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The Egg Abundance of Eastern Baltic Cod *Gadus morhua callarias* (Gadidae) in the 20th Century as a Population Status Indicator

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Abstract—Data on the egg abundance of cod *Gadus morhua callarias* in the ichthyoplankton of deepwater basins of the Baltic Sea in 1903–2000 are presented. The maxima of the total cod egg abundance that were observed in 1947–1956 and 1976–1981 are associated with the activation of cod reproduction in the northeastern areas of the sea and coincide with the period of growth in the salinity of the near-bottom water layer. The cod reproduction is characterized by alternating periods of expansion of spawning ground area (owing to the Gotland Basin in the northeast) and its decrease, with the maintenance of the annual reproduction only in the Bornholm Basin (the southwest of the sea). It is assumed that the dynamics of the egg abundance in the periods of mass cod spawning in northeastern areas was opposite in the Gotland and Bornholm basins.

Keywords: eastern Baltic cod *Gadus morhua callarias*, egg abundance, spawning ground fluctuations

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The Baltic Sea is only connected with the World Ocean by the narrow Danish Straits. As a result of sporadic North Sea water inflows, a relatively high salinity is recorded only in the deepwater basins of the sea. The reproduction of eastern Baltic cod *Gadus morhua callarias* in these basins is a unique example of adaptation to low-salinity conditions in combination with unstable oxygen saturation of near-bottom waters. Ichthyoplankton studies in the Baltic Sea were initiated by German scientists as early as the beginning of the 20th century (Strodtmann, 1906; Apstein, 1911). The generalization of the data on the cod egg abundance in the ichthyoplankton that have been accumulated over 100 years allows us to analyze the relationship between its long-term variability and some of the limiting environmental factors.

MATERIALS AND METHODS

Data on the cod egg abundance at the main spawning grounds of the Baltic Sea (Bornholm, Gdansk, and Gotland deepwater basins) (Fig. 1) were obtained from the AtlantNIRO database and publications that contain primary ichthyoplankton survey materials and estimates of the average abundance by Soviet, German, Latvian, Polish, Danish, and Swedish researchers (Strodtmann, 1906, 1918; Apstein, 1911; Heinen, 1912; Mielck, 1926; Poulsen, 1931; Mielck and Künne, 1935; Kändler, 1944, 1949; Mankowski, 1948, 1950, 1951a, 1951b, 1954, 1955, 1959, 1972; Kazanova, 1952; Grauman, 1958, 1966, 1970, 1971, 1980, 1984; Siudzinski, 1965; Lindblom, 1973; Krenkel, 1981; Müller and Bagge, 1984; Makarchouk, 1996; Karasiova and Voss, 2004). Long-term sets of data on the abundance of cod eggs and larvae in the Bornholm Basin (since 1954) and in the eastern areas of the sea (since 1970) according to the data of German (Kiel Institute for Marine Sciences) and Soviet (AtlantNIRO and BaltNIRKH (Baltic Research Institute of Fisheries)) ichthyoplankton surveys were taken from the report on the International CORE Project (1998).

The number of stations that were carried out in the deepwater part of the sea gradually increased from 230 in 1903–1938 to approximately 5000 in 1986–2000. Ichthyoplankton sampling gears included a 67-cm diameter Hensen net with a mouth opening area of 0.35 m^2 (Germany, Denmark, and Poland), an IKS-80 net (80 cm and 0.5 m^2, respectively) (Soviet Union, Russia, and Latvia), a ring net (100 cm and 0.78 m^2) (Sweden), and a WP-2 net (28 cm and 0.25 m^2) (Germany). Eggs were collected based on vertical hauls in the bottom-surface layer; eggs were also collected since the 1970s on the basis of oblique tows using a Bongo-60 net equipped with a flow counter (Müller and Bagge, 1984; CORE, 1998). According to comparative studies, Hensen, IKS-80, and Bongo-60 nets have a similar catch efficiency for fish pelagic eggs in the Baltic Sea (Oeberst et al., 1981; Wieland and Makarchouk, 1997).

Since the number of samples that were collected in the first half of the 20th century (up to 1970) was relatively low, the values of the maximum egg abundance

