Oceanological and Hydrobiological Studies
International Journal of Oceanography and Hydrobiology
Vol. XXXVI, No.3

Institute of Oceanography (113-130) University of Gdańsk
ISSN 1730-413X 2007 eISSN 1897-3191

DOI 10.2478/v10009-007-0025-2
Review paper

Received: *August 25, 2006*
Accepted: *July 25, 2007*

Estuaries - a biological point of view

Maciej Wołowicz[1], Adam Sokołowski, Rafał Lasota

University of Gdańsk, Institute of Oceanography
Laboratory of Estuarine Ecology
Al. Marszałka Piłsudskiego 46, 81-378 Gdynia, Poland

Key words: estuaries, biodiversity, ecosystem functioning, Baltic Sea

Abstract

Estuaries are considered adverse environments for many living organisms because of their unstable environmental conditions. Variability in salinity, temperature and oxygen concentration of the water, diverse substrata and geomorphological structures are major contributors to increased ecological stress in estuaries. These variations contribute to the characteristic estuarine spatial and temporal changes of physico-chemical properties, which operate even at small scales.

In terms of biology estuaries represent fascinating environments - transition zones between freshwater and marine biomes. Freshwater entering an estuary has a major influence on the ecology of the system, its productivity, diversity and the distribution of organisms, with a high variability of niches favouring an increase of biodiversity and biomass. Many estuarine species/organisms show broad and efficient physiological adaptations (ecotypes) in response to these environmental factors. Under locally specific conditions, even different genetic clades (groups) can be formed. Estuaries serve as vital nursery systems for many fish and unique feeding grounds for migratory birds. On the other hand, estuaries are often seriously degraded habitats, hence providing an ideal environment for combining studies on ecology, nature conservation and human impact.

[1] Corresponding author: *ocemw@univ.gda.pl*; tel.: + 48 58 5236858; fax: + 48 58 523 66 78

Copyright© by Institute of Oceanography, University of Gdańsk, Poland

INTRODUCTION

For many years estuaries[2] have presented a challenging research subject to physical oceanographers, marine biologists and ecologists, and more recently also to ecophysiologists, geneticists and ecotoxicologists. Broad, and often multiscale and multidisciplinary, scientific concern on aspects of the structure and functioning of estuaries has implied a variety of criteria and definitions of *estuary*. This is often as a result of different methodological approaches employed by the various disciplines, for example geomorphology, oceanography and ecology, and in the literature several tens of definitions of an estuary have so far been attempted. In recent years, the growing interest in estuaries by ecophysiologists and ecotoxicologists, as well as geneticists, has been specifically related to potential effects of global climate changes on the biodiversity and functioning of these systems, and the subsequent responses (adaptation, acclimatisation, etc.) of organisms to these environmental disturbances. Of special interest are the evaluation and integration of human activity, including contamination, aquaculture, nutrient enrichment, invasion by non-native species, tourism, shipping, etc., that need a more integrative approach at different levels of system organisation.

In most studies estuaries are defined as part of a tidal coastal system with clearly detectable changes in the concentration of inorganic salts, the role of a salinity gradient hence being highlighted (Pritchard 1967, Day 1980, Fairbridge 1980). Using this criterion, the entire Baltic Sea as well as the White Sea, Black Sea and several other seas can be considered estuaries (e.g. Gustafsson, Andersson 2001; Peneva et al. 2003; Kaiser et al. 2005), with some physical oceanographers and ecologists also including here coastal lagoons (Zienkiewicz 1963). To describe the Mediterranean lagoons and bahiras, Guelorget & Perthuisot (1983) adopted the term *paralic ecosystems*, which corresponds to a common definition of an estuary except the presence of tides (http://memebres.lycos.fr/gredopar/paralic.htm). Variation in salinity along an estuary can be also induced by local climatic conditions. Salinity gradients in subtropical and tropical estuaries, for example (in contrast to the temperate zone) may occur only temporarily, being primarily driven by increased freshwater input during the rainy season and by intense water evaporation in dry months. In addition, estuaries may also differ in scale (size) and the areal extent of low-salinity waters, ranging from small lagoons and bays of a limited water exchange with the open sea to large coastal estuaries, which can have

[2] Estuary (*aestus* = *tide*): coastal water-basin with a connection to open (tidal) sea where sea water is diluted with freshwater of inland origin (river mouths, shallow bays among others).

Copyright© by Institute of Oceanography, University of Gdańsk, Poland

significant offshore impacts e.g. the Amazon River, Volga River, Yangtze River (e.g. Lie, Cho 2002; Gallo, Vinzon 2005)

Estuaries characteristically include a transition between freshwater and marine (saline) realms and, from an ecological point of view, should be treated not as an isolated entity but rather as a natural continuum from river to sea with no clearly defined boundaries. Another distinguishing attribute of estuaries is the elevated hydrodynamics that, combined with the tidal influence, makes these systems exceptionally variable in space and over time. Tides change local environmental conditions along the coast, and strongly affect spatio-temporal patterns of basic environmental factors such as a rate and direction of currents, water temperature, oxygen saturation, salinity but also suspended particulate concentration and distribution of nutrients and contaminants. Diurnal and seasonal variations in the ambient living conditions cause ecological stress to the inherent communities, which might be temporarily exposed to extreme parameters, e.g. during emersion in winter. Transient adversity of environmental factors is therefore thought to shape community structure and species diversity. Due to this high level of variability, estuaries are often considered the most naturally stressful of all aquatic systems. Furthermore, estuaries are ephemeral over geological time, particularly in temperate and boreal regions. Most of these were formed during the last postglacial sea level rise about 6,000-10,000 years ago (Kaiser et al. 2005). As a result the short evolutionary time is of crucial relevance for species introduction, colonisation and the (bio)diversity of these systems.

This overview focuses specifically upon selected properties of the Baltic Sea, which meets the commonly agreed criteria to be definable as an estuary, and may have relevance to the discussion on the concept of this water-basin.

