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Cod populations in the Eastern Baltic Sea and the White Sea: the environmental extremeness as a factor of two unique reproduction strategies formation

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ABSTRACT

Two populations of numerous cod stocks in the Northeastern Atlantic Ocean – the eastern Baltic cod *Gadus morhua callarias* and the White Sea cod *Gadus morhua maris-albi* – are inhabiting the intra-continental seas, where reproduction conditions are close to the extreme ones to the species as a whole. Some aspects of their reproductive strategy are considered with reference to the determining influence of the environment conditions extremeness. The unique feature of the White Sea cod consists in coincidence of its reproduction peak with the hydrological winter season and negative water temperatures. The biological sense of this adaptation is to avoid summer decline of the surface salinity leading to decrease of eggs buoyancy. As a result of adaptation to maturation and reproduction at the extreme temperature conditions, the White Sea cod strategy is directed to reduction of expenses for power-consuming functions: fecundity and growth rate. The reproductive strategy of the Baltic cod is under the combined impact of salinity and oxygen content variability and the reproductive volume is the integral index of this impact. Highly significant duration of the Eastern Baltic cod spawning and shift of mass spawning period from spring to summer after the prolonged absence of the North Sea water inflows became the result of reproduction association with the restricted near-bottom water volume. As a result, it is assumed that salinity is a general factor, which to a significant extent controls reproduction and eggs survival of two populations considered.

Keywords: cod of the Baltic and White Sea, environmental extremeness, reproduction strategy.

INTRODUCTION

Only two populations of numerous cod stocks in the North Atlantic inhabit the intra-continental seas, where reproduction conditions are close to the extreme ones to the species as a whole. These are the White Sea cod *Gadus morhua maris-albi* Derjugin and the eastern Baltic cod *Gadus morhua callaris* Linneus. In spite of their spawning biotopes are quite different (coastal zone for the White Sea cod and deep basins for the Baltic Sea cod), obviously, the general control factor, which determines seasonal reproduction dynamics in many respects, can be revealed in there habitat. This factor is determined by restricted seawater exchange with the ocean and relatively lower salinity in the White Sea and Baltic Seas.

The aim of this paper is comparison of reproduction strategies of the White Sea cod and Baltic Sea one, which provide their adaptation to the extreme living conditions.

MATERIAL AND METHODS

Literary data on the White Sea hydrographic regime (Kuznetsov, 1960; Beklemishev et al.,1980; Biology of the White Sea, 1980,; Oceanographic conditions..., 1991), spawning timing of the White Sea cod and environmental conditions during the reproduction season (Maslov, 1952; Soin, 1980; Makhotin et al., 1986), fecundity, length and weight at age (Andriyashev, 1954) were used.

Out of two Baltic cod populations (Bagge et al, 1994) the most numerous Eastern Baltic cod, which reproduces in the deeps of the Central and Eastern Baltic, is considered.

Characteristic of hydrographic conditions and spawning timing of the eastern Baltic cod is based on the database of the Baltic Sea Laboratory of AtlantNIRO on hydrography and ichthyoplankton as well as literary sources (Kaleis, Yula, 1974,1978; CORE, 1998; Wieland, Zuzarte, 1991; Zezera, 2002; Karasiova, Voss, 2004). Long-term ichthyoplankton investigations of AtlantNIRO were carried out by net IKS-80 with the vertical haul in the layer bottom-surface from February till October.

The ichthyoplankton sampling in the White Sea was also conducted by net IKS-80 (Makhotin et al., 1986).

Also literary sources on fecundity (Dmitrieva, 2001), weight and linear growth (Biryukov, 1970; Baranova, Uzars, 1986; Karpushevskiy, 2002) of the Eastern Baltic cod were used.

RESULTS

The White Sea and Baltic Sea are semi-enclosed intra-continental seas with restricted water exchange with the open ocean.

The vertical structure in the White Sea and Baltic is characterized by existence of two water masses in winter season and three ones in summer season - surface, intermediate and deep – with strongly pronounced temperature gradients in the vertical interface zones (Beklemishev et al., 1980; Zezera, 2002).

In the White Sea relatively the less saline surface water mass (with salinity < 26 psu) is warmed up to 12^{o}C in summer season (Beklemishev et al, 1980). The deep water mass has the maximum salinity (29-30 psu) and the minimum temperature (< - 1°C).

In the Baltic Sea the surface and the intermediate layers have low salinity (6 -8 psu), but these layers are strongly different in water temperature in spring and summer. While the surface layer is well warmed up from winter to summer, the intermediate layer is characterized by low winter temperature till the autumn homothermy. The deep water mass, separated from the intermediate one by halocline, has the maximum salinity and higher water temperature in comparison with the intermediate layer. The near-bottom salinity reduces from the south-west to the north-east: from 14.5 – 20 psu in the Bornholm Basin to 11-13 psu in the Gdansk Deep and Gotland Basin.

Summer warming-up and strongly pronounced seasonal water temperature variability in the White Sea cover the layer not more than 50 m (Kuznetsov, 1960). Because of the more southern geographical location of the Baltic Sea the surface water temperature exceeds that of the White Sea by 2°- 4° C on average during all the year (Fig. 1).