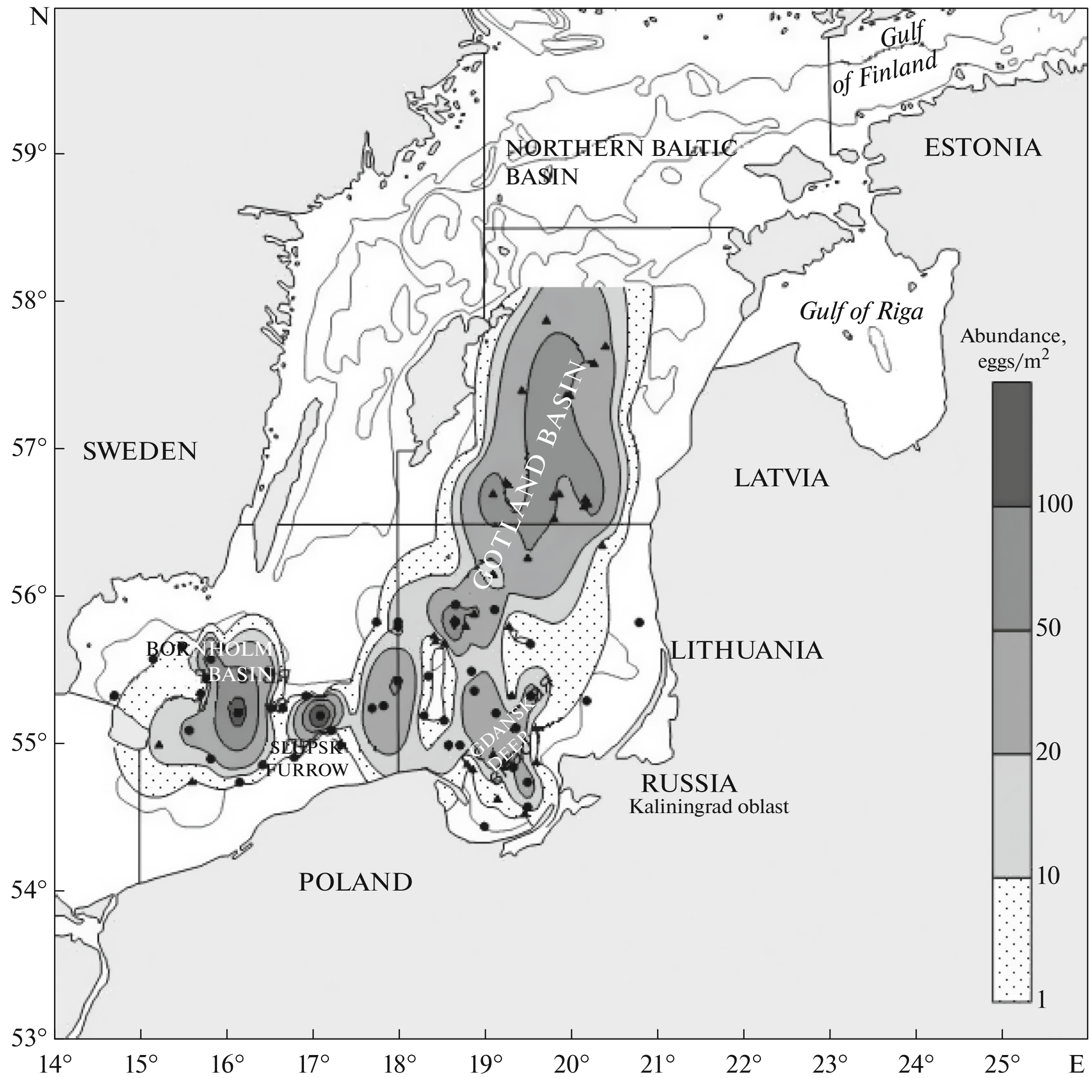

Fig. 1. Baltic Sea map and the distribution of eggs of cod *Gadus morhua callarias* in 1956. According to the data of (▲) AtlantNIRO (Soviet Union) and (●) the Institute of Marine Fisheries (MIR, Poland).

of cod in the spawning area over the reproduction season (eggs/m^2) were also analyzed along with the average abundance. The ratio between the values of the average (N) and maximum (N_{max}) egg abundance that was calculated according to the data for the 1960s to 1970s is described by the following equation: $N = 21.039 \ln N_{max} - 69.409$ (Fig. 2). This correlation was used in three cases, each including a single catch that was carried out during the spawning season showing a high egg abundance: in the Gdansk Deep in 1925 and 1926 and in the central part of the Gotland area in May 1949. The total abundance of eggs was calculated taking into account the area of their distribution ($N \times S$, $\times 10^{10}$ eggs). The total cod larva abundance and the ratio of the larval abundance to the egg abundance (%) were calculated for 1976–1981.

The average egg abundance was estimated taking into account the seasonal dynamics of the cod egg occurrence: the mean value was calculated for April to July in the years until 1990, i.e., before the regime shift period, and for May to August in the 1990s. For the late 1950s to the mid-1960s (when there were no records of cod in the central part of the Gotland Basin due to the cod leaving from this area), the missing values were reconstructed by the ratio of the cod egg abundance in the southern and central parts of the basin. The proportion of the reconstructed values in the total volume of the data used does not exceed a few per cent. When there were several sources of information, the data were combined with respect to the years and study areas. A map of cod egg distribution in different sea areas in 1956 according to the data of the AtlantNIRO and Polish Institute of Marine Fisheries is given as an example of this combination (Fig. 1).

As a rule, the average cod egg abundance was calculated for the depths of over 60 m (Bornholm Basin) and over 80 m (Gdansk Deep and Gotland Basin) according to the CORE method (1998). In the first half of the 20th century, sampling was not annual and did not always cover the same years in different areas; in addition, it was interrupted by two world wars. Therefore, during the analysis of the century-long dynamics due to the fluctuations of near-bottom salinity, the data on the total egg abundance were combined by the time intervals with the highest sample frequency (1938 and 1952–1955) and by 5-year intervals since the 1950s. The salinity of the near-bottom water layer was characterized using literature sources (Soskin, 1963; Zezera, 2009) and the AtlantNIRO electronic database.

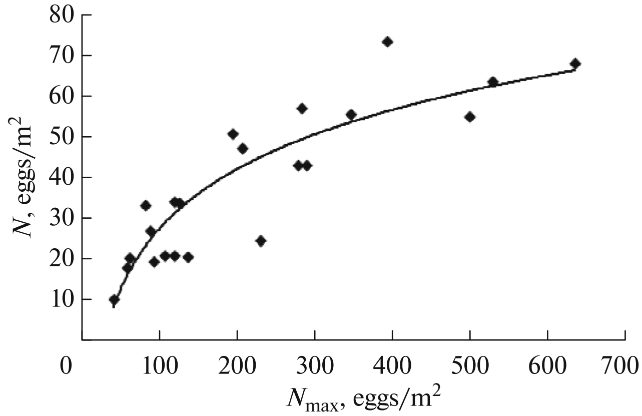

Fig. 2. Logarithmic regression between the maximum (N_{max}) and average (N) egg abundance of cod *Gadus morhua callarias* in the 1960s–1970s: $N = 21.039 \ln N_{max}$, 69.409, $R^2 = 0.7872$.

