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Dynamics of Baltic ecosystems and causes of their variability

E. Gargas, K. I. Dahl-Madsen, H. Schrøder* and J. Rasmussen*

Water Quality Institute, Hørsholm, Denmark and * Danish Hydraulic Institute, Hørsholm, Denmark

Abstract

Dynamics of Baltic ecosystems and causes of their variability are discussed and special attention is paid to the use of ecological models as a tool for research and management. - The causes of the observed changes in salinity, temperature, and oxygen of the deep water of the Baltic Sea are reviewed and discussed. - The work has led to the formulation of a hypothesis by which it appears possible to explain the oxygen development and the long-term development of other hydrographic components. The analyses indicate that the change of the level of the interface from -80 m at the beginning of the century to about -60 m today has increased the quantity of dead organic matter sinking down through the halocline as a consequence of the increased area of contact between the surface water and the deep water. The increased contact area has led to a corresponding increase in all fluxes through the halocline driven by turbulent gradient diffusion including an increase in the upward flux of nutrients. This has led to a fertilization of the surface water which has increased organic production in the surface zone. This in turn increases the amount of dead organic matter supplied to the deep water. At the same time the temperature increase has increased the rate of oxygen consumption. The net result is that oxygen in the deep water is being consumed at a much higher rate today than previously. It is estimated that the rate of consumption has increased about 110% since the end of the last century. This implies an increase in the primary production of about 40%. - The supply of oxygen to the deep water has increased primarily as a consequence of the increase in the area of contact between the surface water and the deep water, and secondly as a consequence of an increase in the vertical oxygen concentration gradient. However, the rate of increase of supply has been smaller than the rate of increase of the consumption. The relative dif $ference\ between\ the\ consumption\ and\ the\ supply\ has\ increased\ from\ 0\ at\ equilibrium$ conditions at the end of the last century to about 10% today. Although this change in the balance between supply and consumption appears to be marginal, it is nevertheless sufficient to bring about the dramatic decrease of the oxygen concentration in the deep water from about 3 ml/l at the end of the last century to close to 0 ml/l today. - The model introduced represents a preliminary step towards a Baltic model, which necessarily must take the changing position of the halocline and related effects into account.

Zusammenfassung

Dynamik der Ostsee-Ökosysteme und Ursachen für deren Veränderlichkeit

Die Dynamik der Ökosysteme der Ostsee und die Gründe für ihre Veränderlichkeit werden diskutiert, wobei die Verwendung von ökologischen Modellen als Hilfsmittel für Forschung und Management besonders berücksichtigt werden. - Die Ursachen der beobachteten Salzgehalts-, Temperatur- und Sauerstoffänderungen des Ostsee-Tiefenwassers werden besprochen. Die Arbeit führte zur Formulierung einer Hypothese, wonach es möglich erscheint, die O2-Entwicklung und die Langzeitentwicklung anderer hydrographischer Komponenten zu erklären. Die Analysen haben gezeigt, daß der Anstieg der Sprungschicht von 80 m Tiefe zu Beginn des Jahrhunderts auf etwa 60 m heute eine Zunahme der toten organischen Substanz bewirkt hat, die aufgrund der vergrößerten Kontaktzone zwischen Oberflächen- und Tiefenwasser durch die Salzgehaltssprungschicht hinabsinkt. Dieser größere Kontaktbereich hat zu einer entsprechenden Zunahme aller Austauschprozesse durch die Halokline geführt, die durch turbulente Gradientendiffusion und eine Zunahme des nach oben gerichteten Nährstofftransportes unterstützt wird. Dies hat zur Düngung des Oberflächenwassers geführt und eine Zunahme der organischen Produktion im Oberflächenbereich bewirkt. Letztere wiederum erhöht die Menge an toten organischen Substanzen, die dem Tiefenwasser zugeführt werden. Gleichzeitig hat der Temperaturanstieg die O2-Verbrauchsrate erhöht. Die Folge ist, daß der Sauerstoff im Tiefenwasser heute viel schneller verbraucht wird als früher. Seit dem Ende des letzten Jahrhunderts wird die Zunahme der O2-Verbrauchsrate auf 110 % geschätzt. Dies deutet einen Anstieg der Primärproduktion um ca. 40 % an. Die O_2 -Zufuhr zum Tiefenwasser hat hauptsächlich aus zwei Gründen zugenommen: erstens aufgrund des vergrößerten Kontaktbereiches zwischen Oberflächen- und Tiefenwasser und zweitens wegen einer Zunahme des vertikalen O2-Konzentrationsgradienten. Jedoch ist die Steigerungsrate der O2-Zufuhr geringer als die des O2-Verbrauchs. Der relative Unterschied zwischen Verbrauch und Angebot ist von 0 bei Gleichgewichtsbedingungen zur Zeit der Jahrhundertwende auf ca 10 % heute angestiegen. Obwohl diese Veränderung des Gleichgewichts zwischen Angebot und Nachfrage geringfügig erscheint, hat sie ausgereicht, um die dramatische Abnahme der O₂-Konzentration im Tiefenwasser von ca. 3 ml/l am Ende des letzten Jahrhunderts auf nahezu 0 ml/l heute hervorzurufen. - Das eingeführte Modell stellt einen ersten Schritt zu einem Ostseemodell dar, das notwendigerweise die sich verändernde Lage der Halokline und die damit verbundenen Wirkungen berücksichtigen muß.

Introduction

Investigations of the structure and function of aquatic ecosystems involve a collection of physical, chemical, and biological observations. This often results in a large number of data. The use of mathematical models is a convenient and an economical way to treat the data, to plan and coordinate future activities, and to explain and predict causes and changes in the behaviour of the ecosystem.

The models which have been developed can have different approaches and aims. By simple descriptive statistical models a summation and determination of parameters of simple quantitative relationship of collected data can be made. By explanatory models it is possible to obtain information about the mechanisms by which the system operates, and to express this knowledge in the form of quantitative

relationships. By predictive models it is possible to make predictions about future levels of concentrations of state variables and rates of processes in the system.

According to LUCAS (1964) models can be classified into rational models and empirical models with regard to their internal structure.

The purpose of empirical models is to describe the essential characteristics of the available data related to two or more variables. Therefore, the construction of empirical models is seen when the available data are decribed in terms of generalized functions such as polynomials of arbitrary order. Empirical models may be used for predictive purposes. The greatest failing of the empirical models is that predictions made outside the range of the independent variables, for which data are available, are quite unreliable. In contrast to empirical models rational models are more highly structured and admit a minimum of arbitrariness. Rational models are based on experimental or observational data and on accepted knowledge about the way various components in the real system operate. Rational models may be reductionistic or holistic.

Reductionistic models presuppose that each part of the system must be known in order to describe the behaviour of the entire system. Elaboration of reductionistic models causes an increase in number of state variables and processes and the complexity of the submodels.