Temperatures of the deep water masses are significantly different. In the White Sea, from a depth of 50 m, during all the year negative temperatures (-1.2° – 1.6°C) are observed, while in the Baltic Sea the near-bottom layer temperature usually varies in the range of 4°- 8° C between years. (Fig. 2). Despite of higher salinity in the White Sea the vertical salinity distribution in both water bodies has the general tendency of increasing at the deep layer (Fig. 3). In both Seas the seasonal variability of temperature and salinity in the deep layer is almost insignificant.

Because of the extremely low water temperature below 50 m isobath the White Sea cod inhabits the coastal zone (Makhotin et al., 1986). The main area of its reproduction is the Kandalaksha Bay (Fig. 4), but it could spawn in the Onega Bay (Maslov, 1952). Spawning takes place at a depth of 9-20 m (Kuznetsov, 1960). It begins in the middle of March under the ice when the water temperature is from -1,6° to -1,4°C (Makhotin et al., 1986). The spawning peak observes at the first half of April, when the water temperature is not higher than -1°C. The second half of the reproduction season lasts under the significant water temperature increasing (to 9°C) and salinity decreasing because of the ice thawing. Spawning ends in May. The peak of the surface layer desalination occurs in June (Fig. 5) in accordance with the seasonal trend of salinity in the layer 0-10 m.

As the White Sea cod eggs have a neutral buoyancy under salinity 24 psu (Makhotin et al., 1986), the salinity decreasing by 2 - 4 psu causes a sinking of eggs to the bottom and its death (Soin, 1980).

The eastern Baltic cod spawns in the Baltic deeps under the halocline. Spawning takes place at a depth of more than 50 m in the Bornholm Basin close to the Danish Straits and more than 80 m – in more eastern the Gdansk Deep and Gotland Basin.

During the period of maximum spreading of cod habitat in the Baltic (1950s, 1970s) the reproductive area had the significant extension from the south to the north: from 54°40' N in the Gdansk Deep till 58°30'N in the central part of the Gotland Basin (Fig. 6). In 90s the main reproduction of cod took place in the Bornholm Basin of the Baltic Sea (Fig. 7; CORE, 1998; Koester at al, 2003). However, according to experimental data the cod eggs have the positive buoyancy only in the Bornholm Basin when the near-bottom salinity is more than 14 psu (Nissling and Vallin,1996). Favorable environmental conditions for cod egg development are restricted by salinity not less than 11 psu and oxygen content not less than 2ml/l (CORE, 1998).

As the salinity level and oxygen content in deep basins depend on frequency and intensity of the North Sea water inflows the cod reproduction conditions become strongly worse during their prolonged absence. Spawning of the eastern Baltic cod lasts from February to October inclusive. In some years the cod eggs in ichthyoplankton appeared in January (Karasiova, 2006). During the prolonged period (late 40s – early 80s) the mass cod reproduction was observed in April-June. From the beginning of 90s the spawning peak timing shifted to July-August (Fig. 8).

Whereas the White Sea cod does not migrate and its distribution is restricted by the coastal zone, the eastern Baltic cod is an active migrant, especially during the feeding after spawning (Biryukov, 1970). However, the extension of migrations, as well as a part of migrating component, decreases with reduction of the population abundance.

The White Sea cod has lower fecundity (Fig. 9) and rate of linear and weight growth, which are indicated by distribution of length and body weight at ages (Fig. 10, 11).

Data characterized the spawning conditions and some biological characteristics of cod of the Baltic and White Sea are presented in the Table.

DISCUSSION

The White Sea and eastern Baltic Sea cod are belong to the Atlantic cod group (Andriyashev, 1954), but significantly differ from the majority of cod populations in the North-Eastern Atlantic with their adaptive responses.

So, spawning timing for the North Sea and Arctic Norwegian populations shifted northwards for 2-4 weeks in some connection with the difference of water temperature (Brander, 1993). Thermal regime of those Atlantic cod populations, which inhabit the northernmost part of species area under the oceanic salinity, is one of the main factors, which determines the reproductive success (Ozhigin et al., 1999).

Thermal conditions for mass reproduction of the White Sea cod are unique and not observe for the other populations in the North-Eastern Atlantic. Obviously, shift of the reproductive temperature optimum to negative temperatures was a consequence of restrictive impact of the seasonal salinity decrease on buoyancy and surviving of cod eggs. It is well-known that the variability of salinity regime is the restrictive factor, which limits distribution of hydrobionts. Obviously, adaptive responses of the White Sea cod are aimed to avoid a coincidence of the mass reproduction with the seasonal salinity minimum. As a result they caused the shift of spawning peak to hydrological winter with negative water temperature. Therefore, it is the sharp salinity decreasing in the late hydrological spring that impedes a reproduction of the White Sea cod under the more favorable thermal regime.

Obviously, the costs for adaptation to extreme thermal conditions are low fecundity and rate of weight and linear growth, absence of migrating behavior (resident life strategy).

In contrast to the Baltic cod, the life history strategy of the White Sea one is directed to a reduction of expenses for energy-consuming functions such as producing of spawning products, growth and migration activity. The regulative factors, responsible for these differences, are low water temperature in winter- spring season and smaller duration of productive period.

