very roughly five times that of macrofauna (GERLACH, 1971. Applies to both respiration and production, per unit biomass, and therefore probably also to food ingested). For comparative purposes we may therefore calculate a rough ''metabolic index'' by multiplying the meiofauna biomass by five, and adding it to the macrofauna biomass. We then find a total energy use by ''benthos-feeding'' meio + macrofauna* which is about 5 times higher in the Bothnian Sea and the northern Baltic proper, than in the Bothnian Bay (Table 1). We estimated the total north-south increase in primary production to be by a factor of 3–6 over that in the Bothnian Bay, but for the Bothnian Sea a factor 2–4, and for the northern Baltic proper 3–5, may be more appropriate. Considering the very limited accuracy of the estimates we are dealing with, we can thus conclude that the total energy flow through the ''benthos-feeding'' macro- and meiofauna increases about as much as the primary production, as we go south from the Bothnian Bay to the northern Baltic proper. What remains to be explained is the changed ratio of macro- to meiofauna.

Table 1
Baltic benthic metabolic index

| | Biomass, g.m^{-2} | | METABOLIC INDEX | | | |
	Meio	Macro (benthos-feeders)	5 × Meio biomass	1 × Macro biomass	Σ	Ratio over Bothnian Bay
Bothnian Bay	1.8	0.7	9	0.7	9.7	1
Bothnian Sea	6.5	14.7	32.5	14.7	47.2	4.9
northern Baltic	7.5	16	37.5	16	53.5	5.5

Data for Gulf of Bothnia from ELMGREN et al. (in press).
Data for northern Baltic proper are estimates derived as a mean of two groups of data, from the Askö-Landsort area (ANKAR and ELMGREN, 1976) and Askö Laboratory's ''Joint sampling'' stations above the halocline in the Baltic proper (see map, Fig. 1).

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* *Macoma baltica* is known to be both a suspension- and a deposit-feeder (ANKAR, 1977) but since it has the potential ability to utilize the phytoplankton, it has been excluded from the ,,benthos-feeders'' in this summation.

The hypothesis has been advanced (ELMGREN et al., in press; ELMGREN, 1976), that in areas of very low benthic food supply, such as the deep sea (cf. THIEL, 1975) or the Bothnian Bay, the meiofauna has a competitive advantage over the macrofauna, since small organisms can better utilize a sparse and finely particulate food source, such as organically poor bottom sediments. As food input increases, so do initially both macro- and meiofauna. Since macrofauna also utilizes the meiofauna as food (ELMGREN, 1976), further increase in the meiofauna will gradually be limited, leading to stable or even decreasing meiofauna biomasses as macrofauna biomass increases (Fig. 6). This hypothesis seems to explain the facts, but needs much further evidence before it can be considered proved.
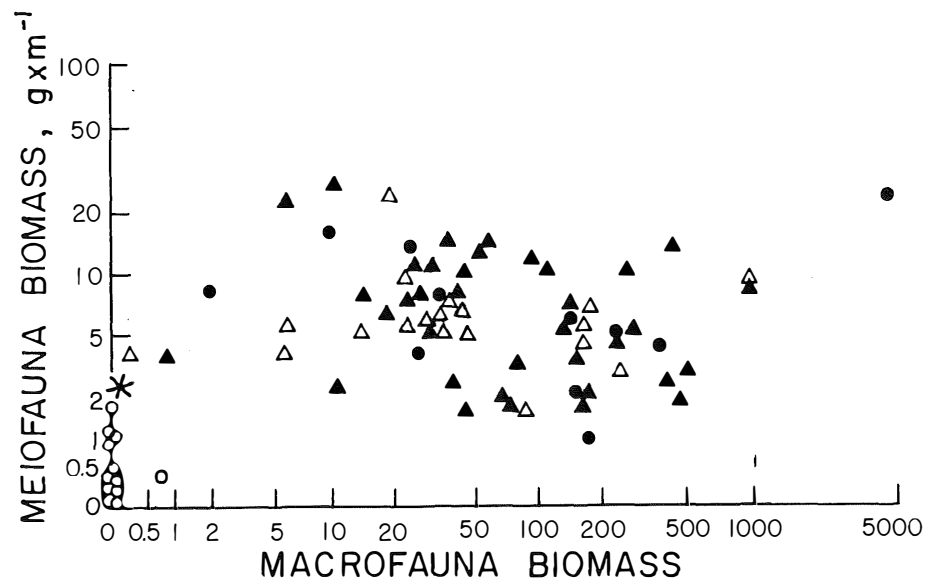

Figure 6

Relationship between macro- and meiofauna wet weight biomass in the Baltic Sea (total N = 79). Based on a diagramme in ELMGREN et al. (in press). Filled circles: Baltic proper, above 80 m (N = 12); open circles: Baltic proper, below 80 m (N = 12). Triangles: Askö-Landsort area (also Baltic proper, from ANKAR and ELMGREN, 1976, N = 36); open triangles: Bothnian Sea (N = 19), star: Bothnian Bay (N = 1). Note logarithmic biomass scales = $\log_{10}$ [1 + (biomass in g)].

Baltic"deserts"

One of the most intensively studied aspects of the Baltic Sea in recent years, has been the oxygen deficiency below the halocline in the western Baltic, Baltic proper and the Gulf of Finland. Its devastating impact on the macrobenthos has prompted many papers, the most recent and comprehensive by ANDERSIN et al. (1977, in press), and can be seen clearly also in Figs. 2 and 3. The meiofauna has been studied by LEPPÄKOSKI (1969, 1976) and ELMGREN (1975, 1976) (see also Fig. 4). I will restrict myself here to giving a further example from a transect from Askö out towards the Landsort Deep.

The oxygen conditions in the Landsort Deep have deteriorated fairly steadily since the beginning of this century, and reached zero values around 1968 (FONSELIUS, 1969).

