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Kieler Meeresforsch., Sonderh. 6, 7 – 17 Kiel 1988

History of benthic research in the Northern Baltic Sea: from description to prediction

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Abstract

The history of studies of benthic flora and fauna in the Northern Baltic Sea (N of 58° N, including the Gulfs) is briefly reviewed from the early naturalists of the Linnaean period (mid–18th century) to the early 1970's.

Introduction

The aim of this review is to briefly summarize the main trends and developments in the knowledge of macroscopic phyto- and zoobenthos in the Northern Baltic Sea area until the early 1970's. For more detailed information some earlier bibliographic reviews should be consulted, among them the classical works of WÆRN (1952), SEGERSTRÅLE (1957a) and ZENKEVITCH (1956, 1963). Comprehensive bibliographies covering the years 1953–1973 were compiled by SEGERSTRÅLE (1964a, b, 1975). The most extensive monograph ever published on the benthic fauna of the Baltic is the work of JÄRVEKÜLG (1979). In this book a voluminous quantitative material is presented from the Eastern Baltic (north of 56° N, incl. the Gulf of Finland) and related to available earlier data (1173 references). For all important benthic species, both animals and plants, distribution maps are presented covering the whole Baltic Sea (for the first generation of maps, see VÄLIKANGAS 1933).

The review covers the northern Central Basin (from 58° N), the northern parts of the Gulf of Riga, the Gulf of Finland and the Gulf of Bothnia (Fig. 1). Our interest lies mainly in field studies. Studies in anatomy, morphology, systematics and physiology on benthic organisms are not included. Great steps forward have been taken since the beginning of our century in benthos research concerning mesopsammon and other meio- and microfauna and -flora of the Baltic Sea. This field of research has been omitted from our paper; for early works on, e.g., Protozoa, Turbellaria, Rotatoria, Nematoda, Ostracoda and other meiobenthic crustaceans, see references in LUTHER (1957) and SEGERSTRÅLE (1957a).

Some names on epochs in ecology and generations of biologists have been adopted from the comprehensive review on the ecologists and ecologization of Sweden by SÖDERQVIST (1986).

The early natural historians

The start of benthic investigations in the Northern Baltic was rather late: it dates back to the 1840's. Italy, Denmark and Germany were the first countries to investigate the sea bottom (RASMUSSEN 1977) since the middle of the 18th century, i.e. some 100 years earlier than in the Northern Baltic. There might be three main reasons for this delay in the north. For the first, the impoverished fauna and flora of the highly diluted waters of the Northern Baltic (salinity generally $< 7^0/_{00}$) with a very low richness in species and forms did not evoke enthusiasm and inspiration among the pioneers of comparative morphology