Thermal regime is more favorable for reproduction of the Baltic cod, than for the White Sea one. In spite of the considerable extension of the Baltic cod spawning area northwards, impact of thermal factor on reproduction periods is recovered by the combined impact of salinity and oxygen content variability.

The integral index of this impact is a value of the so-called “reproductive volume” of waters with favorable conditions for survival of the cod eggs (CORE, 1998). As a result the successive displacement of spawning periods northwards was not observed in the Baltic Sea, but the shift of the mass reproduction timing could took place depending on the value of reproductive volume observed (Karasiova, 2006).

The consequence of reproduction association of the Baltic Sea cod with the restricted near bottom water volume is an adaptive response of population which one reveals itself in decelerating of maturation in seasonal cycle and shift of mass reproduction periods from spring to summer after the prolonged absence of the North Sea water inflows.

In the long-term dynamics of the cod egg number in ichthyoplankton and spawning ground sizes it could be observed the periods of their significant increasing corresponding to the stage with high intensity of inflows. On contrary the periods of both sharp cod egg abundance and spawning ground reduction corresponded to the stage of the prolonged absence of the North Sea water inflows.

As a result of periodically occurring unconformity between environmental capacity and the number of adult part of population the Baltic Sea cod has a very long reproduction period (February - October) without any analogues with the other populations in the North Eastern Atlantic. Also salinity and oxygen regimes in spawning biotope of the Baltic Sea cod have no analogues.

Evidently it was an extremeness of environment that caused specific adaptations distinguishing cod populations under consideration from others in the North Atlantic.

It can be assumed, that salinity is a general factor, which to significant extent controls reproduction and eggs survival of two populations considered.

Climatic warming, which causes the water temperature increasing, because of specific hydrographic features of the Baltic and White Seas, leads to faster oxygen depletion that can impact negatively on reproduction of both populations in the current epoch.

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Table. Comparison of spawning timing, reproduction conditions and size-weight characteristics of the White Sea and Eastern Baltic cod populations.

Characteristic of spawning timing and conditions	The White Sea cod	The Baltic Sea cod
Beginning of spawning: Peak of spawning: End of spawning:	March April - May	February April-May, 50-s. July-August, 90-s. October
Duration of spawning	2.5 months	8 months
Vertical localization of spawning	9 – 20m	55-80m, Bornholm 80-110m, the Gdansk Deep 90-130m, the Gotland Basin
Water temperature	Beginning of spawning: -1.6°; -1.4°C End of spawning: +9, + 10°C	3° – 7°C
Salinity	Beginning of spawning: to 30 psu End of spawning: 24 psu June: to 15 psu	11psu – 18 psu
Oxygen content in the layer with developing eggs	>8 ml/l, April	> 2 ml/l, inflow < 2 ml/l, stagnation
Environmental factors, which cause the extremeness of reproduction conditions	Seasonal decreasing of salinity; temperature during spawning starting	Reproductive volume fluctuations as a result of salinity and oxygen content variability in the Gdansk Deep and the Gotland Basin
Length, cm Weight, g (age from 2 to 7 years)	20.6 – 42.9 73 – 842	31.2 – 63.8 269 – 2920

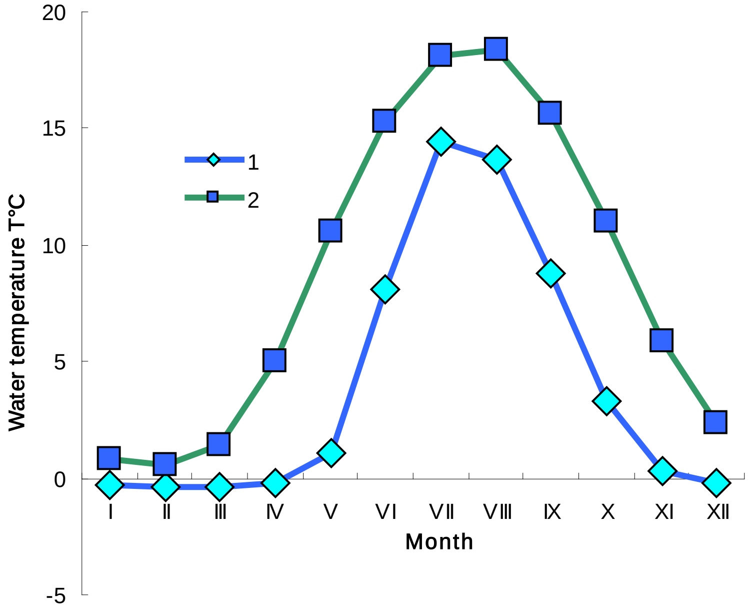


Fig.1. The seasonal dynamics of surface water temperature: 1 - the Baltic Sea, 2 - the White Sea