Since then oxygen concentrations below the halocline have remained low. There have been intermittent periods with somewhat better conditions at intermediate depths, but no major improvements (such as periodically occurs in the Bornholm basin, e.g. LEPPÄKOSKI (1969). ELMGREN (1975) described the oxygen dependent depth zonation of the meiofauna along this transect, and compared it to the very similar zonation found in the Black Sea by BACESCU (1963). Later samples from the transect have confirmed the validity of the proposed zonation (ELMGREN, unpubl.), and CEDERWALL (pers. comm.) has shown that the macrofauna, too, can be included in the same zonation (modified from ELMGREN 1975):

1. An upper zone of continuously high oxygen content, extending down to about 50 m, where both macro- and meiofauna are rich and taxonomically relatively diverse.

2. An intermediate zone, around the primary halocline, where the mean oxygen values decrease with depth and strong fluctuations occur. The macrofauna gradually disappears in this zone, and at its lower border only an occasional *Harmothoe sarsi* will be found. Most meiofauna taxa also disappear successively, and only nematodes remain abundant throughout the zone.

3. A lower, continuously oxygen-poor zone, which is virtually devoid of macrofauna and has an extremely impoverished meiofauna, generally consisting of a few thousand nematodes per square meter only. This is a bottom "desert", in the sense of ZMUDZINSKI (1977).

The biomass relationship between macro- and meiofauna along this transect is shown in Fig. 7 (based on ELMGREN, 1975 and unpublished, for meiofauna, and CEDERWALL, unpublished, for macrofauna). In the upper zone macrofauna biomass is always larger than meiofauna biomass. As the macrofauna is impoverished, while nematodes remain abundant in the intermediate zone, the ratio shifts in favour of the meiofauna, which generally dominates below about 70 m. In the deepest zone the macrofauna disappears completely, leaving the notoriously anoxia-resistant nematodes totally dominant. The stippled area in Fig. 7 is between ratio 4 and 6, and using the earlier mentioned rough estimate that meiofauna metabolic rate is 5 times higher per unit biomass, this gives an idea about where meio- and macrofauna have about equal shares of the benthic energy flow. It is clear that the relative importance of the meiofauna increases in the oxygen-poor zones, and even in the deepest basins, which are frequently totally devoid of oxygen, some nematodes seem always to be present.

Dynamics of Baltic benthos

A case study: Production of *Pontoporeia*

Very large bottom areas of fine sediment in the Gulf of Bothnia, Gulf of Finland, Gulf of Riga and the northern and central Baltic proper are dominated by one or the other of two small, congeneric, deposit-feeding amphipods, *Pontoporeia affinis* and *P. femorata* (see eg. ZENKEVITCH, 1963:315). The *Pontoporeia* community in this wider sense is probably the Baltic community with the largest areal extension. CEDERWALL (1977, in press) has recently completed a two-year study of the macrofauna production of a soft bottom at 45 m depth near Askö, and he has kindly allowed me to use his basic data for some further calculations. The two *Pontoporeia* spp. have about equal abundance and biomass at this station, and together constitute over 80 % of the shellfree macrofauna biomass. Both species basically have a two year life cycle at this station, but a few individuals survive longer and spawn only after three years.

The study is summarized in Fig. 8, which shows the variation in *Pontoporeia* biomass over the two years (B, bottom), and the variations in production (P, where black is somatic production and white is release of young by the females) and elimination (E),
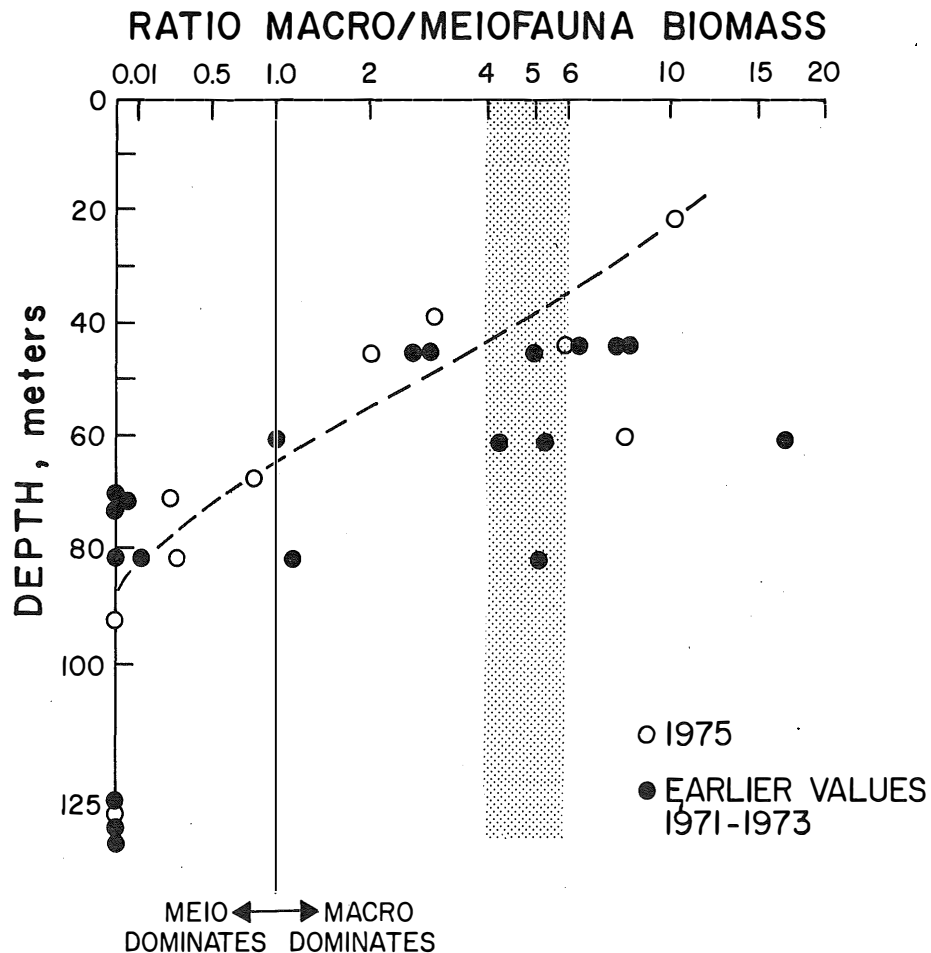
RATIO MACRO/MEIOFAUNA BIOMASS