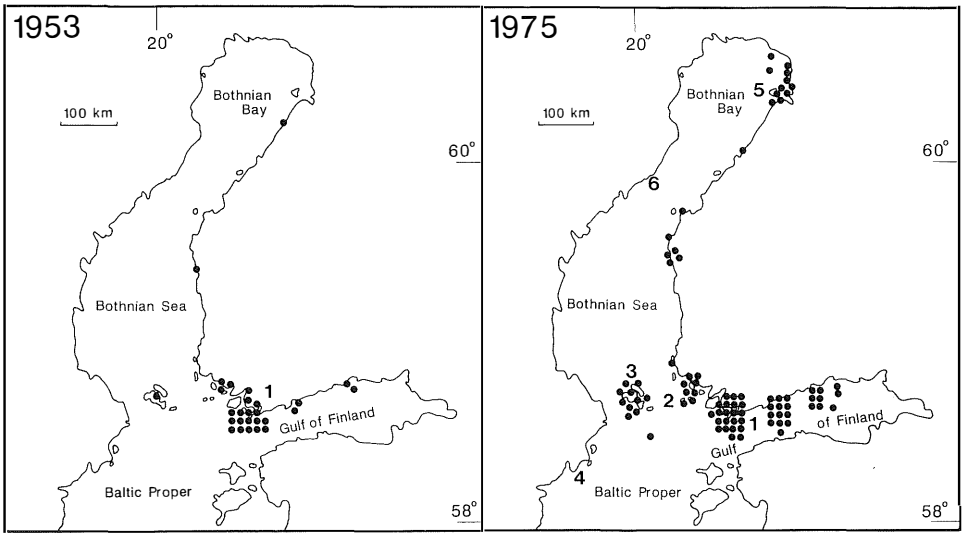

Figure 1

Geographical distribution of studies on macrobenthic fauna and flora performed in Finland in 1953 and 1975 (dots, redrawn from JYLHÄ-PYYKÖNEN 1979), and the location of biological field stations in the northern Baltic Sea. 1 = Tvärminne Zoological Station, 2 = Archipelago Research Institute, 3 = Husö Biological Station, 4 = Askö Laboratory, 5 = Bothnian Bay Research Station, 6 = Norrby Laboratory

and systematics. For the second, there is almost no immediate economic interest in bottom-living organisms of the inner parts of the Baltic. The only exceptions might be earlier, local use of seaweeds (mainly *Fucus vesiculosus*) washed ashore as manure (LINNAEUS 1745). Not until our century resources of industrially applicable red algae (*Furcellaria fastigiata* and *Phyllophora brodiaei (= truncata)*) studied by, e.g., KIRAYEVA (1961), have been harvested in western Estonian coastal waters since 1966 (TREI 1975). Harmful benthic species causing trouble in fisheries were already described by GADD (1769) whereas technical problems and economic losses caused by fouling organisms in power plants were not looked for in a scientific sense before the 1980's.

For the third, there were no adequate scientific bodies established in biology in the area concerned during the 18th and the first decades of the 19th century. The chair held by Carl von Linné and his followers in Uppsala, Sweden, was attached to the Faculty of Medicine for more than a century (SÖDERQVIST 1986). At Åbo Academy, Finland, a chair in economics (mainly applied natural science) was established in 1746. The first holder of this chair was Pehr Kalm, a Finn who had studied under Linné at Uppsala.

There are a lot of macrobenthic species among the Northern Baltic fauna and flora first described by Linné, from poriferans (*Ephydatia fluviatilis*) to crustaceans (*Mesidothea entomon, Gammarus locusta*), molluscs (*Mytilus edulis, Macoma balthica*) and algae (*Fucus vesiculosus, Furcellaria lumbricalis*), but it is not known to us whether the specimens studied in the 18th century by Linné and the early Linneans in Uppsala originated from northern Baltic waters or not.

The first scientific notes on benthic animals of the Northern Baltic might date back to a thesis published under the supervision of GADD (1769) in which two "insects", *Idotea entomon (Oniscus)* and *Gammarus pulex* were described as damaging fishing tackle. Studies specifically of benthic organisms were started in the middle of the 19th century.

V. SIEMASCHKO (1847) reported some bivalves from the Gulf of Finland. LINDSTRÖM (1855) described the occurrence of a great variety of benthic animals in the Stockholm archipelago. His approach was in part taxonomic (*Bathyporeia pilosa* and *Pontoporeia affinis* described as new species), in part ecological: he gave a discussion of the penetration of lacustrine species of invertebrates and vascular plants into the more saline waters of the outer archipelago, and of species originating from the sea in the opposite direction. Famous names to bear in mind from the 1860's are S. Lovén (see below) and ZENGER (1870, cf. JÄRVEKÜLG and VELDRE 1963). The works of N. ZENGER were continued by GRIMM (1877), BRAUN (1884) and KOJEVNIKOV (1892). There are also some sporadic notes from the late 19th century on crustaceans and molluscs in Finnish coastal waters, from the western Gulf of Finland up to the Northern Quark (NORDENSKIÖLD and NYLANDER 1856, CAJANDER 1869, LEVANDER 1899, 1901a, b). In the 80's, NORDQVIST (1890) sampled invertebrates at several localities from Tornio/Torneå in the north to southern Arhipelago Sea and performed some dredgings in the Åland Sea down to 230 m depth. The first systematically organized biological expeditions to the northern Baltic were undertaken in 1907–1909 by the Russian naval transport ship "Kompass". Results on benthic fauna of the open sea, the Gulf of Riga and Gulf of Finland were published by KNIPOVITCH (1909).

