THE SEASONAL AND INTER-ANNUAL VARIABILITY OF ICHTHYOPLANKTON BIODIVERSITY IN THE GDANSK DEEP OF THE BALTIC SEA DURING LAST DECADES

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ABSTRACT

The assemblage of pelagophilous fishes, which reproduce in the Baltic Sea deeps, has formed under the influence of environmental conditions that extremely limited its species richness. The composition of ichthyoplankton from the Gdansk Deep usually includes eggs of 4 fish species only (cod, sprat, flounder, rockling), co-occurrence of which is observed in spring season. Extremeness of reproduction conditions (low salinity and recurring oxygen deficiency) is one of the main reasons of species composition poorness, which becomes even more pronounced in some seasons with a decrease in frequency and intensity of the North Sea water inflows. Based on AtlantNIRO investigations for 1992 – 2006, and the analysis of literature data published in previous decades, significant seasonable and decade-to-decade changeability of Shannon's index of general diversity and Simpson's domination index were revealed under the invariable species richness. Over the period greater than 50 years (beginning from late 40s), the index of general diversity exhibited a stable downward tendency, whereas the domination index permanently increased. It was structural reorganization of the pelagophilous fish community, which reproduced in the deeps, that resulted in transition from the polydominant to the monodominant ichthyoplankton assemblage. The influence of abiotic environment on spatial variability of Shannon's index is also shown. The mechanisms that compensate low species saturation, and augmenting other kinds of the ichthyoplankton assemblage diversity are considered. At present the assemblage structural elements remained as well as a possibility of recurrence to a former state in case of adequate climatic changes.

Keywords: ichthyoplankton, deeps, diversity and domination indices, long-term trends.

INTRODUCTION

According to present-day concepts, all self-organizing living systems need a minimal diversity of species to participate in phyto- and chemosynthesis and provide cyclic redistribution of energy fluxes between the producers, consumers and decomposers. There exists a biodiversity threshold, below which the ecosystem cannot function, and the importance of biodiversity lies exactly in its role aimed at ecosystem resiliense (Perrings et al., 1995). The Baltic Sea is an example of a successful ecosystem functioning, given a small-scale diversity of the biota inhabiting it. The reasons of this phenomenon are rooted in geological youth of this water body and unique peculiarities of its abiotic environment.

The richness of pelagofilous (i.e. spawning pelagic eggs) fishes, which reproduce in the Baltic Sea deepwater basins, is limited, as a rule, to several species: from 6 species in the Bornholm Basin to 4 species in the Gdansk Deep and Gotland Basin. However, it is the poorness of the species structure that makes the ichthyoplankton in the open part of the sea a convenient object for studying some aspects of intra-seasonal and inter-annual variability in biodiversity.

MATERIAL AND METHODS

Long-term data on the species structure and ichthyoplankton abundance (pelagic eggs of the fish) in the Southeast Baltic Sea based both on literary sources (Kaendler, 1949, Mankowski, 1948, 1950, 1951, Grauman, 1967, 1969, 1980, 1984, 1987) and the investigations of the Baltic Sea Laboratory in AtlantNIRO are used in this paper. Also, the ichthyoplankton data obtained during the cruises of German RV "*Alkor*" within the framework of the STORE project were used. Ichthyoplankton nets, mainly IKS-80, and also Hensen net in the 40s and 50s, were used as a sampling gears for vertical fishing of the bottom-surface layer.

The abundance was given as sp./sq.m.
The total number of fish eggs species in the ichthyoplankton S was used as the index of species richness.
The Shannon's index (Shannon, Weaver, 1963) was used to characterize the general diversity:

$$\hat{H} = - \Sigma (n_i / N) \log_2 (n_i / N),$$

where $\hat{H}$ – general diversity index, n_i – number of specimens of each species,
N – total abundance.

The domination index C (Simpson, 1949) was used to characterise the domination degree in the ichthyoplankton assemblage :

$$c = \Sigma(n_i / N)^2,$$

where n_i – number of specimens of each species,
N – total abundance.

The data on hydrographic conditions in the Gdansk Deep were obtained from the AtlantNIRO database and literary sources (Glowinska, 1972, Zezera, 2002).

RESULTS

1. **Conditions of pelagofilous fish reproduction in the Gdansk Deep**.
The assemblage of pelagofilous fishes, reproducing in the Baltic deepwater basins, was formed under the influence of environmental factors, which extremely limited its species richness. Extreme conditions for reproduction is one of the main reasons of poorness of the species composition with low salinity, in the first place, being one of them. In the second half of the XX century, the near-bottom salinity in the centre of the Gdansk Deep fluctuated from the maximum in May 1952 (above 15 ‰) to the minimum in 1990 (below 10‰) (Fig 1). The surface layer salinity was considerably lower, usually not exceeding 6-7 ‰ in that area of the sea. As a result of sharply expressed stratification, vertical distribution of oxygen content is in inverse to salinity distribution, and is usually characterized by the near-bottom minimum. Periodical oxygen depletion near the deep bottom in the absence of the North Sea water inflows makes the reproduction of adult individuals and survival of early ontogenetic stages in the layer of the highest salinity impossible. The existence of a cold intermediate layer in the spring-summer season, the temperature of which after cold winters may drop below 1°C (Fig.2), imposes restriction on spawning timing and survival of the thermofillous fish offspring.

2. **The species composition, temporal and spatial variability in ichthyoplankton distribution**.
According to literary data and long-term investigations in the AtlantNIRO Baltic Sea Laboratory, the ichthyoplankton species composition in the Gdansk Deep of the Baltic Sea includes the eggs

of 4 pelagofillous fish species:

1) cod *Gadus morhua callarias* L.
2) flounder *Platichthys flesus trachurus* Duncker
3) rockling *Encheleopus cimbrius* L.
4) sprat *Sprattus sprattus balticus* (Schneider).