RESULTS

Long-term sets of data on maximum cod egg abundance (1903–1970) evidence a significant changeability of these parameters (Fig. 3). In the first half of the 20th century, two small peaks of N_{max} values can be distinguished in the Bornholm Basin and Gdansk Deep using Poulsen (1931) and Kändler (1944) data; these peaks covered the early 1920s and late 1930s. Whereas the maximum egg abundance in the Bornholm Basin did not exceed 15–18 eggs/m^2 in 1903–1905, it was 168 and 344 eggs/m^2 in 1923 and 1938, respectively (Fig. 3a). In the Gdansk area, high N_{max} values were recorded for 1925 and 1938: 74 and 68 vs. 12 eggs/m^2 in 1903–1909, respectively (Fig. 3b). According to highly limited data on the Gotland Basin, the maximum cod egg concentrations were at the level of 15 and 21 eggs/m^2 in 1925 and 1931. The cod egg abundance reached the century-long maximum in all areas under consideration in the late 1940s to the early 1950s. The highest N_{max} values were recorded in 1952 for the Bornholm Basin (1078 eggs/m^2), in 1949 for the Gdansk Deep and central part of the Gotland Basin (600 and 348 eggs/m^2, respectively), and in 1951 for the southern part of the Gotland Basin (275 eggs/m^2).

Estimates of the average cod egg abundance show a similar time dynamics (Fig. 4). From 1903 to 1970, the peaks of the maximum and average abundance in the Bornholm and Gdansk areas and southern part of the Gotland Basin were observed in the same years (1952, 1949, and 1951); the N values in these years were 151.4, 106.0, and 56.3 eggs/m^2, respectively (Figs. 4a–4c), while the average abundance peak (53.3 eggs/m^2) was recorded at a later time in the central part of the Gotland Basin, namely, in 1954. The coefficients of correlation between N_{max} and N estimates in the Bornholm, Gdansk, and Gotland areas were 0.784, 0.823, and 0.861, respectively, in 1903–1970 ($p < 0.01$).

The years of 1949–1954 became the period of the century-long maximum of the cod egg abundance in all main reproduction areas in the Baltic Sea (Fig. 5). This was followed by a decrease in the number of spawned eggs in the late 1950s to early 1960s, which was particularly noticeable in eastern areas. The new growth began in the late 1960s and rapidly changed to some decline in 1971–1975. The second, rather long-term period of high cod egg abundance was observed in the mid-1970s to the early 1980s. It was highly pronounced in the Gotland Basin, rather poorly pronounced in the Bornholm area, and not observed in the Gdansk Deep. It should be noted that the periods of growth in the cod egg abundance in the Baltic usually started from the Bornholm area. This was observed according to the data for 1964 to the 1970s. From 1985, the abundance of cod eggs began to sharply decrease in all sea areas, followed by their almost complete disappearance in the Gotland Basin. In the 1990s, the growth in the egg abundance was rarely recorded only in the Bornholm Basin, which has become the main reproduction area for the population in the current period.

The highest total cod egg abundance was recorded in 1953–1955: 257.55×10^{10} eggs. The following peaks did not reach the value of the first peak: in particular, this parameter was 1.4 times lower in 1976–1980 (185.52×10^{10} eggs). The dynamics of the total cod egg abundance ($N \times S$) is very similar to fluctuations in the egg abundance at the Gotland spawning ground (r = 0.744, $p < 0.01$) (Fig. 6a). In the pre-war period, the contribution of the Gotland Basin as a spawning ground varied from 11 to 18%; from the 1950s to the mid-1980s, its contribution to the cod reproduction increased markedly (up to 25–49%); however, it was only 3–7% in the late 1980s and 1990s. In addition, the general dynamics of the total cod egg abundance is consistent with the variability in the near-bottom