Notes on the benthic flora of the Estonian coastal waters from the middle of the 19th century are given by EICHWALD (1849, 1852). GOBI (1874, 1877) and ARTSIKOVSKI (1905) studied the red and brown algae in the Gulf of Finland. From the south coast of Finland there are some notes on aquatic plants from the 1840's as well (NYLANDER 1844, HISINGER 1857). In 1859 NYLANDER and SAELAN published a plant list, Herbarium Musei Fennici, which also included the first records of macroalgae in Finland. From the Archipelago Sea there exists just one paper on phytobenthos from the last century, namely that of STRÖMFELT (1884). Early notes on algae from the Stockholm area in Sweden are given by Carl von Linné (ref. in WÆRN 1950, 1952). An investigation of the algal flora along the Swedish east coast was made in the 1860's by KROK (1869). Other Swedish phycological studies from the 19th century worth mentioning are works by AGARDH (1817), ARESCHOUG (1850) and KJELLMAN (1890).

The approach of the pioneer benthologists was mainly faunistic and floristic; they were generally all-round natural historians. The habitats were not described and nothing was mentioned about ecological conditions. An exception was perhaps the mentioned work of Krok, where the effects of decreasing salinity and bottom conditions on the distribution of marine species in the Baltic are discussed. Gradually benthic investigations were directed towards biocoenology, in an attempt to demonstrate the affinity of organism species to each other and to certain species assemblages and elucidate causal relationships between these and the most important environmental factors and gradients (water depth and type of bottom). Consequently a gradual "ecologization" of brackish water biology took place; the term ecology was used first among botanists around 1900 (SÖDERQVIST 1986).

During this period, marine invertebrates were highly preferred for studies in embryology, anatomy, morphology etc. The material used by Swedish scientists originated mainly from the west coast of Sweden, where the first permanent base for marine biological research in Scandinavia, the Kristineberg Zoological Station, was founded in 1877. In the south, studies on the benthic animals of the Sound (Öresund) were initiated during the first decade of our century. The Northern Baltic coasts of Sweden were largerly neglected until the early 1960's (see below). Zoological research in Stockholm was concentrated upon the comparative anatomy of vertebrates until the early 1950's, whereas Uppsala zoology already developed towards a famous school of biogeographers at the beginning of our century (SÖDERQVIST 1986).

In Russia (St. Petersburg), Estonia and Finland the choice of the Baltic as a study area was natural. The only attainable oceanic coast belonging to Finland (until the end of the World War II) was a narrow strip of coast (Petsamo) between Norway and Russia on the Arctic Sea. In Turku/Åbo, at the first Åbo Academy (founded 1640, the predecessor of the present Helsinki/Helsingfors University), there was obviously no interest in brackish water biology among the later Linneans. In the late 1800's, some biologists at Helsinki University (the only university in Finland until 1918), focused their interest upon brackish water biota. Prof. J.A. PALMÉN worked actively for 30 years (until his death in 1919) to create a field base for studies in brackish water zoology. He became further inspired by his visits to Naples (1876), Bergen (1881) and Rostock (1891). A small summer laboratory was established in 1889 on an island (Esbo-Lövö) some 10 km SW from Helsinki. This island was occupied by PALMÉN and a group of young zoologists (with K.M. LEVANDER as a driving force) until 1899 (for publications from Esbo-Lövö see A. LUTHER 1957).

Tvärminne Zoological Station was founded by PALMÉN in 1902, and this was the starting point of more regular and systematic investigations of fauna and flora in the entrance area to the Gulf of Finland. During the first 50 years of Tvärminne's history, some 370 papers were published, covering virtually all the important taxonomic groups, both aquatic and terrestrial, in the area (see A. LUTHER 1957 for a bibliography). Before World War I, the benthic groups studied at Tvärminne included Turbellaria (A. LUTHER), Nematoda (G. SCHNEIDER), Nematomorpha (K. M. LEVANDER), Oligochaeta (LEVANDER, E. MUNSTERHJELM, D. TOIVONEN), Ostracoda (N. HIRSCHMANN), Decapoda (LEVANDER), Trichoptera (A. J. SILFVENIUS/SILTALA), Mollusca (LEVANDER, A. LUTHER) and algae (E. HÄYRÉN, C. SKOTTBERG). The research work of this pre-war generation of early ecologists tended to answer the questions "What?" and "Where?". Today the general structure of the major macrobenthic subsystems (phytal and soft-bottom) of the northern Baltic is relatively well-known but to answer these most elementary questions one has still to go to very sporadic sources of local character and back to the authors mentioned above from the early years of the present century.

