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The decline of macrofauna in the deeper parts of the Baltic proper and the Gulf of Finland*)

A.-B. Andersin, J. Lassig, L. Parkkonen and H. Sandler

Institute of Marine Research, Helsinki, Finland

Abstract

An attempt is made to describe the large-scale changes in the benthic soft bottom macrofauna in the deep parts of the Bornholm Basin, the Gulf of Gdańsk, the Central Basin and the Gulf of Finland, from the beginning of Baltic zoobenthos research to the present day. The authors also try to correlate these changes with fluctuations in the oxygen content and salinity in near-bottom water layers. The paper surveys the literature and presents recent, earlier unpublished results.

During the later part of last century and the first decades of the twentieth century no area of the Baltic Sea seems to have been totally devoid of macrofauna. Unfortunately there are considerable gaps in our knowledge of the time before the middle of this century. The most striking decline has taken place, generally speaking, after the exceptionally great inflow in 1951–1952, and the subsequent prolonged stagnation.

The first records of "dead" bottoms in the Bornholm Basin are from 1948, when no macrofauna was recorded below 80 m. Records from 1954 show that the deepest parts of the Eastern Gotland Basin and the deep area between Öland and Gotland were devoid of macrofauna at that time, but that the deep areas of the northernmost Baltic proper and the Gulf of Finland were still populated.

The change continued, and during the 1960s the communities dominated by lamellibranchs in the Bornholm and Gdańsk Deeps disappeared, and were subsequently replaced by polychaete cummunities. These have been wiped out during periods of bad oxygen conditions, but quickly re-established when conditions had improved. The lamellibranch community has not been restored. In the Northern Central Basin and the Gulf of Finland the depopulation of the deep bottoms probably began later, in the late 50s. In the 70s practically no macrofauna has been recorded below the permanent halocline in the Central Basin (except the southernmost parts of it) and the Gulf of Finland.

During the 60s and 70s the area with periodically unfavourable oxygen conditions has covered about 100000 km^2, which is c. 25 % of the total area of the Baltic Sea.

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Zusammenfassung

Die Abnahme der Makrofauna in den tiefen Bereichen der eigentlichen Ostsee und des Finnischen Meerbusens

Es wird der Versuch unternommen, die großräumigen Veränderungen der Weichboden-Makrofauna in den tiefen Bereichen des Bornholm-Beckens, der Danziger Bucht, des Zentralbeckens der Ostsee und des Finnischen Meerbusens von den Anfängen der Zoobenthosforschung bis zur Gegenwart zu beschreiben. Die Autoren versuchen außerdem, diese Änderungen mit den Schwankungen des Sauerstoffgehaltes und Salzgehaltes in den bodennahen Wasserschichten zu korrelieren. Die Arbeit gibt einen Überblick über die Literatur und präsentiert neue, bisher unveröffentlichte Ergebnisse.

Im letzten Teil des vergangenen und in den ersten Jahrzehnten des zwanzigsten Jahrhunderts scheint kein Bereich der Ostsee völlig frei von Makrofauna gewesen zu sein. Leider sind unsere Kenntnisse über die Zeit vor der Mitte dieses Jahrhunderts recht lückenhaft. Insgesamt ist die auffälligste Abnahme der Makrofauna nach dem 1951–1952 erfolgten außergewöhnlich starken Wassereinstrom und der darauf folgenden verlängerten Stagnation eingetreten.

Die ersten Angaben über „toten" Meeresboden im Bornholm-Becken sind aus dem Jahre 1948, als keine Makrofauna mehr unterhalb von 80m Tiefe registriert wurde. Angaben aus dem Jahre 1954 zeigen, daß die tiefsten Teile des östlichen Gotlandbeckens und der Tiefenbereich zwischen Öland und Gotland zu der Zeit frei von Makrofauna waren. Die tiefen Bereiche des nördlichsten Teils der eigentlichen Ostsee und der Finnische Meerbusen waren aber noch besiedelt.

Die Veränderung dauerte an, und während der sechziger Jahre verschwanden die von Muscheln dominierten Gemeinschaften im Bornholm-Becken und im Danzig-Tief und wurden darauf durch Polychaeten-Gemeinschaften ersetzt. Diese wurden während der Perioden mit schlechten Sauerstoffbedingungen ausgelöscht, wurden aber schnell wiederhergestellt, wenn die Verhältnisse sich besserten. Die Lamellibranchier-Gemeinschaft wurde nicht wiederhergestellt. Im nördlichen Zentralbecken und im Finnischen Meerbusen begann die Verarmung in der Besiedlung der tiefen Böden später, Ende der fünfziger Jahre. In den siebziger Jahren wurde unterhalb der dauerhaften Salzgehaltssprungschicht im Zentralbecken (außer in den südlichsten Teilen) und im Finnischen Meerbusen praktisch keine Makrofauna mehr registriert.

Während der sechziger und siebziger Jahre nahm der Bereich mit periodisch ungünstigen Sauerstoffbedingungen etwa 100000 km² ein, was etwa 25% der gesamten Fläche der Ostsee entspricht.

Introduction

In the history of marine biological work in the Baltic Sea, the benthic macrofauna was one of the first parameters studied. This presentation is an attempt to describe the large-scale changes in the benthic macrofauna communities during the last 100 years in those parts of the Baltic Sea where stagnation has resulted in permanently or periodically unfavourable oxygen conditions. Such conditions have occurred in the subhalocline areas of the Baltic proper and the Gulf of Finland; the isolated Gulf of Bothnia has a different hydrographical regime, and its oxygen conditions have not been critical.

The Institute of Marine Research, Helsinki (IMR) started zoobenthic studies in the Baltic in 1954, on the first expedition of the research vessel Aranda. After being discontinued for a while, the studies were resumed in 1961 at the recommendation of ICES.

Hydrography

The inflow of saline water from the North Sea into the Baltic Sea has been studied by several scientists since the later half of the nineteenth century (e.g. JACOBSEN 1873, EKMAN and PETTERSSON 1893, PETTERSSON and EKMAN 1897, GEHRKE 1910, WITTING 1912, KALLE 1943, WÜRTKI 1954, MANKOWSKI 1958, FONSELIUS 1962, 1967, 1969, 1975, SOSKIN 1963, FONSELIUS and RATTANASEN 1970, NEHRING and FRANCKE 1971, MATTHÄUS 1972, 1973). The compilations by FONSELIUS (see above) for the Baltic proper and the Gulf of Bothnia, and by BUDANOVA (1972) for the Gulf of Finland deserve special mention, since they cover the period from the turn of the century right up to recent times.

The increasing trend of salinity, the decrease in the oxygen content, and the duration of the stagnation periods, especially the last two factors, have been of decisive importance for the changes in the bottom fauna communities in the deep areas of the Baltic Sea during the present century. Figs. 1 and 2 include the salinity and oxygen diagrams of FONSELIUS (1962) for the Bornholm Deep and the Gotland Deep with additional data for recent years. The diagrams for the Bornholm Deep have also been supplemented with data from the period 1900–1938 (GEHRKE 1910, SCHULZ 1956). Corresponding diagrams have been prepared for the Gdansk Deep, station BCS III-10 in the southernmost part of the Central Basin, station F 74 in the Northern Central Basin and station LL 7 in the Gulf of Finland (Figs. 1, 2 and 3).

Inflows of saline water cause rapid changes in the hydrographical conditions of the Bornholm Basin, while only the greatest inflows have marked effects in the Gotland Deep and the Northern Central Basin. In the Gulf of Finland the effects of such inflows are still less pronounced. The irregularities seen in the diagram for the Gulf of Finland (Fig. 2) may be explained by movements of the halocline caused by changing meteorological conditions (see PALMEN 1930).

On the whole, the oxygen level was higher at the end of last century and during the first half of the present century than during subsequent years. In the Bornholm Basin GEHRKE (1910) noted very low oxygen values at the end of the period 1902–1907, but the duration of the periods with critical oxygen conditions was only a few months. Scattered data from the years 1925–1938 indicate that at that time the oxygen conditions in the Bornholm Basin were generally very good, but signs of stagnation could be seen in 1931 and 1937 (SCHULZ 1956). The first records on the oxygen content in the Gotland Deep are from 1893, when concentrations of about 1 ml/l were noted (PETTERSSON and EKMAN 1897). However, none of the values record before World War I were below 1 ml/l. In the 1902s very low oxygen values were recorded (cf. Fif. 2), but it was not until 1931 that hydrogen sulphide (H_2S) was first observed in the Gotland Deep (GRANQVIST 1932). This was the consequence of a period of stagnation extending from 1922 right up to 1933 (cf. KALLE 1943, FONSELIUS and RATTANASEN 1970).

The only data available from the time of World War II are sporadic records on the salinity in the Bornholm Basin. Hydrographic investigations started again in the late 1940s in the southern and central Baltic. The data from that time do not indicate that any drastic changes had occurred during the war.

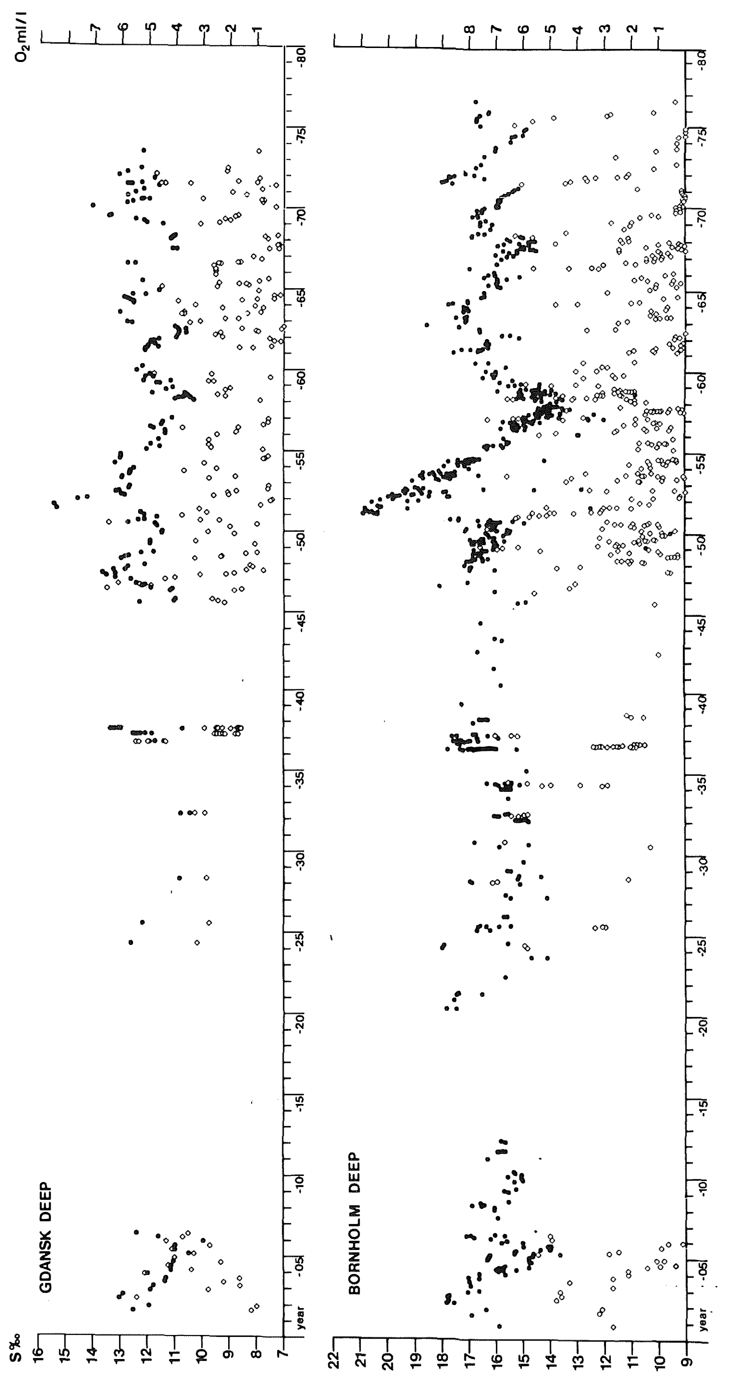


Figure 1

Salinity (●) and dissolved oxygen (◇) values recorded for the Bornholm Deep (below 80 m) in 1901–1977 and the Gdansk Deep (below 90 m) in 1902–1974