Under favourable thermal, salinity and oxygen content conditions in the near-bottom layers, the eggs of cod, flounder and sprat may occur as early as February. At the beginning of the 50s, sporadic occurrence of cod and sprat eggs was recorded in January in the western part of the Gdansk Deep. All four ichthyoplankton species occur simultaneously in March, April and May (Fig.3). Due to termination of flounder reproduction, the eggs of three fish species are available in the ichthyoplankton in June, July and August. In September and October, only cod and rockling eggs can be found in the ichthyoplankton, as the sprat spawning ends in August. Thus, the least recorded duration of occurrence in the ichthyoplankton is that of flounder, and the highest – of the East Baltic cod population (Fig. 3). It should be mentioned that exceedingly prolonged are the spawning and, accordingly, egg occurrence in the ichthyoplankton only of the East Baltic cod population unlike the West Baltic population, the conditions of reproduction of which in the Kattegat and Arkona Basin are not extreme (Fig. 4).

In the long-term aspect, the timing of mass cod reproduction in the Gdansk Deep is characterized by a considerable variability (Fig. 5). While the peak of cod spawning fell on May-June in early 50s, in the second half of the 90s it was recorded in July-August.

The timing of mass sprat reproduction also underwent the variability, caused mainly by alternation of cold and warm winters (Fig. 6).

Seasonal variability was also identified for vertical sprat eggs distribution (Fig. 7). While the largest amount of sprat eggs was concentrated in the near-bottom layer at the beginning of the spawning period, in summer season a significant amount of the eggs appeared in the surface layer.

Although a total number of pelagic egg species remained invariable through several decades, their percentage ratio sharply changed in the 90s as against in 1948-55 (Fig. 8). If the sprat egg abundance in the middle of the last century averaged to 40% in March-August, it reached 99% in the late 90s. Quite the opposite, the share of cod eggs reduced from 48% in 1948-55 to 0.3% in 1998-1999.

3. Variability of diversity indices.

The indices of general diversity in May tended towards a decrease, especially distinct in the late 90s as compared with the late 40s and beginning of the 50s (Fig. 9). But for all that the species richness remained permanent (4 species).

A decrease of the diversity index through several decades was attributed to a significant rise of the domination index as a result of a sharp increase of sprat eggs abundance which had reached the maximum in the late 90-s (Karasiova, Voss, 2004).

Seasonal dynamics of the diversity and domination indices also had opposite trends (Fig. 10). Inter-decade differences in the diversity index were most pronounced in April-June, when the intensity of sprat reproduction and, accordingly, the abundance of their eggs in the ichthyoplankton sharply increased (Fig. 10).

Though, on the whole, the diversity index in the 90s was considerably lower than in the 50s and 70s, it notably increased in the years of strong advections of the North Sea waters (1994, 2003) as compared with the years of prevailing development of stagnation processes in the Southeast Baltic (Fig. 11). The increase of the Shannon index in the years of inflow events was mainly

related to a rise of cod eggs abundance in the ichthyoplankton.
Also, the spatial variability in the species richness reaching the maximum in the central part of the Deep above the depths more than 80m and sharply decreasing above the depths less than 70m, was well traced in the years of advection along the transects across the Gdansk Deep (in latitude 54°50'N) (Fig. 12). That decrease was caused by falling the cod and rockling eggs out of the ichthyoplankton composition due to a considerable drop of the near-bottom salinity at the depths less than 70m.

DISCUSSION

Many scientists, starting on the whole with Moebius and Heinke (1884), contributed greatly in the investigation of the Baltic Sea biota biodiversity and the ichthyofauna in particular. At present, it is generally recognized that the fauna of this young water body in terms of geology was formed in the post-glacial period**,** and was heterogeneous in its origin and composition, including the sea, fresh and brackish water components (Rimsh, 1994). Under the theory of critical salinity put forward by Khlebovich (1974), the minimal biodiversity is observed at the salinity of 5-8 ‰. It increases with the shift of salinity both towards a decrease (to the entirely fresh water) and towards an increase to the level of the oceanic water (Aladin, 1988).

In accordance with the decrease in salinity from the Danish Straits to the Gulf of Finland, the number of the sea species inhabiting the Baltic Sea successively decreases in that same direction (Rimsh, 1994).

The central part of the Southeast Baltic is occupied by mesohaline waters, which allows to consider the ecosystem of the sea as that of brackish waters (Aladin et al., 2007). In addition to a decisive influence of low salinity upon diversity formation, there exist additional limiting factors.

For bottom fishes (cod, flounder and rockling) salinity and oxygen content are major environmental factors determining the size of the near-bottom layer favourable for their reproduction. Their successful reproduction may be possible at the salinity no less than 12‰ and oxygen content no less than 2ml/l (Nissling et al., 2002, STORE, 2003). The water temperature exerts significant influence on sprat reproduction (Grauman et al., 1987), the near-bottom layer temperature being essential at the beginning of their reproduction season, and the temperature of the cold intermediate layer and surface water being of importance in the end of spring – beginning of summer (Karasiova, Zezera, 2000, Karasiova, 2002). Respectively, a drop of salinity, temperature and oxygen content below the optimal level sharply increases the extremeness of reproduction conditions for these fishes in the Baltic Sea.

Extremely low species richness of the ichthyoplankton in the open part of the Baltic Sea is compensated to a certain degree by other diversity indices. So, the population of the East Baltic cod contains the aggregations of mature individuals with quite differing maturation and reproduction timing.