Figure 7

Macro- to meiofauna biomass ratio in a transect from Askö towards the Landsort deep (Location of most stations shown in ELMGREN, 1975). Open circles: 1975, Filled circles 1971–73. Dashed line eye-fitted to values of 1975. Further explanations: see text. Sources: meiofauna: ELMGREN, 1975 and unpublished; macrofauna: CEDERWALL (unpublished). Note logarithmic x-axis ($\log_{10}[1 + \text{Ratio}]$).

which govern these biomass variations. Both P and E are calculated according to CRISP (1971)*. Also shown are respiration estimates (R), based on the assumption that the weight-temperature-respiration relationship determined for North American *P.*

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* my P calculations for *P. femorata* differ slightly from those of Cederwall, since I have not used his mean individual cohort weights for June, which are clearly anomalous (see CEDERWALL 1977:159, Fig. 2). Instead, I have used an average of the preceding and following weights. The resulting difference is very slight when computed as total annual production, but eliminates an impossibly high production value for the 0 group, followed by an almost as large negative production value. Both of these are clearly artifacts, due to the method of estimating individual weight from a linear log length to log weight regression, which in June is unduly influenced by the presence of large spent and moribund females, which have very low dry weights.
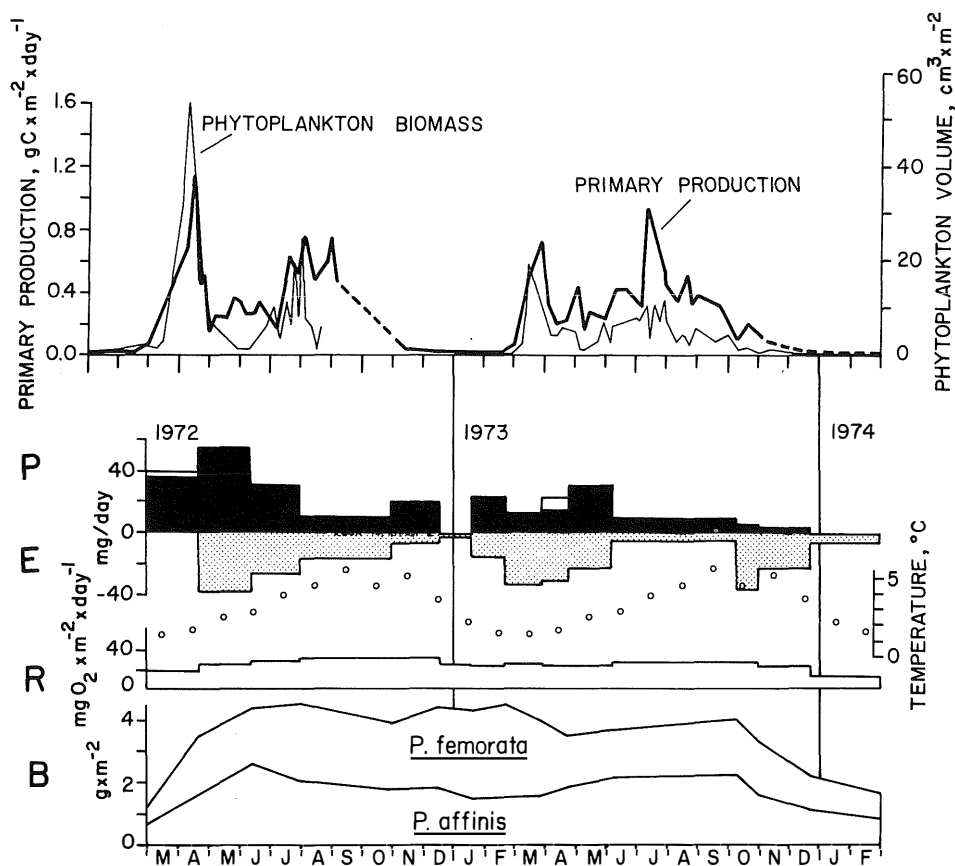
Figure 8

Pontoporeia production study. Top: Phytoplankton primary production and biomass in the Askö area (HOBRO and NYQUIST, unpublished). Below: P = Production, dry weight (black = somatic, white = egg production); E = Elimination, dry weight (stippled); R = Respiration; B = Biomass, dry weight. (Both species summed, except for biomass where P. *affinis* alone is also given. Upper B line is sum of both species). Based on data from CEDERWALL (1977, in press, and unpublished); A generalised temperature curve for 40–50 m is also given (not actual measurements from 1973–1974).

affinis by JOHNSON and BRINKHURST (1971) is valid for both *Pontoporeia spp.* in the Baltic. The approximate mean temperatures used in this calculation are also given, and vary from 1 to 5° C. At the top of the diagram, finally, phytoplankton biomass and primary production during most of the two years of investigation are given (HOBRO and NYQUIST, pers. comm). The estimates for both species have been pooled, both for simplification, and to smooth out sampling variability.