The holistic models are based on the principle that a system is more than the sum of its components. Examples of holistic models are the maximum power principle of ODUM and ODUM (1976), and the hypothesis of all ecosystems behaving linearly as stated by PATTEN (1968).

Another way to classify models is in deterministic models and stochastic models.

By a deterministic model is meant a rational model, that is so structured that the value of the dependent variable is predicted (but not necessarily accurately, depending on the quality of the model) from exact values of the independent variables.

By a stochastic model is meant a rational model that is so structured that it can calculate the probability that a future value of the independent variable will lie between certain specific limits. The central objective of the stochastic model does not imply a conviction that the system is truly random.

The aim of the models may be the following:

- a tool for research, or
- a tool for survey planning, or
- a tool for management.

Models as a research tool involve the testing of a hypothesis on the processes described (submodels) as well as testing the behaviour of the total ecosystem, i. e. stability, sensitivity, diversity etc.

Models as a survey planning tool are based on available knowledge of a given water system. These models can be used for defining survey activities, survey localities, survey periods, and survey frequencies.

Models as a management tool involve calculations of consequences of a given management policy and calculations of allowable loadings. The types of problems which can be elucidated by these types of models are constructions of causeways, predictions of changes in water quality due to changes in loadings of organic compounds, nutrients, pathogens, pesticides, heavy metals, thermal effluents, etc.

The increasing exploitation of natural resources and technical interventions have caused disturbances in the ecological balance. Our present knowledge of the behaviour of ecosystems and how they respond to any changes is not sufficient. The increasing use of ecological models in research and management has gradually increased our understanding of the ecosystems and their responses to the influence of man.

Models as a research tool

From an ecological point of view the Baltic may be considered as a body of water comprising different ecological subsystems in which the energy is transported through a great number of state variables on different trophic levels. Following the maximum-power principle of ODUM and ODUM (1976), the systems that survive in the competitions among alternative choices are those that develop more power inflow and use it to meet the needs of survival. The systems do this by:

- 1) developing storages of high quality energy,
- 2) feeding back from the storages to increase inflows,
- 3) recycling materials as needed,
- 4) organizing control mechanisms that keep the system adapted and stable, and
- 5) setting up exchanges with other systems to supply special energy needs.

Investigations of these mechanisms give important information about the dynamics of the ecosystem, the causes of their variability and explain why certain systems survive and other systems do not. To carry through this research in its utmost consequence, however, enormous resources are required. Through formulation of models the large computers and EDP-technique which are available today have given ecologists much better possibilities of understanding the structure and function of ecosystems.

The scientists at the Askö Laboratory, the Swedish marine station in the Baltic, were among the first research groups who started investigations on dynamics and energy flows in the Baltic ecosystems by means of ecological models. The work carried out by this group has mainly been based on the energy circuit language by H. T. ODUM (1972), and JANSSON (1972), and simulations by the analogue computer technique. Most of the ecosystem analyses and ecosystem simulations carried out by the Askö group and other Baltic scientists have been carried out on:

1) the phytal subsystem, 2) the soft bottom system, and 3) the pelagic subsystem (ACKEFORS, 1973; ELMGREN and GANNING, 1974; A. M. JANSSON, 1974; B. O. JANSSON, 1975; ACKEFORS, 1975; PROBST, 1975; ANKAR and ELMGREN, 1976; WALLENTINUS, 1976; MCKELLER and HOBRO, 1976; ANKAR, 1977; B. O. JANSSON and WULFF, 1977; SCHRAMM and GUTERSTAM, in print and others). Through these works important knowledge of the behaviour of the Baltic ecosystems has been obtained, and ecological models of different complexities have been constructed.

By nature these models are analogue to a part of the real system. A given system can be abstracted in any number of ways, and a near infinite variety of models from very simple to extremely complex ones can be hypothesized. Whether or not such models are relevant to a problem depends on whether or not the models will accept the available input data and produce output corresponding to the output which is desired. If the system which is to be modelled is poorly understood, the model may contain hypotheses about interactions of processes as well as rate constants, which will influence the output. When the research project is complex, some of these hypotheses will be rejected and new functional interactions will be suggested. Through this work the knowledge of ecosystem behaviour is increased, and the models become more and more reliable.

Models as a management tool

The previously mentioned work on system analysis and energy flow has increased our knowledge of the behaviour of ecological subsystems in the Baltic and prepared the way for development of ecological models for the total Baltic Proper to be used as a tool for management. Such models are justified by the ecological changes which have been observed in the Baltic during the last century. Some of these changes are man-made, and others are due to natural hydrographic and climatic changes.

Based on the long series of hydrographical measurements by the Fishery Board of Sweden, FONSELIUS (1969) was able to show a decrease in the oxygen concentration below the halocline. The stagnation culminated in 1968–69, when a large part of the Gotland Basin and the Gulf of Finland contained hydrogen sulphide. At the end of 1968 water flow from the North Sea through the Belt Sea increased, and the North Sea water reached the northern Baltic almost a year later. This resulted in a mixing of the nutrient-rich water mass below the halocline with the surface water of the Gotland Basin.

The concentration of phosphate has increased considerably during the last 40 years in the water mass below the halocline (FONSELIUS, 1972b). The frequency of inflow of water from the North Sea increased, which has resulted in the raising of the halocline from a level close to 80 m below the surface at the beginning of the century to the present level 60 m below the surface. A rough calculation shows that this has increased the volume of the deep water by about 2000 km³ to about 6000 km³. Furthermore, it is of great importance to note that the area of contact between the deep water and the surface water has increased from about 100,000 km² at the beginning of the century to about 150,000 km² at present.

Since the beginning of the century the salinity of the deep water in the northern Baltic Proper has increased about $1^{\circ}/_{\circ o}$ and the temperature has increased about 1.5° C, according to FONSELIUS (1969) and MATTHÄUS (1972). The increase in salinity is a result of a combination of changes in the processes governing the salt balance:

- 1) a general decrease in the fresh water inflow, and
- 2) an increase in the supply of water and salt to the deep water as a consequence of 1)

DICKSON (1971) has studied variations of the salinity in the Northern Atlantic and adjacent waters over long periods. He found that salinity fluctuations are closely related to changes in the atmospheric circulation which have been observed over a long period and concluded that any acceleration of the inflow to the continental area is accompanied by an acceleration of the inflow to the Kattegat, the Belt Sea, and the Sound.

It is a well-established fact that the oxygen concentration of the deep water has decreased from about 3 ml/l at the end of the 19th century to a negligible concentration today. Fig. 1 shows the development of oxygen concentration at 100 m depth in the northern Central Basin from 1900 to 1967, (after FONSELIUS, 1969).