An extremely law ichthyoplankton species richness in the open Baltic Sea is compensated to a certain degree by other diversity manifestations. Thus, the East Baltic cod population contains the aggregations of sexually mature specimens with highly differing timings of maturation and reproduction. The seasonal occurrence of the East Baltic cod eggs includes late winter, spring, summer and the first half of the autumn, thus covering at least 9 months. As distinct from the East Baltic cod, the reproduction season of the most cod populations in the Northwest Atlantic lasts from 3 to 5 months due to higher salinity and favorable oxygen rate (Brander, 1993, Bagge et al., 1994).

Apart from long reproduction period, the East Baltic cod population and, in particular, its part reproducing in the Gdansk Deep is characterized, in a long-term aspect, by a considerable variability in spawning peak timing, which shows in seasonal distribution of cod eggs in different time periods. The shifts of the Baltic cod mass reproduction timing can be attributed to the long-term variability in environmental conditions in the near-bottom deep layers (Wieland et al., 2000, STORE 2002, Karasiova, 2006).

The water temperature is the main environmental factor influencing the Baltic sprat reproduction timing. Since the sprat spawn over a vast area, including the Bothnian Sea and the western part of the Gulf of Finland, the timing of their mass reproduction falls to later time, and the total duration of reproduction reduces in the south to the north direction (Grauman, 1980). The dependence of sprat reproduction on the environmental conditions can be also well traced within the limits of local spawning grounds (Kraus et al., 2004).

The seasonal variation of the Baltic sprat spawning biotope is the most specific feature of their reproduction, which distinguishes them from the populations in other areas of the Northeast Atlantic. In February, March and April, the sprat spawn in deep-water layers in the upper part of the halocline. In May, their reproduction begins in the surface layer above the thermocline or in its upper part (Grauman, 1969). As a result, in summer their reproduction area exceeds the bounds of deepwater basins, extending also to relatively shallow areas.

According to Chernov (2005), the compensation of the species depletion in the biota is especially clearly pronounced under the extreme conditions confining the species diversity. The mechanisms of manifesting the compensative phenomena differ, and may involve the increase of individual species population density, extension of ecological niches, increase of intraspecific diversity, including the rise of morpho-ecological differentiation degree (Chernov, 2005). Evidently, the presence of cod, rockling and sprat aggregations with differing timing of seasonal maturation and spawning should be regarded as a compensating response of the pelagofillous fishes community to a decrease in taxonomic diversity. Besides, the Baltic sprat show the features of polytopeness by switching from reproduction in the near-bottom layer early in spring to reproduction in the surface layer in summer. Thus, in summer the Baltic sprat occupy the spawning biotope, which in the Black Sea and other seas in the Mediterranean region is occupied by anchovy and sardine.

It is worth noting that the sprat inhabiting the Baltic Sea are usually considered as a single stock (ICES WGBAS Report 2006). The Baltic cod are subdivided into two populations: the West Baltic relatively scanty population reproducing in the Kattegat and the Arkona Basin, and the East Baltic numerous population reproducing in the Bornholm, Gdansk and Gotland Deeps. The flounder in the Baltic Sea are likely to have a more complicated population structure, which is formed, a according to the data of different authors (Aro, 1989, Florin, Hoeglund, 2005), by 9 to 15 populations. However, as regards the spawning ecology, the Baltic flounder is subdivided into two ecological forms, one of which reproduces in deep-water sea basins at relatively high salinity providing its buoyancy, and the other on shallow banks on the bottom substrate at a lower salinity (ICES WGBAS Report 2006).

Thus, different Baltic Sea flounder populations use various spawning biotopes.

These peculiarities of reproduction should apparently be ascribed to the category of phenomena compensating low species diversity, and thus increasing the stability of the community functioning. So, a few fish species having settled in the Baltic Sea deepwater basins for reproduction possess advanced aptitude for ecological divergence and extension of their niches, the increase of the ecological space volume used under favourable ecological conditions.

Through the recent 50 years, in many Baltic Sea areas, including the Gdansk Deep, a tendency has been traced to the transition from polydominance of fish community to its monodominance, which reflects in a decreased index of general diversity. This process was caused by a decline of the bottom fish species abundance and a rise of sprat abundance under the conditions of weakened inflows of the North Sea waters, warming of the climate, and increased eutrophication of the sea (Koester et al, 2003). Considering a growing human impact on the Baltic Sea ecosystem, it should be noted that the observed tendency has been caused both by climatogenic and anthropogenic factors (MacKenzie, Koester, 2004).

Based on the presented data, it may be deemed that in the long-term dynamics of the ichthyoplankton community diversity there exists a periodical component, which can be traced within the limits of the time interval several decades long.

A sharp drop of cod abundance (which, being the predator, represent the upper level of the trophic pyramid) increases a probability of the resource reconsumption by pelagic fishes and, hence, the eventuality of the ecological crisis. However a high abundance of this species is still maintained in the Bornholm Deep, the closest to the Danish straits, where it continues to successfully reproduce (STORE. 2003). With occasional inflows of the North Sea waters, cod reproduction is getting intensified in the Gdansk deep, and renewed in the Gotland Deep, though on a very small scale. Thus, the potential for the increase of cod abundance in the Baltic Sea has not been lost yet.

At present, the community of the fishes, reproducing in the sea deepwater depressions, has undergone a transition to a new equilibrium state, having maintained, however, its structural elements and a possibility to recover the former status under adequate climatic changes.

CONCLUSION

1. The community of pelagophilous fishes, reproducing in the Baltic deepwater basins, formed under the influence of environmental factors, which extremely limited its species richness. Extreme reproducing conditions is one of the main causes of species composition poorness.

2. Four species of pelagophilous fish species, reproducing in the Gdansk Deep of the Baltic Sea, are characterized by protracted period of their eggs occurrence in the ichthyoplankton (especially cod and rockling), considerable variability in timing of the peak eggs abundance in the ichthyoplankton (cod, rockling, and sprat), use of different spawning biotopes (sprat and flounder).