BALTIC SEA - CASE STUDY

Environmental parameters

The Baltic Sea is a continental inland sea with an area of 385,000 km^2 and an average depth of 62.1 m (Håkanson et al. 2003). Because of a very small tidal range, which usually does not exceed 10-20 cm, the sea has not traditionally been defined as an estuary. The drainage area (1,745,000 km^2) with more than 200 rivers and an annual freshwater discharge of about 450 km^3 is more than four times greater than the area of the sea (HELCOM 1998). The aquatic balance is positive, the mean depth of the Sound and the Belts is only 14.3 m which restricts the exchange with the North Sea, and the retention time for water in the Baltic is approximately 25-30 years (Glasby, Szefer 1998; Håkanson et al. 2003). Due to higher salinity of deep-water masses that are

occasionally supplied by more saline, oxygenated waters from the North Sea, and the strong thermo-haline stratification of the water column (a well-developed permanent thermo-halocline occurs at a depth of 60-80 m; Samuelsson 1996), salinity changes occur along the vertical profile. There is also an apparent horizontal salinity gradient, the salinity of surface waters decreases from the west (25 PSU) to the east and north (3 PSU), reaching a minimum of < 3 PSU in the northern part of the Gulf of Bothnia.

A distinctive feature of the Baltic Sea, as compared to estuaries in tidal areas, is the topography and geomorphology of the sea bottom. Along the shoreline of tidal estuaries are characteristic salt marshes, swamps and mudflats that result from tidal action on the littoral zone and deposition of fine-grained sediment particles and clays transported by rivers and sea currents. Salt marshes and swamps, which serve as vital reproduction and nursery systems for many fish and shellfish species, as well as unique breeding and feeding grounds for migratory birds, show high biodiversity of benthic communities, ichthyo- and avifauna. As a result of appreciation of their role as a biome, coastal wetlands are widely protected, for instance a third of the European Union's wetlands are located on the coast, as are more than thirty percent of the Special Protection Areas designated under the "Directive on the Conservation of Wild Birds" (79/409/EEC). Wetlands and swamps, with elevated species and habitat diversities, are also found along the shoreline of the Baltic, some of them being protected (Natura 2000) to conserve and maintain their exceptional ecological value e.g. halophilic and nitrophilic flora on the sea coast (perennial vegetation), *Salicornia* inland swamps, coastal salt marshes and inland halophilic meadows (http//mos.gov.pl/natura.2000). In contrast to intertidal mudflats, where marine-derived, fine-grained, organic-rich fractions are predominantly deposited in the middle reaches of the estuary through flocculation (smectittes and iron oxyhydroxides) and aggregation at the hydrological front of mixing the freshwater and seawater, in the Baltic lithogenous and organic particles that are discharged into the sea with riverine waters sediment to the bottom, notably in the upper littoral zone. However, the fine (mainly illites and chlorites) and organic particle load of big rivers such as the Neva River, Vistula River or Dwina River, tend to be distributed further seaward by currents, and thus sediment in the deeper regions, the processes being additionally favoured by the syncline topography of the sea bottom in many coastal areas (decantation basin; Kunzendorf et al. 1998). Organic matter content and the silt fraction of sediments are, for example, observed to be higher below the permanent thermo-halocline and the wave-base level in the Gulf of Gdansk and in the Gdansk Deep (Sokołowski et al. 2001). Such a distribution pattern reflects the overall scheme of sorting and sedimentation processes of suspended matter that is typical for estuarine areas (Kępińska, Wypych 1990; Witkowski, Pempkowiak

Copyright© by Institute of Oceanography, University of Gdańsk, Poland

1995; Leipe et al. 1998). From an ecological point of view, the basic characteristics and ecological role of muddy organic-rich sediments seem similar in tidal areas and the tideless Baltic Sea. They present habitats that are difficult to colonise because of the mobility and fine structure of the substratum, preventing macrophytes, sessile organisms and their planktonic larvae from successful settlement. Muddy and silty sediments are preferentially inhabited by suspension- or deposit-feeding infaunal species such as oligochaetes, polychaetes and some bivalves. In the Baltic, soft-bottom communities consist primarily of deposit feeders, e.g. polychaetes *Hediste diversicolor*, *Marenzelleria viridis* and *Pygospio elegans*, the oligochaete *Paranais littoralis*, and the facultative deposit feeding Baltic clam *Macoma balthica.*

Biocenosis with special emphasis on benthos

A wide spatial variation in salinity is one of the most important factors that affects the survival and distribution of estuarine organisms. Longitudinal variability is directly related to species richness and distribution in the Baltic Sea; biodiversity decreases with salinity from the Danish Straits towards the Gulf of Finland and the Gulf of Bothnia (Fig. 1). Floral and faunal populations of the Baltic are often considered as direct extensions of the stocks of the North East Atlantic (Väinöla, Varvio 1989), with intrusions of freshwater species which primarily inhabit the northern-most territories and the regions adjacent to the mouths of big rivers. The Baltic is inhabited by both typically marine (*Ulva lactuca*, *Fucus vesiculosus, Zostera marina, Aurelia aurita, Arctica islandica, Astarte borealis, Sagitta elegans baltica, Fritillaria borealis*, *Gadus morhua, Clupea harengus*) and freshwater (*Chara* sp.*, Branchionus* sp., *Cyclops* sp., *Theodoxus fluviatilis, Lymnea peregra, Esox lucius*, *Abramis brama, Perca fluviatilis*) species. Due to broader salinity tolerances, and consequently better performance under osmoregulatory stress, brackish species make a substantial contribution to the biota, including typically estuarine taxa such as *Enteromorpha*, *Hediste diversicolor*, *Neomysis integer*, *Praunus flexuosus*, *Crangon crangon* and bivalves, the most important of these with respect to abundance and biomass being *Mytilus trossulus*, *Macoma balthica*, *Cerastoderma glaucum* and *Mya arenaria*. Besides the salinity constraint, an important factor that shapes the biota of the Baltic, and determines its structure and organization, is geological history. During recent periods of glaciation and deglaciation, Baltic organisms were exposed to drastic changes in the ambient environment, leading often to their contemporary or complete disappearance. Only the most resistant taxa, that were able to stand adverse conditions, could survive in local refuges (if they existed), serving later as ancestors for development of local populations. Over the last 8,000 years, the Baltic has gone



Fig. 1. A total number (in circles) and distribution limits of plant and animal species in different regions of the Baltic Sea (after Tidlund, 1998).

through three distinct phases; a marine phase, a freshwater phase and an arctic phase. The relics of the latter (e.g. *Priapulus caudatus*, *Halicryptus spinulosus*, *Saduria entomon*, *Mysis relicta*, *Triglopsis quadricornis*) that remained in deep cold waters from the probable interconnection with the White Sea around 9,000 to 7,000 BC (Rheinheimer 1995) are important constituents of Baltic communities. It is debatable whether the same species or genetically different forms (subspecies, races) recolonised estuaries in subsequent phases of the history of the Baltic, and whether current populations evolved from the refugees

Copyright© by Institute of Oceanography, University of Gdańsk, Poland

that adapted under strongly selective environmental conditions, as suggested by Barnes (1994), or were formed *de novo* from species that invaded the sea during the post-glacial period. The community composition and species distribution in the Baltic suggest that their ancestors, at least in part, derive directly from the faunal communities that remained after each development phase of the sea. The refugees might have colonised deep-water regions first, and continued into shallower areas with the retreat of the ice sheet. In addition, melting ice brought about a sea level rise of 60 to 150 m over the last 8,000 years, flooding an upper region of the continental shelf and river valleys and thus establishing a variety of habitats for colonisation by non-native species.