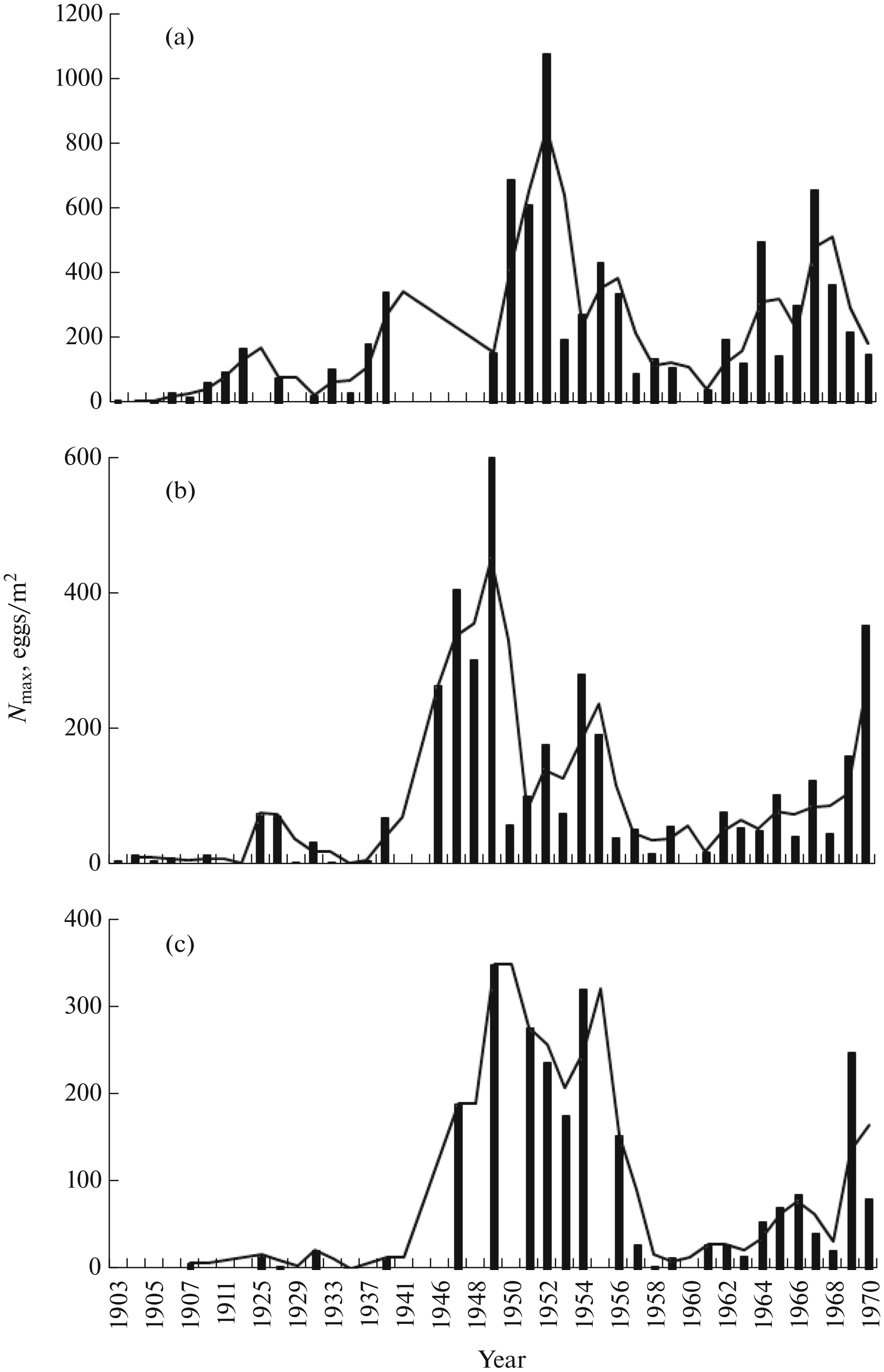

Fig. 3. Maximum egg abundance (N_{max}) of cod *Gadus morhua callarias* in the (a) Bornholm Basin, (b) Gdansk Deep, and (c) Gotland Basin in 1903–1970: (■) actual data, (—) trend lines.

salinity in the Gotland Basin (Fig. 6b). The century-long maximum of near-bottom salinity that was recorded at the beginning of the 1950s coincided with the century-long peak abundance of cod eggs in the Baltic Sea.

One should note an inverse correlation ($r = -0.75$) in the egg dynamics of the Gotland area vs. Bornholm Basin during the period of intensification of cod reproduction in this area (1976–1981), resulting in the emergence of high-yield cod generations (ICES, 2014) (Fig. 7a). In this period, the egg abundance of cod in the center of the Gotland Basin increased only the next year after the abundance growth in the Bornholm area. In contrast, when the number of eggs signifi-

