Spatial distribution of cod in the Baltic Sea in relation to abiotic factors - a question of fish-age and area.

J. Hjelm, J. Simonsson and M. Cardinale

Abstract

The eastern Baltic cod (*Gadus morhua*) is the main piscivore in the Baltic Sea. Unfortionatly, it has decreased during the last two decades. The decrease is thought to be due to a combination of high fishing pressure and possibly suboptimal environmental conditions. One specific problem in the Baltic Sea is that inflows from the North Sea determine the water turnover and oxygen and saline concentrations, but also the yearly nutrient loading. During the last 15 years only two major inflows have occurred and as a consequence, areas with hypoxic and anoxic conditions have commonly occurred.

In this study, we investigate the distribution of 1-, 3- and 5-year old cod in relation to oxygen, salinity, and temperature between 1988 and 2004 (first quarter) in subdivisions 25-28 in the Baltic Sea. We explored the spatial distribution of cod analytically but also graphically. The highest abundance of cod of all ages during all years was found in Subdivision 25, independently of oxygen and total biomass of cod (based on XSA estimates). At a smaller spatial scale, within subdivision 25, 3- and 5-year old cod had similar distributions, offshore in deep waters, whereas 1-year old cod occurred at more coastal areas. Within the other three subdivisions explored, no clear patterns could be detected. We found a positive relationship between oxygen concentration, as well as salinity, and the total abundance of cod (all age-classes), independently of total biomass of cod and recruits. An additional exploration confirmed oxygen to be the main factor affecting cod density and distribution. Furthermore, there is a negative correlation between oxygen concentration and a scaled abundance measure of 3- and 5-year old cod indicating that oxygen affects the survey abundance index used in cod assessment. Therefore, an increased awareness of the Baltic cod distributional response to a decreasing abundance and fluctuations of hydrographical conditions may enable an increase accuracy of stock size estimations, which may ensure the future of the Baltic cod and the Baltic cod fishery.

Keywords: Cod; oxygen concentration; distribution

Joakim Hjelm, Jessica Simonsson, and Massimiliano Cardinale: National Board of Fisheries, IMR, PO Box 4,

Lysekil. E-mail: joakim.hjelm@fiskeriverket.se

Introduction

The distribution of fish and other organisms vary due to many factors including prey/predator abundance, overall environmental conditions but also due to migratory behaviour during spawning and feeding (Aro, 1989). By migrating to different areas for reasons such as feeding and reproduction, an individual can optimise its fitness and the exploitation of the surrounding environments as well as minimising the negative impacts of a fluctuating environment (Aro, 1989).

The Baltic Sea is a large stratified estuary, with a two-layer salinity structure, a low-salinity surface layer and a more saline deep layer (Tomkiewicz *et al.*, 1998) and can be considered a highly variable environment due to its hydrographical properties. Irregular inflow of water from the North Sea, which is oxygen rich and highly saline, play an important role in governing the environmental conditions and hydrographical properties of the Baltic Sea. For example, only two major inflows have occurred since the 1990's, at the beginning of 1993 and 2003 (ICES, 2004b), which has had a major impact at many trophic levels in the Baltic ecosystem.

At the top trophic level, the Baltic cod (*Gadus morhua*) (Neuenfeldt and Köster, 2000) has decreased since 1985 (Aro, 2000) and in 1992 a historical low was reached, but the stock size has remained at a low level sins that period (ICES, 2004a). Unsuccessful recruitment in recent years in combination with a high fishing mortality is two factors that can be hypothesised to be responsible for the current state of the cod stock (Wieland *et al.*, 2000). Normally, cod is able to live in the whole Baltic Sea except the Bothnian Bay and the far east of the Gulf of Finland (Aro, 2000), but the main spawning ground for the eastern Baltic cod population is the Bornholm Basin (ICES, 2004b). This is probably related to the fact that adult cod have a preferred range of hydrographical conditions. Tomkiewicz *et al.* (1998) showed that the majority of the cod occurs at oxygen levels between 3.9 and 7.2 $ml \cdot L^{-1}$ and at salinities between 11and 15 psu. It is also known that the cod reproduction success (fertilisation and survival of eggs) is determined by oxygen concentration, salinity and temperature (Nissling and Westin 1991, Nissling et al. 1999), and a small change in these parameters may have a great influence on the success of reproduction (Bleil and Oeberst, 2002). Based on these assumptions, it is generally accepted, but not confirmed, that cod avoid low oxygen areas by migrating horizontally. This will in turn affect the estimation of cod stock size. That is, in years with low oxygen concentration the estimate of cod abundance may be high whereas in years with high oxygen concentration it may be low, given the same real density in different years. Increased knowledge of how the environmental and hydrographical conditions influence the spatial distribution and recruitment of cod has been suggested to improve the accuracy of stock size estimations (Tomkiewicz *et al.*, 1998). Thus, this study try to explore the spatial distribution of Baltic cod within in subdivisions 25 - 28 and comparing those with oxygen, salinity and temperature conditions. Cod abundance data was obtained from the Swedish National Board of Fisheries surveys between 1988 and 2004, first quarter, and hydrographical information during the same time period from the Swedish Meteorological and Hydrographical Institute. The distributions and its relationship to abiotic factors were examined both analytically and graphically.