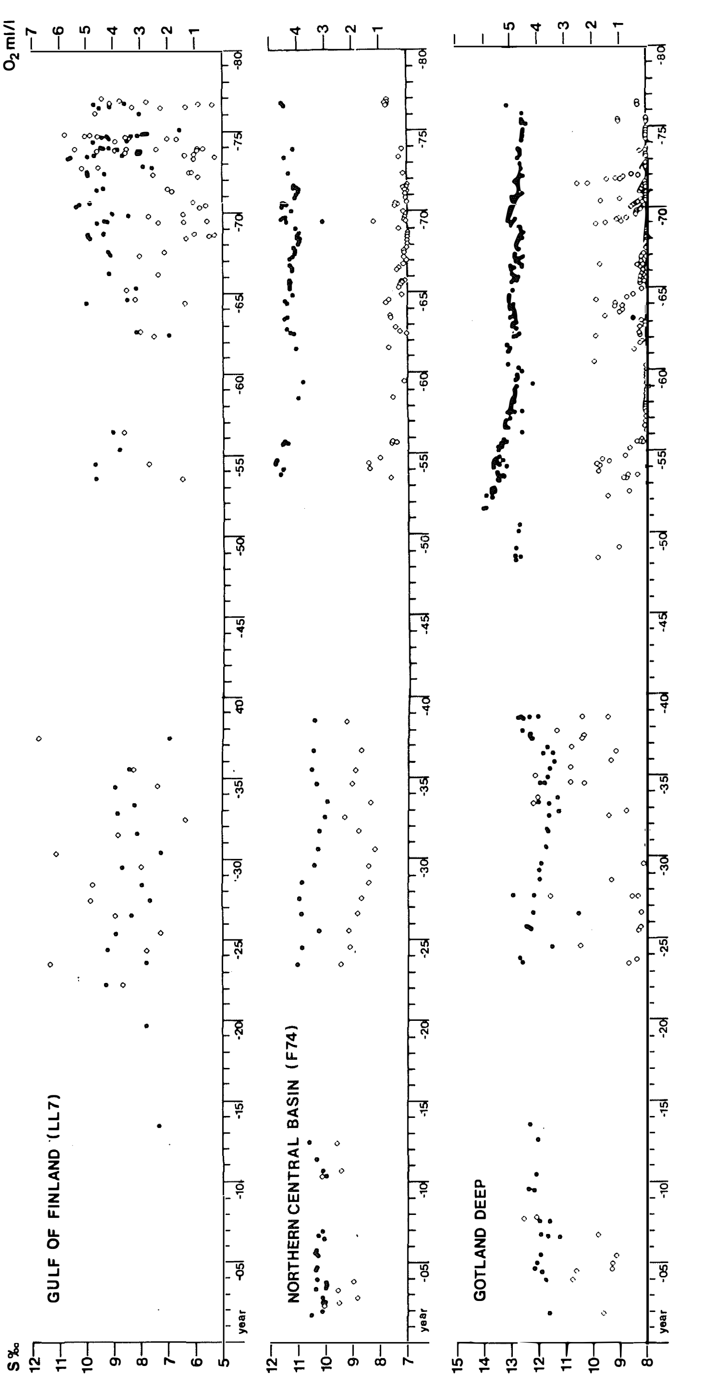


Figure 2

Salinity (●) and dissolved oxygen (◇) values recorded for the Gotland Deep (c. 200 m) in 1902–1977, the Northern Central Basin (below 150 m) in 1902–1977 and the Gulf of Finland (80 m) in 1914–1977

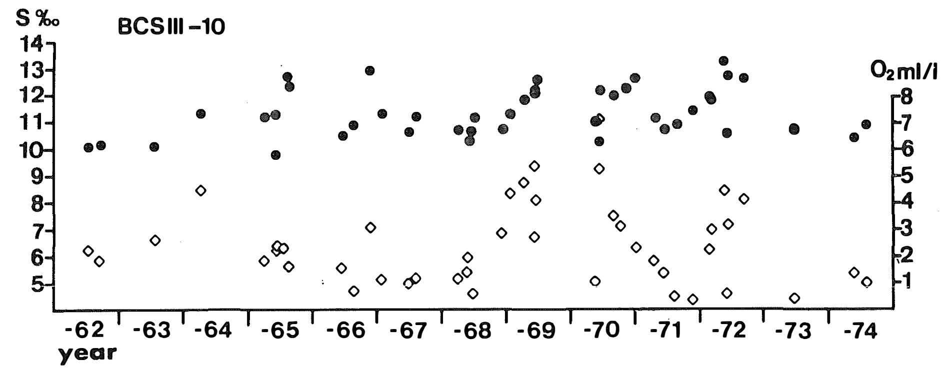


Figure 3

Salinity (●) and dissolved oxygen (◇) values recorded for the southernmost part (station BCS III–10) of the Central Basin (c. 90 m) in 1962–1974

The greatest saline water inflow to the Baltic Sea ever registered took place in 1951 (cf. WÜRTKI 1954). This inflow was followed by prolonged stagnation, which caused an oxygen deficit in all the deep basins in the Baltic proper (Figs. 1 and 2, see also FONSELIUS 1969). In the Bornholm Basin anoxic conditions were recorded in 1953 and 1954 (Fig. 1), but unfortunately no data are available on the occurrence of H_2S. In the Gotland Deep H_2S was not observed until 1957, and did not disappear until 1961 (FONSELIUS and RATTANASEN 1970). Although considerable inflows have been observed later, none of them has been large enough to raise the oxygen concentrations to the same level as before 1951. Figure 4 shows the largest area covered with H_2S during each of the years 1963–1975. Both in the Bornholm Basin and in the Gotland Deep H_2S was formed in 1963, although it disappeared again in 1964 and did not reappear until 1966. Since that time the periods with oxic conditions in the deeps have been very short. The most unfavourable oxygen conditons were recorded in 1968, 1969 and 1972. In 1969, 1970 and 1972 the area with H_2S even extended far into the Gulf of Finland. In 1973 and 1974 a clear improvement could be seen due to a large inflow registered in the Arkona Basin in April 1972 (FILARSKI 1974). After a decline in 1975 the oxygen conditions improved due to a series of inflows that began late in 1975 (TIEWS 1976, 1977, ENGSTRÖM 1977a, 1977b, 1977c, FONSELIUS 1977, NEHRING 1977).

Material and the methods of the Institute of Marine Research, Helsinki

The information for the time before 1954 was obtained exclusively from the literature. For the periods 1954–1956 and 1961–1964, data from the literature were supplemented with material obtained at the IMR from the northern part of the Baltic proper and the Gulf of Finland. From 1965 onwards, the descriptions of the benthos communities in all the deep basins are chiefly based on the material of the IMR.

The material collected at the IMR from the northern and central Baltic proper, including the Gulf of Finland, covers the period 1954–1977, while the material from the southern Baltic proper covers the period 1965–1974. Since the main aim of this article is to describe the long-term changes in the deep areas of the Baltic Sea, only those deep stations have been included that are situated in areas for which reference material is available from earlier times (Fig. 5).

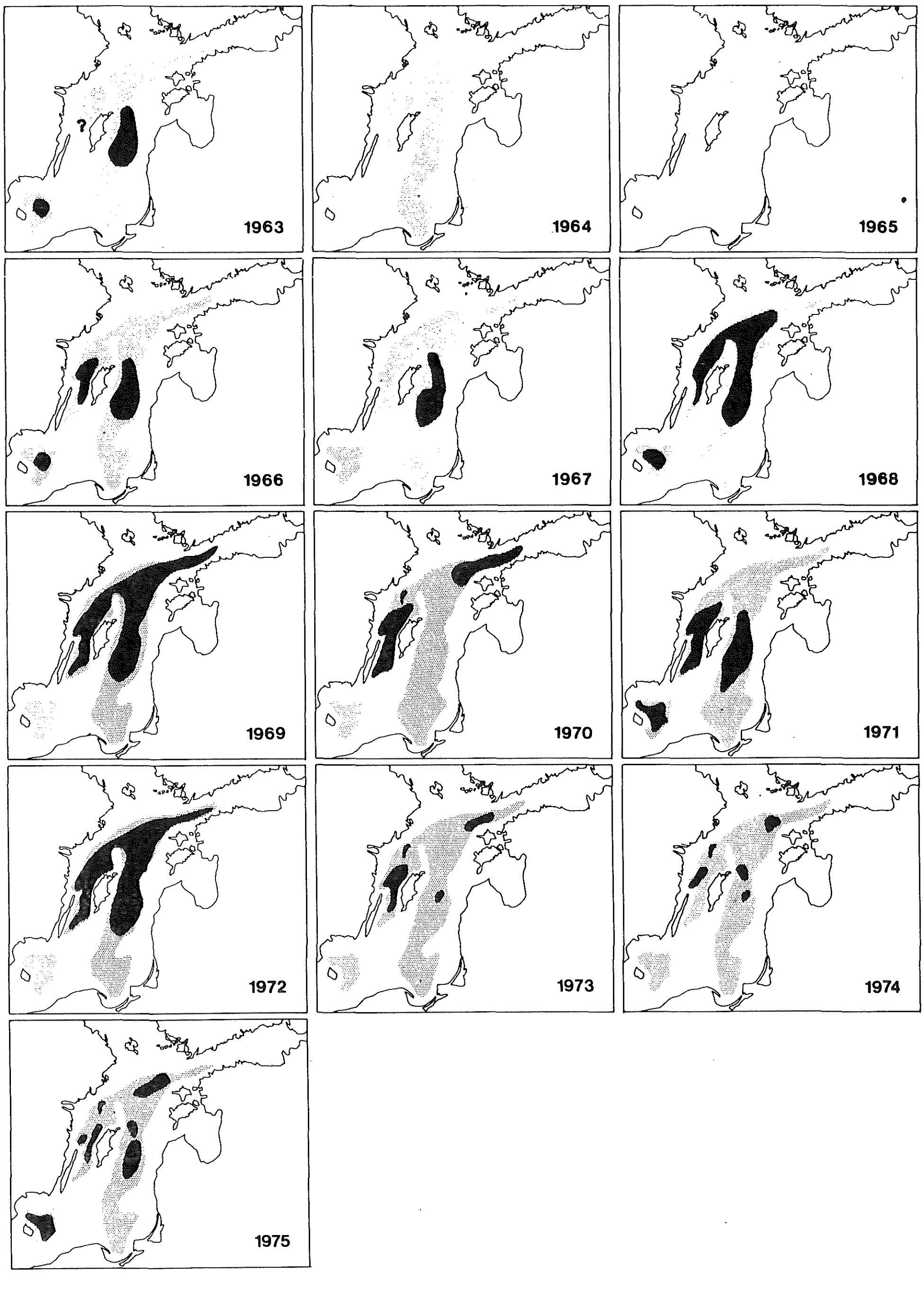


Figure 4

The occurrence of hydrogen sulphide (black areas) in the Baltic deep basins during the period 1963–1975. The shading indicates the areas where the oxygen concentration of the bottom water has been below 2 ml/l. The figure shows the most unfavourable conditions for each year