Besides the increase in transport of nutrients from the water mass below the halocline into the water mass above the halocline, also an increase in the domestic and industrial loading of nutrients and organic matter has taken place. Because of lack of national investigation programmes, however, only the total loading of nutrients and BOD into the Baltic can be given. ICES/SCOR (1977) states that the

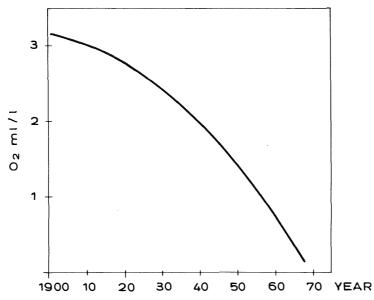


Figure 1
Oxygen concentration at 100 m in the Northern Central Basin – after FONSELIUS (1969)

total input of BOD amounts to 1000,000 tons/year. The sewage loading into the Baltic amounts to about 77,000 tons/year of nitrogen (excluding loadings from the industries) and 27,000 tons/year of phophorus. Of these loadings about 40% of the direct and 20% of the indirect input are discharged without any treatment. About 50% of the waste water input along the western and southern borders of the Baltic results from domestic sewage. The proportions are smaller for the eastern part of the Baltic Proper, the Gulf of Finland, the Bothnian Sea and the Bothnian Bay. Crude estimates of the river transport of total phosphorus to the Baltic vary from 10,000 tons/year (VOIPIO, 1969) to 14,000 tons/year (FONSELIUS, 1972a) and 32,000 tons/year (SEN GUPTA, 1973). According to AHL and ODEN (1972) for river discharge and ENGWALL (1972) for urban and industrial outlets, in total about 80% of the discharged phosphorus and 50% of the discharged nitrogen from Sweden is caused by man's activities.

Due to the increased loadings of nutrients, the production of phytoplankton and hereby the turbidity of the water has increased (FONSELIUS, 1971; KAISER and SCHULTZ, 1975; SCHULTZ and KAISER, 1975; LINDAHL, 1975; LINDAHL, 1977; EDLER, 1977). In the off-shore areas the blooms of the blue-green algae *Nodularia spumigena* seem to have increased during the last few years and experiments have shown that this alga is stimulated by increasing phosphate concentrations (HORSTMANN, 1975). The seaweeds, especially the brown algae such as *Fucus*, are forced seawards (PEUSSA and RAVAESKO, 1975), the number of the green algae *Cladophora* and *Enteromorpha* has increased, and the normal vertical stratification of seaweed has changed (LINDGREN, 1975). The population of zooplankton and the stock of herring and sprat have increased (SEGERSTRÅLE, 1965; SCHULTZ, 1970; ACKEFORS and HERNROTH, 1972). Due to changes in the salinity and oxygen concentrations the bottom fauna below the halocline, however, has suffered heavily (HAGBERG, 1972 and SCHULTZ and KAISER, 1973), and the

hatching of bottom fish like cod and off-shore flounder has become critical, too (DYMENTYEVA, 1972 and LINDBLOM, 1973). The common jellyfish *Aurelia aurita* has extended further north (LINDQVIST, 1962), and the recolonization of the Baltic Basin after the great stagnation in the late sixties shows clear features of oceanization in the distribution of species, zoogeographical elements and feeding types (LEPPÄKOSKI, 1975).

According to JENSEN et al. (1969 and 1972), the total contents of DDT and PCB in herring, salmon and seal were up to ten times higher than the concentrations in the same organisms in the North Sea. Both DDT and PCB are found in higher concentrations in the eastern Bornholm Basin than in the western part of the basin. Also high concentrations of Hg have been observed in Baltic animals, i. e. especially in pike (ACKEFORS, 1971).

As is seem from the above-cited authors, the physical, chemical and biological conditions in the Baltic have changed drastically during the last century. In order to obtain a better understanding of the overall mechanisms which are responsible for and control these changes, it is necessary to develop a combined predictive transport-dispersion and water quality model of the Baltic. The importance of making this kind of model has recently been recognized by B. O. JANSSON (1976) and WULFF (1976). Budgets for salinity, oxygen and nutrients have been formulated by FONSELIUS (1972a) and BOLIN (1972a, b and 1973), and a preliminary ecological model has been developed by SJÖBERG et al. (1972 a, b). In the present paper the hydrographic mechanisms which may have caused some of the ecological changes that have been observed are discussed, and a simple salinity model has been procured. The results of this work are intended as a contribution to the current discussions of the lines of action to be taken in future research of the Baltic.

Hydrographical mechanisms and their influence on the change in the hydrographical and ecological conditions in the Baltic

System analysis

To establish the order of magnitude of some important hydrographic parameters a simple two-segment model of the Baltic is considered, see Fig. 2.

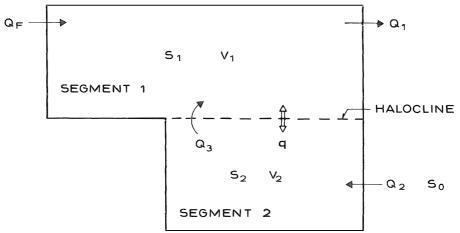


Figure 2
A two segment model of the Baltic showing transport terms

 S_1 and S_2 denote average salinities in the upper and lower segment respectively. V_1 and V_2 are the volumes and Q_2 and Q_F the deep water and the fresh water inflow respectively.

The salt flux across the halocline is composed of two contributions: 1) the advective flux, which is the product of the flow and the salinity at the interface, and 2) the salt flux generated by turbulent diffusion over the interface. This term is traditionally expressed as:

Salt flux due to diffusion =
$$AD_z \frac{dS}{dz}$$
 (1)

where A is the total area of the interface, D_Z is the effective diffusion coefficient in the vertical direction and $\frac{dS}{dz}$ is the salinity gradient at the interface.

In the model the vertical mixing is defined by an effective exchange volume, q:

$$\Delta S \int_{A} \frac{D_{z}}{\Delta z} dA = q \Delta S$$
 (2)

Conservation of water in the segments requires:

$$\frac{dV_1}{dt} = Q_F + Q_3 - Q_1 \tag{3}$$

$$\frac{dV_2}{dt} = Q_2 - Q_3 \tag{4}$$

Conservation of salt in the segments requires:

$$\frac{d}{dt} (V_1 S_1) = Q_3 \frac{1}{2} (S_1 + S_2) + q (S_2 - S_1) - Q_1 S_1$$
 (5)

$$\frac{d}{dt} (V_2 S_2) = Q_2 S_0 - Q_3 \frac{1}{2} (S_1 + S_2) - q (S_2 - S_1)$$
 (6)

where S_0 is the average salinity concentration in the inflowing water.

The change in the total amount of salt in the volume considered by the model is obtained by adding the equations: $\dot{}$

$$\frac{d}{dt} (V_1 S_1) + \frac{d}{dt} (V_2 S_0) = Q_2 S_6 - Q_1 S_1$$
 (7)

It is possible to perform computations of the time varying transport parameters Q_2 and q using equations (3) through (7). Records of salinities on the Baltic water $(S_1,\,S_2)$ have been extracted from data reported by FONSELIUS (1962, 1967 and 1969) and NILSSON and SVANSSON (1974). Time series of Q_F and S_0 are taken from MILJØSTYRELSEN (1976). All input data to the computations are in the form of annual means over the period 1920 to 1970, see Figs. 3 and 4.