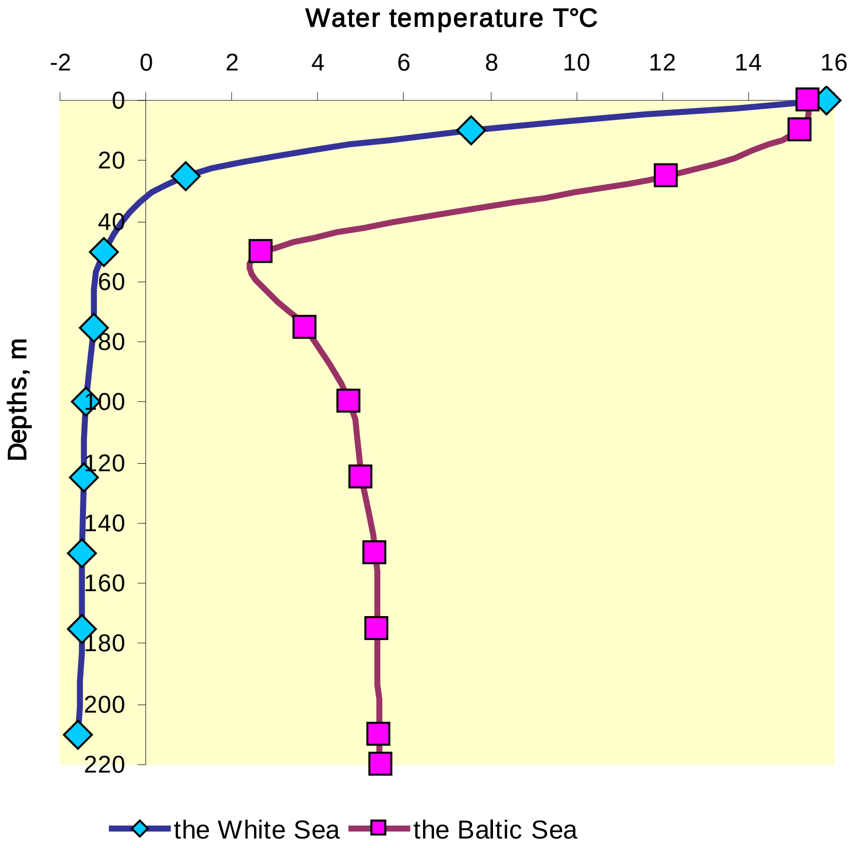


Fig. 2. The vertical distribution of water temperature in deep areas of the White and Baltic Seas in summer season

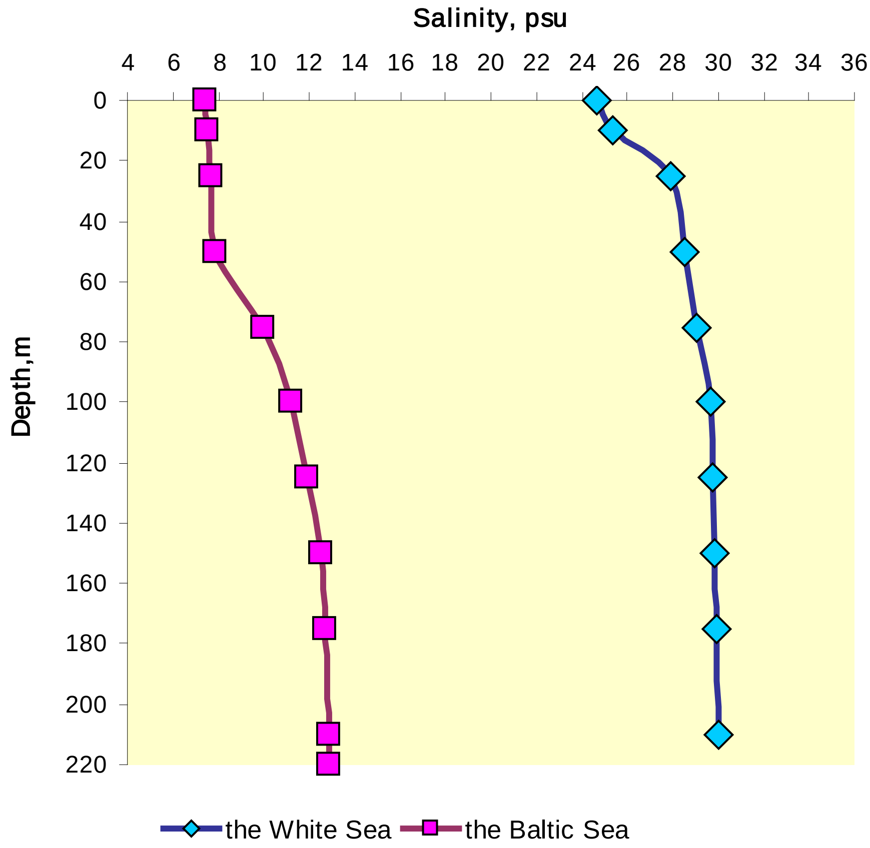
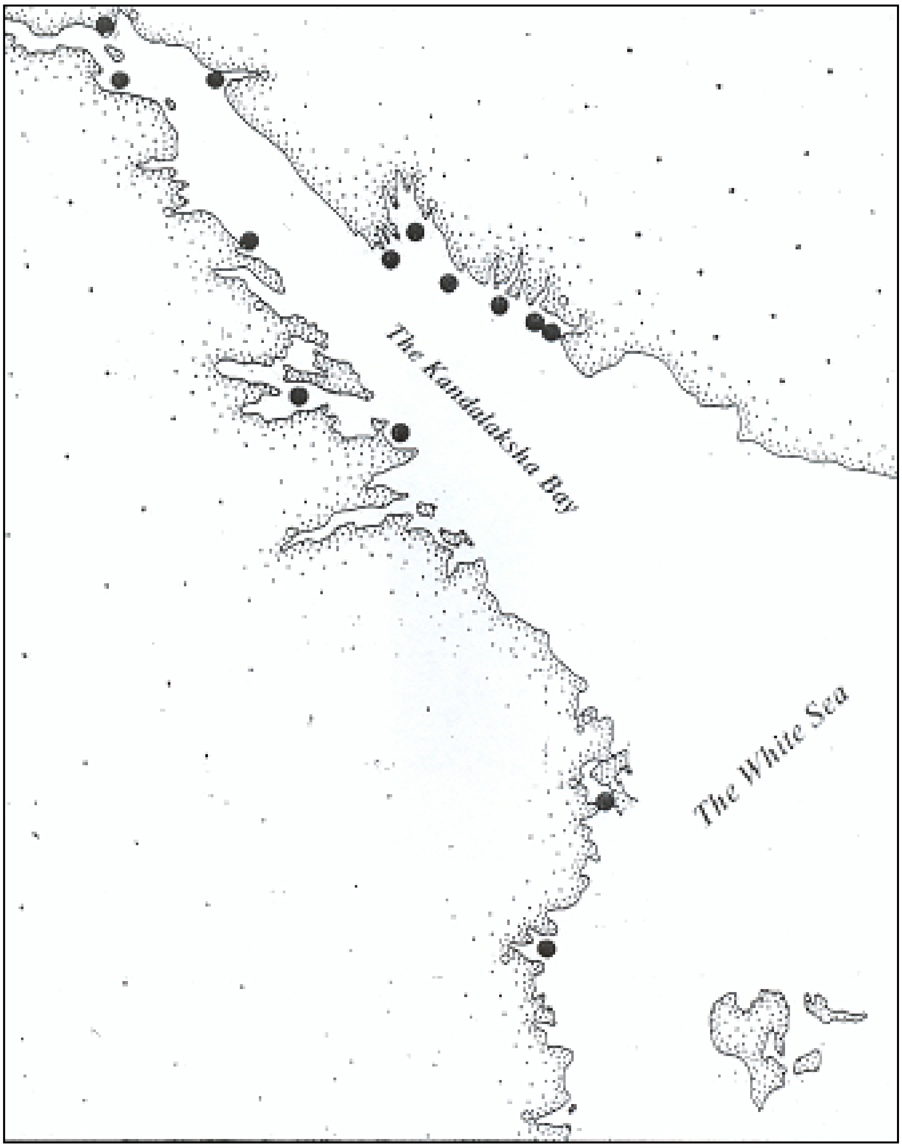