3. Apparently, these peculiarities of reproduction should be ascribed to the category of phenomena compensating low species diversity, and thus increasing the resilience of the community functioning. Consequently, few fish species that have settled in deepwater basins of

the Baltic Sea evidently possess advanced aptitude to ecological divergence, and expansion of their biotopes in space and time under definite environmental conditions.

4. There exists a periodical component in the long-term dynamics of the ichthyoplankton community diversity, which can be traced within the limits of the time interval several decades long. In the present-day epoch, a transition from polydominance of pelagophilous fish community to monodominance has resulted in the decrease of general diversity index.

5. At present, the community of the fishes, reproducing in deepwater parts of the sea, underwent a transition to a new equilibrium state having, however, maintained its structural elements and a possibility to recover the former status under adequate climatic changes.

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LEGENDS

Fig. 1. Long-term variability in salinity and oxygen content at the Gdansk Deep bottom.
Fig. 2. Long-term variability in temperature in the upper part of the intermediate layer (30-40m) in the Gdansk Deep.

Fig. 3. Seasonal variability in different fish species eggs abundance in the Gdansk Deep in the Baltic Sea.

Fig. 4. Seasonal variability in cod eggs abundance (%) in the West Baltic (the Bay of Kiel) and East Baltic (the Gdansk Deep) populations (Kaendler, 1949, Mankowski, 1949, 1951, 1955).

Fig. 5. Seasonal variability in cod eggs abundance in the Gdansk Deep in different time periods (Karasiova, 2006).

Fig. 6. Seasonal variability in sprat eggs abundance in cold (1947, 1968-71, 1996) and warm (1949, 1973-75, 1998) years (Karasiova, 2002).

Fig. 7. Vertical distribution of Baltic sprat eggs in spring (April) and summer (June) seasons (according to Grauman data, 1969).

Fig. 8. Variation in ichthyoplankton species ratio in the Gdansk Deep in different time periods.

Fig. 9. Long-term variability in Shannon's H diversity index and Simpson's domination index in the ichthyoplankton of the Gdansk Deep in the Baltic Sea.

Fig. 10. Seasonal dynamics of diversity indices H (a) and domination indices C (b) in the ichthyoplankton of the Gdansk Deep in different time periods.

Fig. 11. Seasonal variability in diversity index in the Gdansk Deep in the years of advections (1994, 2003) and stagnation of environmental conditions.

Fig. 12. Variability in some ichthyoplankton parameters along the transect made across the Gdansk Deep in May 2003 depending on the depth: a)species richness S, b) egg abundance N, sp./m^2.

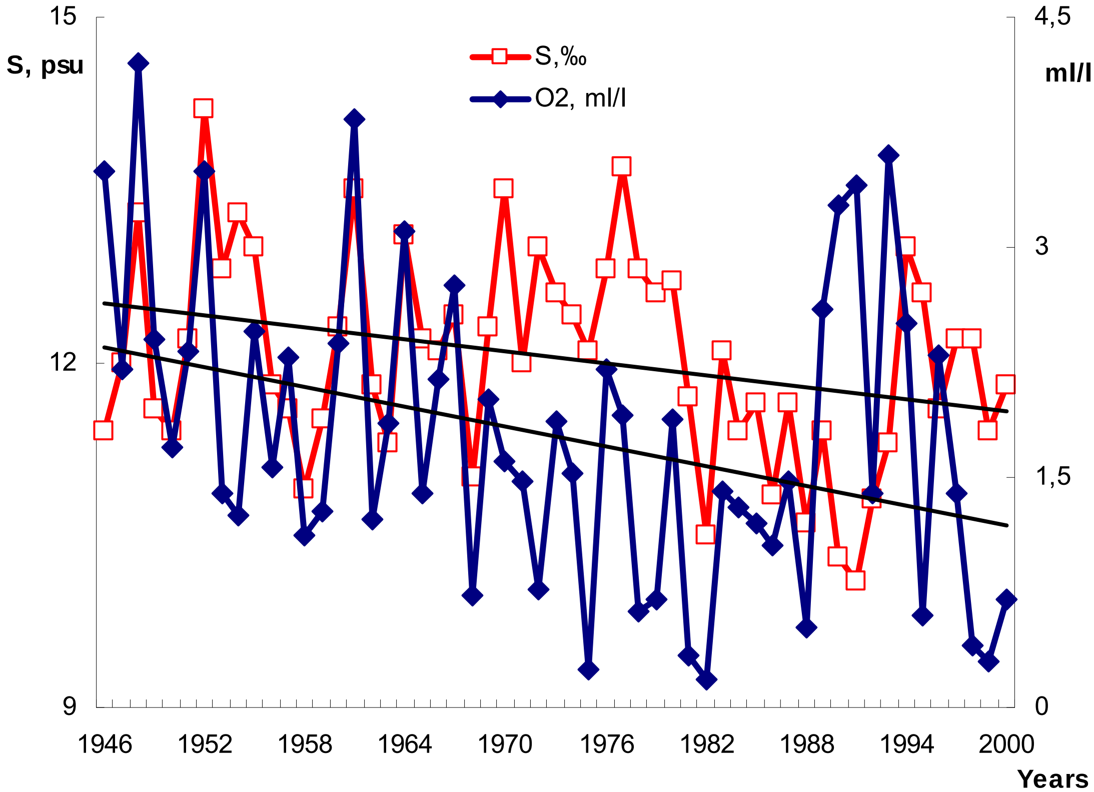


Fig.1. Long-term variability in salinity and oxygen content at the Gdansk Deep bottom