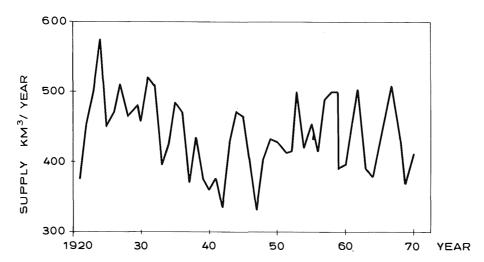


Figure 3
The annual mean of net fresh water supply to the Baltic

It should be noted that the term $\frac{d~(VS)}{dt}$ has been approximated by $V\frac{dS}{dt}$ which is

a fair approximation implying that $Q_3 = Q_2$. Maximum errors arising from the approximation are estimated at about 15%.

The results of the computation are depicted in Fig. 5, showing 5 year running means of the inflow to the deep water and the effective exchange volume.

The effective exchange volume may be made equivalent to an effective turbulent diffusion coefficient using equation (2), assuming that the turbulent diffusion is uniformly distributed over the interface. By doing so it appears that the computed diffusion coefficients fall in the range 0.004–0.03 cm²/s with an average of 0.015 cm²/s. Dye tracer experiments performed in the Arkona and Bornholm basins near the halocline yielded vertical diffusion coefficients in the order of 0.03 cm²/s (KULLENBERG, 1974).

The computed magnitude of the inflow to the deep water (Q_2) compares well with that given by BOLIN (1972 b), while the value given by FONSELIUS (1969) is somewhat higher. The salinity of the inflowing water is assumed to be $17.1^{\circ}/_{\circ\circ}$, corresponding to the average salinity at Gedser Rev Lightship. This value would appear to be too high since further mixing between the surface water and the inflowing bottom current will take place before the bottom current reaches the halocline level. However, the product Q_2 S_0 , which is the total amount of salt transported to the Baltic deep water, will still have the correct order of magnitude.

It should be stressed that the present approach suffers from a serious drawback. This is due to the fact that the continuity equations cannot predict changes in the magnitude of the inflowing water as a result of changes in the fresh water inflow. If one attempts to do so, the meaningless result that an increased fresh water inflow would increase the deep water inflow emerges. This is of course not so. On the contrary, an increased fresh water inflow to the Baltic will decrease the supply of water and salt to the Baltic deep water since higher outflow velocities produce an increased resistance to the deep water flow through the Belt Sea.

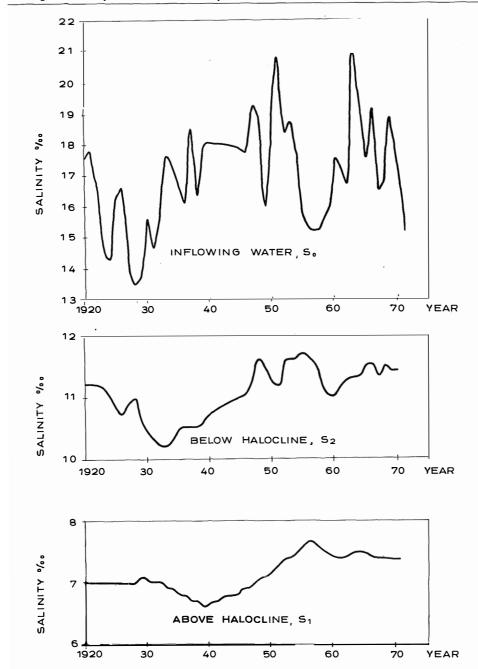


Figure 4

Annual means of salinities of inflowing water and of the Baltic deep and surface water

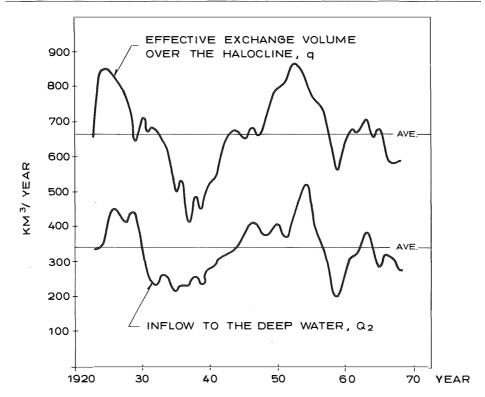


Figure 5 Five years running means of the effective exchange volume and the inflow to the deep water (computed from eqs. (5)–(7))

The computed time series of Q_2 and q can for the reason stated above not be expected to be correct in detail. It should furthermore be made clear that the decreasing trend in the magnitude of the fresh water inflow has two very important effects: 1) an increase in the supply of water and salt to the Baltic deep water which tend to lift the level of the halocline and 2) an increased vertical exchange across the halocline, none of which are reproduceable by the conservation equations. It is therefore not surprising that the results do not show an increasing trend in these quantities, which is indicated by both theory and observations.

Since the temperature below the halocline can be regarded as a conservative tracer, a conservation of temperature equation can be set up for segment 2. A characteristic feature of the hydrography of the Baltic is the presence of a temperature minimum immediately over the halocline due to thermal convection. The temperature at this level is about 2°C corresponding to the temperature at which water with a salinity of $8^{\circ}/_{00}$ attains its maximum density. Since the temperature of water flowing into the Baltic is always higher than 2°C the heat flux in the bottom water is always directed upwards.

The conservation of the temperature equation for segment 2 reads:

$$Q_2 T_0 = q \Delta T + Q_2 \overline{T}$$
 (8)

where the terms not previously defined are: T_o is the average temperature of the inflowing water, ΔT is the difference in temperature of the deep water and the temperature minimum close to the halocline.

Computations using equation (8) give $T_0 = 10\,^{\circ}\text{C}$ indicating that the bulk of the inflow to the Baltic deep water takes place in the warm season. Judging from the annual variation of the temperature at Gedser Rev Lightship it appears that about $^{3}/_{4}$ of the inflow stems from the period June–November in which the temperature in the inflowing water is above the annual mean, $7.5\,^{\circ}\text{C}$.

Oxygen Supply and Consumption in the Deep Water

The long-term development of the oxygen concentration depicted in Fig. 1 raises the question of its causes and the possibility that man's activities have had an adverse effect. A close examination of the equations expressing the conservation of organic matter and oxygen using the findings derived from the salinity analyses seems to be appropriate.

The conservation of BOD equation for the deep water reads:

$$\frac{d}{dt} \frac{(V_2 L_2)}{dt} = P - k V_2 L_2 \tag{9}$$

where L_2 is the average concentration of BOD (mg O_2/I) in the deep water, t is time, P is the net supply per unit time of BOD, and k is the "BOD decay coefficient".

The conservation of oxygen equation reads:

$$\frac{d}{dt} \left(V_2 C_2 \right) = F - k V_2 L_2 \tag{10}$$

where C_2 is the average concentration of oxygen in the lower segment, and F is the net rate of supply of oxygen to the lower segment.