Estuaries, specifically in tidal areas, are among the most productive ecosystems on Earth. They function as a buffer zone between the land and the sea and usually act as traps for nutrients and detritus that are recycled and supply primary production. Allochthonous organic matter, which originates from rivers and terrestrial run-off, combined with autochthonous organic matter are the main sources of food for suspension feeders. High concentrations of suspended matter, throughout the year, are discharged with riverine input and/or resuspended by tidal currents, and underpin the favourable conditions for many benthic invertebrates, including commercially exploited crustaceans and bivalves. It is therefore not surprising that estuaries are common locations of aquaculture (particularly oysters and mussels), and shellfish production is an important economic input to many European countries (e.g. France, Italy, Spain, Portugal, the Netherlands, the United Kingdom), estuaries thus having socio-economic relevance. One of the largest basins of oyster and mussel production is situated in the Charente River estuary on the Atlantic coast of France (the Marennes-Oléron Bay). Annual oyster production in the Marennes-Oléron Bay represents more than 25% of France's marine seafood production, accounting for 30,000 tons of oysters (*Crassostrea gigas* and *Ostrea edulis*) grown entirely within the Bay and 60,000 tons of mussels (Héral 1990). In the Baltic, despite lower biological diversity and simpler trophic interactions, as compared to the Mediterranean Sea or Atlantic (Loreau 2000), the productivity is reported to be similar to that of the Atlantic. The biomass of filter feeders in the Gulf of Gdansk, for instance, is estimated to be 300-600 g m^{-2}, and of the polychaete *Hediste diversicolor* 30-100 g m^{-2}, with a markedly increasing trend over recent decades (Osowiecki 2000). The regions of high productivity and species richness in the Baltic are, however, mainly restricted to shallow and coastal areas where good thermal, nutritive and oxygen conditions support intense primary production and development of faunal populations. As a result of high organic content in sediments and insufficient mixing of deep waters with upper layers, biological mineralisation of organic matter often leads to oxygen depletion (anoxia) in deeper waters, and hydrogen sulphide and methane may

even be present temporally (Janas, Szaniawska 1996), resulting in massive mortalities of many benthic invertebrates (Cederwall, Elmgren 1990). The detrimental effects of hydrogen sulphide toxicity, including successive impoverishment and decimation of the macrozoobenthos, and in some cases even total extinction, are observed in many areas of the Baltic, e.g. the Baltic Proper and the western Gulf of Finland (HELCOM 2003). Only a few of the most hypoxia-resistant species are present in the deep, organic-rich, soft bottom areas e.g. *Macoma balthica*, *Saduria entomon*, *Hediste diversicolor*. While in tidal estuaries such conditions often occur naturally, enrichment with organic matter and subsequent oxygen deficiency of the overlying bottom water and sediments in the Baltic is usually driven by human factors, which in turn are reinforced by specific thermal conditions. Short periods of summer microbial activity and low dissolved oxygen concentration across the sea bottom and in the interstitial waters throughout much of the year do not allow complete mineralisation of organic matter, leading to anoxic conditions in a layer, which can range from several cm to up to 100 m thick (HELCOM 2003). The area of these anoxic regions, also known as azoic deserts, has been gradually increasing over the last few decades (Gerlach 1994, HELCOM 2004).

Particularly important in terms of the structure and functioning of estuaries is the ichthyofauna, which in the Baltic encompasses a number of both marine and freshwater species (e.g. in Puck Lagoon 57 species was observed at the end of the 80's (Skóra 1993) and only 44 species at the end of the 90's (Skóra 1996)). Ichthyofauna, specifically demersal fish, contributes considerably to benthic-pelagic coupling, being a key factor in energy transfer from the benthic system to the water column, and concurrently a potential transmitter of contaminants to higher trophic levels, including humans. Fish species tend to be more diverse, with more variety in their physiological and morphological forms, in shallow, coastal regions. Coastal and estuarine habitats offer a diverse range of reproduction and nursery grounds (e.g. sea grass meadows, mussel beds) for many fish, and the high abundance and biomass of inherent benthic invertebrates provides an easily accessible, protein-rich food source for juveniles, including some commercial species, e.g. plaice (Sapota, Skóra 1996). The biological productivity of estuarine ecosystems has permitted the development of mariculture in selected regions of the Baltic. Among the Baltic Sea States, mariculture is undertaken in Denmark, Finland and Sweden where the main species farmed are salmon (*Salmo salar*) and rainbow trout (*Onchorynchus mykiss*), and in 1998 the fish production totalled approximately 22,400 tonnes (HELCOM 2002).

Another important ecological role of estuaries is that of bird habitat, acting as hospitable resting areas for migratory sea birds, and often offering unique breeding and feeding habitats for non-migratory wintering birds (more than 30

Copyright© by Institute of Oceanography, University of Gdańsk, Poland

species regularly breed along the shoreline of Puck Lagoon). For example between 1997 and 1999 more than 120 bird species bred, ca. 70 species over-wintered, and more 160 species regularly migrated through the Polish part of the Vistula Lagoon (Mokwa, unpublished observations). Coastal, southern regions of the Baltic, in particular, are on a vital migratory route for waterfowl, geese and waders that nest in the arctic tundra. The abundance of feeding birds in a given region is usually dependent on the area of the estuary and the availability of food, which primarily consists of benthic invertebrates and fish. During the winter (September to April), diving ducks (8 common species, mean number 40,000-90,000 individuals) consume more than 25,000 tonnes of marine organisms, of which about 20,000 tonnes are bivalves (Stempniewicz, Meissner 1999). Avifauna is thus of considerable significance in coupling marine and terrestrial ecosystems and exporting organic carbon between them.