Material and methods

Cod surveys

Abundance data between 1988 and 2004 from the Swedish National Board of Fisheries trawl surveys, with R/V Argos, in Sub-divisions (SD) 25, 26, 27 and 28 in the Baltic Sea from the first quarter of each year were analysed (Fig. 1). The surveys were completed during an approximately three-week long period during the end of February and the beginning of March every year.

For each year, the catch depth and the haul positions were known. The number of hauls conducted varied from year to year both totally and within each SD, though every year the most number of hauls were carried out in SD 25. The total number of trawls per year within all four SDs varied, from the lowest, 25, in 1988 to 59 in 1999. Consequently, the total number of trawls conducted within each SD during all years differs; 325 trawl hauls in SD 25, 43 trawl hauls in SD 26, 122 trawl hauls, in SD 27 and 142 trawl hauls in SD 28. Moreover, in SD 26 no trawl hauls were conduct in 1988, 2001 and 2002. Therefore, no data from SD 26 was included in the analysis for these years, which will have an effect on the accuracy/precision of the graphical presentation as well on the statistics. Nonetheless, all hauls conducted were used in the analysis in order to increase sample size and statistical power.

The sampling method was the same for all years, with two exceptions. Firstly, in 2000 the trawl, GOV (French herring trawl), was replaced with a TV3 930. These two trawls are considered to have approximately the same catch efficiency, nonetheless calibration between the two trawls have been conducted but not analysed at this date. However, preliminary results suggest that the catch efficiency is similar between the two trawl types. In 1997 and one trawl haul in 1988 a third type of trawl were used (Fotö-trawl) but this trawl has similar catch efficiency as the GOV trawl. Secondly, the way of determining sampling locations has varied between years. In 2000 the sampling became randomised and depth stratified, before that the sampling locations were chosen without any respect to depth, i.e. a “fixed sample design”.

Each haul was conducted at 3 knots speed during 30 minutes and the catch data was converted into one-hour hauls. All caught cod specimens were measured (total length, cm classes). In each length class 10 specimens in each SD, predetermined and independently of catch size, were sampled for age analysis, which may result in that for some hauls none of the specimens had been aged. To make the data set complete, the specimens that had not been aged were allocated to an age class using years and SD specific ALK (Age Length Key).

Hydrographical surveys

Hydrographical information was obtained from the Swedish Meteorological and Hydrographical Institute (SMHI) for the same time periods, month and year, as the cod survey in the study. The main part of the data used in the analysis was sampled during the time of the trawling surveys at every trawl station, either before or after the haul. However, at some stations there were no record of oxygen ($ml \cdot L^{-1}$), temperature (^{o}C) and salinity (psu) (either one, two or all of them) at the bottom. To achieve a better resolution of the hydrographical situation at the bottom additional data from the same time periods as the surveys were included. In the first years (1988-1991) of this study there were very few locations where oxygen concentration had been measured at the bottom. Thus, for every haul station we allocated to the nearest measurement of the hydrographical conditions. This meant that some trawls were allocated the same measurements.

Statistical analyses

To explore which of the hydrographical factors (i.e. oxygen, temperature and salinity) explained the most of the variation in cod abundance, a backward and forward stepwise multiple regression analysis was conducted, with a $F_{0.1}$ threshold, for each age class separately and for all the population. To describe the distributional pattern of cod without the effect of variation in oxygen concentration, an ANCOVA with oxygen as covariate and year and SD as random factors, was used for each age class separately and for all the ages combined. For this analysis, the abundances of 3-and 5-year old cod each year were scaled to the total abundance of cod in the east Baltic. Abundance of cod in eastern Baltic is VPA (Virtual Population Analysis) model based and are the official estimates of ICES (ICES 2004a). The numbers of age 1 individuals were not available, and therefore they were estimated using a logistic equation (Hilborn and Walters 1992). The logistic equation is defined as:

$$N_t = N_{t+1} \cdot \exp^{(-F+M)}$$

where N_t is the number of individuals at age t, N_{t+1} is the number of individuals at age $t+1$, F is the fishing mortality and M is the natural mortality. M was assumed 0.2 for all stocks (as within ICES and NAFO assessment framework). A similar correlation analysis was also used to explore the relationship between the oxygen concentration and the density of each age-class. All statistical analyses were performed using SPSS, S-plus and Statistica.