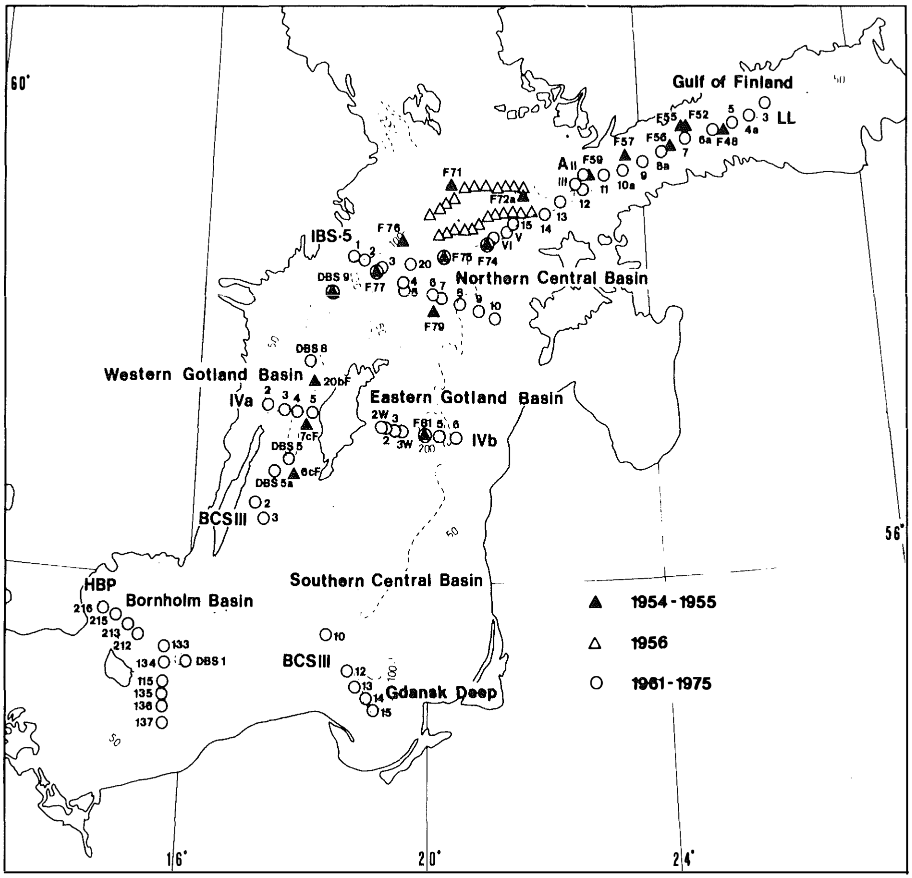


Figure 5

Thw zoobenthos sampling stations of the Institute of Marine Research (Helsinki) in the deep areas of the Baltic proper and the Gulf of Finland

The sampling was carried out on board the R/V Aranda, except for the cruise in March – April 1967 when an opportunity was kindly provided for sampling in the southern Baltic on board the R/V Alkor of the University of Kiel. Sampling was mostly performed only once a year. The samples were taken with a 0.1 m^2 van Veen grab, except at four stations in 1955, when a 0.1 m^2 Petersen grab was used. The samples were washed through a 1 mm sieve. The methods used accord fairly well with the recommendations given by the Baltic Marine Biologists (BMB) (DYBERN et al. 1976). In the period 1954–1956, 1–2 samples were taken per station, in 1961–1972, generally 3 samples, and from 1973 onwards 3–10 samples. The samples were stored in formalin. From 1961 onwards the formalin concentration was 4 % (4 parts concentrated formaldehyde solution and 96 parts fresh water). During the period 1961–1967 the formalin was buffered with borax ($Na_2B_4O_7 \cdot 10H_2O$), and from 1968 onwards with hexamine ($C_6H_{12}N_4$). (For more detailed information on the method, see ANKAR et al., in press.)

Changes in the zoobenthos communities

The following descriptions trace the large-scale changes in the zoobenthos communities of the deep areas of the Baltic proper and the Gulf of Finland since the days of MÖBIUS (1873) and BRAUN (1884).

Bornholm Basin

The information available from the beginning of macrofauna research to World War II indicates that at that time the deep areas of the Bornholm Basin were inhabited by a polychaete-lamellibranch community (Table 1). This type of community was first observed during the Pommerania expedition in 1871 (MÖBIUS 1873). Observations in 1907 (JOHANSEN 1918) and 1908 (KNIPOVIČ 1909, SKORIKOW 1910) likewise reveal a polychaete-lamellibranch community in the Bornholm Basin, although the oxygen content of the deep water had been very low in 1905 and 1906 (Fig. 1). The first quantitative investigations in the Bornholm Basin were carried out in 1921 (THULIN 1922), and further quantitative studies followed in 1925 (HERTLING 1928, see also HAGMEIER 1926) and 1929 (HAGMEIEIER 1930). Below 80 m the abundance values were dominated by *Scoloplos armiger* in 1921 and 1925, and by *Macoma calcarea* in 1929. As regards the biomass, *M. calcarea* was dominant in 1921 and 1929, and presumambly also in 1925, although no biomass values were given for that year.

Unfortunately there was a long gap in the investigations through the 30s and World War II. During the later half of this century the oxygen conditions in the water layer above the bottom have shown rapid changes, with frequent periods of low oxygen content or even anoxic conditions (Fig. 1). The first bottom fauna investigations in this area after World War II were carried out in 1948–1950, when DEMEL and MANKOWSKI (1951) found a benthic community, impoverished, but still of the same type as before the War. The density of animals and the number of species had diminished strongly since the 20s (Table 1). The presence of young specimens of *Astarte borealis* and *Macoma calcarea* in late 1949 (DEMEL and MANKOWSKI 1951) indicated successful colonization by these lamellibranchs. Although no larger inflow was registered until late in 1951, the oxygen values remained high enough to allow a recovery of the lamellibranch population, as shown by the data for 1951–1952 (Table 1). The prolonged stagnation after the inflow in 1951 caused a deterioration of the macrobenthos. According to ZMUDZINSKI (1971), in 1956 and 1957 the area below 80 m was inhabited only by *Astarte borealis* and *Macoma baltica*. In 1961 there seems to have been new colonization by *Scoloplos armiger*, while the lamellibranchs had nearly disappeared. In late 1962 the oxygen content in the deep water was very low, and in May 1963 H_2S was recorded below 90 m (KALEIS and ALEXANDROVSKAYA 1965). When TULKKI (1965) carried out his investigation in January 1963 and January 1964 he found that the fauna below 80 m had almost disappeared.

Our conclusions regarding the period 1965–1974 are mainly based on the results of the IMR, Helsinki (Table 1 and Fig. 6). In 1964–1965 the oxygen conditions were tolerable (Figs. 1 and 4), and in 1965 strong recolonization was observed in the areas below 80 m, especially by *Scoloplos armiger* and capitellids. This was also seen in the results of LEPPÄKOSKI (1969). By July 1966, however, this polychaete community had completely disappeared. In spring 1967 a clear recovery could be observed, but on the whole the period 1967–1968 is characterized by a very sparse fauna (cf. LEPPÄKOSKI 1969). The remarkable inflow in 1968–1969 (cf. e.g. NEHRING and FRANCKE 1971) broke the prevailing stagnation, and recolonization took place in 1969–1970, first by *Harmothoe sarsi*, and later by *Scoloplos armiger* (cf. also SCHULZ 1973). In 1971, when H_2S was again formed in the Bornholm Basin in August, only remnants of the benthic

Table 1

Year	1871	1908	1921	1925	1929	1948 –49	1949 –50	1951	1952	1956	1957	1961	1963	1964
Month						XI –IV	VIII –IV	V VII	II –IV	?	?	?	I	I
No. of stations	1	1	1	1	2	9	6	7	4	13	4	4	6	6
Species														
Nemertea undet.		x	3	16	19	1	1	3	17					
Priapulus caudatus			17		1				1			x		
Halicryptus spinulosus			7	4	6		3	1				x		
Polychaeta undet.				1					2					
Harmothoe sarsi							6	1				x		
Nephtys sp.		x												
Scoloplos armiger	x	x	103	151	59	6	8	23	45			x		
Pygospio elegans									x					
Terebellides stroemi		x												
Diastylis rathkei	x	x		19	50	1	6	1	3			x		
Mesidotea entomon				1										
Pontoporeia femorata				10	9							x		
P. affinis			77											
Caprellasp.		x												
Astarte borealis	x	x			26	2	1	61	85	x	x		1	1
Macoma baltica	x		63			( )	( )							
M. calcarea		x	30	131	94	2	19	10	15	x	x	x		
Total, ind./m^2			300	333	264	12	44	100	174				1	1
Total, wet weight g/m^2			12.97		68.09			14.71	12.69	4.40	3.83	4.78	0.04	0.21

Year	1965	1965	1966	1966	1967	1967	1967	1968	1968	1969	1969	1969	1969	1969
Month	V	VI	VI	IX	III	III IV	VII	VI	VIII	III	IV	VI	X	XI
No. of stations	1	5	3	3	6	7	6	7	5	3	1	3	5	1
Species														
Nemertea undet.		1				1								
Halicryptus spinulosus		1												
Harmothoe sarsi	13	1			8	6	39	2			10	27	8	10
Scoloplos armiger	374	295				20	22	19				1	18	190
Aricidea suecica				1		1								
Pygospio elegans								1						
Capitellidae spp.	526				60	7	42					11		
Diastylis rathkei		2		1		2	1							
Pontoporeia femorata		2												
Pontoporeia affinis		4												
Astarte borealis		( )			1					( )	( )		( )	( )
Macoma baltica						1							2	
M. calcarea		( )								( )	( )		( )	( )
Total, ind./m^2	913	306	none	2	69	38	104	22	none	none	10	39	28	200
Total, wet weight g/m^2	7.45	6.83		0.01	0.27	0.47	0.96	0.17				0.51		

Year	1969	1970	1970	1970	1970	1970	1970	1970	1971	1972	1973	1974	1974
Month	XII	I	III	IV	V	VI	VII	X XI	VI	VI	VI	VI	VIII
No. of stations	5	1	5	5	5	3	5	5	3	7	2	6	3
Species													
Priapulus caudatus								2					
Polychaeta undet.										1			
Harmothoe sarsi	2	10			2	5	2			18	13	15	13
Phyllodocidae undet.											2		
Nephtys sp.												1	
Scoloplos armiger		650	234	148	108	483	154	8			82	16	1
Aricidea suecica			2										
Trochochaeta multisetosa						20					60	10	8
Pygospio elegans										2			
Capitellidae spp.						6					30	2	7
Ampharete acutifrons			2										
Terebellides stroemi										1		1	
Diastylis rathkei											2		1
Pontoporeia femorata											1		
Astarte borealis	( )	( )	( )	( )	( )		( )			2	2		
Macoma baltica										3			
M. calcarea	( )	( )	( )	( )	( )		( )						
Total, ind./m^2	2	660	238	148	110	514	156	10	none	27	192	45	30
Total, wet weight g/m^2						11,75				0.83	1.93	0.57	0.77

community were observed in May (LEPPÄKOSKI 1971) and by June no macrofauna at all was recorded below 80 m. PERSSON (1976a) made similar observations during 1970–1971 at 75 m depth in the northwestern part of the basin. Altohough the H_2S disappeared at the end of 1971, the oxygen values remained very low until the great inflow in August 1972 (Fig. 1). After this the deep area was again recolonized, first by *Harmothoe sarsi*, and later mainly by *Scoloplos armiger*, *Trochocheata multisetosa* and capitellids (i.e. *Capitella capitata* and *Heteromastus filiformis*) (cf. also PERSSON 1975, 1976a). In 1974 the fauna below 80 m deteriorated again. But PERSSON (1975) reports that at 75 m depth recolonization was still continuing in July 1974. In May 1975 the oxygen sank to zero and H_2S was registered. In June PERSSON (1976b) found no macrofauna at all at 75 m depth, and in August only *Halicryptus spinulosus* at about 80 m. In 1976 the same auther reported a polychaete community similar to that observed in 1974 in the northwestern part of the Bornholm Basin (PERSSON 1977).