The terms P and F can be separated into two contributions:

- (1) the contribution due to vertical transport over the halocline, and
- (2) the contribution due to the exchange through the Danish Belts and Sounds.

It is of considerable importance to note that (2) is composed of a positive term expressing the advective influx with the deep water inflow, and a negative term expressing the advective upward flux out of the lower segment due to the continuous erosion of the lower segment (entrainment). An analysis of the magnitudes of these terms show that the upward flux of organic matter as well as oxygen nearly balances the advective influxes so that both the net supply of organic matter and oxygen to the lower segment as a first approximation can be assumed to be a result of vertical exchange processes only.

It should on the other hand be kept in mind that the exchange of water and salt through the Danish Belts and Sounds is of decisive importance for the internal exchange processes in the Baltic and hence for the ecological conditions.

The quantity of P may then be computed as that fraction of the carbon produced in the surface layer which penetrates the halocline before mineralization has taken place. The annual mean production of the Baltic is assumed to be 70 gC/m²/yr. The interface area is in the order of 150,000 km². Assuming that only the organic carbon produced in the water column vertically above the interface has a possibility

of sinking down into the deep water, and that 20% of the organic carbon sinks down below the halocline, one obtains:

$$\begin{array}{ll} P \,=\, _{\alpha} \cdot p \, \cdot \, A \\ &=\, 0.2 \, \cdot \, 70 \, \cdot \, 150,\! 000 \, = \, 2.1 \, \cdot \, 10^6 \; tC/yr. \end{array}$$

The amount of oxygen utilized to decompose this quantity of organic carbon must equal the supply of oxygen under equilibrium conditions. Assuming that 1g C consumes $3.47 \, \mathrm{g} \, \mathrm{O}_2$, the total consumption in the deep water is $7.3 \cdot 10^6 \, \mathrm{t} \, \mathrm{O}_2/\mathrm{yr}$, equivalent to $5.1 \, \mathrm{km}^3 \, \mathrm{O}_2/\mathrm{yr}$. The oxygen supply to the deep water can be calculated as q $\Delta \mathrm{C}$, which, using q = 665 km³/yr, and $\Delta \mathrm{C}$ = 7.5 ml/l yields 5.0 km³/yr.

The quantity of F can on the grounds stated previously be approximated by

$$F = AD_{Z} \frac{dc}{dz}.$$
 (11)

Returning to equation (10) it is evident that the development depicted in Fig. 1 indicates that the right hand side of the equation has been negative over the last 70–80 years. There are, however, clear indications that the quantity F has undergone a considerable increase over that period of time. This implies a similar, even faster rate of increase as far as the supply of organic matter to the deep water is concerned. The discussion below will clarify the statements above:

The supply of oxygen represented by equation (11) has increased considerably since the beginning of the century for two reasons:

- 1. The area of contact between the well aerated surface water and the deep water has increased about 50% as a consequence of the lifting of the halocline.
- 2. The oxygen concentration gradient in the vertical direction has increased as a consequence of the decrease of the concentration below the halocline. Assuming that the vertical distance Δz over which the concentration decrease is concentrated is constant, the increase in the magnitude of the gradient amounts to about 50%.

The diffusion coefficient may have decreased as a consequence of the increased stability of the halocline. However, assuming that $\mathrm{D_{Z}}$ can be taken as inversely proportional to the relative density deficit over the halocline the decrease in $\mathrm{D_{Z}}$ will not exceed about 15%. However, the fact that the halocline has reduced its distance from the surface by 20 m could very well have counteracted this decrease considerably.

If the decrease of the diffusion coefficient is tentatively evaluated as 10%, the resulting ratio of present supply to the supply at the outset of oxygen decrease may be evaluated as $1.5 \cdot 1.5 \cdot 0.9 = 2$.

The supply of organic matter expressed by P = α p A has experienced a similar increase:

The factor α , which denotes the ratio of organic carbon settling down into the deep water to the total amount produced in the water column directly above the halocline, has probably remained unchanged.

The primary production of organic carbon per unit area in the upper layer has probably increased somewhat. The record of values on the primary production is not long enough to form the basis of any definitive conclusion, but it appears fair to assume that productivity has increased since the turn of the century. The main reason for this statement is that the flux of nutrients from the deep water,

where concentrations are about 10 times higher, to the surface water has increased as a consequence of the increased area of contact between the layers. In recent years the more and more frequent occurrences of nutrient releases from bottom sediments under anoxic conditions has further accelerated the supply of nutrients to the surface water.

The area of contact (A) between the surface water and the deep water has increased from about 100,000 km² to about 150,000 km² by the raising of the interface from the 80 m level to today's 60 m level. The areas are computed considering the entire Baltic including the Gulf of Bothnia on the basis of data given by EHLIN (1974).

The development of the supply of organic matter to the deep water cannot be evaluated in detail on the basis of this analysis. However, based on an analysis of eqs. (9) and (10) it may tentatively be concluded that the rate of increase of P has exceeded the rate of increase of F. A closer examination (see below) shows that the increase in P has been about 10% higher than in F. Thus, it is assumed that the resulting ratio of present supply of organic matter to the supply at the outset of the oxygen decrease may be evaluated as $1.0 \cdot 1.4 \cdot 1.5 = 2.1$.

It should furthermore be observed that k, the decay coefficient, has increased as a consequence of the increased temperature in the deep water. The rate of decomposition of organic matter and the rate of oxygen consumption can be expressed as:

$$(T-20) k = k_{20} (1.07)$$
 (13)

where k_{20} is the decay rate at 20° and T is the temperature in °C. Over a period of 80 years the decay rate can be assumed to have increased about 11%. This figure corresponds well with that estimated by KULLENBERG (1970), who pointed out the possible significance of this effect on the long term development of oxygen conditions in the deep water.

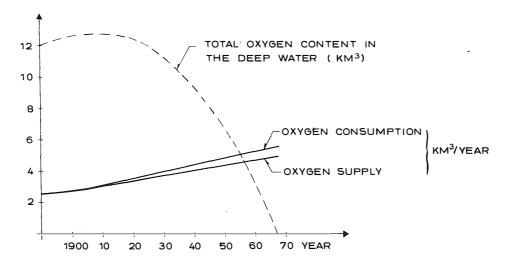


Figure 6
Estimated variation of supply to and consumption in the deep water (full lines) and variation of the total oxygen content in the period 1890 to 1967 (dotted line)

Assuming a linear variation of the magnitude of the halocline area (A) with time and likewise for the variation of D_z , the development of the oxygen supply can be calculated. Knowing the actual development of the oxygen concentration (Fig. 1) and assuming a linear variation of the volume of the deep water it is possible to calculate the oxygen consumption. The result is indicated in Fig. 6.

The figure clearly illustrates the dramatic effect of the slight shift in favour of the consumption. This development is understandable when it is noted that the total content of oxygen is small compared to the quantity which is annually supplied and consumed.