At the start of the study, in March 1972, both *Pontoporeia* spp. had low biomass. Following the release of young by the females in March–April, individual growth was very rapid for all cohorts (CEDERWALL 1977:159, Fig. 2), resulting in a threefold increase in *Pontoporeia* biomass in only three months, in spite of the high mortality of newly released young and the total mortality of spent females. This explosive growth

seems tied to the sedimentation of the phytoplankton spring bloom to the bottom. Within weeks of its culmination as much of 40–50 % of the spring bloom reaches the bottom, much of it undecomposed (sediment trap data for later years, from HOBRO et al., in print; LARSSON, pers. comm.). During the summer the material that sinks down from the pelagic zone is both lower in quantity (about 15 % of the primary production) and of inferior quality (much lower organic carbon content, LARSSON, pers. comm., presumably it is largely zooplankton fecal pellets). This led to a decreased growth rate, and during the rest of the year most of the assimilation went to maintenance (respiration, R), while production could only keep even with elimination. There is another period of higher mortality in October–November, during the copulation period, when the ripe animals swim in the free water, exposing themselves to fish predation, and after which the males die. There was still, however, enough production to compensate for this and keep biomass high into the spring of 1973.

The phytoplankton spring bloom of 1973 was both less intense and of shorter duration than that of 1972, and we can assume that sedimentation was correspondingly lower. Thus the much higher initial population in the spring of 1973 never had a superabundance of food, individual growth was much slower, and production could barely compensate for the mortality of spent females and newly released young. During the summer of 1973 most of the assimilation was used in respiration, while production and elimination were both low and roughly balanced. During autumm und winter production ceased entirely, and even became negative, so that the high mortality connected with the copulation period led to a drastic biomass decline.

This seems to be a rather clear case of a population responding to a favourable period by increasing beyond the carrying capacity of the environment, leading to a population crash. Thus food availability, not predation pressure seems to limit the *Pontoporeia* populations studied. While annual mean biomass (B) is only slightly higher (19 %) in the first year (March '72–February'73), production (P) is 2.7 times higher. Total mortality (=elimination), on the other hand, is virtually identical in both years (up 6 % second year). Growth seems to be directly dependent on food availability, since for each cohort growth is much faster in 1972, starting at a lower, or for young of the year the same weight, but attaining a higher final weight than in 1973 (CEDERWALL 1977: Fig 2; Cederwall also gives reason to exclude temperature differences as a plausible cause for the growth differences). A comparable situation was found by ANDERSIN et al. (1977), who found that in the Bothnian Bay not only was the mean lenght of the oldest cohort of *Pontoporeia affinis* lower, but individuals of a given length were also lighter than in the Bothnian Sea. As argued earlier, the annual phytoplankton primary production and presumably also the benthic food supply is lower in the Bothnian Bay than in the Bothnian Sea.

Several interesting conclusions emerge from this study, such as:

1. The *Pontoporeia* populations seem to be primarily food limited. Only after growth rates had already declined due to food limitation could elimination, which is almost certainly mostly through predation, check or even reverse the biomass increase.

2. The benthic system is intimately coupled to the pelagic system, and may respond to events in the plankton within weeks, even at a depth of 45 metres and on a bottom where suspension-feeders are unimportant.

3. Attempts to estimate production, using P/B quotients, must be made with caution, and may be quite misleading if the population is increasing or decreasing rapidly.

Energy flow in benthic communities

In spite of the many uncertainties involved in production estimates based on indirect
methods, we have made an attempt to estimate approximately the production of the
macro- and meiofauna in the Askö-Landsort area (ANKAR and ELMGREN, 1976). A
stratified random sampling survey of the area gave us the biomass of the dominant
species or groups within the macro- and meiofauna. By using production to biomass
ratios available in the literature, or where no such data was found, number of
generations per year and life-cycle turnover ratios, derived from the theoretical
treatment of WATERS (1969), we could then derive rough production estimates for the
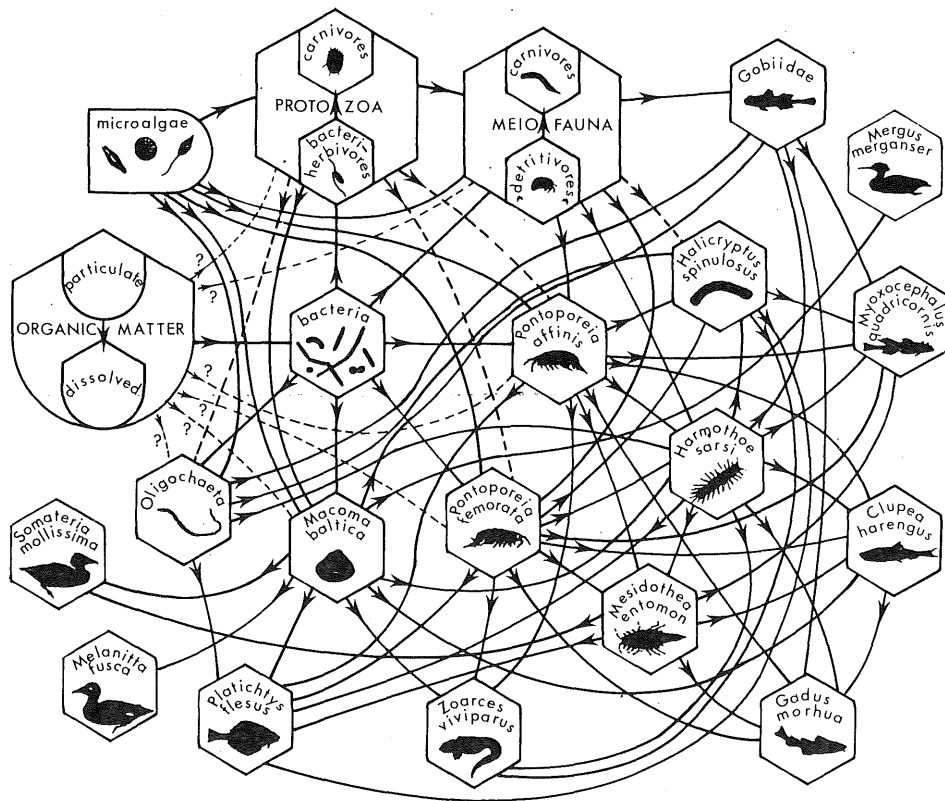various groups involved.