The relationship between oxygen concentration and abundance was also graphically investigated with two different techniques. A non-linear geo-statistical method that generates an interpolated grid, kriging, was used to produce maps of the bottom's oxygen concentration (Surfer 8.0). The kriging method might predict areas with negative values; such areas were treated as areas with 0 ml L^{-1} oxygen. On top of the oxygen estimates the square root of the scaled cod abundance from every trawl station were illustrated with relatively sized bubbles. Hauls with zero catch were illustrated with the smallest sized bubble. Secondly, a linear extrapolation method was used to map each year's oxygen measurements and the distribution and density patterns of each age (note; not scaled to SSB and recruits) were overlaid (Ocean Data View) (Schlitzer, 2003).

Results

Abiotic factors

The abiotic factors, oxygen, salinity and temperature were significantly correlated, both within the total area and within each subdivision. Oxygen and salinity were negatively correlated, and temperature and salinity were positively correlated (Table 1).

Cod abundance versus abiotic factors

Overall, there was a positive correlation between oxygen, as well as salinity, and abundance of all ages of cod. However, when this correlation was further explored with a multiple regression analysis it was suggested that oxygen to be the main factor affecting cod abundance, irrespectively of age.

To test which abiotic factors had an effect on the cod abundance (scaled to SSB) and recruits we used an ANCOVA with oxygen as covariate and year and SD as factors. When all ages were combined the results showed that oxygen had a significant affect on the abundance of cod and that the interaction between year and SD was significant (Table 2). The interaction suggests that the abundance within each SD was affected differently by the variation in total abundance over time. The greatest total abundance of cod, when scaled to oxygen, occurred during all years in SD 25. This was also found when investigating each age separately. The abundance of 1-year old cod has been relatively stable independently of the variation in total abundance of cod and oxygen, while the abundance of 3- and 5-year old cod have decreased over time. The analysis of each age separately suggested that SD and oxygen (Table 3) affected the abundance of 1-year old cod whereas the abundance 3-year old cod was affected by oxygen interaction between year and SD were significant (Table 4). Oxygen, SD and year had all an affect on the abundance of 5-year old cod (Table 5).

We also explored if there is a relationship between oxygen during the year of recruitment and the abundance of 1-year old cod the following year and we found a positive relationship between the number of recruits, scaled to previous year's SSB, and the previous year oxygen concentration (Fig. 2). It was also found that with increasing oxygen concentration the catch-rate of 3- and 5-year old cod decreased, while the catch rate 1-year olds were unaffected by oxygen concentration (Fig. 3).

Maps

Two general patterns were obvious when visually exploring the relationship between oxygen concentration and cod abundance, both for scaled and non-scaled abundance; the abundance of each age-classes peaked in areas with high oxygen concentration (relative to that specific years situation) and cod was often absent in areas with oxygen concentration less than 2 ml·L^{-1}. Secondly was that the abundance of any aged cod was highest in SD 25, when scaled to total biomass and irrespectively to oxygen concentration. Although all years were explored graphically, we only present two other examples to highlight some observed patterns. Example 1: In 1992 and 1993 the abundance of cod was comparable but these years differ drastically in oxygen concentration. In 1992 oxygen concentration was low in most of the area (almost one third of the area had an oxygen concentration of 2 ml·L^{-1} or less), whereas 1993 no area with oxygen concentration of 2 ml·L^{-1} or less. In 1993 1- and 3-year old cod were distributed further north and east, and 5-year old cod distribution had shifted further east compared to the 1992 distribution (Fig. 4, 5 and 6). A similar pattern between these two years distributions was found when the abundances were scaled to the total abundance. Though it should be noted that, there were few years and age-classes deviating from the shown pattern between abundance and oxygen concentration, e.g. 1999. Example 2: The graphical presentations further indicate that the distribution-area is linked to the oxygen situation at the time regardless of the stock size. A comparison between a year with both a large stock and high oxygen concentration, for example 1995, and a year with a small stock and high oxygen concentration, e. g. 2003, showed this relationship. For 3- and 5- year old it can be seen that the occupied area were greater in 2003, despite the smaller stock size. The distribution area of 1-year old was of similar size. A visual comparison of the different ages abundance (both scaled and not scaled to total fish abundance) within subdivision 25 shows that during the major part of this study 1-year old cod had a distribution more closely associated with coastal, shallow waters compared with 3- and 5-year old cod.