Fig.3. The vertical distribution of salinity in deep areas of the White and Baltic Sea in summer season.



● - the White Sea cod spawning grounds

Fig.4. Locations of cod spawning grounds in the White Sea (according to Makhotin at al., 1986)

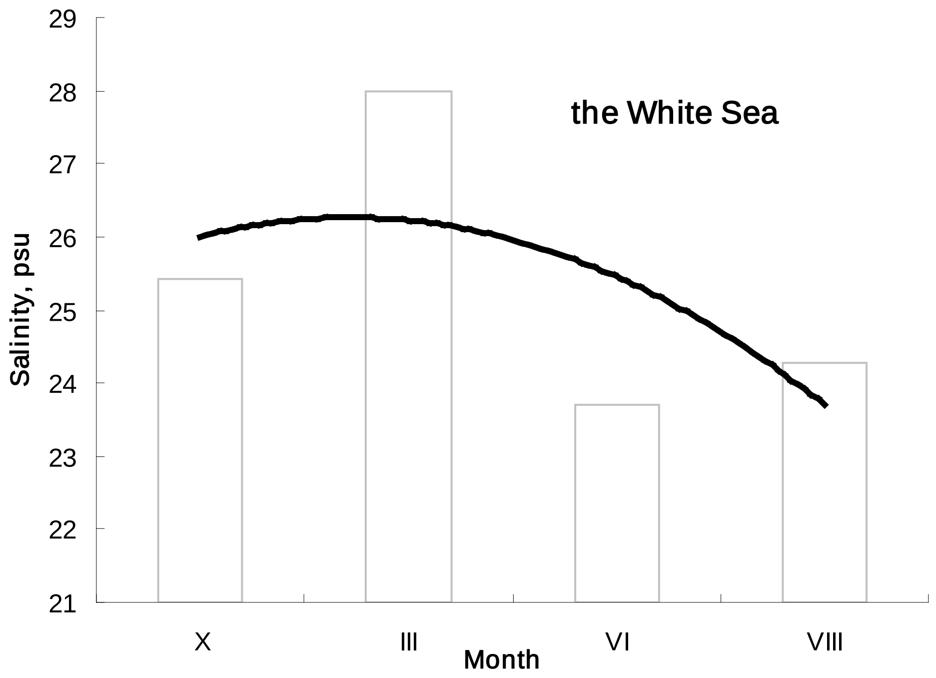


Fig.5. Seasonal changes of salinity at the surface water layer (0 – 10 m) of the White Sea.