Relatively low biodiversity (resulting in free niches), and putatively man-induced changes in the structure and functioning of the Baltic ecosystem (including anthropogenic eutrophication, pollution and overfishing) are considered key factors in causing the exceptionally high rate of introduction of new species to the sea. For example, increasing eutrophication appears to be linked to the rising predominance of freshwater species, and hypoxic/anoxic conditions cause extinctions of Arctic postglacial-relic benthic fauna in the deep basins of the Baltic, e.g. the clam *Macoma balthica* has taken over subhalocline areas where the bivalve *Astarte borealis* was previously abundant (Leppäkoski, Olenin 2001). Non-indigenous species (e.g. the dinoflagellate *Prorocentrum minimum*, the red alga *Polysiphonia harveyi*, the swim-bladder nematode *Anguillicola crassus*, the fishhook waterflea *Cercopagis pengoi*, the oligochaete *Paranais frici*, the spionid oligochaete *Marenzelleria viridis*, the barnacle *Balanus improvisus*, the mud crab *Rhithropanopeus harrisii* ssp. t*ridentatus*, the zebra mussel *Dreissena polymorpha*, the round goby *Neogobius melanostomus*, the Canadian goose *Branta canadensis*, and the American mink *Mustela vison*, among others) contribute increasingly to pelagic and benthic communities (http://www.ku.lt/nemo/mainnemo.html). By the year 2000, a total of 99 species of plants and animals that are known or believed to be non-indigenous have been recorded in the Baltic Sea and adjacent coastal lagoons and lakes. Estuaries and embayments are affected by alien species more frequently than open sea areas (Leppäkoski, Olenin 2001; Olenin, Daunys 2005; Kotta et al. 2006). The latest studies suggest that introduction of alien species to the sea is predominantly based on active natural migration, through natural or artificial waterways such as rivers, inland canals and streams, although human-mediated transfers (e.g. with ballast waters, intentional introductions) are also well documented. Most non-native species in the Baltic originate from North American (ca. 30%) and Ponto-Caspian regions of similar climatic conditions

and water salinity, that is, highly comparable environments. The rate of invasions has substantially increased over the last 50 years, mainly due to increased shipping and international trade. The ecological and economic impacts of introductions on a wider scale are still largely unknown, however evidence resulting from local observations (e.g. *Mnemiopsis* in the Black Sea, *Marenzelleria viridis* in the Baltic Sea) clearly indicate an effect of alien species on community structure and trophic interactions (Jażdzewski et al. 2005, Orlova et al. 2006). In contrast to the Baltic, mechanisms of species introduction in tidal estuaries are primarily linked to intentional human activities such as commercial trade of plants and animals for aquaculture and aquaristics or accidental events (e.g. ballast waters; Leppäkoski, Olenin 2001).

Changes to the Baltic Sea ecosystem

Inherent properties of the Baltic, namely restricted water exchange with the oceanic system, considerable inflow of freshwater and strong halo-thermal stratification, make the sea vulnerable to short- and long-term changes (Wulff et al. 1990). What is more, intense exploitation of the coastal zone and the open sea by humans for a wide range of uses such as industry, energy production, shipping, commercial fishing, extraction of oil, sand and gravel, and dumping of dredged materials have a major impact on the water quality. The Baltic has been subjected to significant anthropogenic inputs of nutrients and pollutant contaminants during the last century, and eutrophication and pollution now have large-scale implications (Ærtebjerg et al. 2001, Wołowicz et al. 2006). Clear-cut alterations in the structure and function of the ecosystem have been observed in the Gulf of Gdansk, and extend, to various degree, across the entire Baltic. These changes are discernible by alterations to numerous abiotic and biotic parameters at different organisation levels, from biocenosis, species, morphology and ecophysiology to genetics.

Changes at species level

One of the most evident alterations in the biocenosis of the Baltic over recent decades has occurred in benthic populations of suspension and deposit feeders. As a result of anthropogenic eutrophication, primary production has approximately doubled (Cederwall, Elmgren 1990), leading to a substantial increase in the total particulate matter (Maksymowska et al. 1997). In consequence, biomass of the suspension and deposit feeders has increased and the spatial distribution and standing stocks apparently changed. For instance, the distribution range of the epifaunal suspension-feeding mussel *Mytilus trossulus* in the Gulf of Gdańsk has extended towards deeper water, from 7-12 m in 1982 to 5-50 m in 1997. The concurrent biomass increase was from 13.4 to

Copyright© by Institute of Oceanography, University of Gdańsk, Poland

326.1 g dry wt m^{-2} at 38 m in a central region of the Gulf, with maximum reports of up to 500.0 g dry wt m^{-2} at 20-54 m (Osowiecki 2000). A similar expansion into deeper water of this mussel has also been reported in other Baltic basins, e.g., the Baltic archipelago (Jansson, Kautsky 1977). Similarly, a concurrent increase in biomass and shift in the distribution range, even down as deep as 90 m, was recorded for the infaunal facultative deposit feeder, the Baltic clam *Macoma balthica* (HELCOM 2003). This is presumed to be as a result of its ability to tolerate low ambient oxygen conditions and the presence of hydrogen sulphide.

Morphological deformations

Geological sediment parameters, namely granulometry and the proportion of organic content, are highly variable across estuaries. These factors are considered to constrain ontogenic variations in the external skeletal morphology of benthic organisms. For example, shell weight of the cockle *Cerastoderma glaucum* has been found to be up to 60% higher on a sandy bottom as compared to muddy sediments (Wołowicz 1984). Soft, muddy and silty sediments have reportedly caused asymmetry in shell architecture and a reduction in the number of ridges, ribs and other spines on external surfaces of cockle shells (Loppens 1923, Mars 1951, Petersen 1958, Remane 1958). A decrease in cockle shell weight and a simultaneous change in shell dimensions towards a more "squat" form (a reduced ratio of length to width) is thought to have an adaptive significance in the functional response of the organism to soft and fluid sediments in preventing it from sinking (Brock 1991). Shell deformations (elongation of the posterior region and apparent flexure on the posterior side) were recently observed in the Baltic clam *Macoma balthica* in the Gulf of Gdańsk. Such morphological modifications are hypothesised to have functional significance in protective response to low ambient oxygen concentrations and soft sediments, allowing the bivalve to extend its siphons higher above the anoxic layer to pump oxygenated water (Fig. 2, Sokołowski et al. 2005).