Gdańsk Deep

The hydrographical changes are less pronounced in the Gdańsk Deep than in the Bornholm Deep (Fig. 1). The inflows are generally observed about three months later in this area (GLOWINSKA 1966). The oxygen values recorded below 90 m during the first half of the present century are relatively high. During the later half of this century oxygen values below 1 ml/l have frequently been recorded.

The information on the bottom fauna community in the Gdańsk Deep during the period 1871–1974 has been compiled in Table 2. The large-scale fluctuations in the community in the deepest parts of the Gulf of Gdańsk follow roughly the same pattern as the fluctuations in the Bornholm Basin. The scanty information available for the first half of the present century indicates a polychaete-lamellibranch community (MÖBIUS 1873, REIBISCH 1902, HERTLING 1928, HAGMEIER 1930, MULICKI 1938). The greatest difference from the Bornholm Basin was the numerous occurrence of *Pontoporeia femorata* in 1925 (HERTLING 1928) and in 1929 (HAGMEIER 1930). However, HAGMEIER (1926, 1930) characterizes th fauna in the deep areas of the Gulf of Gdańsk as a *Macoma calcarea* community both in 1925 and in 1929.
Unfortunately no bottom fauna investigations were carried out in this area between 1938 and 1948. When DEMEL and MANKOWSKI (1951) studied the area in 1948–1950 the lamellibranchs seemed to have almost disappeared, and as regards abundance the community was dominated by *Scoloplos armiger*. Since the oxygen values recorded below 90 m during the period 1946–1951 do not differ significantly from the values recorded in 1925–1938 (t-test), it seems that the change observed in the community structure cannot be due to a deficiency of oxygen. The results of the investigations may not be fully comparable (location of the stations, methodological differences etc.).

Table 1

Synopsis of information on the zoobenthos communities below 80 m depth in the Bornholm Basin between the late nineteenth century and the present day.

1871 Möbius (1873), 1908 Knipovic (1909) and Skorikow (1910), 1921 Thulin (1922), 1925 Hertling (1928), 1929 Hagmeier (1930, 1948–1949 and 1949–1950 Demel & Mankowski (1951), 1951 and 1952 Demel & Mulicki (1954), 1956, 1957 and 1961 Zmudzinski (1971), 1963 and 1964 Tulkki (1965), 1965 (V), 1967 (III) and 1968 (VIII) Leppäkoski (1969), 1969 (III, IV, X, XI, XII) and 1970 (I, III, IV, V, VII, X/XI) Schulz (1973), 1965 (VI), 1966 (VI, IX), 1967 (III/IV, VII), 1968(VI), 1969(VI), 1970(VI), 1971(VI), 1972(VI), 1973(VI) and 1974(VI, VIII) Institute of Marine Research (Helsinki).

Table 2

81 – 90 m

Year	1871	1901	1925	1929	1937 –38	1948	1949	1950	1951 –52	1966	1967	1968	1971	1972	1973	1974
Month										VI	VII	VI	VI	VI	VI	V
No. of stations	3	–	–	1	2	–	–	2	2	–	1	–	1	1	–	–
Species																
Nemertea undet.	x							15			14					
Priapulus caudatus								3			6		9			
Halicryptus spinulosus	x			x	8						41		12			
Harmothoe sarsi									30		46		9	9		
Scoloplos armiger	x							108	38		150		107			
Terebellides stroemi	x			x									246			
Aricidea suecica											32		3			
Oligochaeta undet.									"few"							
Mesidotea entomon				x	3						15					
Diastylis rathkei	x			x	95			3	5		69		3	3		
Pontoporeia femorata				x							333		3			
P. affinis	x															
Astarte borealis											12		20	60		
Macoma baltica	x				98			5	( )		23		9			
M. calcarea				x												
Total, ind./m^2					204			134	73		741		421	72		
Total, wet weight g/m^2				36.75					1.31		16.04		21.24	17.37		

91 – 100 m

Year	1871	1901	1925	1929	1937 –38	1948	1949	1950	1951 –52	1966	1967	1968	1971	1972	1973	1974
Month										VI	VII	VI	VI	VI	VI	V
No. of stations	–	–	–	–	3	–	1	2	2	2	2	2	2	2	–	–
Species																
Nemertea undet.					4											
Halicryptus spinulosus					2		10	18	2							
Polychaeta undet.					2											
Harmothoe sarsi									7	3	26					
Scoloplos armiger					153		150		89		556					
Aricidea suecica										3						
Terebellides stroemi					2											
Diastylis rathkei									2		3	5				
Pontoporeia femorata					13					5	3					
Macoma baltica					13		1	( )	2							
Total, ind./m^2					189		161	18	102	11	588	5	none	none		
Total, wet weight g/m^2									1.76	0,14	6.44	0.03				

101 – 110 m

Year	1871	1901	1925	1929	1937 –38	1948	1949	1950	1951 –52	1966	1967	1968	1971	1972	1973	1974
Month										VI	VII	VI	VI	VI	VI	V
No. of stations	–	1	1	2	1	2	4	1	2	1	1	1	1	1	1	1
Species																
Nemertea undet.						3										
Priapulus caudatus						10	3		5							
Halicryptus spinulosus			3	x		15	8		3							
Harmothoe sarsi		x	3	x		2	3	5	3		5			9		6
Scoloplos armiger			8	x	128	22	14		107		226				4	
Aricidea suecica				x							5	9				
Spionidae undet.			8													
Terebellides stroemi			80	x												
Mesidotea entomon		x	5	x												
Diastylis rathkei							2									
Pontoporeia femorata		x	545	156	6		3		2							
Bathyporeia pilosa			3													
Corbula gibba		x														
Macoma baltica		x				( )	3	( )	2							
M. calcarea			20	x												
Total, ind. /m^2			667		134	52	36	5	122	none	236	9	none	9	4	6
Total, wet weight g/m^2				27.64					2.75		1.88	0.07		0.34	0.01	0.19

The large inflow in 1951 was registered in the Gdańsk Deep in the spring of 1952. After this inflow the oxygen content of the deep waters decreased (Fig. 1). Unfortunately, little information is available on the benthic macrofauna in the 1950s. The information from 1956 and 1957 on the animals below 80 m is not differentiated for depth regions, but the biomass values (1.58 and 0.07 g/m²) (ZMUDZINSKI 1971) indicate that the fauna was relatively poor. The average biomass value reported by ZMUDZINSKI (1971) for 1961 (4.28 g/m²) is considerably higher. This improvement in the bottom fauna can be correlated with an improvement in the oxygen conditions, due to a series of inflows that started in 1958 (cf. ANTONOV 1962). It is regrettable that no information on bottom fauna is available for the following years. It seems probable that the deepest bottoms were completely depopulated in 1963–1964, since anoxic conditions were recorded in 1963 (see Fig. 1). The next information available on the bottom fauna in this area is from 1965–1966, when very low biomass values (0.16 g/m²) were reported below 80 m (ZMUDZINSKI 1971). The results of the IMR from June 1966 show a very poor fauna below 90 m. The recovery in 1967 was much more pronounced in the Gdańsk Deep than in the Bornholm Basin, and a fairly dense *Scoloplos armiger* population was recorded below 80 m (see also ZMUDZINSKI 1971). Both the results of the IMR 1968 and those reported by ZMUDZINSKI (1971) from 1968 and 1969 show a clear deterioration of the fauna. The next visit by the R/V Aranda to the stations in the Gdańsk Deep was made in June 1971. At that time no macrofauna at all was found below 90 m depth (cf. the Bornholm Basin, Fig. 6). Although relatively high oxygen values were recorded when the benthos was sampled in 1972–1974, no signs were observed of a recovery of the bottom fauna below 90 m.

Central Basin

The vast Central Basin fairly continues, without any very pronounced sills between its different parts. It is generally divided in three larger sub-basins, the Eastern Gotland Basin, the Northern Central Basin and the Western Gotland Basin (Fig. 5) (cf. Fonselius 1969).