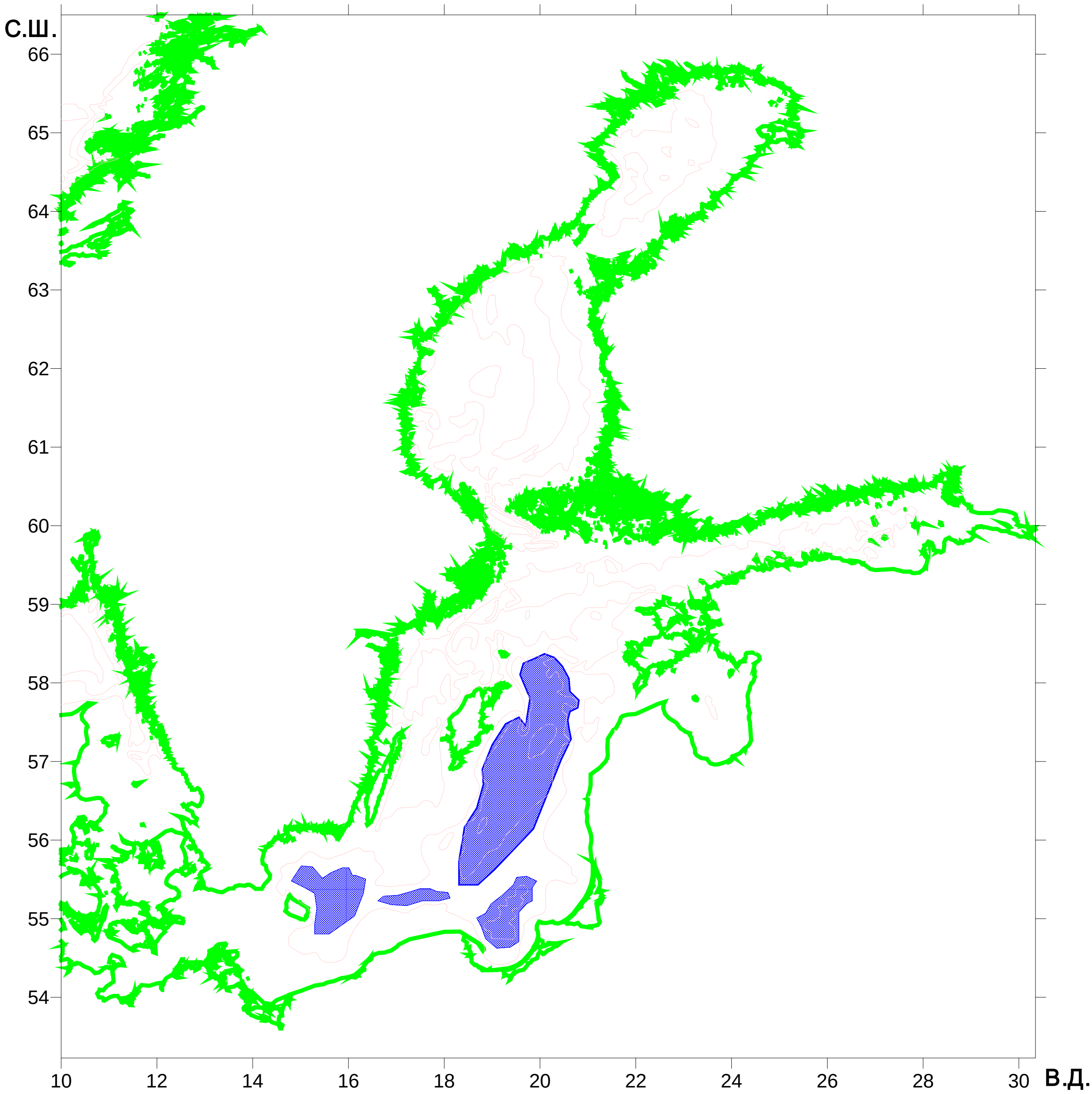


Fig.6. Spawning grounds of eastern Baltic cod in the period of the maximum spatial expansion (1950s, 1970s)