Figure 9

Trophic relations of dominant benthic macrofauna in the Askö-Landsort area from ANKAR (1977).
Continuous lines = documented trophic links, dashed lines = probable links. Question marks
indicate uncertainty concerning use of dissolved organic matter (probably of minor importance
for the metazoa).

A few macrofauna species together dominate the area, 4 species making up more than
90 % of the macrofauna biomass. When ARNTZ (in print) attempted a similar survey of
the Kiel Bay, he had to deal with 20 species of macrofauna and 10 species of demersal
fish. In the Askö area osmotic stress had further simplified the system, so that only
about 6 species of macrofauna and 4 of demersal fish have to be considered. In spite of
this "simplicity", the benthic food web is still extremely complicated, when all known

and probable trophic relationships are included, as shown in Fig. 9 (from ANKAR, 1977). This diagram demonstrates that even in a naturally simple ecosystem we are forced to make many further simplifications, before we can deal with the system as a whole.

After many such simplifications we could sum up our results in an Odum energy flow model (Fig. 10). The benthos was divided into planktivores (suspension-feeders), meiofauna detritivores, meiofauna predators, macrofauna detritivores (deposit-feeders) and macrofauna predators. The total sum of meiofauna production is about half that of the macrofauna in our estimate. If we sum all the production estimates (meio- + macrofauna) we get about 340 kJm^{-2}yr (roughly 7 gCm^{-2}yr), but since much of the detritivore production is used by predators within the system, only part of this is available for export, such as consumption by fish.
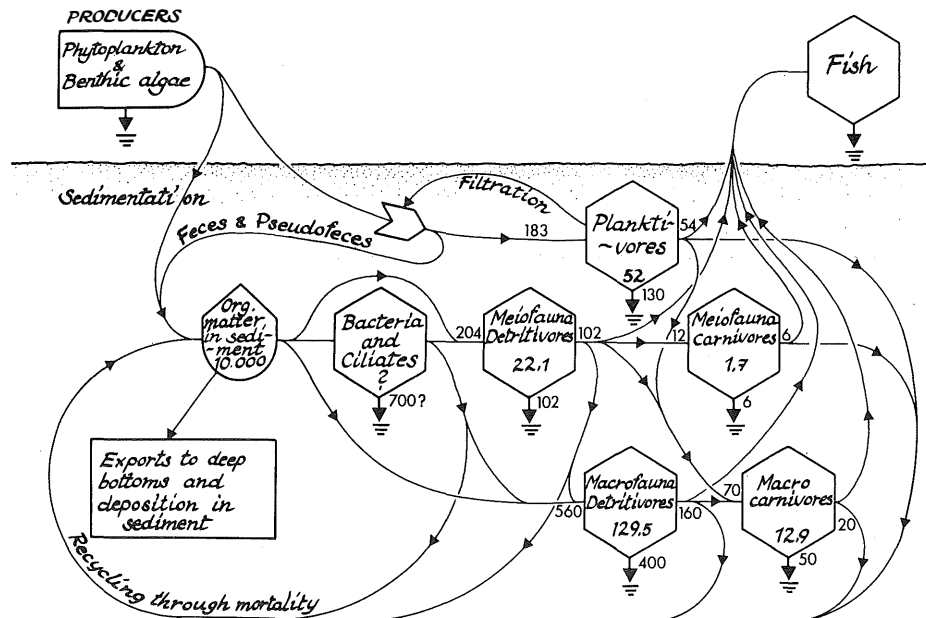

Figure 10

Rough energy flow model (Odum energy circuit language) of the benthic ecosystem of the Askö-Landsort area. Biomass measured, production estimated, respiration guessed at. Storages in kJ·m^{-2}, flows in kJ·m^{-2}·yr^{-1}. Figures to the left of the hexagons indicate assimilation (R + P). Feces and organic excretion are considered never to have left the organic pool in the sediment. (From ANKAR and ELMGREN, 1976).

Another point to emerge from the model is that with macrofauna biomasses as high as in the Askö-Landsort area, meiofauna is unlikely to supply more than a minor fraction of the total food consumption of the benthos-feeding macrofauna.

We also made an effort to estimate respiration, and thus total energy flow (as R + P), for these populations by using respiration-to-production values from literature. These speculations led to an estimated 40 gCm^{-2}yr needed to fuel the entire benthos (including bacteria and microfauna).

ANKAR (1977) has since carried these speculations even further, using instead respiration per biomass values from literature to estimate respiration. His results are slightly higher for the macrofauna, and considerably higher for the meiofauna respiration, and boosts the estimated carbon input needed to $60\,gCM^{-2}yr^{-1}$. The original respiration estimates for the meiofauna were probably too low (ELMGREN 1976:15), and the close agreement for the macrofauna increases our confidence in having reached the right order of magnitude with our calculations, but it is still impossible to say which of the two total input estimates (40 or $60\,gCm^{-2}\cdot yr^{-1}$) is the more realistic. Both figures are compatible with our estimates of primary production and sedimentation in the Askö-Landsort area. Neither calculation, therefore, runs into difficulties such as those experienced by STEELE (1974) and ARNTZ (1976), who could not find enough energy available to supply the needs of their benthos, if bacteria were included in the food web.

Interactions between macro- and meiofauna

A recurring theme in the preceding has been the idea that meiofauna populations are largely controlled by macrofauna predation. There is indeed a large number of observations to show that Baltic macrofauna and fish eat meiofauna (ELMGREN 1976:16–17) – but none of a quality to prove that this may be an important regulator of meiofauna populations. The evidence for this is largely circumstantial, such as, that in the thin mud layer on top of manganese-limonite concretions, where macrofauna is reduced because the sediment is not deep enough to burrow in, meiofauna reaches values of 2 to 3 times normal abundance and biomass (ANKAR and ELMGREN 1976: stations 2:1, 2:2 and 2:3).