Eastern Gotland Basin

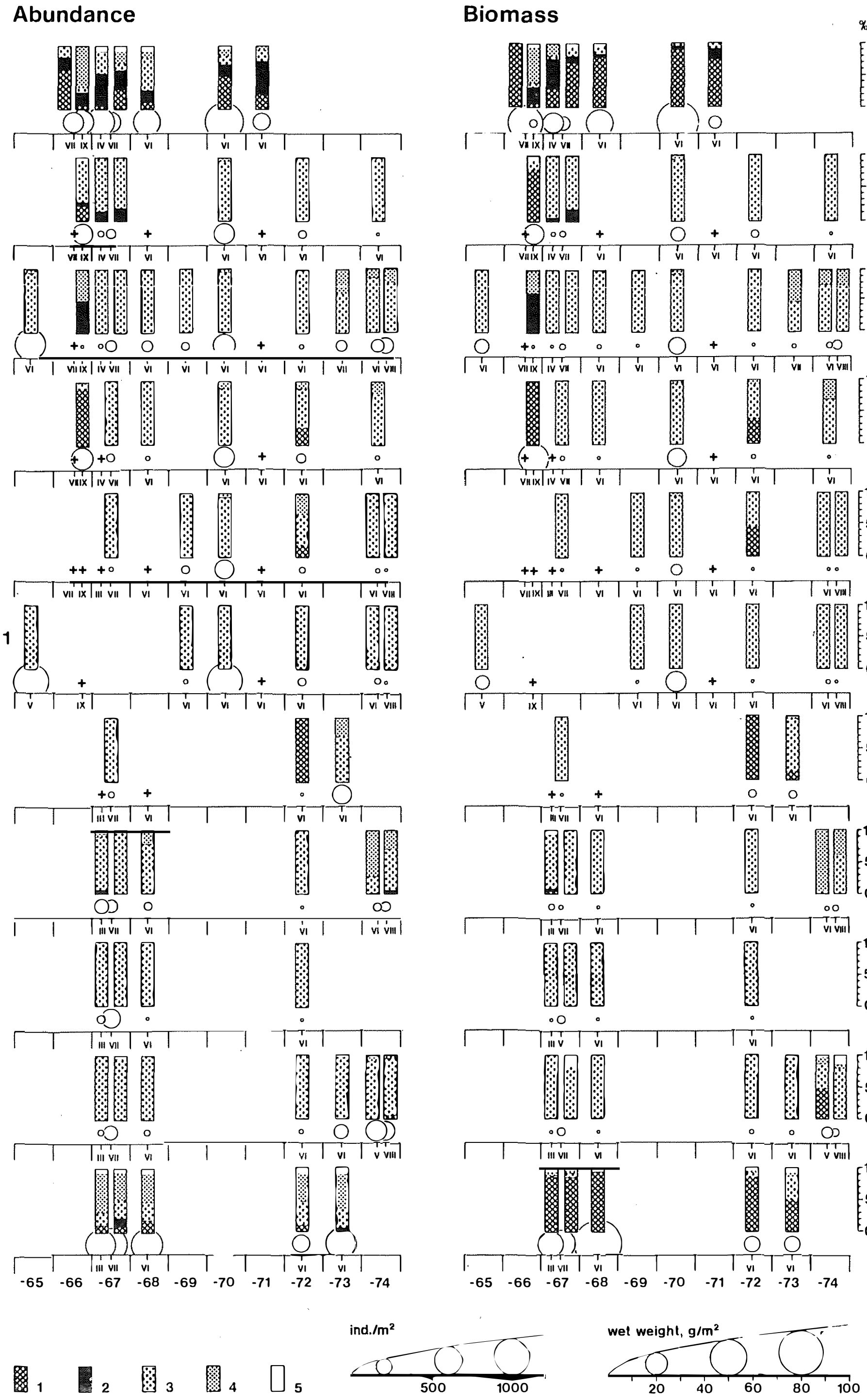
In this huge basin both the hydrographic and depth conditions differ widely between the southern and northern parts. In this paper the Eastern Gotland Basin is represented by two different areas, one situated in the southernmost part of the basin, and the other around the Gotland Deep.

The southernmost part of the Eastern Gotland Basin is represented by station BCS III-10 (Fig. 5). The hydrographical data for the period 1962–1974 (Fig. 3) indicate both higher and more fluctuating oxygen concentrations in this area than in the deeper central and northern parts of the Eastern Gotland Basin (Fig. 2). The earliest information on the bottom fauna of this area is given by KNIPOVIČ (1909), who reported a rich fauna at about 100 m depth in 1908 (see also Skorikow 1910), with very abundant

Table 2

Synopsis of information on the zoobenthos communities in different depth regions in the Gdańsk Deep between the late nineteenth century and the present day.

1871 Möbius (1873), 1901 Reibisch (1902), 1925 Hertling (1928), 1929 Hagmeier (1930), 1937–1938 Mulicki (1938), 1948, 1949 and 1950 Demel & Mankowski (1951), 1951 and 1952 Demel & Mulicki (1954), 1966–1968 and 1971–1974 Institute of Marine Research (Helsinki).


Abundance
Biomass
%
216
54 m
215
80 m
213
80 m
212
84 m
133
94 m
DBS1
90 m
134
92 m
115
81 m
135
83 m
136
73 m
137
57 m
-65 -66 -67 -68 -69 -70 -71 -72 -73 -74
ind./m²
500 1000
wet weight, g/m²
20 40 60 80 100
1 2 3 4 5

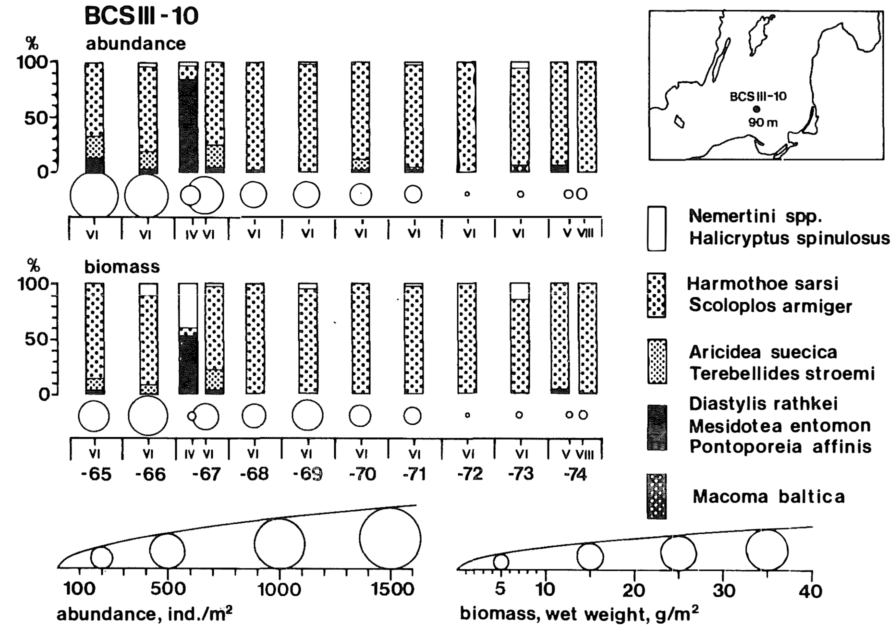


Figure 7

Abundance, biomass and composition of the benthic macrofauna in the southernmost part of the Central Basin during the period 1965–1974 according to the results of the Institute of Marine Research (Helsinki)

Halicryptus spinulosus, *Harmothoe sarsi*, *Terebellides stroemi* and Amphipoda (most probably *Pontoporeia* spp.). The first quantitative investigations were carried out around 1950, when the abundance recorded was about 250 ind./m^2 (DEMEL and MANKOWSKI 1951, DEMEL and MULICKI 1954). In 1949 DEMEL and MANKOWSKI (1951) found a community at 87 m in which *Scoloplos armiger* composed 85 % of the abundance. In 1952 DEMEL and MULICKI (1954) observed a community at 103 m in which *Scoloplos armiger* made up about 50 % of the abundance, and *Pontoporeia femorata* nearly 50 %, while *Macoma baltica* clearly dominated in the biomass.

The data obtained at the IMR on the macrofauna in this area during the period 1965–1974 are presented in Fig. 7. The most striking feature is the continuous decrease in both the abundance and biomass. The stagnation in the early 70s (Fig. 3) is most probably the reason for the very low abundance and biomass values recorded in 1972. During the investigation period the community was dominated by polychaetes, especially *Scoloplos armiger*. The fauna was quite diverse at the beginning of the period, but by 1968 both crustaceans and lamellibranchs already seemed to have disappeared completely (Fig. 7). This area is, however, by no means uniform, as the results of SCHULZ (1973) show. Somewhat north of the station BCS III-10, he found a

◄ **Figure 6**

Abundance, biomass and composition of the benthic macrofauna in the Bornholm Basin during the period 1965–1974 according to the results of the Institute of Marine Research (Helsinki). 1 = Lamellibranchiata, 2 = Crustacea, 3 = polychaetes resistant to oxygen deficiency (i.e. *Harmothoe sarsi*, *Scoloplos armiger*, *Capitella capitata* and *Heteromastus filiformis)*, 4 = other polychaetes, 5 = other species

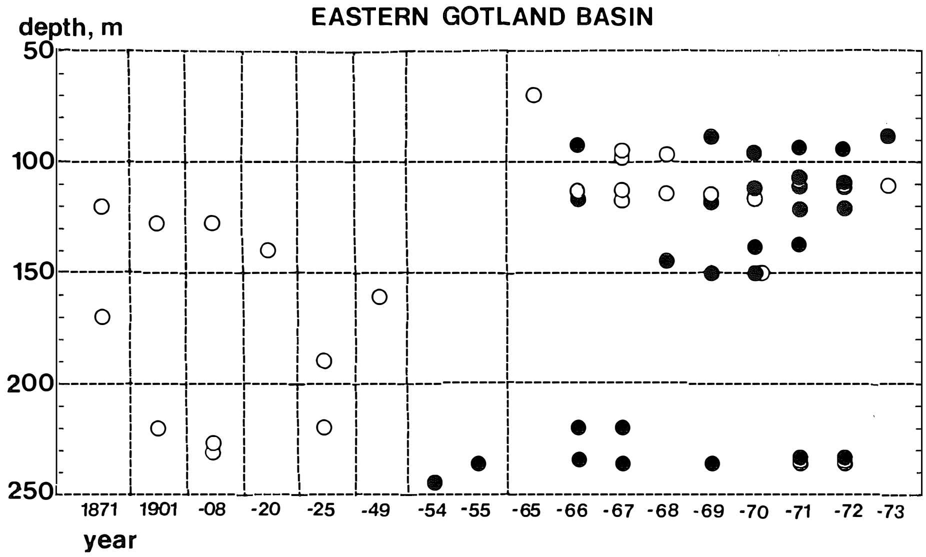


Figure 8

Vertical distribution of benthic macrofauna in the Eastern Gotland Basin. Open circles indicate presence and filled circles absence of macrofauna. 1871 Möbius (1873), 1901 Reibisch (1902), 1908 Knipovic (1909), 1920 Hessle (1924), 1925 Hagmeier (1926), 1949 Demel & Mankowski (1951), 1954 Sjöblom (1955), 1955–1973 Institute of Marine Research (Helsinki)

community at 100 m depth in which *Pontoporeia femorata* still formed a considerable part in July 1970, although *Scoloplos armiger* was dominant.

In the Gotland Deep the stagnation periods following the inflow in 1951–1952 radically lowered the level of the oxygen content below depths of 200 m(Fig. 2). This decrease is clearly mirrored in the occurrence of the benthic macrofauna (Fig. 8). The information available on the bottom fauna below 200 m during the first half oft the present century is limited to the results of a few qualitative investigations (REIBISCH 1902, KNIPOVIČ 1909, SKORIKOW 1910, HAGMEIER 1926). Species observed in all these investigations were *Harmothoe sarsi* and *Scoloplos armiger*. Somewhat more information is available from the depth region 100–200 m. The most frequently occurring species in this depth region were the polychaetes *Harmothoe sarsi*, *Scoloplos armiger* and *Terebellides stroemi* and the crustacean *Pontoporeia femorata*. Unfortunately the only information on the bottom fauna from the stagnation period 1922–1933 (see Fig. 2) is from 1925 (HAGMEIER 1926), when anoxic conditions had not yet been recorded. The occurrence of H_2S in 1931 must have depopulated the deepest areas, at least for some time. The first observation of empty bottoms was made by SHURIN (1961), who reported that the area below 150 m was devoid of macrofauna in 1949–1950. Since then the deepest areas of the Eastern Gotland Basin seem to have been devoid of macrofauna. In the period 1959–1962 the dead area comprised the bottoms below about 100 m (SHURIN 1961, 1962, 1964, 1968). JÄRVEKÜLG (1968, 1976) reported, however, that bottom fauna was found to a depth of 120–130 m west of Ventspils in 1965–1966. The results obtained at the IMR indicate that on the whole the extent of the dead area was the same in 1966–1973 as reported by Shurin in 1959–1962 (see above).