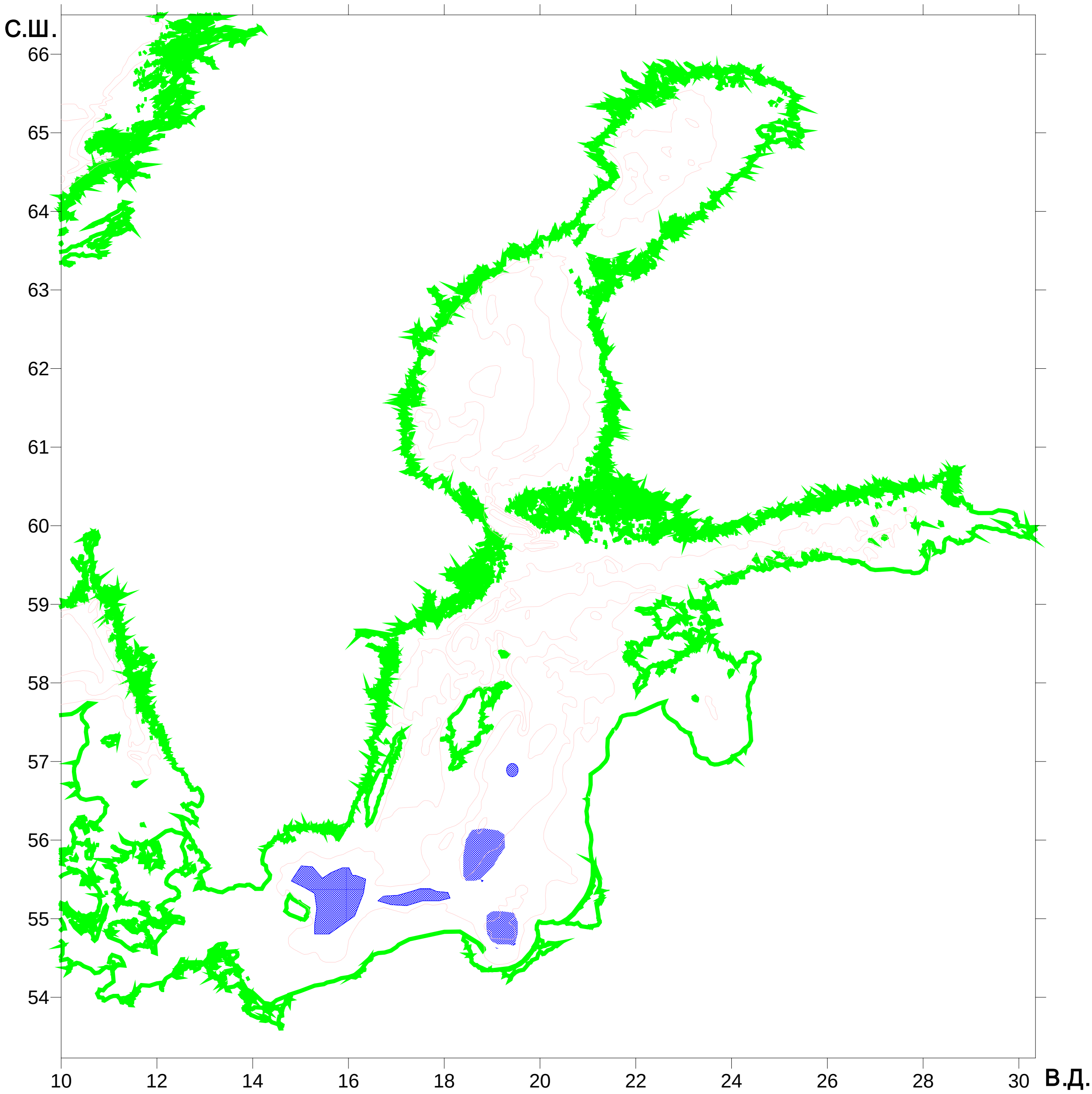


Fig 7. Spawning grounds of eastern Baltic cod in the period of the minimum spatial expansion in 90s (according to CORE, 1998).

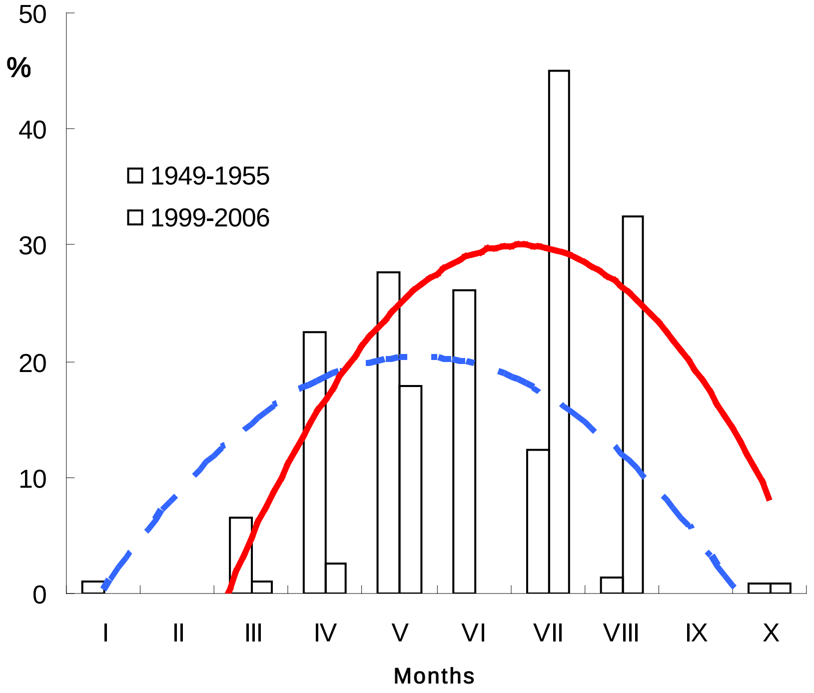


Fig.8. The seasonal dynamics of cod egg abundance (%) in the Gdansk Deep of the Baltic Sea in 1949-1955 and 1999-2006.