Inter-war synecologists

Quantitative (or at least semi-quantitative) sampling methods achieved a foothold in aquatic biology and the synecological analysis of plant and animal communities. These, together with studies in marine biogeography, are characteristic of developments in Baltic biology during the inter-war period. Generally speaking, the number of biologists involved in brackish water ecology in the Northern Baltic area appears to be rather restricted during these decades (see VÄLIKANGAS 1933 for a contemporary summary, and consult the extensive series *Die Tierwelt der Nord- und Ostsee* 1927 –, omitted from our review, for most taxonomic groups living in the Baltic). In Finland S.G. SEGERSTRÅLE started in 1922 his long series of studies dealing with the invertebrate fauna of the *Fucus vesiculosus*-belt (SEGERSTRÅLE 1928) and soft bottoms. Quantitative macrobenthos sampling at Tvärminne was started in 1926. The main study object was the bivalve *Macoma balthica,* the denominator of the *Macoma*-community (*sensu* ZENKEVITCH 1963) which covers most parts of the inner Baltic Sea. These papers made SEGERSTRÅLE the leading figure in Northern Baltic marine biology. His studies included, for example, vertical distribution and population dynamics (recruitment, age, growth, fluctuations in abundance and biomass), in relation to environmental factors, of *M. balthica* and the amphipods *Pontoporeia affnis* and *P. femorata* (SEGESTRÅLE 1927, 1933a, b, 1937). HELLEN (1919a, b) published notes on isopod and amphipod crustaceans in coastal waters. Turbellarian fauna was the object of a long series of studies, the first of which was published by A. LUTHER (1904). On the Finnish south coast ULVINEN (1937) studied macrophytes in the Kotka archipelago. SKULJA (1924) published notes on algae in the Gulf of Riga and observations on the inner

limits of marine algae in the Gulfs of Bothnia and Finland were made by HÄYRÉN (e.g. 1928, 1931, 1938), VÄLIKANGAS (1933) etc. WÆRN (1952) started his comprehensive ecological studies of the algal flora around the coasts of Sweden including parts of the Finnish Archipelago Sea.

From the Northern Central Basin of the Baltic proper there are quantitative zoobenthos data available in the papers of HESSLE (1924), who extended his investigations up to the Gulf of Bothnia, and HAGMEIER (1926). The first quantitative data on benthic fauna in the deep basins of the Gulf of Bothnia seem to be from mid-50's (SJÖBLOM 1955, early results on macrobenthos were summarized and comprehensively reviewed by ANDERSIN et al. 1978, ELMGREN 1978, JÄRVEKÜLG 1979).

The biota of the Baltic consists of marine, brackish water and lacustrine components. Their adaptative capacity and distribution along salinity and other environmental gradients (south-north, west-east, surface-bottom; e.g., the phenomenon of brackish water emergence/submergence) have traditionally been topics of major concern in Baltic benthology (see WÆRN 1965 and REMANE 1971 for a review). In a biogeographical sense the most peculiar feature of the Baltic biota is the post-glacial history of the sea and the immigration of its organisms, verified largely through studies of benthic (or nekto-benthic) fauna and exemplified by species such as *Pontoporeia affinis, P. femorata, Mysis mixta, M. relicta, Mesidothea entomon,* and *Halicryptus spinulosus* (EKMAN 1933, SEGERSTRÅLE 1957b, JÄRVEKÜLG 1962, ZENKEVITCH 1963). The starting point of this fruitful discussion on the post-glacial relicts and different theories on the routes and mode of their invasion was in all probability a lecture given by the Swedish zoologist S. Lovén to the Royal Academy of Sciences in 1860; since then some 60 papers have been published on this subject (see SEGERSTRÅLE 1982 for a review).