Discussion

Oxygen was found to have the greatest effect on the abundance, both scaled and non-scaled, and of all ages of cod (scaled to that years cod population), of the investigated abiotic factors. However, the strong link between salinity and oxygen suggests that salinity may also have an effect on the abundance of cod. The negative correlation found herein has been observed in a previous study of the hydrographical condition in the Baltic Sea (Tomkiewicz *et al.*, 1998). The inflowing water from the North Sea will, due to its higher salinity (and hence density), sink to the bottom where the oxygen is consumed at a high rate by biological processes (ICES, 2004a). Tomkiewicz *et al.* (1998) found that the spatial distribution of spawning Baltic cod that oxygen concentration and salinity are the main hydrographical factors affecting distribution. This study highlights the fact that even before spawning, cod distribution is affected by hydrographical conditions.

Even though the trends in abundance, when scaled to SSB and the number of recruits and without the effect of oxygen, within each Sub-division differs between each other over time, Sub-divisionSD 25 was found to have the highest abundance of all ages every year. This is most likely the result of spawning aggregations seeing that the Bornholm Basin is, at present, the only suitable location for cod to spawn (ICES, 2004a). Though another possible factor, which affect distribution, is the abundance of prey species. Nonetheless, a previous study investigating the cod distribution between 1982 and 1989 concluded that during the first quarter of the year the greatest abundance occurred in SD 26 (Sparholt *et al.,* 1991). However, they used a different approach compared to this study, and did not scale the abundance nor acknowledge the effect of oxygen. (Sparholt *et al.,* 1991). During there study's time period two inflow events occurred (1985 and 1986) and one had occurred prior to the start of the study (1980) (ICES, 2004a). Therefore, it can be assumed that the observed difference in distribution is the result of the oxygen conditions at the time of each study, which in turn supports the fact, that oxygen may shape the distribution of cod.

During the majority of the years included in this study, 1-year old cod abundance peaked at the coastal, shallow waters of Hanö Bay (in Sub-division 25). Settling and survival is crucial to occur in areas with high oxygen concentration, i.e. greater than 2 mL L^{-1}, as they are relatively immobile (Nissling and Westin, 1991, Nissling et al. 1999). This close association to coastal waters is likely the consequence of the immature cod's feeding habits; they are known to feed on benthic organisms. The catch rate of 1-year old cod was found to be unaffected by oxygen concentration, hence they do not disperse further offshore even if the oxygen concentration allows it. The greater part of the mature cod, i.e. 3- and 5-year old, occurred offshore in the deep areas of Sub-division 25. Mature cod is highly mobile and feed upon other fish species, mainly herring and sprat (Rudstam *et al.*, 1994). For these reasons, their distribution is also linked to the distribution of prey species. A corresponding pattern have been identified in past studies, e.g. Sparholt *et al.* (1991) concluded that immature cod have a greater preference for shallower water than mature individuals. This distribution difference between immature and mature cod has also been shown for Atlantic cod (Dalley and Anderson, 1997). Further reasons have been suggested to explain the segregation of immature and mature cod as intraspecific competition and cannibalism (Otterlind, 1985; Aro, 2000). The intensity of cannibalism amongst cod is partly determined by the overlap between mature and immature individuals (Uzars and Plikshs, 2000). In contrast to immature cod, the catch rate of mature cod, i.e. 3- and 5-year old, was found to decrease with increasing oxygen concentration. Consequently, it can be hypothesised that cod disperse over a larger area, hence their density decrease, during favourable oxygen periods. This might indicate that mature cod migrate horizontally to avoid hypoxic bottoms. The maps of the scaled abundance, which shows that areas next to hypoxic areas have a greater abundance than other areas with the same oxygen concentration, further support this hypothesis. Consequently, during periods of low oxygen concentration estimations of the stock size are likely to be overestimated, due to the increased density in areas with better oxygen conditions. Nevertheless, horizontal and vertical migrations are not necessarily mutually exclusive.