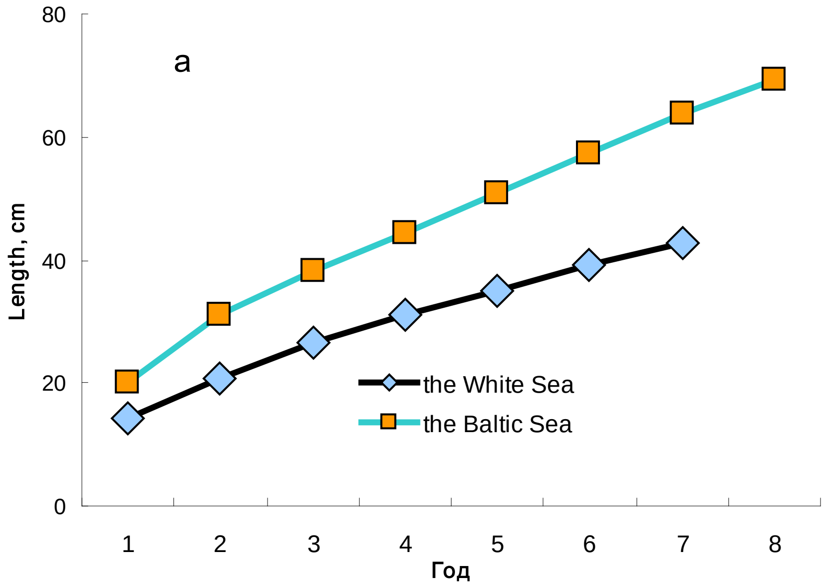


Fig.9. The mean length at age of the White Sea cod and the eastern Baltic cod.

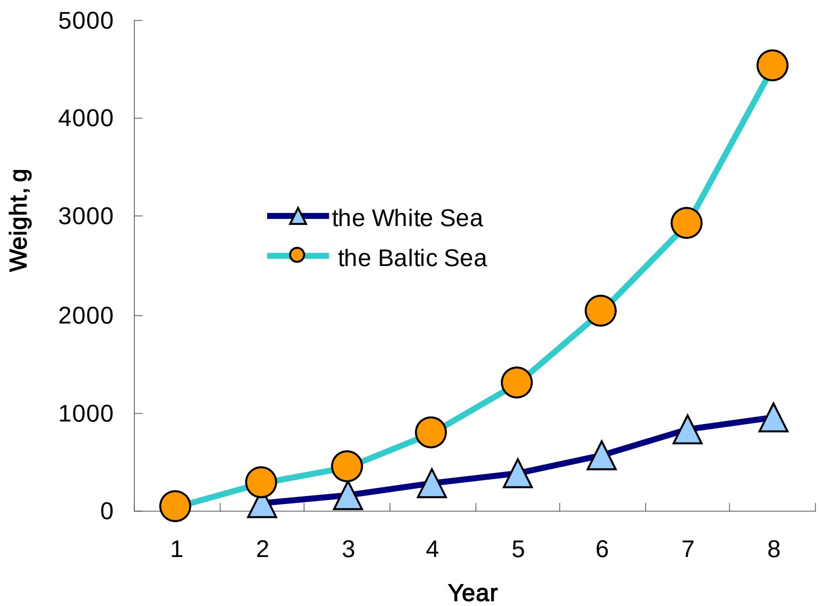


Fig.10. The mean weight at age of the White Sea cod and the eastern Baltic cod

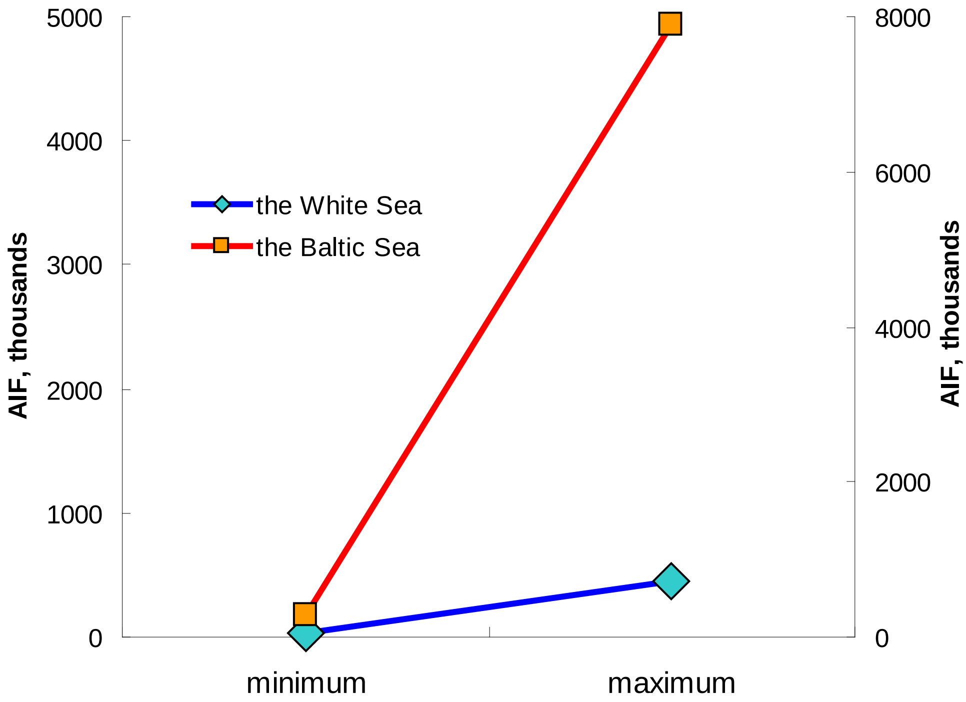


Fig.11. Absolute individual fecundity (AIF, thousands) of the White Sea cod and the eastern Baltic cod

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