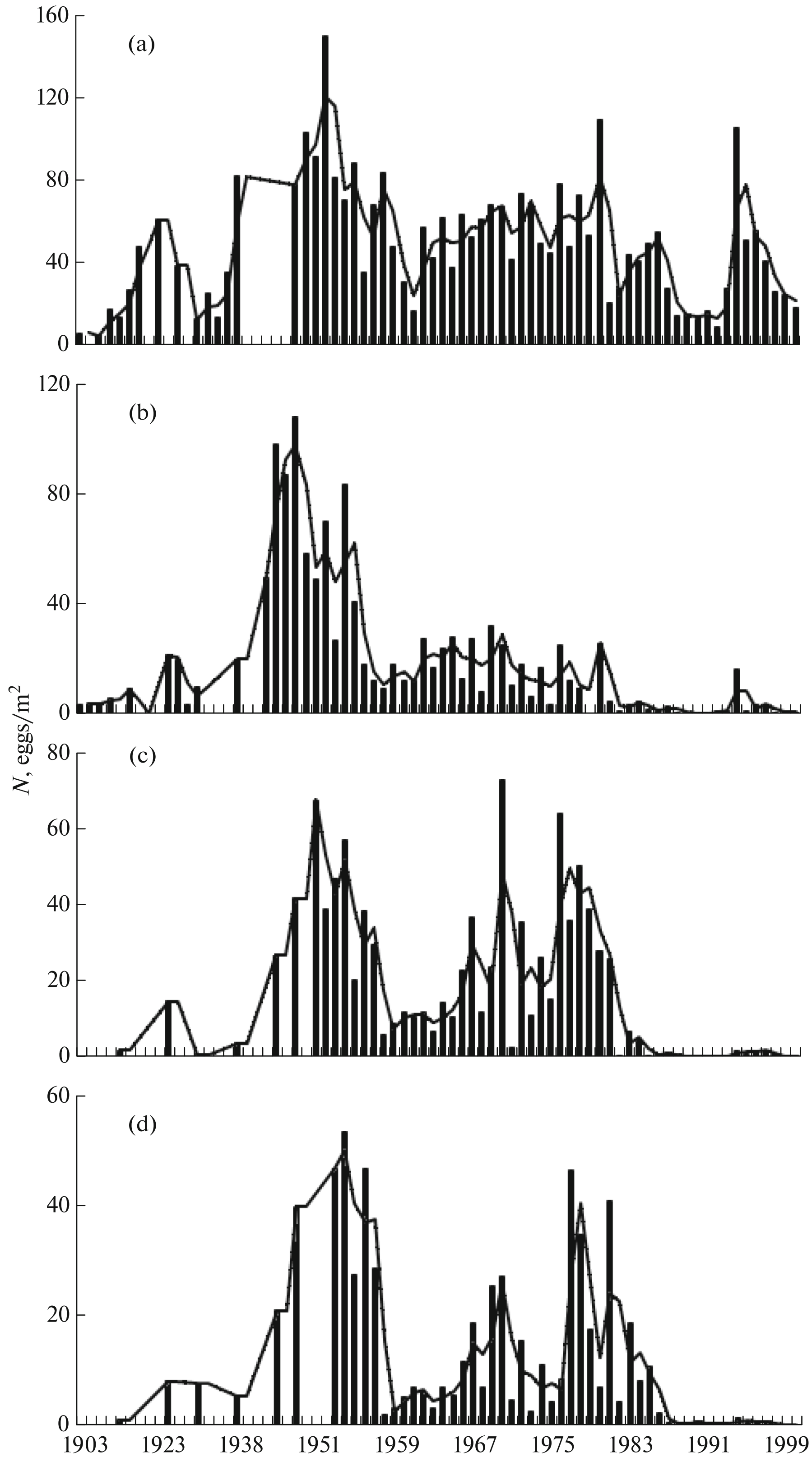

Fig. 4. Average egg abundance (N) of cod *Gadus morhua callarias* in the (a) Bornholm Basin, (b) Gdansk Deep, and (c) southern and (d) central parts of the Gotland Basin in 1903–2000; see the notations in Fig. 3.

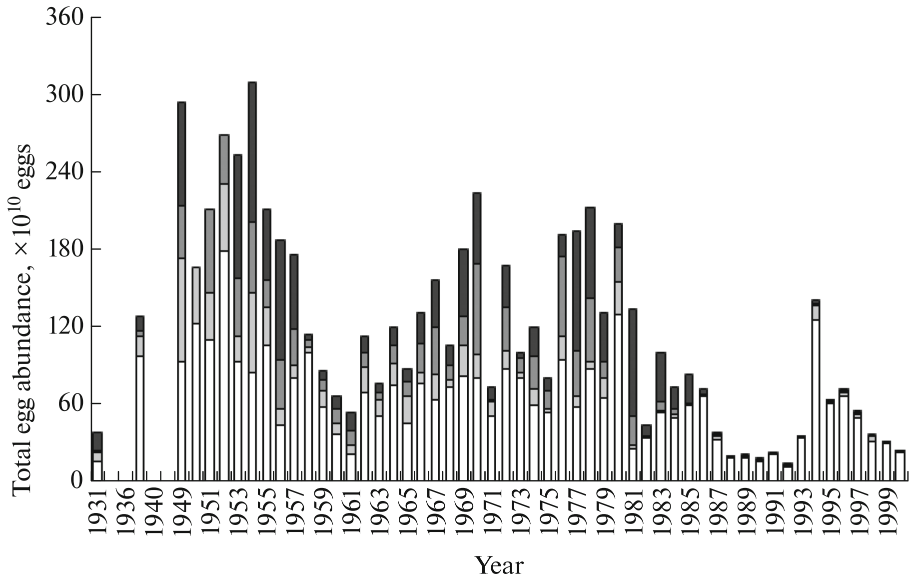

Fig. 5. Total egg abundance of cod *Gadus morhua callarias* in the deepwater basins of the Baltic Sea in 1931–2000: (□) Bornholm Basin, (■) Gdansk Deep, (■) southern part of the Gotland (without taking into account the year of 1950), (■) the central part of the Gotland Basin (without taking into account the years of 1950–1952).