Although SSB doubled and halved during the time period included in this study (ICES, 2004a), stock size were not shown to affect the size of the distribution area. Atkinson *et al.* (1997) in contrast, identified a positive relationship between stock size and the occupied area of the northern cod. A more recent study, also looking at the distribution of the Atlantic cod, drew a similar conclusion for cod aged 1-3 years, but found no relationship for 4-year old cod (Anderson and Gregory, 2000). However, in this study a relationship between oxygen concentration and density was shown, an increase in oxygen concentration results in a decreased density and thus a larger area is occupied. This fact indicates that the cod stock density in SD 25 to 28 is determined by oxygen concentration rather than stock size. Despite the significant relationship between oxygen concentration and abundance the spatial distribution of cod in the Baltic Sea is most likely determined by the interaction of several factors including oxygen. This is supported by the deviations (not presented herein) shown from the relationship between cod abundance and oxygen level, as well as other studies. In an experimental study, Claireaux *et al.* (1995) showed that free-swimming mature northern cod do enter water outside the preferred range of hydrographical conditions if food is present. Furthermore, as the oxygen level decreases cod preferred water with lower temperature, possibly a way to reduce the metabolic rate and hence increase their survival chance (Claireaux *et al.*, 1995). Their results do point out that cod has the ability to sense their surrounding environment and choose the most favourable ones.

The positive relationship between the scaled abundance of 1-year old cod and previous year oxygen concentration were expected, as oxygen is the main factor influencing egg and larvae survival (Nissling and Westin 1991). At an oxygen concentration of 4 ml L^{-1} approximately half of the eggs survive (ICES, 2004b). On the other hand, this is accordance with several studies on the influence of spawning volume and recruitment of the Baltic cod (i.e. MacKenzie et al. 2000, Vallin and Nissling 2000, Cardinale and Arrhenius 2000)

In conclusion, oxygen was identified as the abiotic factor with the greatest effect on the spatial distribution of cod regardless of age. However, there were years that did not support this. Consequently, the distribution is more likely determined by a combination of several important factors, both biotic and abiotic. Another important issue that has been addressed is how cod behaves in the presence of anoxic bottoms. There are two options, which not necessarily are mutually exclusive, vertical or horizontal migration. The later was supported by this study, i.e. a higher density will occur in areas surrounding anoxic bottoms. Thus, this phenomenon should be accounted for at assessment of the Baltic cod stock's size. For example and based on the results presented here, an decrease in average oxygen concentration from 2 to 1.5 ml L^{-1}, the relative catch rate is doubled for larger cod. Overall, the results presented here suggest that oxygen concentration may affect the distribution of cod which in turn affects the catch rate of the research vessels and it can be suggested that tuning indices used could be corrected to compensate this bias.

Acknowledgements

We would like to thank and every one of the staff at Institute of Marine Research in Lysekil. We would like to thank the Swedish Meteorological and Hydrographical Institute for providing the hydrographical data.

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Table 1. Outcome of the partial correlation analysis between oxygen, salinity and temperature. SD = Sub division

Control	Variables	Oxygen	Temperature	Salinity
SD	Oxygen	1		
	Temperature	-0.744	1	
	Salinity	-0.674	0.656	1

Table 2. ANCOVA outcome, with oxygen as covariate, of which factors that have an effect on the scaled abundance of the total abundance of cod. SD = Sub division

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Oxygen	1.739	1	1.739	10.824	0.001
SD	7.658	3	2.553	15.887	< 0.001
Year	3.757	15	0.25	1.559	0.078
SD*year	9.622	42	0.229	1.426	0.038
Error	271.062	1687	0.161		
Total	349.021	1749			
Corrected Total	302.771	1749			

Table 3. ANCOVA outcome, with oxygen as covariate, of which factors that have an effect on the scaled abundance of 1-year old cod. SD = Sub division

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Oxygen	0.337	1	0.377	5.829	0.016
SD	1.361	3	0.454	7.017	< 0.001
Year	1.118	15	0.075	1.152	0.306
SD*year	2.585	42	0.062	0.952	0.56
Error	33.684	521	0.065		
Total	44.045	583			
Corrected Total	40.476	582			

Table 4, ANCOVA outcome, with oxygen as covariate, of which factors that have an effect on the scaled abundance of 3-year old cod. SD = Sub division

Source	Type III Sum Of Squares	df	Mean Square	F	Sig.
Oxygen	1.966	1	1.966	7.078	< 0.001
SD	13.116	3	4.372	15.736	0.001
Year	8.984	15	0.599	2.156	0.008
SD*year	28.631	42	0.682	2.454	< 0.001
Error	144.746	521	0.278		0.007
Total	293.977	583			< 0.001
Corrected Total	216.753	582			