Physiological changes

Alterations, that are convincingly linked to observed environmental changes, particularly anthropogenic eutrophication in the Gulf of Gdańsk over recent decades, have been documented to affect ecophysiological performance of benthic organisms. Comparative studies of the epifaunal mussel *Mytilus trossulus* from two depth zones (10 m and 40 m) over a seasonal cycle revealed ecophysiological differences between the deep- and shallow-water animals. For the same shell-length, the shallow-water individuals were heavier and showed a higher weight-index (dry weight/volume, Fig. 3) than the deep-water mussels.

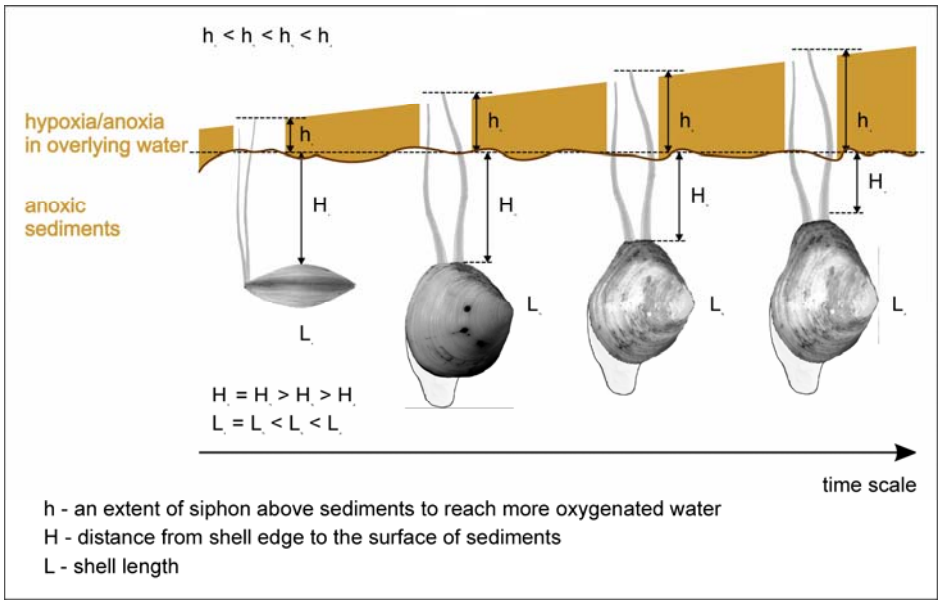


Fig. 2. Hypothesised modification of position (superficial shift) and shell morphology (elongation of posterior region and development of flexure) of *Macoma balthica* in response to increasing and long-lasting hypoxic/anoxic conditions and the presence of hydrogen sulphide in the surficial sediments and overlying water on soft bottom in the Baltic Sea (after Sokołowski et al. 2005).

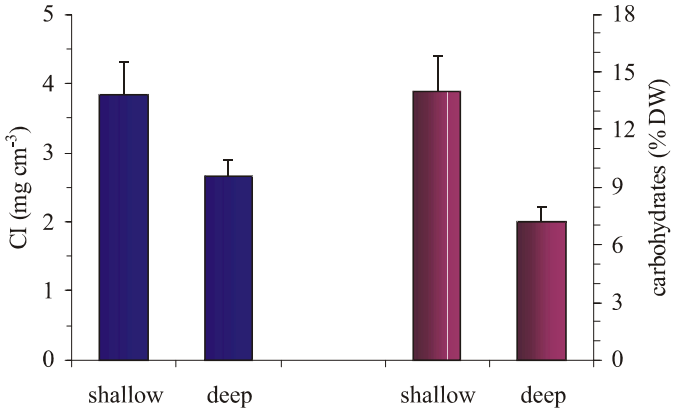


Fig. 3. Condition index (blue bars) and total carbohydrate content (reddish bars) of the mussel *Mytilus trossulus* from two depth zones, shallow (10 m) and deep (40 m) in the Gulf of Gdańsk. Data are presented as mean ±standard error (n=10÷12).

Copyright© by Institute of Oceanography, University of Gdańsk, Poland

Considerable differences were also noted in the biochemical composition, specifically in high-energy storage reserves, the shallow-water mussels contained less protein and more than twice as much total carbohydrate than the deep-water mussels (Fig. 3). The population from the deeper region additionally showed a remarkable dominance of males over females (ratio of males to females averaged 2.9) as compared to the population from shallow area where the sex ratio averaged 1.4, indicating higher female mortality in the deep-water population. The observed ecophysiological phenomena are likely to derive from acclimatisation of the bivalves to the locally different environmental conditions (e.g. temperature, salinity and dissolved oxygen), the availability of food has also been suggested as having a primary impact on the ecophysiological differentiation of the mussels (Wołowicz et al. 2006). Similar depth-related local physiological differences have been also reported for the Baltic clam *Macoma balthica*, whose deep-water subpopulation showed distinct ecophysiological features (condition index, biochemical composition and gonadal development cycle) compared to the shallow-water subpopulation (Bonsdorff, Wenne 1989; Hummel et al. 2000).

Genetic changes

Estuaries are convenient ecosystems in which to study processes of genetic adaptation in aquatic organisms. Unstable and heterogeneous environments may strongly affect the genetic structure of the population. Studies of marine invertebrates have shown that a number of enzyme loci are under strong selection pressure, promoting local adaptation that is evident as differences in allele and genotype frequencies between subpopulations (e.g. Koehn et al. 1983, Johanesson et al. 1995). One example of adaptive clines in allele frequency that is connected to environmental gradients is the correlation between salinity and allele frequencies of the leucine aminopeptidase (*Lap*) locus, which has been reported for the mussel genus *Mytilus* (e.g. Koehn et al. 1983) and the cockle *Anomalocardia brasiliana* (da Silva, Solé-Cava 1994), among others. Similarly, a relationship between water temperature and the isocitrate dehydrogenase (*Idh*) locus was found in the lugworm *Arenicola marina* (Hummel et al. 1997). As well as adaptive changes being reflected in genetic differences, a positive correlation between multilocus heterozygosity and fitness parameters was observed in several bivalve species, suggesting a selective advantage of heterozygotes (e.g. Myrand et al. 2002). Highly heterozygous individuals may have lower maintenance metabolism, resulting in more energy available for growth, reproduction and survival (Hawkins, Bayne 1992), and so show better fitness to adverse conditions. In the case of the Gulf of Gdańsk, high genetic variability, strong population structuring and better performance of