Salinity model of the Baltic

Model Characteristics

A preliminary conservation-of-salt model based on a finite segment approach has been constructed (Fig. 7). Areas and volumes are given in Table 1. Note that the entire Baltic including the Bothnian Bay is included.

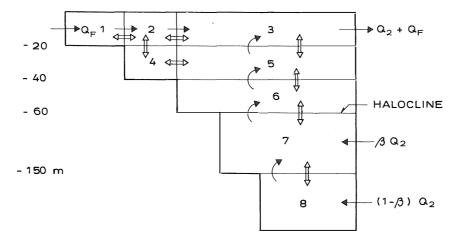


Figure 7

Model segmentation

Advective internal transports of salt are represented as the product of the flow and the average salinity on the segment boundary (central difference approach). On the boundaries advective salt transports are taken as the product of flow times upstream salinity.

Diffusive transports are accounted for by the term AD_ZdC/dz which in the finite segment approach is equivalent to q \cdot Δ C, where Δ C and Δ z are adjusted to fit the real gradient.

The 8 time-dependent conservation of salt equations form 8 ordinary algebraic equations which are set up and solved with a time step of 1 year.

The boundary between adjacent segments is assumed to remain fixed in position. This is probably the most serious drawback in the model since it is known that the changing of the level of the halocline is of considerable importance as far as the oxygen conditions are concerned.

Table 1
Volumes and areas between adjacent segments

Segment	Volume km³	Area km²
1	100	60
2	1 600	50
3	4 400	
4	600	50
5	4 400	220 000
6	3 600	155 000
7	5 860	13 000
8	340	
A_{2_4}		80 000
A _{2_4} A _{3_5}		220 000

As input variables to the model time series of Q_F , Q_2 , and time series of q over the halocline, as described earlier, are used. Effective exchange volumes over the other segment boundaries have been adjusted in a calibration of the model.

Model Results

Model computations covering the period 1920 to 1970 have been performed for various magnitudes and distributions of the exchange volumes at the horizontal segment boundaries. The exchange volumes corresponding to the run which yielded the most satisfactory agreement between observed and computed salinity variations are given in Table 2.

 Table 2

 Exchange volumes and diffusion coefficients found in the calibration of the model

Level	Exchange Volume	Diffusion Coefficient	Estimates of D _z *
m	km³/year	cm²/sec.	cm²/sec.
- 20	24 700	1.5	0.5–1.5
- 40	24 700	1.5	
- 60	665	0.015	0.06
— 150	28	0.06	0.6

^{*} after KULLENBERG (1974)

Fig. 8 shows the comparison between computed salinities (5 year running means) and observed salinities. It appears that the model is capable of reproducing the given salinity variations quite well. This is, of course, essentially a matter of calibration and thus not necessarily expressive for the quality of the predictive capabilities of the model. However, the result of the model calibration, which physically yielded very plausible magnitudes of the diffusion coefficients, is such that it allows one to conclude that the model functions without numerical errors.

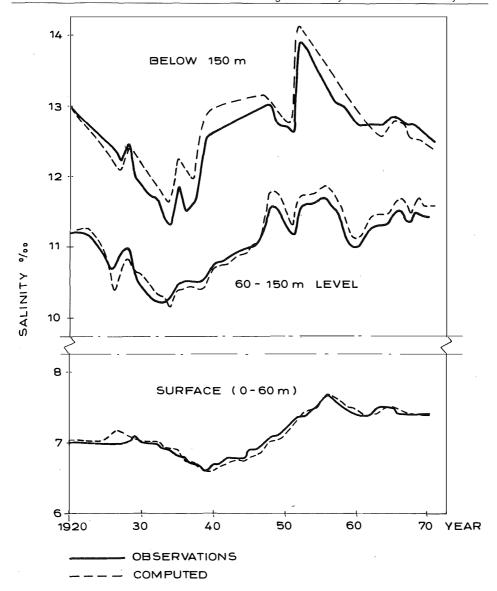


Figure 8
Salinity variations. Full lines are average salinities derived from observations, i. e. FONSELIUS (1969) and NILSSON and SVANSSON (1974). Dotted lines are salinities computed by the calibrated model

It was originally intended to use the salinity model as the basis for construction of an oxygen model. However, the recognition of the importance of the movement of the halocline made it clear that a fixed-boundary model cannot be used to reproduce the observed long-term development of the deep water oxygen content.

Proposed further research

The character and amount of data available on the physical and biological behaviour of the Baltic appear to offer an excellent opportunity to establish cause-effect relationships and to obtain a quantified description of the system. However, due to the complexity of the system this can only be achieved by means of a unified and consistent systematic approach using numerical modelling.

To achieve this goal a number of important physical and biological mechanisms still need to be explored and understood in detail.

Among the physical mechanisms which appear to need further elucidation in order to advance our understanding of the behaviour of the system are the following:

- the processes governing the inflow of water (and salt) to the Baltic deep water, and
- 2) vertical exchange processes.

A thorough understanding of the above-mentioned two items is essential for the description of the observed long-term hydrographical changes. Since the hydrographic changes are intimately correlated to the ecological changes, the question concerning the physical behaviour of the system appears to deserve a high priority in future Baltic research.

Parallel with a study of the basic processes a current development of existing models should take place.

At present, the salinity model presented in this paper may be used, within certain limitations, for the study of long term changes in the vertical distribution of any conservative constituent and any constituent for which a first order decay can be specified provided that the sources and sinks can be specified. Thus it would appear obvious to apply the model to compute the concentration of, for instance, phosphate concentration as a function of time and supply. The drawback with respect to the effect of changes in the fresh water inflow can be overcome by specifying estimated rate of inflow as a given function of the $Q_{\mbox{\sc F}}$ -variation. The model can furthermore serve as a tool in various sensitivity tests which could be performed with the purpose of testing the response of the system to various changes in the variables. This would appear to be the most obvious application since it would aid the general understanding of the system and furthermore throw light on the question regarding priority of further research.

Generally, the results of hydrodynamic and transport-dispersion models are used as input to the water quality models. During recent years the hydrodynamic models have been developed to an advanced stage. Flows in areas such as the Great Belt and the Sound have been modelled sucessfully. Comparisons between measured and calculated results in these areas show good agreement in velocities and interface elevations (BERTHELSEN et al., 1977; HINSTRUP et al., 1977 and RODENHUIS et al., 1977).

In order to predict the consequences of any man-induced disturbances of the ecosystem in the Baltic a water quality model is also needed.

A water quality model which is going to be used as a tool for management policy has to comprise the state variables, processes and forcing functions which are believed to be the most essential for the specific problem, and the model must be calibrated to the conditions prevailing in the water body. A calibration comprises the use of initial concentrations, realistic boundary values, and values of coefficients

During recent years the use of water quality models for research and management of Danish waters has increased. These models are now used for simulating chemical and biological changes in concentrations of state variables and rate of processes in water bodies exposed to technical interventions (DAHL-MADSEN, in press).