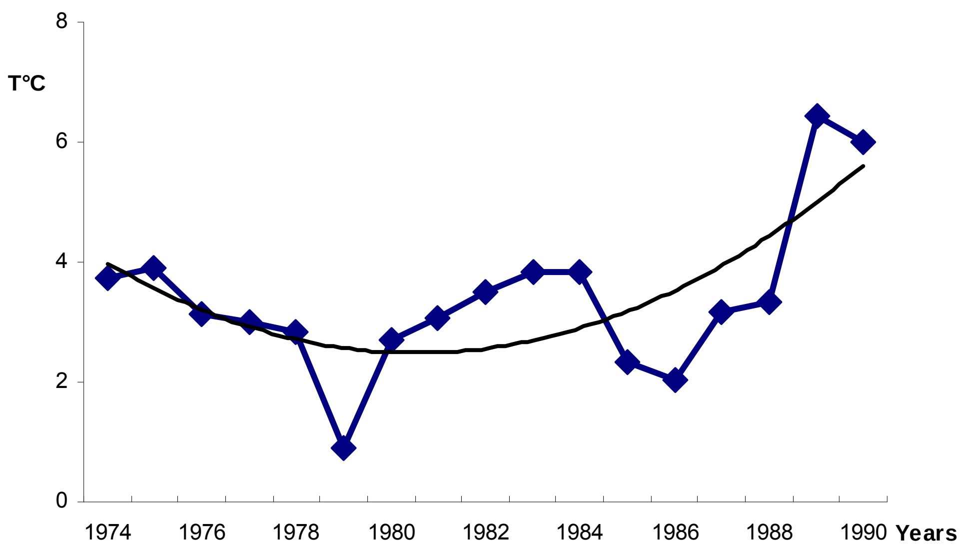


Fig.2. Long-term variability in temperature in the upper part of the intermediate layer (30-40m) in the Gdansk Deep.

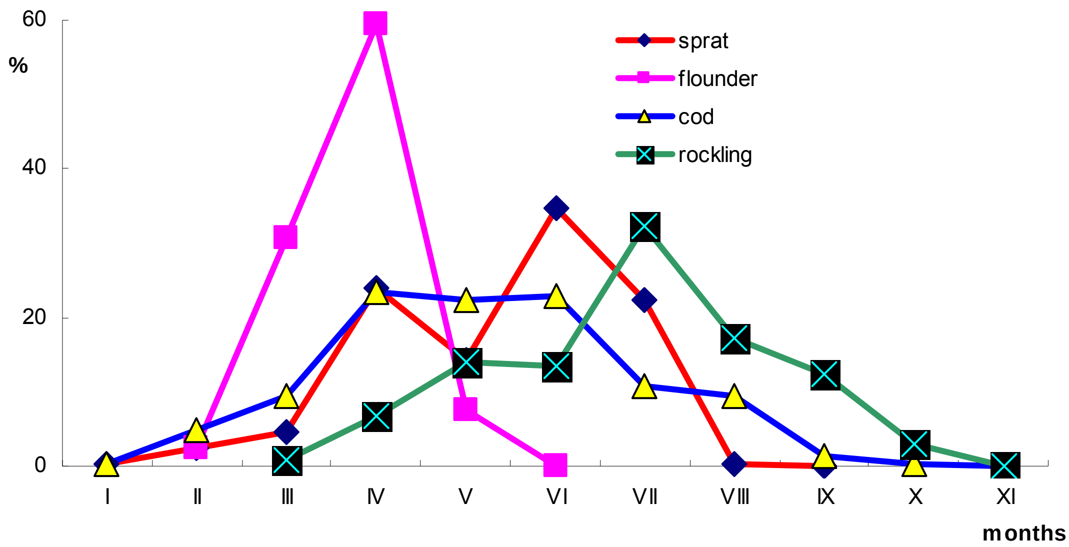
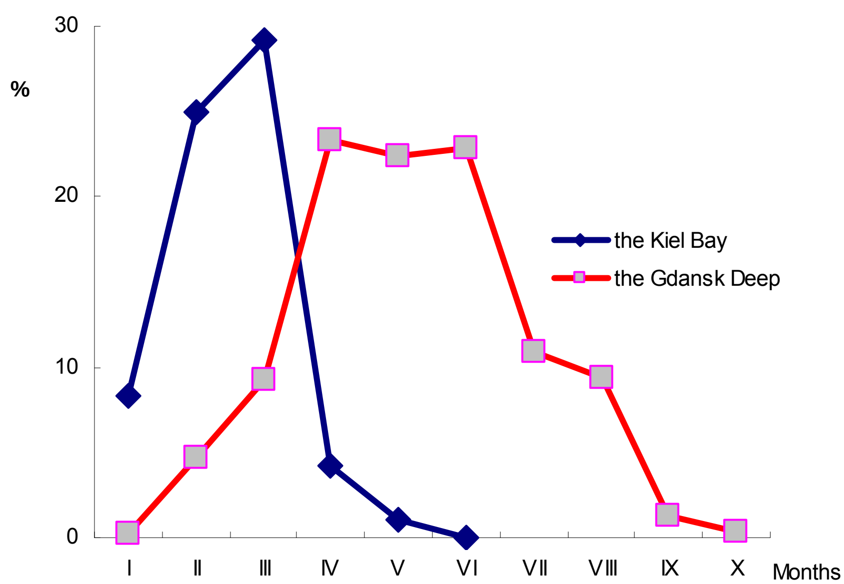


Fig.3. Seasonal variability in different fish species eggs abundance in the Gdansk Deep in the Baltic Sea