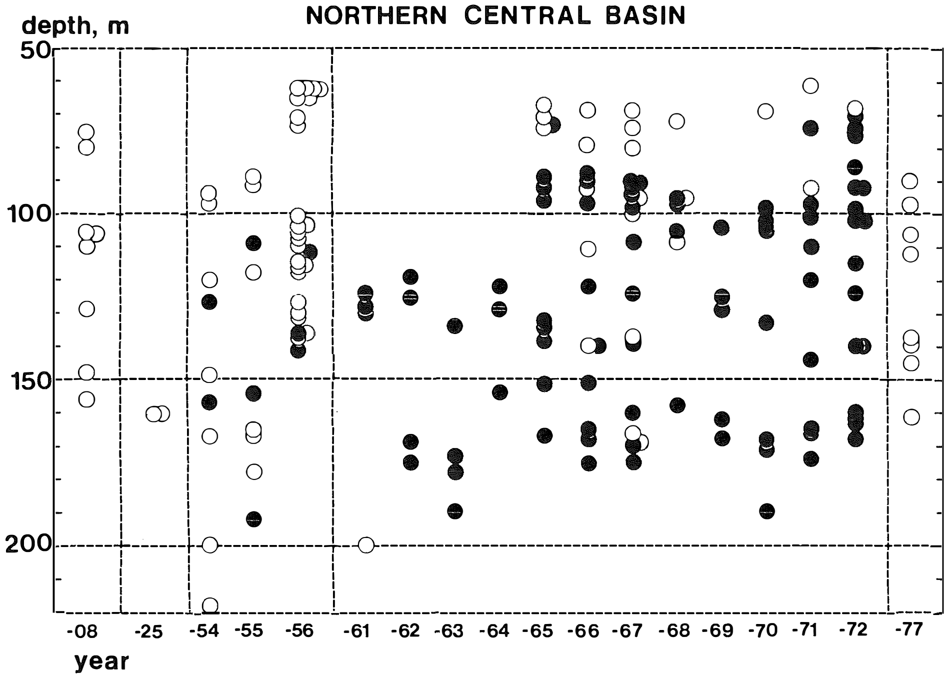


Figure 9

Vertical distribution of benthic macrofauna in the Northern Cantral Basin. Open circles indicate presence and filled circles absence of macrofauna. 1908 Knipovic (1909), 1925 Hagmeier (1926), 1954 Sjöblom (1955), 1955–1977 Institute of Marine Research (Helsinki)

In 1966 and 1967 the following species were observed at about 100 m depth: Nemertea spp., the priapulids *Priapulus caudatus* and *Halicryptus spinulosus*, the polychaetes *Harmothoe sarsi*, *Scoloplos armiger*, Spionidae sp. (problably *Pygospio elegans)* and *Terebellides stroemi*, the crustaceans *Pontoporeia femorata* and *P. affinis* and the lamellibranch *Macoma baltica*. The density recorded for the fauna in 1966 (about 300 ind./m^2) was considerably higher than in 1967 (about 10 ind./m^2). In 1968 only *Halicryptus spinulosus* and *Harmothoe sarsi* were observed, and after that the only species noted was *H. sarsi*.

Northern Central Basin

In the Northern Central Basin the periods of stagnation, evident in the Bornholm Basin and in the Gotland Deep during the first half of this century, did not reduce the oxygen content of the bottom water to a level really critical for the benthic macrofauna (Fig. 9).

The first information on the bottom fauna of this area is from 1908, given by KNIPOVIC (1909), who reported, at depths varying between 76 and 156 m, a fairly diverse community, including *Terebellides stroemi* and amphipods (most probably *Pontoporeia* sp.). In 1025, at 160 m, HAGMEIER (1926) found only *Pontoporeia femorata*.

Although the sparse hydrographic data from the 1950s indicate that the oxygen content of the bottom water was rather low (Fig. 2), the benthos fauna recorded by the IMR was fairly diverse and dense even below 100 m in 1954 (SJÖBLOM 1955), 1955 and 1956

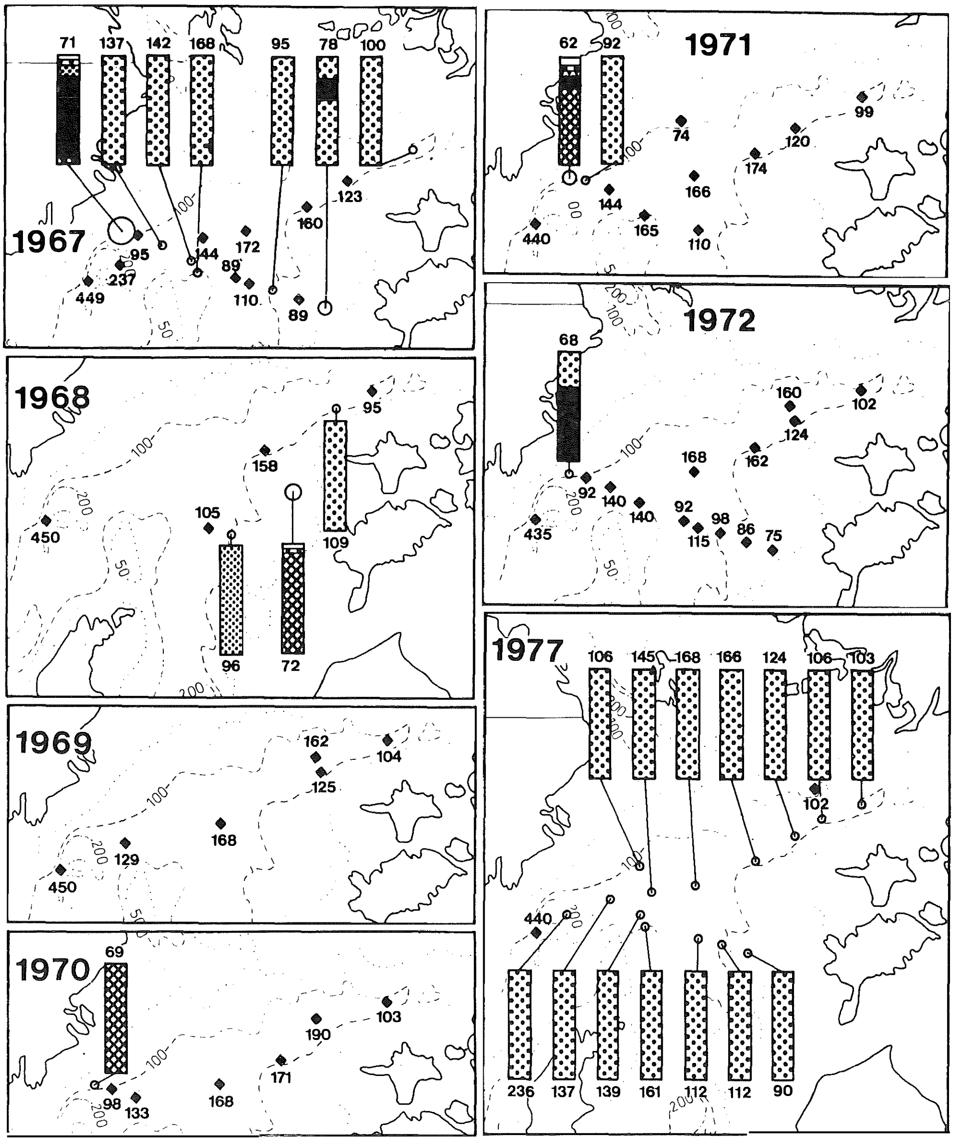
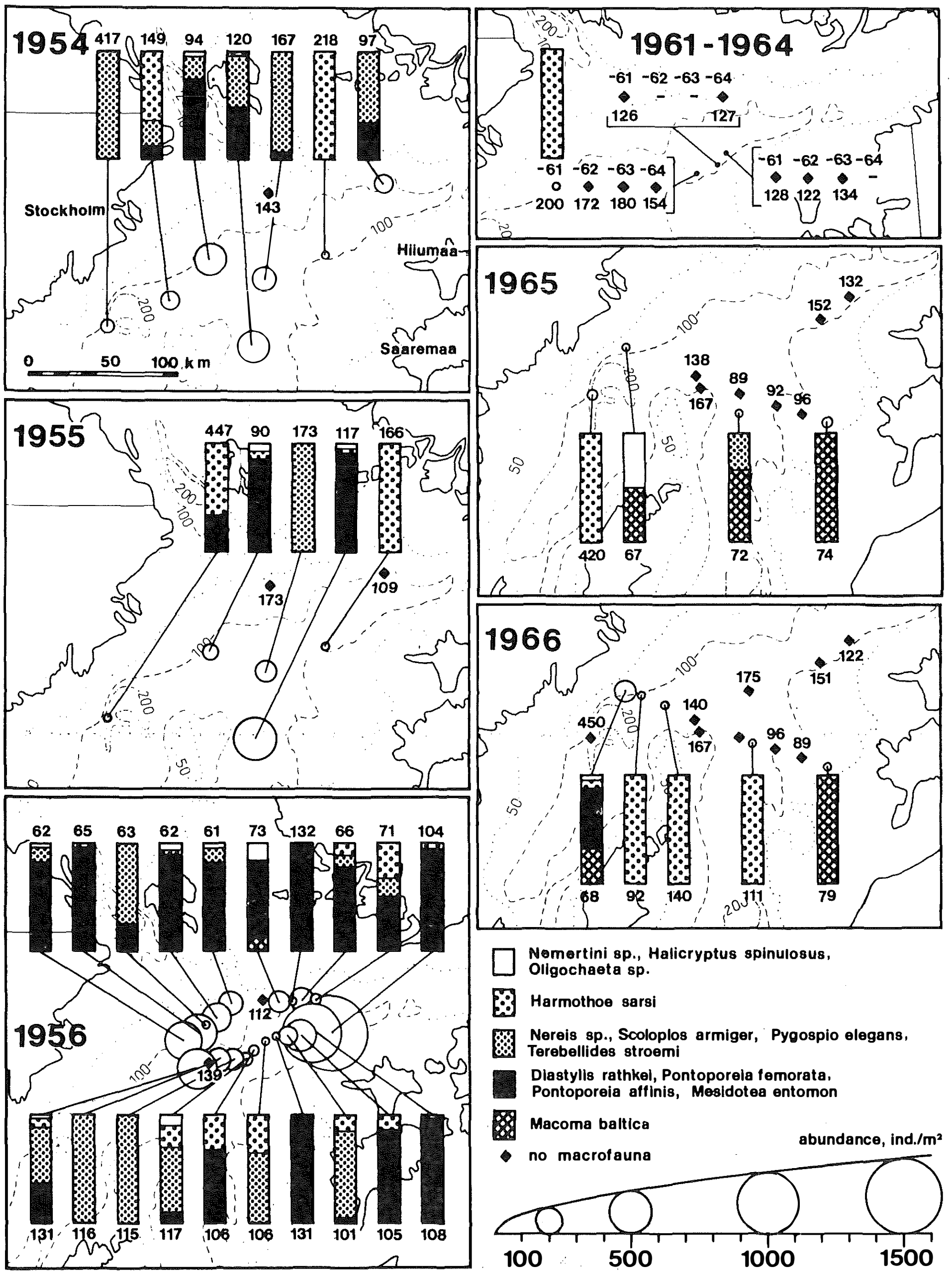


Figure 10

Abundance and composition of the benthic macrofauna in the deep areas of the Northern Central Basin during the periods 1954–1956 and 1961–1977 according to the results of the Institute of Marine Research (Helsinki). The station depths are inserted

(Fig. 10). The most abundant crustacean in 1954 and 1955 was *Pontoporeia femorata*. An exceptional mass occurrence of *Diastylis rathkei* (max. 1485 ind./m²) was observed in 1956, when this species was the dominant crustacean at the stations below 100 m. In these years the most abundant polychaete was *Scoloplos armiger*.