Table 5. ANCOVA outcome, with oxygen as covariate, of which factors that have an effect on the scaled abundance of 5-year old cod. SD = Sub division

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Oxygen	0.106	1	0.106	6.426	0.012
SD	0.143	3	0.048	2.872	0.036
Year	0.693	16	0.043	2.612	0.001
SD*year	0.957	45	0.021	1.283	0.107
Error	9.38	566	0.017		
Total	13.145	632			
Corrected Total	11.82	631			

Figure 1. Map of the Baltic Sea showing bottom topography and position of SD 25-28.

Figure 2. The relationship between numbers of recruits and previous year's SSB and oxygen concentration (ml·L^{-1}).

Figure 3. The relationship between scaled average catch rate of each age-class and the scaled average oxygen concentration (ml L^{-1}).

Figure 4. a) The spatial distribution of 1-year old cod scaled to recruits (left) and total abundance (right) related to oxygen concentration (ml L^{-1}) at the bottom 1992 (low oxygen concentration). To enable visual comparison of the distribution of 1-year old cod in 1992 and 1993 (i.e. Fig. 4a and 4b), their abundances have been scaled to the same total abundance. b) The spatial distribution of 1-year old cod in 1993 (high oxygen concentration) scaled to recruits (left) and total abundance (right) related to oxygen concentration (ml L^{-1}) at the bottom.

Figure 5. a) The spatial distribution of 3-year old cod scaled to SSB (left) and total abundance (right) related to oxygen concentration (ml L^{-1}) at the bottom 1992 (low oxygen concentration). To enable visual comparison of the distribution of 3-year old cod in 1992 and 1993 (i.e. Fig. 5a and 5b), their abundances have been scaled to the same total abundance. b) The spatial distribution of 3-year old cod in 1993 (high oxygen concentration) scaled to SSB (left) and total abundance (right) related to oxygen concentration (ml·L^{-1}) at the bottom scaled to recruits (left) and total abundance (right).

Figure 6. a) The spatial distribution of 5-year old cod scaled to SSB (left) and total abundance (right) related to oxygen concentration (ml L^{-1}) at the bottom 1992 (low oxygen

concentration). To enable visual comparison of the distribution of 3-year old cod in 1992 and 1993 (i.e. Fig. 6a and 6b), their abundances have been scaled to the same total abundance. b) The spatial distribution of 5-year old cod in 1993 (high oxygen concentration) scaled to SSB (left) and total abundance (right) related to oxygen concentration (ml·L^{-1}) at the bottom scaled to recruits (left) and total abundance (right).

Figure 7. The spatial distribution of 1-year old cod scaled to recruits (left) and total abundance (right) related to the oxygen concentration (ml L^{-1}) at the bottom 1995 and 2003 (comparable oxygen concentrations but different total abundance). To enable visual comparison of the distribution of cod in 1995 and 2003 (i.e. Fig. 7, 8 and 9), their abundances have been scaled to the same total abundance. b) 1995, b) 2003.

Figure 8. The spatial distribution of 3-year old cod scaled to SSB (left) and total abundance (right) related to the oxygen concentration (ml L^{-1}) at the bottom 1995 and 2003 (comparable oxygen concentrations but different total abundance). To enable visual comparison of the distribution of cod in 1995 and 2003 (i.e. Fig. 7, 8 and 9), their abundances have been scaled to the same total abundance. b) 1995, b) 2003.

Figure 9. The spatial distribution of 5-year old cod scaled to SSB (left) and total abundance (right) related to the oxygen concentration (ml L^{-1}) at the bottom 1995 and 2003 (comparable oxygen concentrations but different total abundance). To enable visual comparison of the distribution of cod in 1995 and 2003 (i.e. Fig. 7, 8 and 9), their abundances have been scaled to the same total abundance. b) 1995, b) 2003.