HÄYRÉN (1921) was the first to use phytobenthos (plant communities) in brackish water as an indicator of pollution. His saproby classification was based on the system of KOLKWITZ & MARSSON (1902) developed for running waters in Central Europe. As plant communities are rather reliable indicators of the degree of pollution, the investigations of Häyrén off Helsinki/Helsingfors have been repeated several times until quite recently. Written in Swedish and published in a series of limited distribution, his important work remained little known outside the Nordic countries. The first papers on bottom fauna as indicators of pollution date back to the mid–60's.

Post-war diversification of benthic ecology

For obvious reasons there are only a few studies published during the first 10 to 15 years after World War II. In Sweden, HÄGG (1950) and FORSMAN (1956) gave notes on the distribution of littoral and soft-bottom invertebrates along the east coast; the latter had just a few samples north of 58° N but he carefully compiled earlier data available from the whole length of the Swedish Baltic Sea coast. WÆRN (1952), the first diving marine biologist in the Baltic, published his classical work on rocky-shore algae at Öregrund. His exact diving profiles and excellent underwater photographs were of fundamental value for future monitoring. In the Soviet Union, the number of benthic investigations published until the early 60's also remained low with the exception of descriptions of different groups of animals in the series *Classification Keys for the Fauna of the USSR.*

In Finland some comprehensive monographs were published. From the early 30's LINDBERG (1937, 1948) studied the aquatic insect fauna of the upper littoral along the Finnish, Swedish and, in part, also Estonian coasts from the innermost Bothnian Bay to the Sound. PALMÉN (1955) focused his interest on chironomids in brackish waters, SEGERSTRÅLE (1944, 1950) continued his studies on soft-bottom fauna and SMITH (1955) performed a comparative study of the polychaete *Nereis diversicolor* along salinity

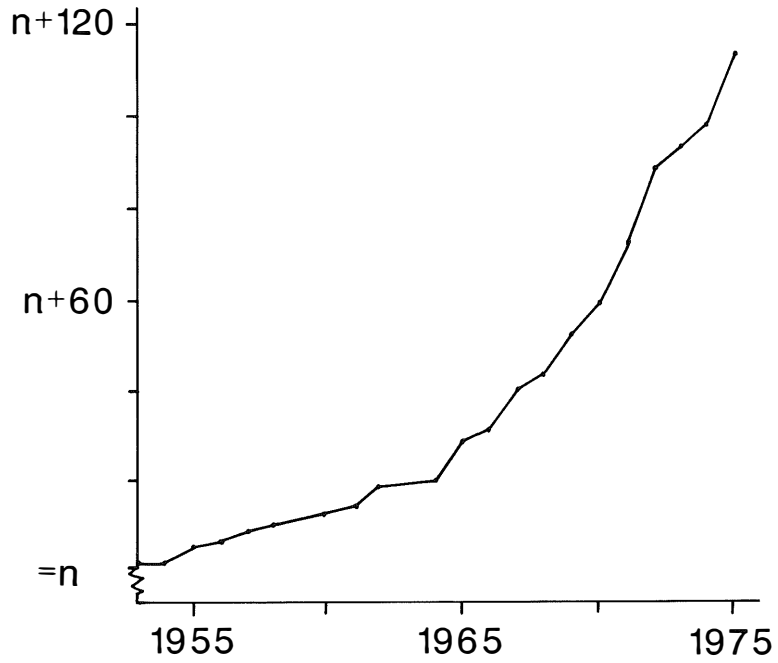

Figure 2

Culmulative number of benthological studies in Finland published in 1953–1975 (from JYLHA-PYYKÖNEN 1979).

gradients in Finnish and Danish waters. H. LUTHER (1951a, b) finished his comprehensive studies on macrophytes in different archipelago zones off Tvärminne, started in the 1930's but interrupted by the war.

Astonishingly there is a gap after KNIPOVIC (1909) for 40 years in benthos research in the Gulf of Finland, until the first sampling trips were undertaken by the Finnish research vessel "Aranda" in the mid–50's (SJÖBLOM 1955). Similarly only two short notes on the benthic fauna of the Bothnian Bay are known from the period between NORDQVIST (1890) and LINDBERG (1948). All earlier records were compiled by HAAHTELA (1964).