Recently a combined transport-dispersion model and water quality model has been used for estimating the effect of a tunnel between Helsingør and Helsingborg on the hydrographic and biological conditions in the Sound (KROGH et al., in press). In Fig. 9 are shown the results of the measured and computed vertical distribution

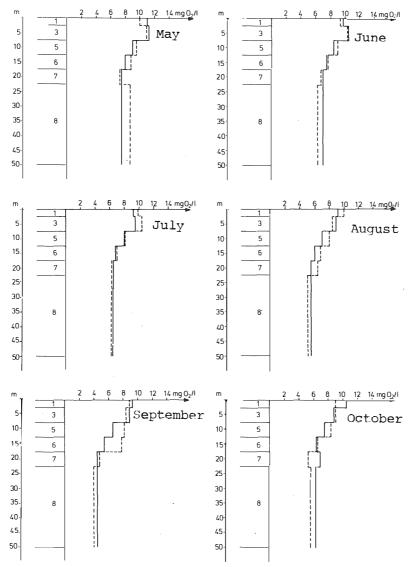


Figure 9

Comparison between measured (————) and computed (———) values of oxygen vertically in the Sound. After KROGH et al. (1978)

of oxygen from May to October in 8 segments from the surface to 50 m. As is seen from the figure, a good agreement between measured and computed results was achieved.

As discussed in the present paper, the biological and chemical conditions in the Baltic have changed drastically during this century. Therefore, there is an urgent need today to get a better understanding of the mechanisms which have caused these changes and to elucidate the possibilities for controlling further damages in the Baltic.

A coordination of the Baltic research activities has already been established (ICES/SCOR, 1977), The authors, however, find that the situation has matured to a point where the development of numerical models to a higher extent than hitherto could be emphasized.

A combined transport-dispersion and water quality model for the Baltic capable of reproducing the observed long term developments and capable of predicting changes as a function of changes in external conditions must take into account the effect of the changing level of the halocline. The development of a moving boundary model and a water quality model calibrated to the conditions prevailing in the Baltic appear to be obvious objects for further Baltic research.

References

ACKEFORS, H.: Mercury pollution in Sweden with special reference to conditions in the water habitat. Proc. Roy. Soc. Lond. B, **177**, 365–387 (1971)

ACKEFORS, H.: Production studies of zooplankton in relation to the total production in the Baltic proper. Merentutkimuslaitoksen Julkaisu, 239 (1973)

ACKEFORS, H.: Production studies of zooplankton in relation to the primary production in the Baltic proper. Merentutkimuslait. Julk./Havforskningsinst. Skr 239, 123–130 (1975)

ACKEFORS, H. and L. HERNROTH: Estimations of the amount of zooplankton and fish in the Baltic proper. Medd. Havsfiskelab., Lysekil, **139**, pp. 16 (1972)

AHL, T. and S. ODEN: River discharges of total nitrogen, total phosphorus and organic matter into the Baltic Sea from Sweden. Ambio Special Report, **1**, 51–56 (1972)

ANKAR, S.: The soft bottom ecosystem of the northern Baltic proper with special reference to the macrofauna. Contrib. Askö. Lab., Stockholm, 19, pp. 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. Contrib. Askö Lab., Stockholm, **11**, pp. 115 (1976)

BERTELSEN, J. AA. and I. R. WARREN: Two-Layer Modelling of The Danish Belts: Collection and Processing of Data and Calibration of the Models. Proceedings XVII Congress IAHR, Baden-Baden (1977)

BOLIN, B.: Some preliminary views on the problem of modelling the Baltic for ecological purposes. Oikos Supp. **15**, 7–8 (1972a)

BOLIN, B.: Model Studies of the Baltic Sea. Ambio Special Report, 1, 115-119 (1972b)

DAHL-MADSEN, K. I.: Modelling of eutrophication in shallow marine water (in press)

DANISH METEOROLOGICAL INSTITUTE: Mean Values of Observations from Danish Light Vessels. Copenhagen. Nautical-Meteorological Annual 1932 (1933)

DICKSON, R. R.: A Recurrent and Persistent pressure-anomaly Pattern as the Principle Cause of Intermediate-Scale Hydrographic Variations in the European Shelf Seas.-Deut. Hydr. Z. **24**, 97 – 119 (1971)

DYMENTYEVA, T. F.: On the causes responsible for changes in fish production of the Baltic Sea. Ambio Special Rep. 1, 63–66 (972)

EDLER, L.: Phytoplankton and primary production in the Sound. Thesis in Marine Botany. University of Gothenburg, pp. 110. Göteborg (1977)

EHLIN, U.: Computer Based Calculations of Volumes of the Baltic Area. 9th Conference of the Baltic Oceanographers (1974)

ELMGREN, R. and B. GANNING: Ecological studies of two shallow brackish water systems. Contrib. Askö Lab. Stockholm, **5**, pp. 56 (1974)

ENGVALL, R.: Swedish municipal and industrial discharges into the Baltic. Ambio Special Rep. 1, 41–49 (1972)

FONSELIUS, S. H.: Hydrography of the Baltic Deep Basins I. Fishery Board of Sweden – Series Hydrography, **13** (1962)

FONSELIUS, S. H.: Hydrography of the Baltic Deep Basins II. Fishery Board of Sweden. Series Hydrography, **20** (1967)

FONSELIUS, S. H.: Hydrography of the Baltic Deep Basins III. Fishery Board of Sweden. Series Hydrography, **23** (1969)

FONSELIUS, S. H.: On the primary production in the Baltic. ICES paper C. M. 1971/L: 16 (1971)

FONSELIUS, S. H.: On Biogenic Elements and Organic Matter in the Baltic. Ambio Special Rep. 1, 29–36 (1972a)

FONSELIUS, S. H.: On Eutrophication in the Baltic Sea. In: Marine Pollution and Sea Life. (FAO) Fishing News Books Ltd., England (1972b)

HAGBERG, A.: Undersökningar över bottenfauna. Meddelande från Havsfiskelab., Lysekil, **117**, 8–9 (in Swedish) (1972)

HINSTRUP, P. I., A. KEJ and U. KROSZINSKY: A High-Accuracy Two-Dimensional Transport-Dispersion Model for Environmental Applications. Proc. XVII Congr. IAHR, Baden-Baden (1977)

HORSTMANN, U.: Eutrophication and mass production of blue-green algae in the Baltic. Merentutkimuslait. Jul./Havsforskningsinst. Skr. **239**, 83–90 (1975)

ICES/SCOR: Studies of the pollution of the Baltic Sea. Coop. Res. Rep. No. 63, ed. G. Kullenberg (1977)

JANSSON, A. M.: Community structure, modeling and simulation of the *Cladophora* ecosystem in the Baltic Sea. Contrib. Askö Lab., Stockholm, **5**, pp. 130 (1974)

JANSSON, B. O.: Ecosystem approach to the Baltic problem. Bull. Ecol. Res. Committee/NFR **16**, pp. 82 (1972)