Figure 1

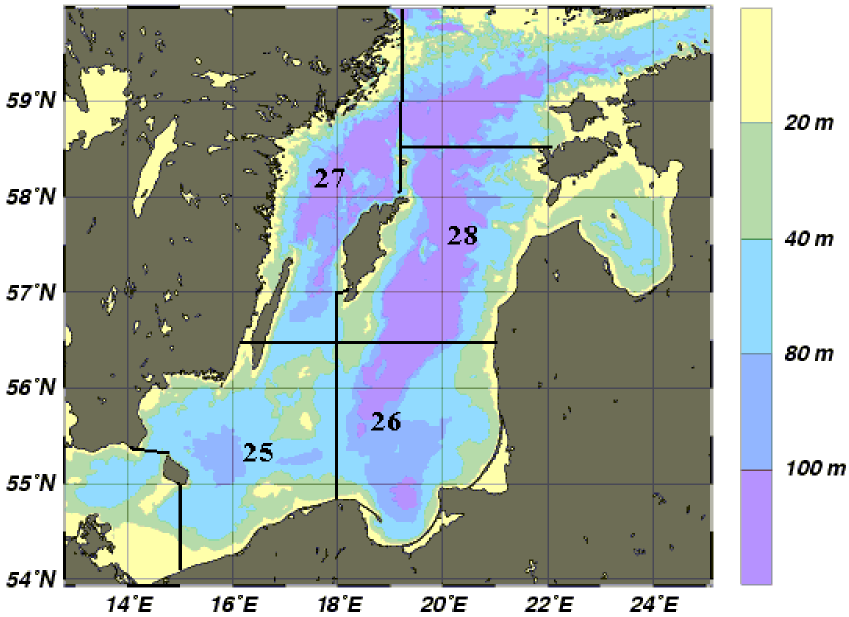

59°N
58°N
57°N
56°N
55°N
54°N
14°E
16°E
18°E
20°E
22°E
24°E
27
28
26
25
20 m
40 m
80 m
100 m

Figure 2.

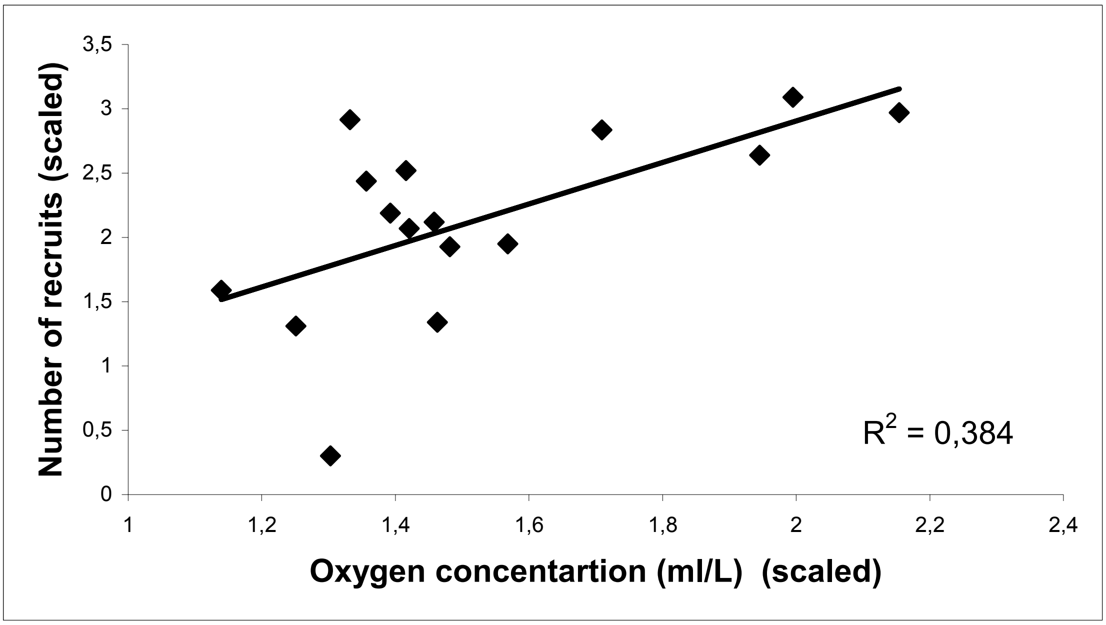

Number of recruits (scaled)
3,5
3
2,5
2
1,5
1
0,5
0
1
1,2
1,4
1,6
1,8
2
2,2
2,4
Oxygen concentartion (ml/L) (scaled)
R^2 = 0,384

Figure 3.