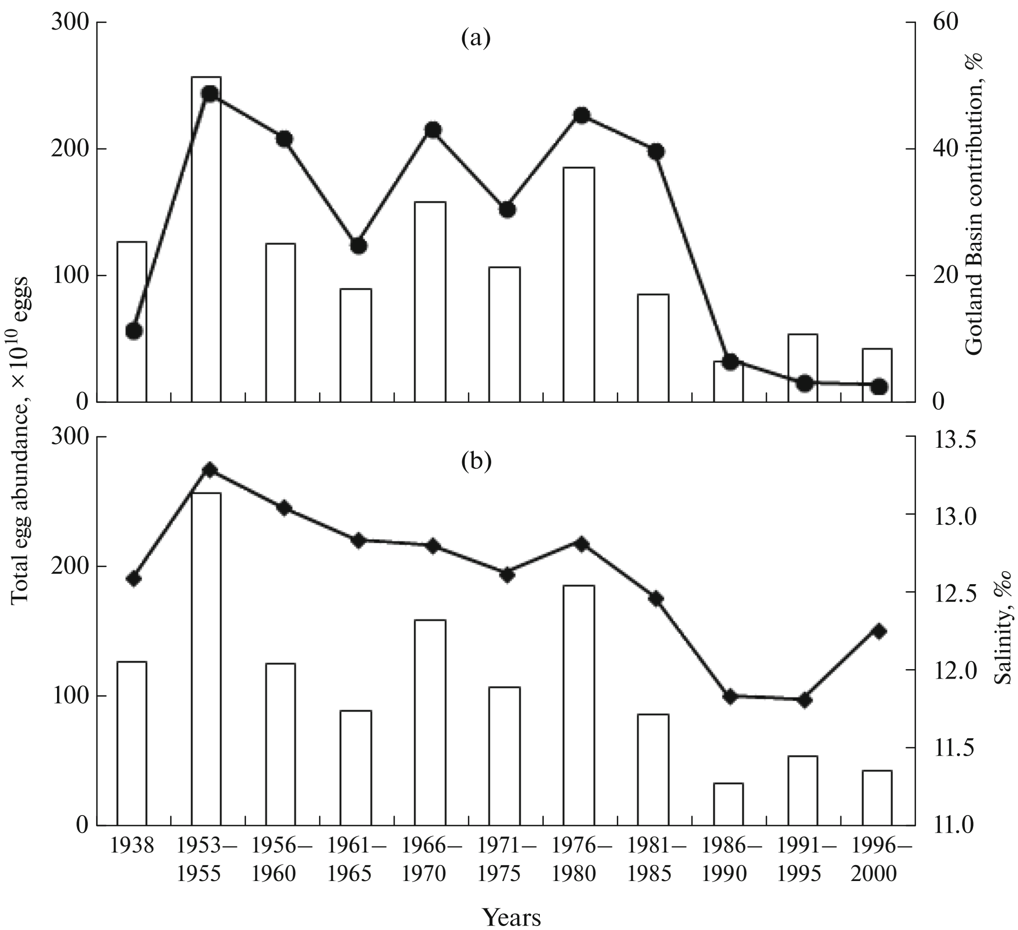

Fig. 6. Total egg abundance (□) of cod *Gadus morhua callarias* in 1938–2000 with respect to: (a) the contribution of the Gotland Basin to this parameter (-●-), (b) the salinity (◆) of the near-bottom water layer in the Gotland Basin.

cantly increased in the Bornholm Basin, their number decreased in the centre of the Gotland area. The same relations were also observed for fluctuations in the total abundance of cod larvae (Fig. 7b) and for the larval and egg abundance ratio (Fig. 7c): the correlation coefficients were negative: –0.69 and –0.79, respectively. The absence of the complete data set for the central part of the Gotland Basin for 1947–1952 makes it difficult to check the absence or presence of this relationship for this whole period of high abundance. However, in 1953–1957, the correlation between the numbers of cod eggs in the Bornholm and central Gotland areas was also negative ($r = -0.426$).

The existence of this correlation might be determined by the features of the spread of Kattegat water inflows in the near-bottom layers of the Baltic Sea (Matthäus, 2006). These water flows initially penetrate into the Bornholm Basin; the water renewal in the Central Gotland Basin and, accordingly, the growth in salinity often takes place only in the following year. Therefore, the coefficient of correlation between the levels of salinity of the near-bottom water layer usually increases in these areas with a 1-year forward shift of the time series for the Gotland Basin vs. the series for the Bornholm Basin (Table 1). The exception was observed only in 1981–1990 when the intensity and frequency of North Sea water inflows sharply decreased. As a result, this was the only decade over the 100-year period when the high correlation between the levels of salinity in these basins was observed with no shift in the data set.

Therefore, the low level of the abundance that was recorded at the beginning and end of the past century coincides with the localization of the main reproduction in the Bornholm Basin and its sharp decrease in the Gotland area. The cod reproduction in the Bornholm area is characterized by the highest stability, while the periods of spawning intensification alternate with the periods of its reduction in the Gotland Basin.

Table 1. Coefficients of correlation between the salinity of the near-bottom water layer in the Bornholm Basin and central part of the Gotland Basin

Years	Without a shift	1-year shift
1904–1910	0.019	0.780*
1029–1939	0.409	0.829**
1947–1960	0.211	0.698**
1961–1970	0.047	0.713*
1971–1980	0.042	0.500
1981–1990	0.716*	0.588
1991–2000	0.218	0.689*
1902–2000	0.369**	0.550**

The correlation between the areas is significant at p: * <0.05, ** <0.01.

DISCUSSION

The results of ichthyoplankton studies in the Baltic Sea made it possible to draw the first generalized conclusions on the dynamics of the cod egg abundance as early as the late 1940s to early 1950s (Kändler, 1944, 1949; Mankowski, 1951). Kändler (1949) provided the mean values of the egg abundance by months and combined them with respect to time intervals (1903–1911, 1926–1935, 1937–1938, and 1946–1947) with the indication of maximum values. Mankowski (1951) published a report that contained the primary information by month for 1903–1949 with some inaccurate data for the first years of the 20th century. Both publications indicate a significant growth in the cod egg abundance, which initially began in the late 1930s in the Bornholm Basin and then (in the 1940s) also covered the eastern basins (Gdansk and Gotland areas).

Kändler (1949) believed that the cod egg abundance in the Baltic Sea increased by 5–10 times over the first half of the 20th century, which was due to a significant growth in the stock of this species. While recognizing the Bornholm Basin to be the most important area for the reproduction of Baltic cod, he considered a sharp increase in the egg abundance in the Gdansk Deep in 1947 compared to the beginning of the century (400 vs. 12 eggs/m^2) as an unusual phenomenon, which he explained by an increase in salinity in the near-bottom sea layers. The same opinion was shared by Mankowski (1951), whose findings were based on the increase in the maximum egg concentrations in all deepwater areas; he believed that these changes were also caused by an increase in salinity, which began in the late 1930s.