We have tried to show such predation more convincingly by keeping surface mud with a natural meiofauna population in jars with varying numbers of Pontoporeia affinis (1 1/2-year old specimens) (SUNDELIN and ELMGREN, unpublished). After two months results show a decrease of small nematodes in jars with Pontoporeia (which are known to eat small nematodes), while large nematodes are unaffected (Fig. 11). From the slope of the line we can estimate a decrease of 6 small nematodes per amphipod per day. At this rate, a normal Pontoporeia population might eliminate several millions of nematodes per year. This is still not entirely convincing, however, since the conventional level of significance is not reached. Thus, while there is a lot of soft evidence, convincing proof is still elusive. Such proof is not likely to be found in evidence from field surveys, but will require experimental work, in the laboratory or the field.

Thus far we have concentrated on negative interactions between macro- and meiofauna, such as predation and competition. There are also other, more positive interactions. ANKAR (1977) has described how meiofauna is concentrated in the narrow oxidized micro-zone created around the siphons of Macoma baltica, in otherwise black, anoxic sediments. The Pontoporeia community mentioned earlier may be another example. Here 8000 small amphipods per square metre fill and empty their gut several times per day, and not unexpectedly the top two to three centimetres of sediment often consist almost entirely of Pontoporeia fecal pellets. Since Pontoporeia only ingests fine particles (ANKAR 1977, MOORE, 1977), it cannot reingest its own fecal pellets, unless these are first broken down to finer fragments. Here the millions of meiofauna may have a crucial role to play, in speeding up the breakdown of the fecal pellets through bioturbation, thus making the attached microorganisms available to Pontoporeia (cf. LEVINTON et al., 1977). Indeed, the experiments of TENORE et al. (1977) suggest that a proper balance between different size categories of the benthos is necessary for the remineralization of organic matter to proceed with maximum efficiency.
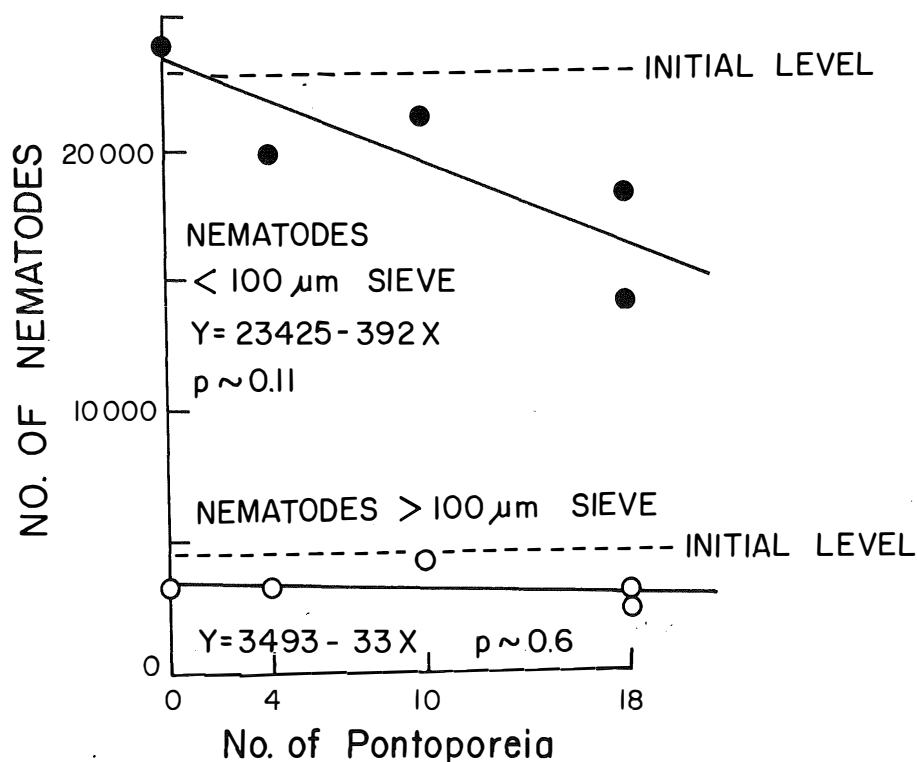
Figure 11

Changes in nematode abundance over 64 days as a function of *Pontoporeia affinis* density in jars with surface mud from 40 m depth in the Askö area. Mud area 143 cm², depth 2 cm. Initial level based on two subsamples. SUNDELIN and ELMGREN (unpublished).

Acknowledgements

References

ACKEFORS, H., L. HERNROTH and O. LINDAHL: Studies on the primary and secondary production of plankton in the Baltic. Ann. Biol. **31**, 73–75 (1976)

ARNTZ, W.: Biomasse und Produktion des Makrobenthos in den tieferen Teilen der Kieler Bucht im Jahr 1968. Kieler Meeresforsch. **27**, 36–72 (1971)

ARNTZ, W.: The "upper part" of the benthic food web: the role of macrobenthos in the Western Baltic. In: Joint Oceanographic Assembly 1976, General Symposia. Ed. by H. Charnock and G.E.R. Deacon, Plenum Press (in press)

ARNTZ, W. and D. BRUNSWIG: An approach to estimating the production of macrobenthos and demersal fish in a western Baltic *Albra alba* community. Merentutkimuslait. Julk. **239**. 195–205 (1975)

ARNTZ, W. and D. BRUNSWIG: Studies on structure and dynamics of macrobenthos in the western Baltic carried out by the joint research programme "Interaction Sea – Sea bottom" (SFB95–Kiel). 10th European Symp. Mar. Biol. Ostend, Belgium, Sept. 17–23, 1975: **2**, 17–42 (1976)