heterozygotes have been found in the key bivalve the Baltic clam *Macoma balthica*. Genetic surveys in 1995, 1997 and 1998, based on allozyme electrophoresis on clams collected from a depth range of 5-85 m, showed strong genetic differentiation (mainly in locus *Idh*) in 1995: clams below 30 m resembled Atlantic populations while those from shallow stations formed a distinct Baltic group. In the following years, all populations resembled the Atlantic type, probably due to the inflow of North Sea water and/or different environmental selection pressures (Hummel et al. 2000). Similarly, in *Mytilus trossulus* from the Gulf of Gdańsk the allele frequencies of the octopine dehydrogenase locus (*Odh)* showed a tendency to vary with depth, suggesting a possible role of this enzyme in adaptation to deep-water habitats (Hummel et al. 2001, Wołowicz et al. 2006). In addition to naturally occurring genetic changes, human driven alterations (for example resulting from pollution) have been shown in recent studies. Pollution can exert a direct influence on DNA, causing gene mutations and chromosomal aberrations, or can create environmental selection pressure, impacting on allele and genotype frequencies (Hummel, Patarnello 1994). The influence of pollutants on genetic structure has been illustrated in field and laboratory surveys on several marine and estuarine molluscan and crustacean species (see Hummel, Patarnello 1994 for review). In the highly eutrophic and polluted Gulf of Gdańsk advanced cases of neoplasia (related to a high level chromosomal aneuploidy) were observed in *Macoma balthica* and *Mya arenaria*, with an average prevalence of 31% and 16%, respectively (Smolarz et al. 2005). For the teleost fish *Myoxocephalus quadricornis*, Gyllensten & Ryman (1988) it has been observed clear changes in allozyme frequencies at some polluted sites in the Baltic Sea that could be a direct effect of selective pressure and/or invasion of the polluted sites by new stock.

SUMMARY

Due to highly variable environmental conditions (e.g. salinity, temperature, dissolved oxygen, substratum type, pollution, etc.) estuaries are considered to be extreme environments, causing significant ecological stress to the inherent biota. Estuaries therefore represent excellent systems in which to study the comparative behaviour, ecophysiology, ecotoxicology and genetics of aquatic organisms.

The low biodiversity of the Baltic Sea derives primarily from its short geological and evolutionary history (ca. 8,000 years) and the major environmental modifications that it experienced during its development. It is an exceptional ecosystem as a result of its unique combination of freshwater, marine and typically estuarine (brackish) species, as well as Arctic relics.

Copyright© by Institute of Oceanography, University of Gdańsk, Poland

Similar to other estuaries the Baltic is a highly productive system, containing (e.g. the Gulf of Gdańsk) a range of favourable habitats for benthic organisms, vital nursery grounds for fish and breeding and staging areas for over-wintering and migratory sea birds. However, the highly industrialised, urbanised and densely populated lands that surround the sea, combined with increasing human activities in the marine sector (exploitation of mineral and biological resources, including aquaculture, shipping, coastal engineering, etc.) are impacting on this ecosystem, causing ecological disturbances, such as a decrease in biodiversity and invasions of non-native species. Observed alerting changes to the ecosystem over recent decades have resulted in the introduction of broad conservation measures designed to protect the unique ecology of the Baltic Sea (Water Directive, directives on the conservation of wild birds, habitats, Natura 2000, Baltic Sea protected areas, etc.)

ACKNOWLEDGEMENTS

The information contained in this paper was presented during a scientific conference "*Water exchange in estuarine waters in the Southern Baltic - hydrology and ecology*" organized by the Institute of Oceanography, University of Gdansk on April 21, 2006. The conference was dedicated to Professor **Jerzy Cyberski** in celebration of his scientific career which has spanned forty-five years.

REFERENCES

Ærtebjerg, G., Carstensen, J., Dahl, K., Hansen, J., Nygaard, K., Rygg, B., Sørensen, K., Severinsen, G., Casartelli, S., Schrimpf, W., Schiller, C, Druon, J. N. (2001). *Eutrophication in Europe's coastal waters*. Copenhagen: European Environment Agency. (Topic report 7/2001)

Barnes, R.S.K. (1994). *The brackish-water fauna of NW Europe*. Cambridge: Cambridge University Press.

Bonsdorff, E. & Wenne R. (1989). A comparison of condition indices of *Macoma balthica* (L.) from northern and southern Baltic Sea. *Neth. J. Sea. Res.* 23, 45-55.

Brock, V. (1991). *An interdisciplinary study of evolution in the cockles Cardium (Cerastoderma) edule, C. glaucum, and C. lamarcki*. Vinderup: Vestydsk Forlag.

Cederwall, H. & Elmgren R. (1990). Biological effects of eutrophication in the Baltic Sea, particularly the coastal zone. *Ambio* 19, 109-12.

da Silva, E. P. & Solé-Cava A. M. (1994). Genetic variation and population structure in the tropical marine bivalve *Anomalocardia brasiliana* (Gmelin) (Veneridae). In A. R. Beaumont (Ed.), *Genetics and evolution of aquatic organisms* (pp. 71-82). London: Chapman and Hall.

Day, J. H. (1980). *Estuarine ecology with particular reference to southern Africa*. Rotterdam: Balkema Books.

Fairbridge, R. (1980). The estuary: its definition and geodynamic cycle. In E. Olausson & I. Cato (Eds.), *Chemistry and geochemistry of estuaries* (pp. 1-35). New York: John Wiley and Son.

Gallo, M.N. & Vinzon S.B. (2005). Generation of overtides and compound tides in Amazon estuary. *Ocean Dynam.* 55(5-6), 441-448. DOI: 10.1007/s10236-005-0003-8.

Gerlach, S.A. (1994). Oxygen conditions improve when the salinity in the Baltic Sea decreases. *Mar. Poll. Bull.* 28, 413-416. DOI: 10.1016/0025-326X(94)90126-0.

Glasby, G.P. & Szefer P. (1998). Marine pollution in Gdansk Bay, Puck Bay and the Vistula Lagoon, Poland: an overview. *Sci. Total Environ.* 212 (1), 49-57. DOI: 10.1016/S0048-9697(97)00333-1.

Guelorget, O. & Perthuisot J.P. (1983). *Le domaine paralique-expressions geologiques, biologiques et economiques du confinement*. Paris: Press de l`Ecole Normale Superieure.