JANSSON, B. O.: Modeling of Baltic ecosystems. Ambio Special Rep. 4, 157–169 (1976)

JANSSON, B. O. and F. WULFF: Ecosystem analysis of a shallow sound in the northern Baltic – A point study by the Askö Group. Contrib. Askö Lab., Stockholm, 18, pp. 160 (1977)

JANSSON, B. O.: Systems analysis and simulation of the green algal belt (*Cladophora*) in the Baltic, Havsforskningsinst. Skr., **239**, 240–247 (1975)

JENSEN, S., A. JOHNELS, M. OLSSON and G. OTTERLIND: DDT and PCB in marine environment. Fauna och Flora **64**, 142–148 (in Swedish) (1969)

JENSEN, S., A. JOHNELS, M. OLSSON and G. OTTERLING: DDT and PCB in herring and cod from the Baltic, the Kattegat and the Skagerrak. Ambio Special Rep. 1, 71–85 (1972)

KAISER, W. and S. SCHULTZ: On primary production in the Baltic. Merentutkimus-lait. Julk./Havsforskningsinst. Skr., **239**, 29–33 (1975)

KROGH, O., K. I. DAHL-MADSEN, E. GARGAS and H. SCHRØDER: A numberical model of oxygen conditions in a two-layered marine environment. International Conference on water resources engineering. Bangkok, Thailand 10–13 January, 1978 KULLENBERG, G.: On the Oxygen Deficit in the Baltic Deep Water. Tellus **22**, 357 (1970) KULLENBERG, G. E. B.: Some Observations on the Vertical Mixing in the Baltic. 9th Conference of the Baltic Oceanogr. (1974)

LEPPÄSKOSKI, E.: Macrobenthic fauna as indicator of oceanization in the Southern Baltic. Merentutkimuslait. Julk./Havsforskningsinst. Skr., 239, 280–288 (1975)

LINDAHL, O.: Primary Production Measurements in the Hanö Bight. Intern rap. Inst. Mar. Res., Lysekil, Sverige (1975)

LINDAHL, O.: Studies on the production of phytoplankton and zooplankton in the Baltic in 1976, and a summary of results from 1973–1976. Medd. Havsfiskelab., Lysekil, **220**, pp. 30 (1977)

LINDBLOM, R.: Abundance and horizontal distribution of pelagic fish eggs and larvae in the Baltic Sea. Medd. Havsfiskelab., Lysekil, **140**, 33 pp. (1973)

LINDGREN, L.: Algal zonation on rocky shores outside Helsinki as a basis for pollution monitoring, Merentutkimuslait., Julk./Havsforskningsinst. Skr., 239, 334–347 (;1975)

LINDQVIST, A.: Sjökalven i Bottenhavet. Östkusten, 4, 9, (in Swedish) (1962)

LUCAS, H. L.: Stochastic elements in biological models; their sources and significance. In: Stochastic Models in Medicine and Biology. Ed. by J. GURLAND. Publ. No. 10 Math. Res. Center, U.S. Army. Univ. of Wisconsin, Madison (1964)

MATTHÄUS, W.: Zur Hydrographie der Gotland See I. Säkulare Variationen von Salzgehalt und Temperatur. Beiträge zur Meereskunde, **29**, 35–51 (1972)

McKELLAR, H. and R. HOBRO: Phytoplankton-zooplankton relationships in 100-liter plastic bags. Contrib. Askö Lab., Stockholm, **13**, 83 pp. (1976)

MILJØSTYRELSEN: The Belt Project – Physical Investigation (in Danish) (1976) NILSSON, H. and A. SVANSSON: Long-Term Variations of Oceanographic Parameters in the Baltic and Adjacent Waters. Medd. Havsfiskelab. **174** (1974)

ODUM, H. T.: An energy circuit language for ecological and social systems: its physical background. In: Systems analyses and simulation in ecology II, pp. 592. Ed. by B. C. PATTEN. New York: Academic Press (1972)

ODUM, H. T. and E. C. ODUM: Energy basis for man and nature. 297 pp. New York, London and Paris: McGraw-Hill Book Company (1976)

PATTEN, B. C.: Mathematical models of plankton production. Int. Rev. Ges. Hydrobiol, **53**, 357–408 (1968)

PEUSSA, M. and O. RAVANKO: Benthic macroalgae indicating changes in the Turku sea area. Merentutkimuslait. Julk./Havsforskningsinst. Skr., **239**, 339–343 (1975)

PROBST, B.: Ein Modell zur Darstellung des pelagischen Kreislaufes in einem marinen Flachwasserökosystem der westlichen Ostsee. Dissertation, Kiel, 53 pp. (1975)

RODENHUIS, G. S., O. BRINK-KJÆR and J. AA. BERTELSEN: A North Sea Model that can provide Detailed Hydrographic Information. Paper to IX Annual Offshore Technology Conference in Houston, Tex., May 2–5 (1977)

SCHRAMM, W. and B. GUTERSTAM, (in press): Studies of the metabolic activity in *Fucus* communities from the Baltic. IV. BMB Symposium, Gdańsk, Poland, October 1975

SCHULTZ, S.: Der Lebensraum Ostsee. Ökologische Probleme in einem geschichteten Brackwassermeer. Biol. Rundschau, **8**, 209–218 (1970)

SCHULTZ, S. and W. KAISER: Biological effects of the salt water influx into the Gotland Basin in 1969/70. Oikos Supp. **15**, 21–27 (1973)

SCHULTZ, S. and W. KAISER: Some Pecularities of the Primary Production during the Last Years in the Baltic and Their Causes. Presented at the IVth Symposium of BMB, Gdansk, 13–18th October 1975

SEGERSTRÅLE, S.: On the salinity conditions off the south coast of Finland since 1950, with comments of some remarkable hydrographical and biological phenomena in the Baltic area during this period. Commentationes Biologicae **28**, 28 pp. (1965)

SEN GUPTA, R.: Budget of nitrogen and phosphorus in the Baltic. Mar. Chem. (1973)

SJÖBERG, S., F. WULFF and P. WAHLSTRÖM: Computer simulations of hydrochemical and biological processes in the Baltic. Contrib. Askö Lab., Stockholm, 1, pp. 90 (1972a)

SJÖBERG, S., F. WULFF and P. WÅHLSTRÖM: The use of computer simulations for systems ecological studies in the Baltic. Ambio, **1**, 217–222 (1972b)

VOIPIO, A.: On the cycle and the balance of phosphorus in the Baltic Sea. Suomen Kemistilchti A 42, 48–54 (1969)

WALLENTINUS, J.: Environmental influences on benthic macrovegetation in the Trosa-Askö area, northern Baltic proper. – I. Hydrographical and chemical parameters and the macrophytic communities. Contrib. Askö. Lab., Stockholm, **15**, pp. 134 (1976)

WULFF, F.: Ecological data and the model. Ambio Special Rep. 4, 171–177 (1976)