ARNTZ, W. and D. BRUNSWIG: Zonation of macrobenthos in the Kiel Bay channel system and its implications for demersal fish. Prace morsk. Inst. ryb. Gdyni. (in press)

ALHONEN, P.: The stages of the Baltic Sea as indicated by diatom stratigraphy. Acta Bot. Fennica **92**, 1–18 (1971)

ANDERSIN, A.–B., J. LASSIG, L. PARKKONEN and H. SANDLER: The decline of the macrofauna of the deeper parts of the Baltic proper and the Gulf of Finnland. Kieler Meeresforsch. Sonderh. **4**, 23–52 (1978)

ANDERSIN, A.–B., LASSIG and H. SANDLER: Community structure of softbottom macrofauna in different parts of the Baltic. In: Biology of Benthic Organisms, 7–20. Ed. by B.F. Keegan and P.O. 'Ceidigh. London: Pergamon Press (1977)

ANKAR, S.: The soft Bottom Ecosystem of the Northern Baltic Proper with Special Reference to the Macrofauna. Contr. Askö Lab. Univ. Stockholm. **19**, 1–62 (1977)

ANKAR, S. and R. ELMGREN: The benthic macro- and meiofauna of the Askö-Landsort Area (Northern Baltic proper) A stratified random sampling survey. Contr. Askö Lab. Univ. Stockholm **11**, 1–115 (1976)

BACESCU, M.: Contribution a la biocoenologie de la Mer Noire. L'etage periazoique et les facies dreissenifere. Leurs characteristiques. Rapp. P.–v. Reun. Comm. int. Explor. Scient. Mer. Mediterr. **17**, 107–122 (1963)

BECKER, K.H.: Beitrag zur Kenntnis der Copepoda Harpacticoidea Sublitoraler Weichböden in der Kieler Bucht. Kieler Meeresforsch. **26**, 56–73 (1970)

CEDERWALL, H.: Annual macrofauna production of a soft bottom in the northern Baltic proper. In: Biology of benthic organisms, 155–164. Ed. by B.F. Keegan and P.O.'Ceidigh. London: Pergamon Press (1977)

CEDERWALL, H.: Production of *Pontoporeia affinis* in the northern Baltic proper. Prace morsk. Inst. ryb. Gdyni, (in press)

CHRISTIANSEN, F.B. and T.M. FENCHEL: Theories of Populations in Biological Communites. 144pp. Berlin: Springer-Verlag (1977)

CRISP, D.J.: Energy flow measurements. In: Methods for the study of marine benthos. I.B.P. Handbook **16**, 197–279. Ed. by N.A. Holme and A.D. McIntyre. Oxford: Blackwell (1971)

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

DEMEL, K. and Z. MULICKI: Quantitative investigations on the biological bottom productivity of the South Baltic. (In Polish, with English summary) Prace morsk. Inst. ryb. Gdyni **7**, 75–126 (1954)

ELMGREN, R.: Benthic meiofauna as indicator of oxygen conditions in the northern Baltic proper. Merentutkimuslait. Julk. **239**, 265–271 (1975)

ELMGREN, R.: Baltic benthos communities and the role of the meiofauna. Contr. Askö Lab. Univ. Stockholm **14**, 1–31 (1976)

ELMGREN, R., R. ROSENBERG, A.-B. ANDERSIN, S. EVANS, P. KANGAS, J. LASSIG, E. LEPPÄKOSKI and R. VARMO: Benthic macro- and meiofauna in the Gulf of Bothnia (Northern Baltic). Prace morsk. ryb. Gdyni, (in press)

FONSELIUS, S.: Hydrography of the Baltic deep basis. III. Rep. Fish. Board Swed. ser. Hydrogr. **23**, 1–97 (1969)

GERLACH, S.A.: Die Nematodenfauna der Uferzonen und des Küstengrundwassers am Finnischen Meerbusen. Acta Zool. Fennica **73**, 1–32 (1953)

GERLACH, S.A.: Die Nematodenfauna der sublitoralen Region in der Kieler Bucht. Kieler Meeresforsch. **14**. 64–90 (1958)

GERLACH, S.A.: On the importance of marine meiofauna for benthos communities. Oecologia (Berl.) **6**, 176–190 (1971)

GRAY, J.S.: Animal-Sediment relationships. Oceanogr. Mar. Biol. Ann. Rev. **12**, 223–261 (1974)

HAGMEIER, A.: Die Bodenfauna der Ostsee im April 1929 nebst einigen Vergleichen mit April 1925 und Juli 1926. Ber. dt. wiss. Komm. Meeresforsch. **5**, 78–95 (157–173) (1930)

HESSLE, C.: Bottenboniteringar i inre Östersjön. Medd. Kung. Lantbruksstyr. **250**, 1–51 (1924)

HOBRO, R., U. LARSSON and F. WULFF: Dynamics of a phytoplanton spring bloom in a coastal area of the Northern Baltic. Prace morsk. Inst. ryb. Gdyni, (in press)

JANSSON, B.–O.: Ecosystem Approach to the Baltic Problem. Bull. Ecol. Res. Comm. NFR **16**, 1–82 (1972)

JANSSON, B.-O.: The Baltic – A systems analysis of a semi-enclosed sea. In: Joint Oceanographic Assembly 1976. General Symposia. Ed. by H. Charnock and G.E.R. Deacon, Plenum Press (in press)

JOHNSON, M.G. and R.O. BRINKHURST: Production of benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish Res. Bd. Canada **28**, 1699–1714 (1971)

LAPPALAINEN, A. and P. KANGAS: Species diversity of macrofauna in a *Zostera marina* community in Tvärminne, Finland. Merentutkimuslait. Julk **239**, 316–324 (1975)