Gustafsson, B.G. & Andersson H.C. (2001). Modelling the exchange of the Baltic Sea from the meridional atmospheric pressure difference across the North Sea. *J. Geophys. Res.* 106 (C9), 19731-19744. DOI: 10.1029/2000JC000593.

Gyllensten, U. & Ryman N. (1988). Biochemical genetic variation and population structure of fourhorn sculpin (*Myoxocephalus quadricornis*; Cottidae) in Scandinavia. *Hereditas*. 108, 179-185.

Håkanson, L., Lundin L.-C., Savchuk O., Ionov V., Musielak S. & Furmanczyk K. (2003). The Baltic Sea. In L. Rydén, P. Migula & M. Andersson (Eds.), *Environmental Science: Understanding, protecting and managing the environment in the Baltic Sea Region* (pp. 120-147). Uppsala: The Baltic University Press.

Hawkins, A.J.S. & Bayne B.L. (1992). Physiological interrelation and the regulation of production. In E.M. Gosling (Ed.), *The mussel Mytilus: ecology, physiology, genetics and culture* (pp. 171-222). Amsterdam: Elsevier.

HELCOM (2004). *HELCOM Indicator Fact Sheets 2004*. Retrieved 21 May, 2004, from http://www.helcom.fi/environment2/ifs/archive/ifs2004/en_GB/

HELCOM (2003). *The Baltic Marine Environment 1999-2002*. Balt. Sea Environ. Proc. 87.

HELCOM (2002). *Environment of the Baltic Sea area 1994-1998*. Balt. Sea Environ. Proc. 82B.

HELCOM (1998). *The Third Baltic Sea Pollution Load Compilation (PLC-3)*. Balt. Sea Environ. Proc. 70.

Héral, M. (1990). Traditional oyster culture in France. In G. Barnabe (Ed.), *Aquaculture* (*Vol. I)* (pp. 342-387). Chichester: Ellis Harwood.

Hummel, H. & Patarnello T. (1994). Genetic effects of pollutants on marine and estuarine invertebrates. In A. R. Beaumont (Ed.), *Genetics and evolution of aquatic organisms* (pp. 425-434). London: Chapman and Hall.

Hummel, H., Sommer A., Bogaards R.H. & Pörtner H.O. (1997). Variation in genetic traits of the lugworm *Arenicola marina*: temperature related expression of mitochondrial allozymes? *Mar. Ecol. Prog. Ser.* 159, 189-195.

Hummel, H., Sokołowski A., Bogaards R.H. & Wołowicz M. (2000). Ecophysiological and genetics traits of the Baltic clam *Macoma balthica* in the Baltic: differences between populations in the Gdańsk Bay due to acclimatization or genetic adaptation? *Internat. Rev. Hydrobiol*. 85, 621-637. DOI: 10.1002/1522-2632(200011)85:5/6<621:AID-IROH621>3.0.CO;2-F.

Hummel, H., Colucci F., Bogaards R.H. & Strelkov P. (2001). Genetic traits in the bivalve *Mytilus* from Europe with an emphasis on Arctic populations. *Pol. Biol.* 24, 44-52. DOI: 10.1007/s003000000174.

Janas, U. & Szaniawska A. (1996). The influence of hydrogen sulphide on macrofaunal biodiversity in the Gulf of Gdansk. *Oceanologia*, 38(1), 127-142.

Jansson, A., & Kautsky N. (1977). Quantitative survey of hard bottom communities in a Baltic archipelago. In B.F. Keegan, B.O. Ceidigh & B.J.S. Boaden (Eds.), *Biology of benthic organisms* (pp. 359-366). New York: Pergamon Press.

Copyright© by Institute of Oceanography, University of Gdańsk, Poland

Jażdżewski, K., Konopacka A. & Grabowski M. (2005). Native and alien Malacostracan Crustacea along the Polish Baltic Sea Coast in the twentieth century. *Oceanol. Hydrobiol. Stud*., 34(1), 175-193.

Johannesson, K., Johannesson B. & Lundgren U. (1995). Strong natural selection causes microscale allozyme variation in a marine snail. *Proc. Natl. Acad. Sci. USA*, 92, 2602-2606.

Kaiser, M.J., Attrill M.J., Jennings S., Thomas D.N., Barnes D.K.A., Brierley A., Polunin N. & Rafaelli D. (2005). *Marine ecology: processes, systems and impacts*. Oxford: Oxford University Press.

Kępińska, U. & Wypych K. (1990). Osady denne. In A. Majewski (Ed.), *Zatoka Gdańska* (pp. 55-65). Warszawa: Wydawnictwo Geologiczne.

Koehn, R.K., Zera A.J. & Hall J.G. (1983). Enzyme polymorphism and natural selection. In M. Nei & R.K. Koehn (Eds.), *Evolution of genes and proteins* (pp. 115-136). Sunderland: Sinauer Associates.

Kotta, J., Kotta I., Simm M., Lankov A., Lauringson V., Pollumae A. & Ojaveer H. (2006). Ecological consequences of biological invasions: three invertebrate case studies in the north-eastern Baltic Sea. *Helgol. Mar. Res.* 60, 106-112. DOI: 10.1007/s10152-006-0027-6.

Kunzendorf, H., Emeis K.-C. & Christiansen C. (1998). Sedimentation in the Central Baltic Sea as viewed by non-destructive Pb-210 dating. *Danish J. Geogr.* 98, 1-9.

Leipe, T., Tauber F., Brügmann L., Irion G. & Hennings U. (1998) Schwermetallverteilung in Oberflächensedimenten der westlichen Ostsee (Arkonabecken, Mecklenburger/Lübecker Bucht und Kieler Bucht). *Meyniana*, 50, 137-154.

Leppäkoski, E. & Olenin S. (2001). The meltdown of biogeographical peculiarities of the Baltic Sea: the interaction of natural and man-made processes. *Ambio*, 30, 202-209.

Lie, H.-J. & Cho C.-H. (2002). Recent advances in understanding the circulation and hydrography of the East China Sea. *Fish. Oceanogr.* 11(6), 318-328. DOI: 10.1046/j.1365-2419.2002.00215.x.

Loppens, K. (1923). La variabilite chez *Cardium edule*. *Ann. Soc. Zool. Belg.* 54, 33-67.

Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos,* 91, 3-17.