The dynamics of the abundance of cod eggs and larvae in the 1970s to 1990s has been studied most thoroughly. Our estimates of the total egg abundance in the Bornholm area during this period coincide with the previously published data, while they are 1.17 and 1.38 times lower for the whole Gotland Basin and for its central part, respectively (Köster et al., 2001, 2009). These differences are presumably determined by the difference in the estimate of the size of this area, which depends on the range of selected depths. The cod egg abundance in the Gotland Basin can be calculated for depths of over 80 m (CORE, 1998) or over 60 m (Köster et al., 2003). However, as in previously published data (Köster et al., 2001), one can also observe a negative relationship between the cod egg abundance and cod larval abundance in the Bornholm Basin and central part of the Gotland Basin in 1976–1981, despite the above-mentioned differences. The increase in the ratio between the abundance at early larval and egg stages indicates a high survival of larvae in the spawning season (Köster et al., 2017).

Fluctuations in the egg abundance of Baltic cod are determined both by the climate driven variability in the abiotic environment and by trophic interactions

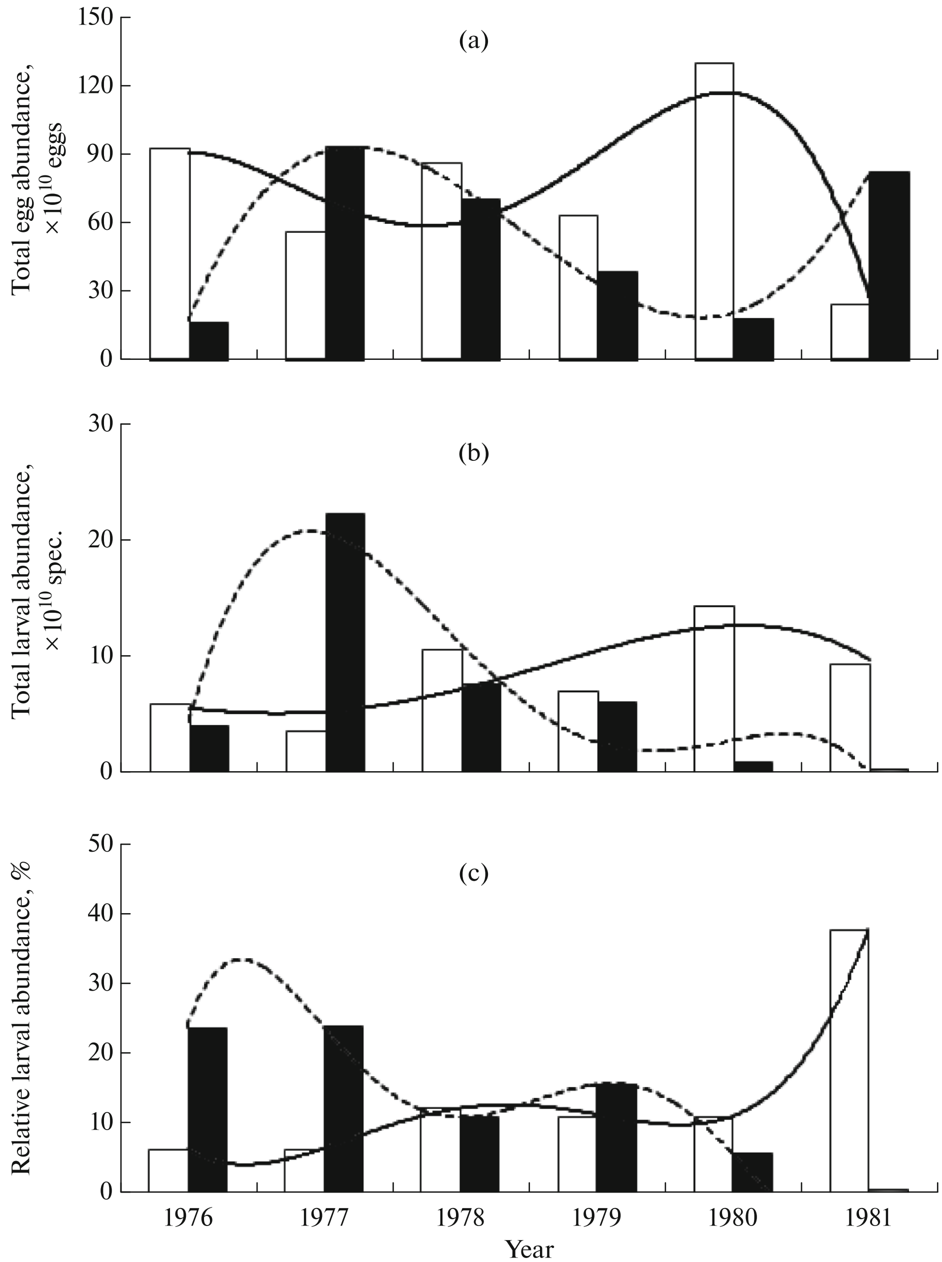

Fig. 7. Total abundance of (a) eggs and (b) larvae and (c) relative abundance of larvae of cod *Gadus morhua callarias* in the Bornholm Basin and central part of the Gotland Basin in 1976–1981; (□) and (■) actual data, (—) and (- -) polynomial trends.