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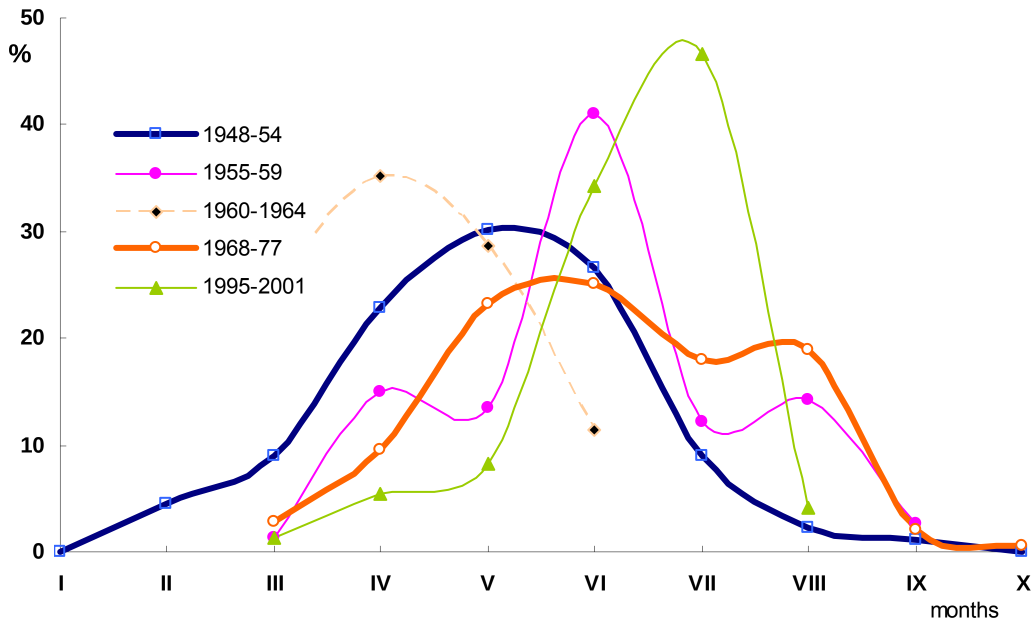
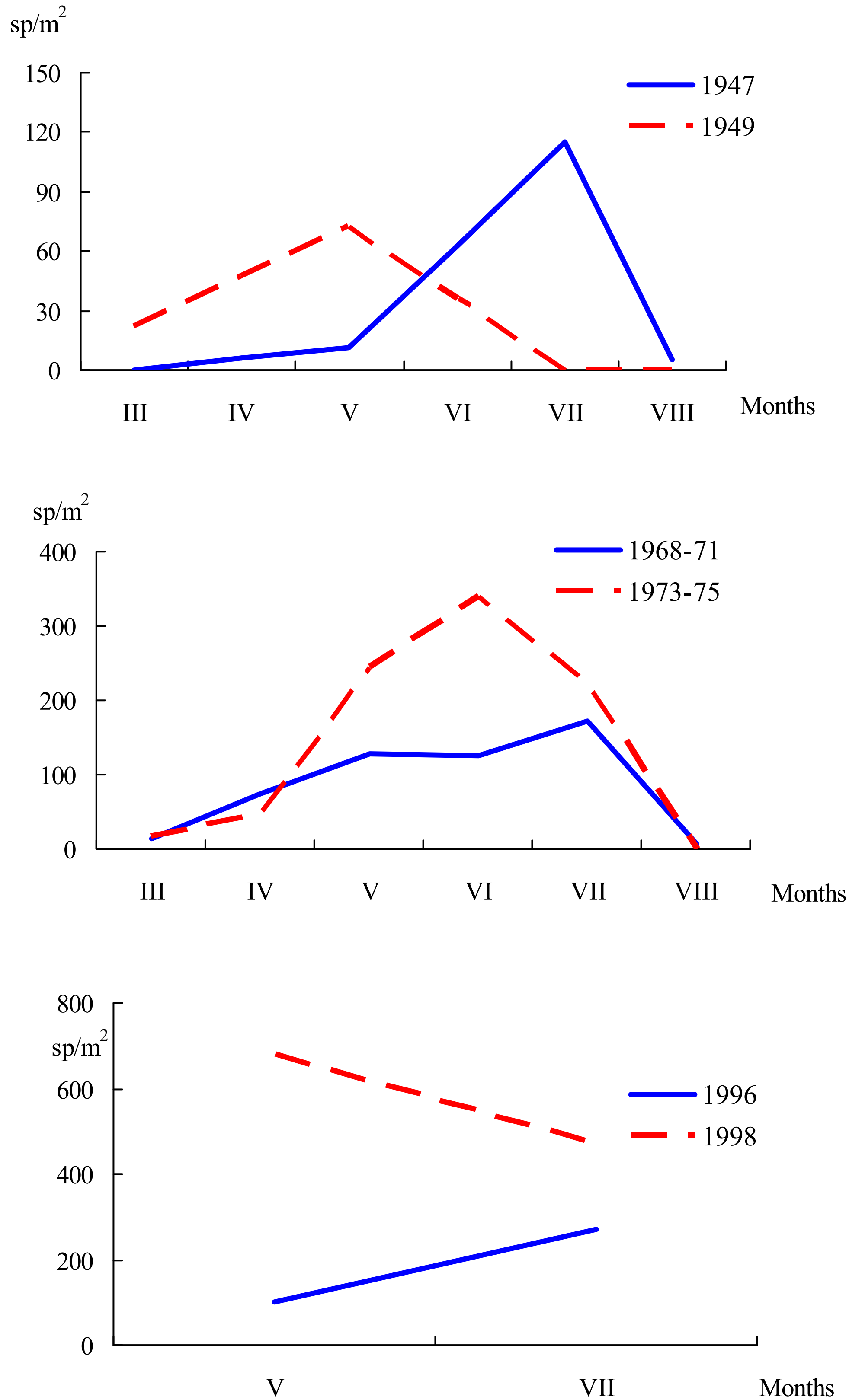


Fig.5. Seasonal variability in cod eggs abundance in the Gdansk Deep in different time periods (Karasiova, 2006).