Maksymowska, D., Feuillet-Girard M., Piekarek-Jankowska H. & Heral M. (1997). Temporal variation in the accumulation of organic carbon and nitrogen in the suspended matter and silty surface sediment of the western Gulf of Gdańsk (southern Baltic Sea) comparisons with the Atlantic Bay of Marennes-Oleron. *Oceanol. Stud.* 26, 91-116.

Mars, P. (1951). Essai d`interpretation des formes generalement groupees sous le nom de *Cardium edule* Linne. *Bull. Mus. Hist. Nat. Marseille*, 11, 1-31.

Myrand, B., Tremblay R. & Sévigny J.-M. (2002). Selection against blue mussels (*Mytilus edulis* L.) homozygotes under various stressful conditions. *J. Hered.* 93, 238-248. DOI: 10.1093/jhered/93.4.238.

Olenin, S. & Daunys D. (2005). Invaders in suspension-feeder systems: variations along the regional environmental gradient and similarities between large basins. In R. Dame & S. Olenin (Eds.), *The Comparative Roles of Suspension-Feeders in Ecosystems* (pp. 221-237). NATO Science Series. IV Earth and Environmental Series - 47. DOI: 10.1007/1-4020-3030-4_13.

Orlova, M.I., Telesh I.V., Berezina N.A., Antsulevich A.E., Maximov A.A. & Litvinchuk L.F. (2006). Effects of nonindigenous species on diversity and community functioning in the eastern Gulf of Finland (Baltic Sea). *Helgol. Mar. Res.* 60, 98-105. DOI: 10.1007/s10152-006-0026-7.

Osowiecki, A. (2000). *Kierunki wieloletnich zmian w strukturze makrozoobentosu Zatoki Puckiej*. Gdynia: Centrum Biologii Morza PAN, Crangon 3.

Peneva, E., Stips A., Bolding K. & Stanev E. (2003). Black Sea-Azov Sea numerical model: analysis of climatic and mesoscale circulation based on GETM. *GRA*, 5, 09845.

Petersen, G.H. (1958). Notes on the growth and biology of the different *Cardium* species in Danish brackish water areas. *Medd. Danm. Fisk.-og Hav*. 2, 1-31.

Pritchard, D.W. (1967). What is an estuary: a physical view point. In G.H. Lauff (Ed.), *Estuaries* (pp. 3-5). Washington D.C.: American Association for the Advancement of Science, Publication No. 83.

Remane, A. (1958). Ökologie des Brackwassers. In A. Remane & C. Schlieper (Eds.), *Die Biologie des Brackwassers - Die Binnengewässer* (pp. 1-216). Stuttgart: Schweizerbart'sche Verlagsbuchhandlung.

Rheinheimer, G. (1995). *Meereskunde der Ostsee*. Berlin: Springer Verlag.

Samuelsson, M. (1996). Interannual salinity variations in the Baltic Sea during the period 1954-1990. *Cont. Shelf Res.* 16, 1463-1477. DOI: 10.1016/0278-4343(95)00082-8.

Sapota, M. & Skóra K.E. (1996). *Fish* abundance in shallow inshore waters of the Gulf of Gdańsk. In Proceedings of Polish-Swedish Symposium on Baltic Coastal Fisheries, Resources and Management, 2-3 April 1996 (pp. 215-224). Gdynia: Sea Fisheries Institute.

Skóra, K.E. (1993). Ichtiofauna. In Korzeniewski K. (Ed.), *Zatoka Pucka* (pp. 455-467). Gdynia: Instytut Oceanografii UG.

Skóra, K.E. (1996). A comparison of changes in the composition of fish catches in the Polish lagoons in 1960-1989. In Proceedings of Polish-Swedish Symposium on Baltic Coastal Fisheries, Resources and Management, 2-3 April 1996 (pp. 225-242). Gdynia: Sea Fisheries Institute.

Smolarz, K., Thiriot-Quiévreux C. & Wołowicz M. (2005). Recent trends in prevalence of neoplasia in the Baltic clam *Macoma balthica* (L.) from the Gulf of Gdansk (Baltic Sea). *Oceanologia* 47(1), 61-74.

Sokołowski, A., Wołowicz M. & Hummel H. (2001). Distribution of dissolved and labile particulate trace metals in the overlying bottom water in the Vistula River plume (southern Baltic Sea). *Mar. Poll. Bul.* 42(10), 967-980. DOI: 10.1016/S0025-326X(01)00069-8.

Sokołowski, A., Pawlikowski K., Wołowicz M., Garcia-Meunier P. & Namieśnik J. (2005). *Abnormal features of the Baltic clam Macoma balthica (Bivalvia) in the Baltic Sea as indices of environmental changes?* Presented at Est. Res. Found. Conf., Norfolk, USA.

Stempniewicz, L. & Meissner W. (1999). Assessment of the zoobenthos biomass consumed yearly by diving ducks in the Gulf of Gdansk (southern Baltic Sea). *Ornis Svecica*. 9, 143-154.

Tidlund, A. (1998). *Marine research at Stockholm Marine Research Centre.* Stockholm: Printgraf AB.

Väinölä, R. & Varvio S.L. (1989). Biosystematics of Macoma balthica in northwestern Europe. In J.S. Ryland & P.A. Tyler (Eds.), *Reproduction, genetics and distributions of marine organisms* (pp. 309-316). Fredensborg: Olsen & Olsen.

Witkowski, A. & Pempkowiak J. (1995). Reconstructing the development of human impact from diatom and ^{210}Pb sediment dating (The Gulf of Gdańsk - Southern Baltic Sea). *Geogr. Polon.* 64, 63-76.

Wołowicz, M. (1984). *Cardium glaucum* (Poiret, 1789) population from Gdańsk Bay (Baltic Sea). *Pol. Arch. Hydrobiol.* 31, 33-44.

Wołowicz, M., Sokołowski A., Salem Bawazir A. & Lasota R. (2006). Effect of eutrophication on the distribution and ecophysiology of the mussel *Mytilus trossulus* (Bivalvia) in southern Baltic Sea (the Gulf of Gdańsk). *Limnol. Oceanogr.* 51, 580-590.

Wulff, F., Stigebrandt A. & Rahm L. (1990). Nutrient dynamics of the Baltic Sea. *Ambio,* 19, 126-133.

Zienkiewicz, L. (1963). *Biology of the seas of the U.S.S.R.* London: Cloth.

Copyright© by Institute of Oceanography, University of Gdańsk, Poland