LEPPÄKOSKI, E.: Transitory return of the benthic fauna of the Bornholm Basin, after extermination by oxygen insufficiency. Cah. Biol. Mar. **10**, 163–172 (1969)

LEPPÄKOSKI, E.: Kökarrännan – en utpost for bottendjur? (In Swedish, with English summary) Husö Biol. Stat. Medd. **18**, 23–28 (1976)

LEVINTON, J.S., G.R. LOPEZ, H. H. LASSEN and U. RAHN: Feedback and structure in deposit feeding marine benthic communities. In: Biology of benthic organisms, 409–416. Ed. by B.F. Keegan and P. O.'Ceidigh. London: Pergamon Press (1977)

LUKSENAS, YU. K.: Zoogeographical complexes of benthic invertebrates in the southern parts of the Baltic. Oceanology **7**, 516–521 (1967)

LUKSENAS, YU. K.: Biocoenoses and trophic groups of bottom invertebrates in the southern part of the Baltic Sea. Oceanology **9**, 866–874 (1969)

McARTHUR, R.H.: Patterns of species diversity. Biol. Rev. **40**, 510–533 (1965)

MESKUS, E.: The primary production of phytoplankton in the northeastern Bothnian Bay. Acta Univ. Oul. A. **42**. Biol. **3**, 55–62 (1976)

MILLS, E.L.: The community concept in marine zoology, with comments on continua and instability in some marine communities: a review. J. Fish. Res. Bd. Canada **26**, 1415–1428 (1969)

MOORE, J.W.: Importance of algae in the diet of subarctic populations of *Gammarus lacustris* and *Pontoporeia affinis*. Can. J. Zool. **55**, 637–641 (1977)

NOODT, W.: Zur Ökologie der Harpacticoidea (Crust. Cop.) des Eulitorals der Deutschen Meeresküste und der angrenzenden Brackgewässer. Z. Morph. u. Ökol. Tiere **46**, 149–242 (1957)

NOODT, W.: Zur Ökologie der Copepoda Harpacticoidea des Küstengebietes von Tvärminne (Finnland). Acta Zool. Fenn. **128**, 1–35 (1970)

PETERSEN, C.G.J: Havets Bonitering II, Beretning til Landbrugsministeriet fran den Danske Biologiske Station, **21**, 1–68 (1913)

PETERSEN, C.G.J. and P. BOYSEN JENSEN: Havets Bonitering I. Beretning til Landbrugsministeriel fra den Danske Biologiske Station, **20**, 1–77 (1911)

REMANE, A.: Verteilung und Organisation der benthonischen Mikrofauna der Kieler Bucht. Wiss. Meeresunters. Kiel **21**, 161–221 (1933)

REMANE, A.: Die Brackwasserfauna. Verh. dt. Zool. Ges. 34–74 (1934)

REMANE, A.: Einführung in die zoologische Ökologie der Nord- und Ostsee. Tierw. Nord- u. Ostsee **Ia**, 238pp (1940)

REMANE, A.: Ökologie des Brackwassers. Die Binnengewässer **22**, 1–216 (1958)

ROSENBERG, R., K. NILSSON and L. LANDNER: Effects of a sulphate pulp mill on the benthic macrofauna in a firth of the Bothnian Sea. Merentutkimuslait. Julk. **239**, 289–300 (1975)

SCHEIBEL, W.: Quantitative Untersuchungen am Meiobenthos eines Profils unterschiedlicher Sedimente in der Westlichen Ostsee, Helgoländer wiss. Meeresunters. **28**, 31–42 (1976)

SEGERSTRÅLE, S.G.: Studien über die Bodentierwelt in südfinnländischen Küstengewässern. I & II Soc. Scient. Fenn. Comm. Biol. **4**, (8), 1–64 and (9), 1–79 (1933)

SEGERSTRÅLE, S.G.: Baltic Sea. Mem. Geol. Soc. Am **67**, 757–800 (1957)

STEELE, J.H.: The structure of marine ecosystems. 128pp. Oxford: Blackwell (1974)

STEPHENSON, W., W.T. WILLIAMS and S.D. COOK: Computer Analyses of Petersen's Original Data on Bottom Communities. Ecol. Monogr. **42**, 387–415 (1972)

TENORE, K.R., J.H. TIETJEN and J.J. LEE: Effect of meiofauna on incorporation of aged Eelgrass, *Zostera marina*, detritus by the Polychaete, *Nephtys incisa*. J. Fish. Res. Bd. Canada **34**, 563–567 (1977)

THIEL, H.: The size structure of the deep-sea benthos. Int. Revue ges Hydrobiol. **60**, 575–606 (1975)

THULIN, G.: Bottenboniteringar i södra Östersjön i samband med fisktrålningar. Sv. Hydrogr.-biol. Komm. Skr. **7**, 1–9 (1922)

WATERS, T.F.: The turnover ratio in production ecology of freshwater invertebrates. Am. Naturalist **103** (930), 173–185 (1969)

WEFER, G. and G.F. LUTZE: Benthic Foraminifera biomass production in the Western Baltic. Kieler Meeresforsch. Sonderheft **3**, 76–81 (1976)

WULFF, F., C. FLYGH, M. FOBERG, S. HANSSON, S. JOHANSSON, H. KAUTSKY, T. KLINTBERG, H. SAMBERG, K. SKÄRLUND, T. SÖRLIN and B. WIDBOM: Ekologiska Undersökningar i Luleå Skärgård 1976. Slutrap. Statens Naturvårdsverk, kontrakt 5860401–8. 322pp. Stockholm: Univ. Stockholm (Mimeo) (1977)

ZENKEVITCH, L.A.: Biology of the seas of the U.S.S.R., (transl. from Russian by S. Botcharskaya). 955pp. London: Allen and Unwin (1963)

ZMUDZINSKI, L.: The Baltic deserts. Ann. Biol. **32**, 50–51 (1977)