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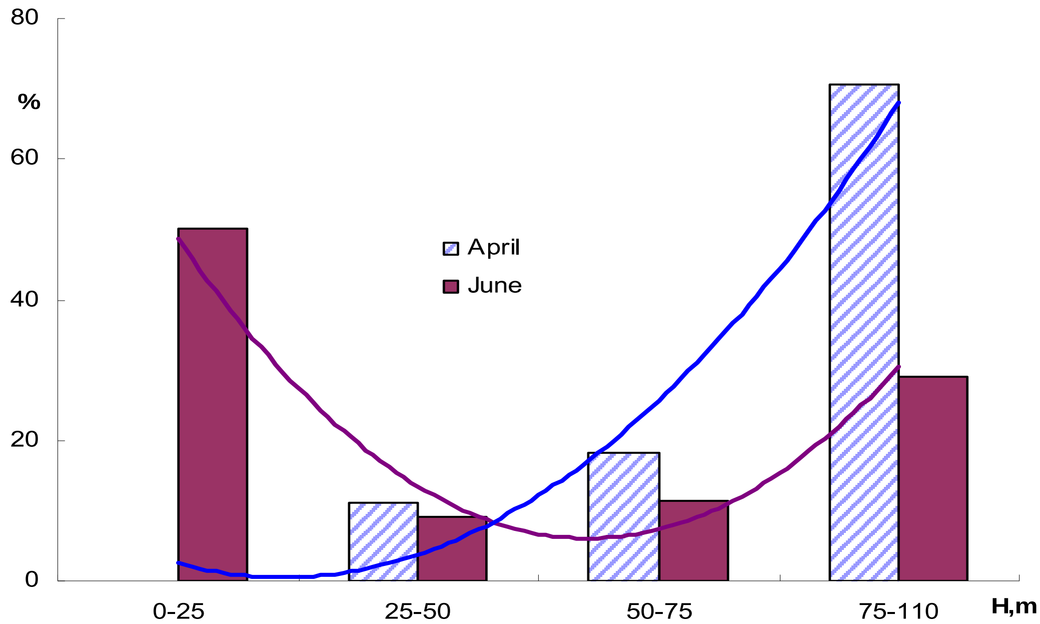

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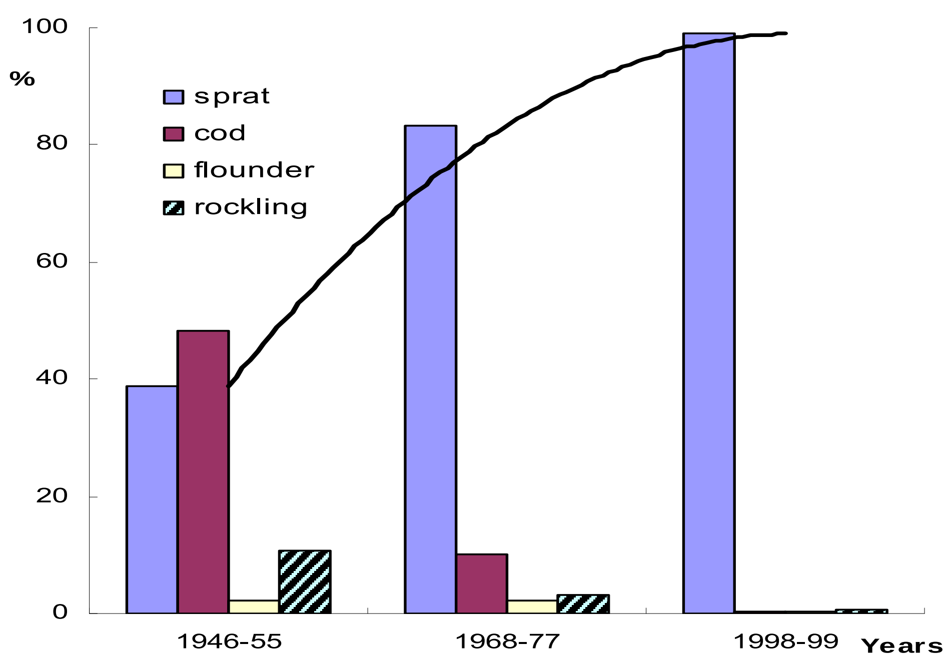

Fig.8. Variation in ichthyoplankton species ratio in the Gdansk Deep in different time periods.

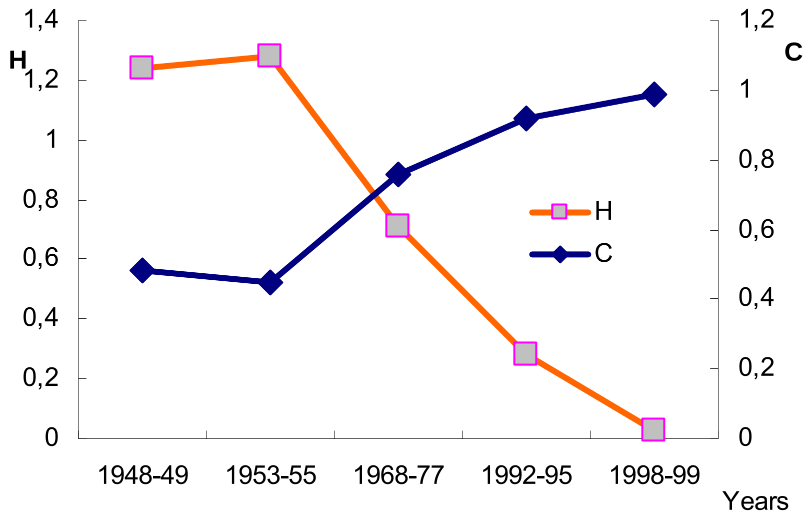

Fig.9. Long-term variability in Shannon's H diversity index and Simpson's domination index in the ichthyoplankton of the Gdansk Deep in the Baltic Sea.