(Köster et al., 2005). Taking into account the limited area of spawning grounds and, accordingly, the limited reproductive resource in the Baltic Sea, the success of cod reproduction in this area is significantly determined by abiotic conditions (Hinrichsen et al., 2011). The most important of them are salinity (not less than 11 psu) and oxygen content (not less than 2 ml/L), which eventually determine the so-called reproductive volume of waters that are suitable for cod spawning (CORE, 1998). The emergence of such conditions primarily depends on saline and oxygen-saturated advections from the North Sea. The term of advections (or water inflows) usually implies water masses that are formed below the halocline and (in the course of their movement) that gradually renew waters in the chain of deepwater basins separated by shallow-water thresholds. This near-bottom circulation, which is limited by the deepwater layers of the western part of the Gotland Basin, can be called a Baltic saline conveyor (Döös et al., 2004). Nonsimultaneous inflows to the Bornholm Basin and central part of the Gotland Basin determine the possibility of the inverse relationship between cod numbers in these areas during the periods of an increased intensity of inflows.

The positive influence of intense water inflows on cod reproduction in the Gotland area is most clearly observed in the case of the penetration of two successive inflows (a water inflow cluster according to Matthäus terminology) (Matthäus, 2006). In these cases, a continuous spawning cod biotope is formed in the vast water area; in the Gotland Basin, this biotope covers the layer at depths from 80 to 120–130 m (Karaseva and Zezera, 2016). This leads to the emergence of a migration pathway that allows cod to migrate from southwestern to northeastern areas. This resulted in the mass emergence of spawning cod in the central part of the Gotland Basin as well as in its presence in areas further north, up to 59° N. In years with high cod egg abundance (1947–1956 and 1976–1981), the heterogeneity of environmental conditions at different spawning grounds in the Gotland area compensated the reproduction failure in one area by successful reproduction in another.

The expansion of mature cod to northeastern areas allowed it not only significantly to expand the areas of its spawning grounds but also to assimilate the food resources of these areas. It can be assumed that it is the lack of food supply in the first quarter of the 20th century that hindered the growth in the cod abundance in the central part of the sea even under favorable abiotic conditions. However, the periods of cod expansion were short in the generally unstable Baltic environment. The long-term absence of North Sea inflows led to the leaving of spawning cod from northeastern areas, and these grounds lost their significance in its reproduction. The longest contemporary period of water inflow reduction is widely considered as the result of the regime shift that occurred in the late 1980s (Alheit et al., 2005). Presumably, when environmental changes go beyond the adaptive capacities of the system, the alteration in the level of its stabilization becomes biologically advantageous (Shilov, 2002). In the current period, the population of eastern Baltic cod has developed into a new, relatively stable state, which is characterized by a significantly lower abundance and the shift of the reproductive part of the range to the southwestern part of the central Baltic.

If the stock increases on the basis of involving new areas that are free of fishery, this growth does not lead to an adequate increase in the yield. The first peak of egg abundance (1947–1956) was recorded in the period of weak fishing intensity in the central part of the Gotland Basin. During this period, some coastal states (Sweden and Finland) practiced cod hook-and-line fishery in vast areas with heavy grounds, where ships should be equipped with echo sounders and trawls with bobbins for cod catching (Karaseva, 2013). The specific feature of Soviet fishery in the Gotland area in the late 1940s until the mid-1950s was that the immature part of the population in the coastal zone was more severely exposed to the fishing pressure than spawning cod in deepwater areas (Dement'eva et al., 1957). The Soviet cod fishery fleet was modernized only in the late 1950s (Lablaika et al., 1991) when cod began to leave the Gotland Basin.

During the second peak of the egg abundance (the second half of the 1970s–early 1980s), the cod fishing intensity was generally significantly higher due to the cod distribution throughout the water area of the sea. Cod forms the densest concentrations during the prespawning period; therefore, a significant portion of the fish stock in the 1970s–1980s was caught before fish spawning. Apparently, the higher degree of the fishing impact on the spawning stock in the 1970s–1980s than in the 1940s–1950s was one of the causes of the lower cod egg abundance in this period. The second cause might be related to mass skipped spawning. In 1979–1985, this phenomenon was recorded for cod in the Gotland area (Uzars et al., 1989; Karaseva, 2016). The skipped spawning caused by oocyte resorption is an adaptive response of the reproductive capacity of the population to changes in the environmental conditions (Shatunovskii and Ruban, 2010). In Baltic cod, it was caused by the deterioration of spawning conditions and a reduction in food supply. Whereas in the past overfishing or unfavorable reproduction conditions in one of the spawning areas might be compensated by the successful survival of progeny at another spawning ground, the current cod population has become more dependent both on environmental conditions and on the fishing pressure in the reduced range.

Therefore, the population functioned in two different regimes during the 20th century. The first of them was characterized by adaptation to several spawning grounds, which provided the flexible use of the reproductive resource, resulting in a high population abundance. The feature of the second regime was that the reproductive part of the range decreased to one annually used spawning area, leading to a decrease in the abundance. The population control strategy should be aimed at preserving the biotopes and spawning part of the population (Pavlov, 2010). Cod biotope conditions in the Gotland area generally depend on the frequency and intensity of North Sea water inflows as well as on the degree of anthropogenic eutrophication (Elmgren, 1989). The timely reduction of the intensity of catches of spawning cod might have mitigated the consequences of the collapse in the early 1990s.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. This article does not contain any studies involving animals performed by any of the authors.

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