In the 1960's there was a huge increase in benthos and other marine biological studies in the Northern Baltic area (Fig. 2), not only in the published volume of research but also in the diversity of benthological studies. Entirely new perspectives were opened, new approaches and ecological concepts adopted and new methods developed at an increasing rate (see SEGERSTRÅLE 1964b, 1976 for contemporary reviews). There are some apparent reasons for this expansion. New universities and new field stations were founded (Fig. 1), and positions opened for marine biologists. The increasing awareness of eutrophication and other environmental problems resulted in legislative reforms (national and local water authories, water courts, etc.) in all three countries concerned in this article. Applied (environmental) marine ecology now played a significantly greater role. Several scientific or administrative bodies were founded in order to facilitate international cooperation in this field: the Nordic Council for Marine Biology (1956), Baltic Marine Biologists (BMB) (1968), the International Biological Programme-Productivity Marine (IBP-PM) (1968), the Committee for the Gulf of Finland (1969), the ICES/SCOR Working Group on the Study of Pollution of the Baltic (1971), the Committee for the Gulf of Bothnia (1972) and the (interim) Helsinki Commission (1974).

In Finland the quantitative expansion of benthos investigation started in about 1965 and resulted successively in a more even geographical distribution of the studies along the coasts (Fig. 1). Benthic studies from this period can very roughly be classified as follows. The "Turku school" was established around TULKKI's (1960, 1964) quantitative studies on littoral and deeper soft-bottom benthos of the inner Archipelago Sea. This school more and more focused upon assessment of the degree of pollution on the basis of macrozoobenthos, in close cooperation with Kristineberg Zoological Station (see LEPPÄKOSKI 1975 for a review), and on the effects of mechanical disturbance on benthic communities, caused by wave effect from ships traffic (FAGERHOLM 1975, RÖNNBERG 1975), dredging, embankments and sand suction. Pollution studies performed by JÄRVEKÜLG (1970, 1982) and co-workers in Estonian waters were conceptually closely related to this approach. At Tvärminne and the Bothnian Bay research station (Fig. 1) the dynamics of the littoral ecosystems in natural state were studied within the IBP-PM Programme (H. LUTHER et al. 1975). The "Askö school" at Stockholm University first focused upon the *Cladophora*-system of the upper littoral (A.-M. JANSSON 1967) and concentrated considerable effort on a project "Energy Flow Through the Baltic Ecosystems" (see B.-O. JANSSON 1972 for background documentation). Marine botanists from Uppsala studied the influence of nutrients on the submarine vegetation along the Swedish coasts, especially in the Stockholm archipelago (NORIN and WÆRN 1973, PEKKARI 1973).

No forum for coordinated publication of results of biological research within the Baltic Sea was available until 1968. Since the first Baltic marine biology symposium held by BMB in Rostock, GDR, a total volume (incl. the 9th symposium in 1985) of approx. 380 papers has been published in the proceedings from these symposia. Of these 160 (= 42 %) deal with macrobenthos (nektobenthic forms not included).

Towards the end of the 70's, the quantitative expansion continued. Even newer methodologies and approaches were adopted in benthos research demonstrating both advances in theoretical ecology and practical, Baltic-specific, needs: field experiments, e.g., colonization studies, ecogenetic and ecotoxicological (incl. eco-epidemiological) studies, recovery subsequent to the elimination of pollution or other forms of disturbance, benthic primary and secondary production, energy flow, systems analysis and modelling, multispecies testing of pollutants in model ecosystems (micro- and mesocosms), systematical monitoring of long-term changes in littoral and soft-bottom benthal sub-systems and trends in the body burdens of different environmental pollutants in selected species.

Most scientists belonging to the present-day generation of benthologists are looking for answers to the questions of central importance in benthic ecology: "Why?" and "How?" The first "why's" were stated by LINDSTRÖM (1855) and KROK (1869) and their contemporaries who realized the importance of salinity and depth gradients. The last "how" will never be answered.

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