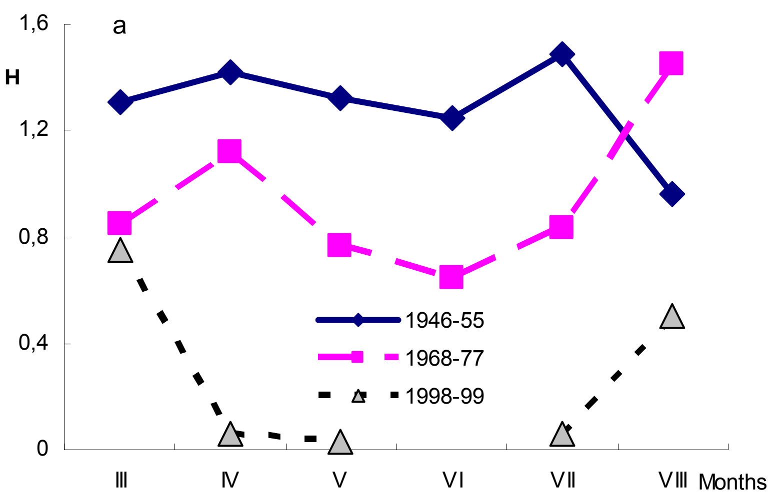

Fig.10. Seasonal dynamics of diversity indices H (a) and domination indices C (b) in the ichthyoplankton of the Gdansk Deep in different time periods

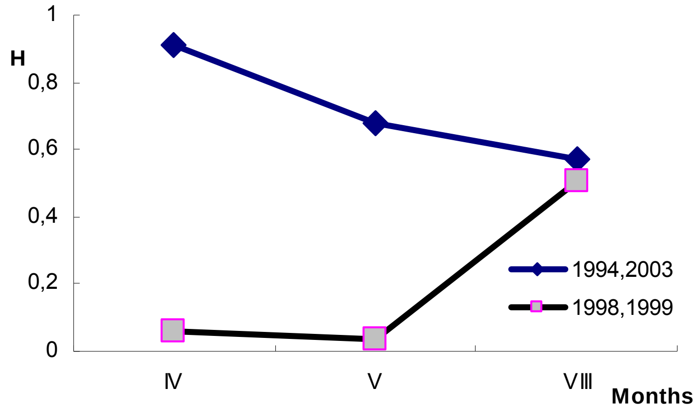

Fig.11. Seasonal variability in diversity index in the Gdansk Deep in the years of advections (1994, 2003) and stagnation of environmental conditions

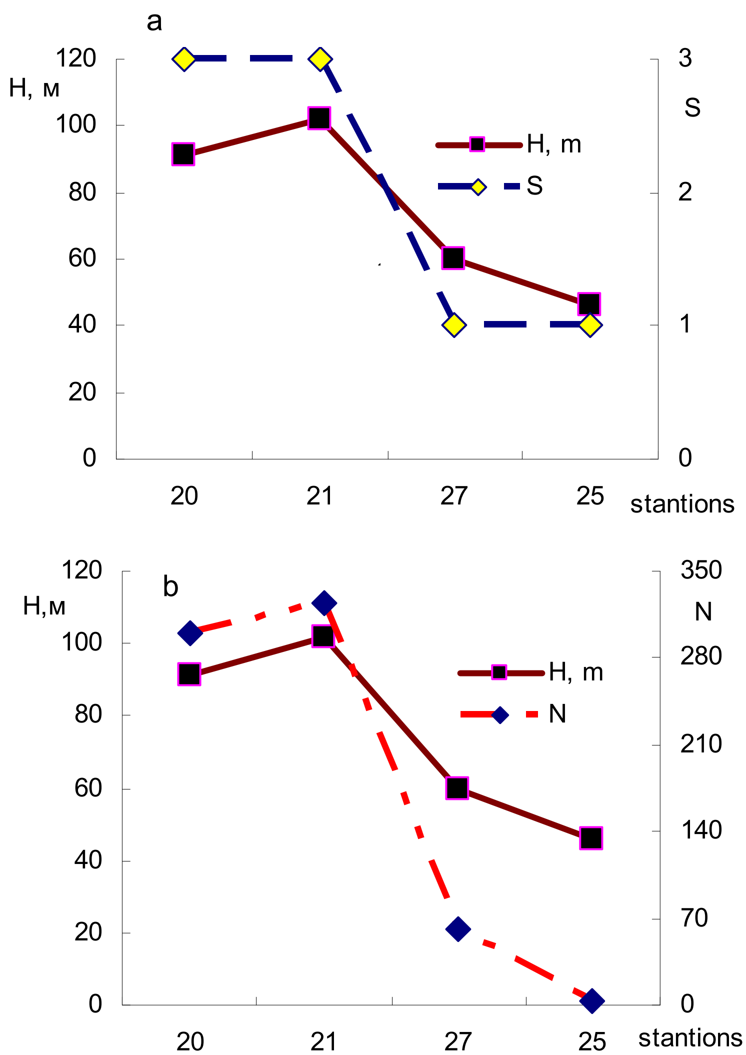

Fig.12. Variability in some ichthyoplankton parameters along the transect made across the Gdansk Deep in May 2003 depending on the depth: a)species richness S, b) egg abundance N, sp./m^2.