Continuation of Figure 10

The first records of the influence of the stagnation following the inflow in 1951–1952 are given by SHURIN (1962), who reported empty bottoms in this area in 1959. In 1960 the area devoid of macrofauna had widened, and extended into the Gulf of Finland (SHURIN 1962). The later studies of the IMR started in 1961 and during the first four years only three stations were sampled in the Northern Central Basin. The results indicated that the deepest bottoms were depopulated at that time (Figs. 9 and 10) (cf. also SHURIN 1964). The unfavourable situation continued during the period 1965–1972 (Figs. 9 and 10), although a slight recovery could be noted in 1966 and 1967. From 1968 onwards H_2S has been recorded frequently in the deep parts of this area also (Fig. 4). In the period 1968–1971 the areas below about 100 m depth were completely depopulated. In 1972 dead bottoms were observed even at 75 m depth. *Scoloplos armiger* and *Diastylis rathkei*, which were abundant in 1954–1956, have not been observed in the material of the later studies of the IMR. The most common species in the deep bottom communities from 1961 onwards has been the polychaete *Harmothoe sarsi*.

Unfortunately there was a pause in the investigations of the IMR in 1973–1976, and the next zoobenthos sampling in this area was carried out in 1977. In the autumn of 1976 the oxygen conditions were observed to have improved (ENGSTRÖM 1977a), and the preliminary results of the benthos sampling in 1977 show a very clear recolonization of the deep bottoms by *Harmothoe sarsi* (Fig. 10).

The Landsort Deep

The Landsort Deep, the deepest spot in the Baltic Sea (c. 450 m), represented by station DBS 9 and situated in the transition area between the Northern Central Basin and the Western Gotland Basin (Fig. 5), is in some respects atypical of both the neighbouring areas (see e.g. Grasshoff 1975). Despite of the great depth anoxic conditions with formation of H_2S did not occur until 1968, although a clear deterioration of the oxygen values could be seen from the mid 50s onwards (FONSELIUS 1969, 1975). This deterioration is clearly reflected in the occurrence of the bottom fauna. In 1925 HAGMEIER (1926) found a sparse population of *Mesidotea entonom* and *Pontoporeia femorata* at 380 m depth. In 1954 SJÖBLOM (1955) reported *Scoloplos armiger* at 450 m and in 1955 *Harmothoe sarsi* and *Pontoporeia femorata* were found (Fig. 10). At the next sampling, in 1965, only *Harmothoe sarsi* was found, while sampling in 1966–1969 and 1971–1972 failed to reveal any macrofauna. In 1977, when the oxygen conditions had improved (FONSELIUS 1977), the benthos sampling did not yield any macrofauna in the coarse fraction (1 mm sieve). However, *Harmothoe sarsi* was found in the fine fraction (0.6 mm sieve), which is not dealt with in this paper.

Western Gotland Basin

The Western Gotland Basin must nowadays be considered the most unfavourable part of the Baltic Sea as regards the benthic macrofauna (Fig. 11). In 1871 MÖBIUS (1873) reported only *Mesidotea entomon* at a depth of about 100 m. The first quantitative investigation in this area was made in 1920; at depths around 100 m HESSLE (1924) reported a *Pontoporeia-Macoma* community, where *P. femorata* predominated in the abundance and *Macoma baltica* in the biomass values. At 100 m in 1925 HAGMEIER (1926) found a very poor fauna consisting of *Terebellides stroemi, Mesidotea entomon* and *Pontoporeia femorata*. The results of investigations carried out in 1954 (SJÖBLOM 1955) and in 1959 (SHURIN 1968) indicate that the deep bottoms in this area had become depopulated. In 1963–1975 the oxygen content of the bottom water did not exceed 2 ml/l in this area, and during the period 1968–1975 H_2S was recorded annually (Fig. 4) The results of the benthos investigation of the IMR in 1965–1973 indicate that the bottoms below 80 m were devoid of macrofauna (Fig. 11).

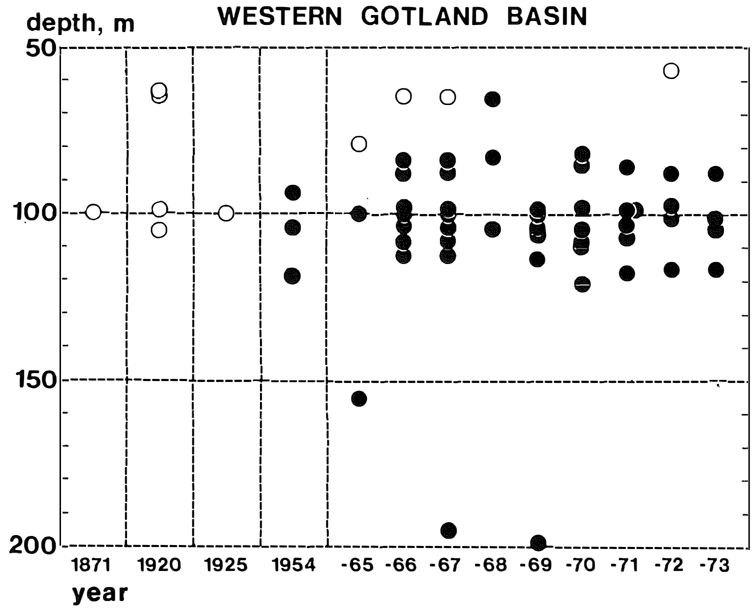


Figure 11

Vertical distribution of benthic macrofauna in the Western Gotland Basin. Open circles indicate presence and filled circles absence of macrofauna. 1871 Möbius (1873), 1920 Hessle (1924), 1925 Hagmeier (1926), 1954 Sjöblom (1955), 1965–1973 Institute of Marine Research (Helsinki)

Gulf of Finland

The Gulf of Finland is not divided from the Baltic proper by any very pronounced sills, and thus forms a direct continuation to the Central Basin. However, the very rough bottom topography leads to local differences, and makes the results of different studies difficult to compare. A decreasing trend in the oxygen content of the bottom water has been described by FONSELIUS (1969) and BUDANOVA (1972). This decrease has been more pronounced during the later half of this century.

The information on the benthic macrofauna from the late nineteenth century (BRAUN 1884) and the beginning of the present century (KNIPOVIC 1909) shows a fairly diverse fauna, even in the deepest parts of the Gulf of Finnland. It is notable that *Diastylis rathkei* was recorded from the entrance to the Gulf (BRAUN 1884).

After the study of KNIPOVIC (1909) there is a gap of 40 years in the benthos investigations. In 1949 SHURIN (1968) reported very low biomass values in the deepest parts of the Gulf of Finland. In 1954 and 1955 bottom fauna was recorded at all stations visited by the R/V Aranda in this area (Fig. 12). The communities were mostly dominated by *Pontoporeia* spp. In 1959 a small area devoid of macrofauna was reported at the entrance to the Gulf (SHURIN 1968) and in 1960 this area had grown to comprise the bottoms below 80 m (SHURIN 1962). The results of the IMR from 1961 onwards indicate a slow deterioration of the fauna below 60 m depth (cf. also BAGGE and ILUS 1973). In the years 1970–1972 the situation was at its worst, and most of the bottoms below 60 m seemed to be almost devoid of macrofauna. The records from station LL 3 (Fig. 13) in the eastern half of the Gulf give an idea of the changes occurring

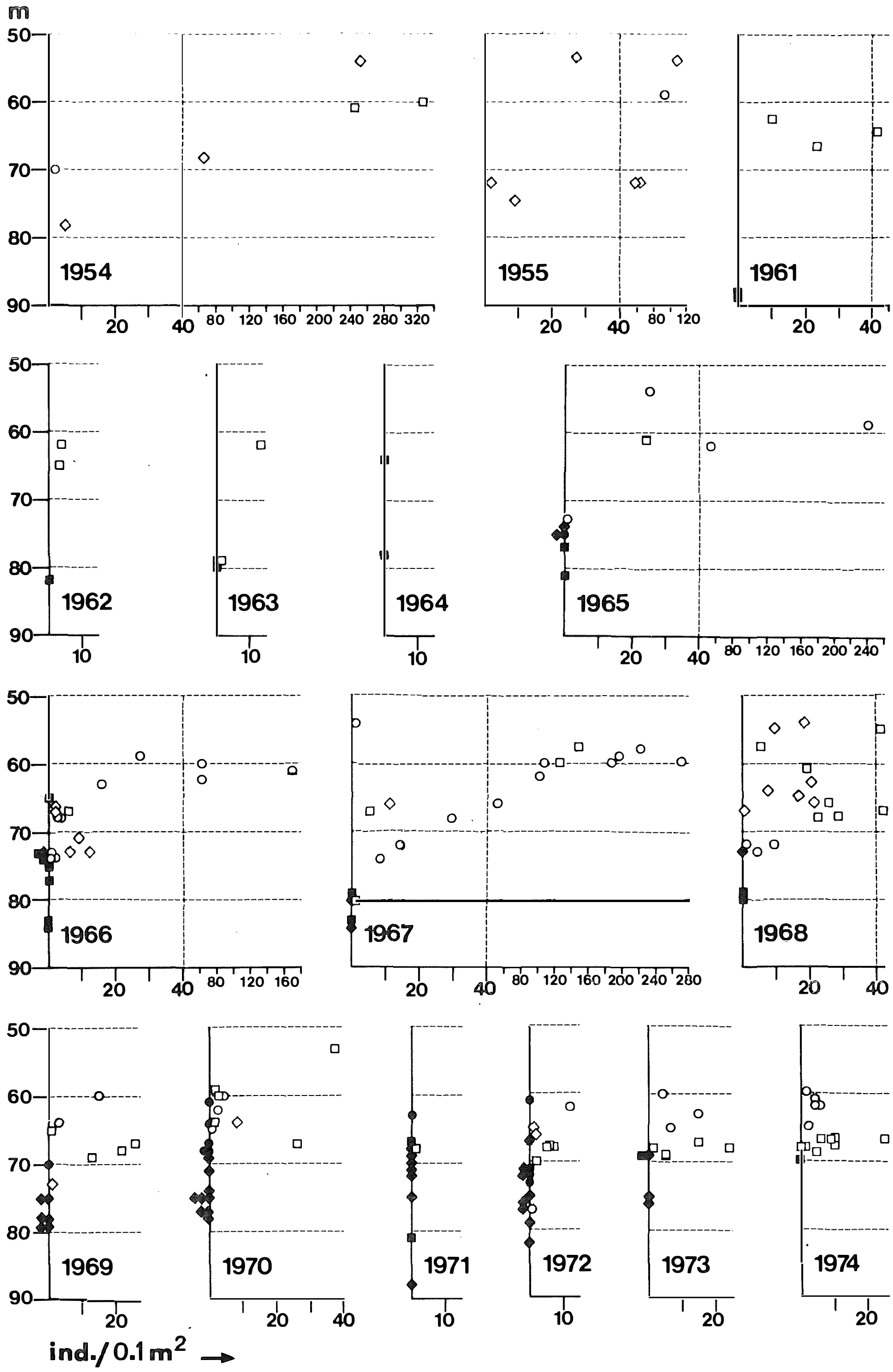


Figure 12

The abundance of benthic macrofauna (ind./0.1 m²) versus depth in the Gulf of Finland during the periods 1954–1955 and 1961–1974 according to the results of the Institute of Marine Research (Helsinki). ○ = the area east of Helsinki, ◇ = the area between Helsinki and the Hanko peninsula, □ = the entrance to the Gulf of Finland. Filled symbols indicate absence of macrofauna

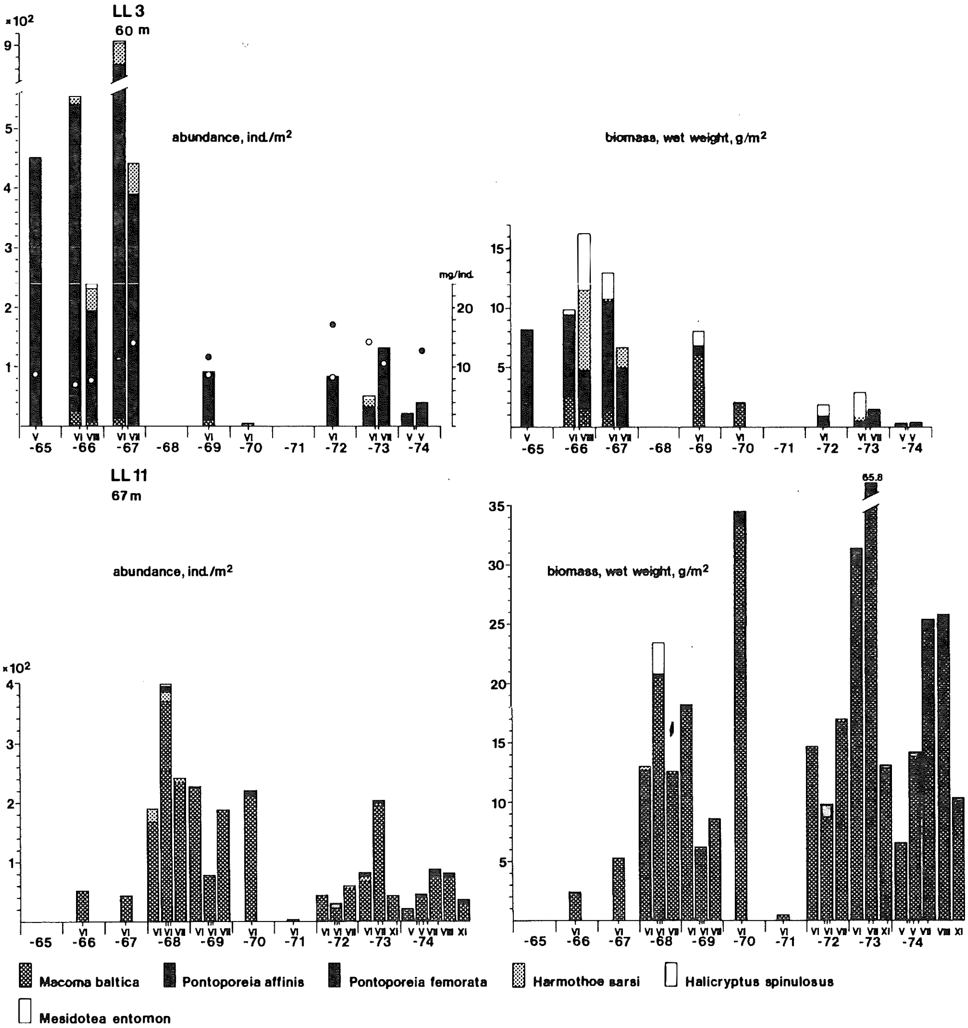


Figure 13

Abundance, biomass and composition of the benthic macrofauna at station LL 3 in the eastern half of the Gulf of Finland from 1965–1974 and at station LL 11 at the entrance to the Gulf of Finland from 1966–1974. Circles indicate the men weight per specimen of *Pontoporeia affinis* (○) and *Pontoporeia femorata* (◑) at station LL 3

in 1965–1974. A dense *Pontoporeia* population was recorded in 1965–1967, but by the next continuous sampling period, 1972–1974, this population had strongly diminished. The results from station LL 11 at the entrance to the Gulf of Finland reflect the changes in a *Macoma baltica* community during the period 1966–1974 (Fig. 13). A decreasing trend can be observed in the abundance values, while the biomass values show the opposite trend. These trends can be explained by examining the size distribution of *Macoma baltica* during this period (Fig. 14). At the beginning of the study the population was rather young, and the peak at 3 mm in 1968 presumably originates from

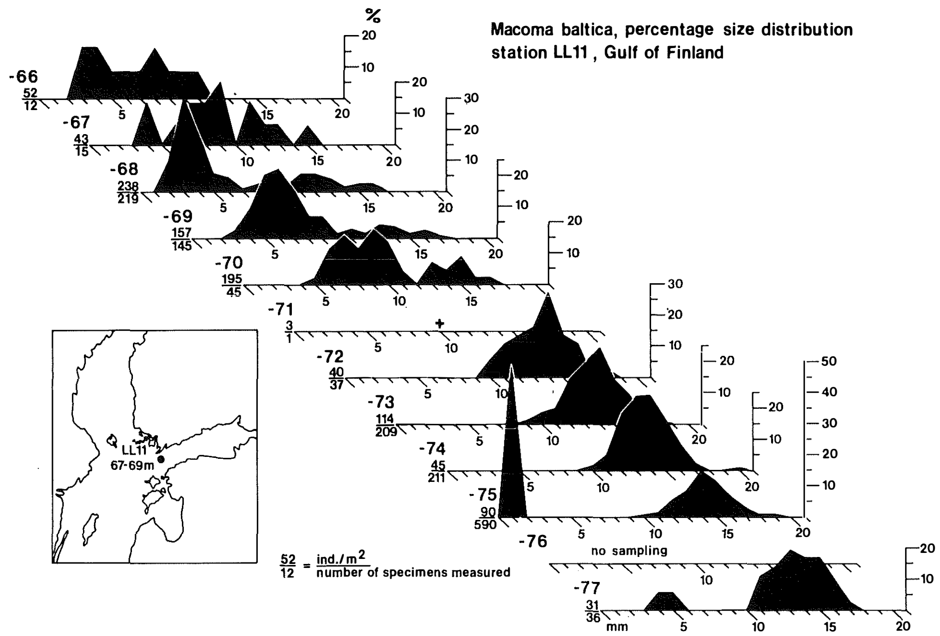


Figure 14

Percentage size distribution of *Macoma baltica* at station LL 11 at the entrance to the Gulf of Finland. + = empty shells only

a successful spatfall in 1966. The growth and numerical decline of the generations can be followed throughout the investigation period. It was not until 1975 that evidence of the next successful spatfall was observed.

Discussion and Conclusions

The conditions for the benthic communities in the deep areas of the Baltic proper and the Gulf of Finland were radically changed by the exceptionally great inflow in 1951–1952, and the subsequent prolonged stagnation. These hydrographical events introduced the era of depopulation that is still prevailing.

In the southern deeps of the Baltic, i.e. the Bornholm and Gdańsk Deeps, the periods with critical oxygen conditions, frequently occurring during the last few decades, have caused temporary depopulation of the bottoms. By the beginning of the 60s the lamellibranch community observed during the first half of this century, and still observed 1951–1952 in the Bornholm Basin, had completely disappeared from these deeps. The bottoms in this part of the Baltic are apparently recolonized very rapidly, and after only short periods of improved oxygen conditions polychaete communities, consisting mainly of *Scoloplos armiger*, can be observed. According to LEPPÄKOSKI (1971), the rapid recolonization in the Bornholm Basin may be caused by strong bottom currents connected with the inflows, which may transport surface sediments containing juvenile specimens and non-pelagic larvae of bottom animals. Up to the time of the last observation (1974), however, the periods with improved oxygen conditions had not been long enough to allow re-establishment of the former lamellibranch community (cf. LEPPÄKOSKI 1975).

In the Eastern Gotland Basin the first observations of empty bottoms were made by SHURIN (1961) in the area of the Gotland Deep in 1949–1950. However, a temporary disappearance of the macrofauna below 200 m depth must have occurred much earlier, as a result of the anoxic conditions in 1931 and 1932 (see Fig. 2). The first observations of empty bottoms in the Western Gotland Basin were made in 1954 (SJÖBLOM 1955). In the Northern Central Basin and the Gulf of Finland the depopulation of the deep bottoms probably began later, in the late 50s.

In the southern part of the Baltic Sea the periods of stagnation have caused temporary depopulation and a change in the community structure, but in the northern parts of the Baltic proper and the Gulf of Finland their influence has been still more severe. There the depopulated area can clearly be observed to have increased during the last twenty years. In these regions the periods with oxygen conditions good enough to allow recolonization are shorter and less frequent than in the southern part of the Baltic Sea (Figs. 1 and 2). Moreover, when the oxygen conditions temporarily improve, recolonization is clearly slower than in the southern Baltic. Once the deep areas of the Central Basin and the Gulf of Finland have lost their bottom fauna it takes a long time until a new community has developed. One reason for this may be less effective transport of young individuals by the bottom currents connected with inflows (cf. above). Another reason for the slow recolonization is the shortage of species resistant to oxygen deficiency. The only species known to be resistant in these areas is *Harmothoe sarsi*. *Scoloplos armiger* which is one of the first colonizers in the southern Baltic, has not been observed in the deep areas of the northern Baltic since 1956. In these northern waters its tolerance of low oxygen concentrations is presumably weakened by the extra stress factor of low salinity.

By the early 70s the area of bottoms periodically or permanently devoid of macrofauna had grown to cover about 60000 to 80000 km^2 (ZMUDZINSKI 1975). According to the present study, during the period 1963–1974 the area with periodically or permanently unfavourable oxygen conditions ($<$ 2 ml/l) comprised about 100 000 km^2. One reason for the growth of this area is that the permanent halocline has risen by about 20m since the 1920s (see e.g. GRASSHOFF 1975). As is seen in Figs. 1 and 2, the frequency of periods with anoxic conditions has also increased during the last few decades. However, the mechanisms of this complicated process – involving both physical, chemical and biological elements of the water mass, the sediment, and the sediment-water interface – are not fully clarified. It has been suggested that especially the increased salinity and temperature observed in the Baltic Sea have contributed to this development. For references on this complicated topic, see e.g. the compilation by GRASSHOFF (1975). The pollution load imposed on the Baltic Sea during recent decades has increased strongly, and thus cultural eutrophication has had an indirect influence on the rate of oxygen consumption in the deep layers. The contribution of man to the whole process is, however, very difficult to determine quantitatively. To what extent the deterioration of the benthic communities is caused by large-scale natural phenomena, and to what extent by human activities is still an unsolved probelm.

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Since the programme started in 1961 a great number of young assistants have spent thousands of hours, often in bad weather, sieving the samples on the deck of the research vessel. Thank you all of you.

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