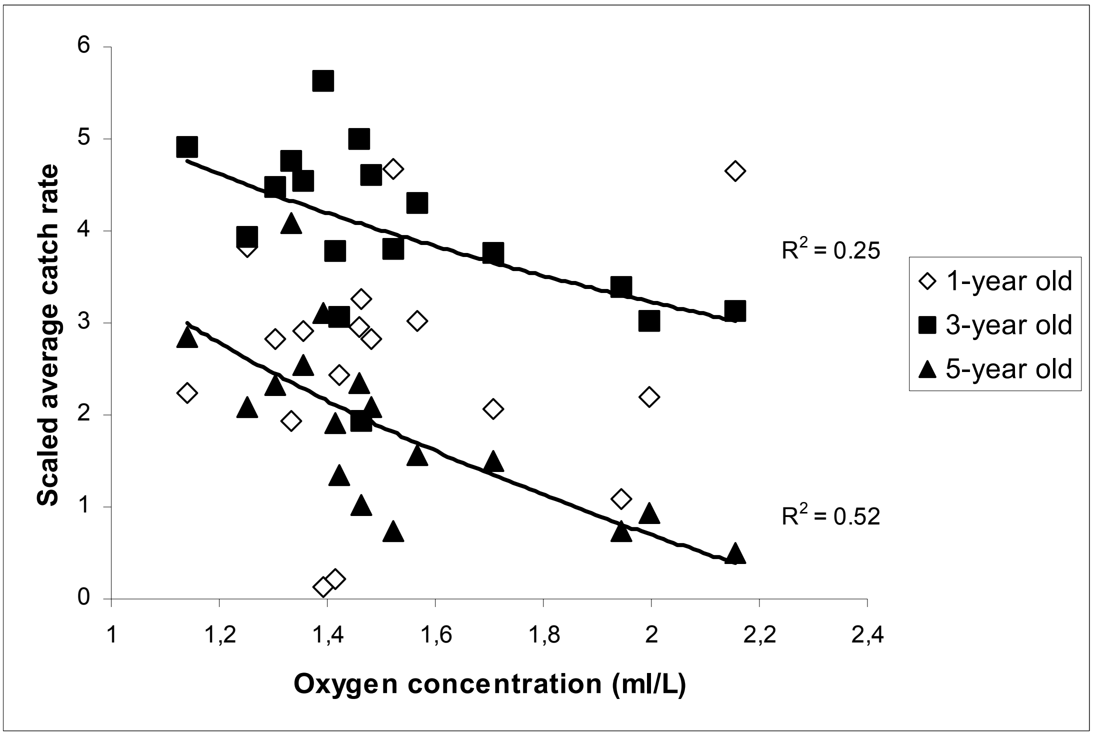
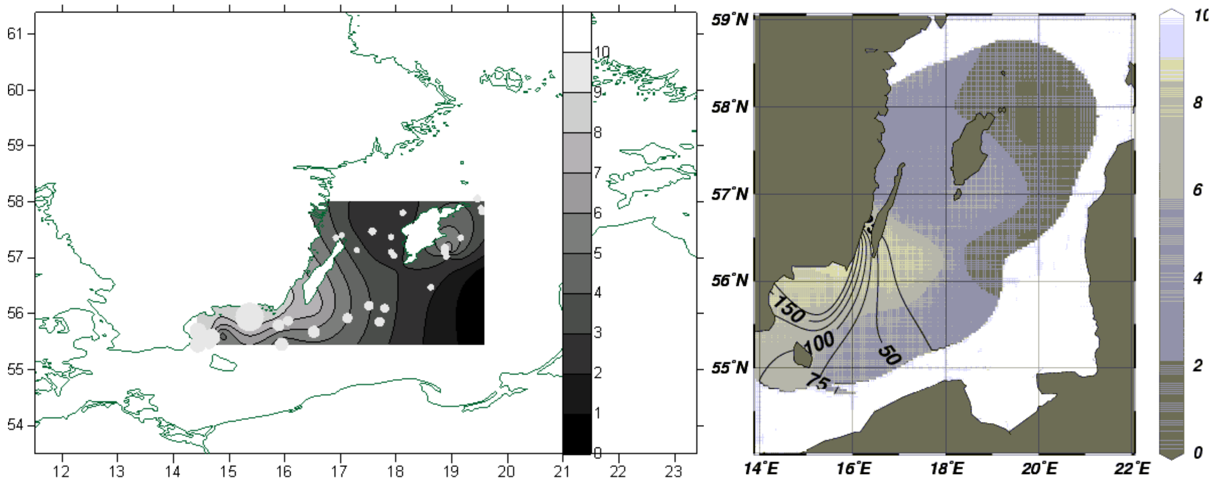

Scaled average catch rate
Oxygen concentration (ml/L)
0
1
2
3
4
5
6
1
1,2
1,4
1,6
1,8
2
2,2
2,4
R2 = 0.25
R2 = 0.52
1-year old
3-year old
5-year old

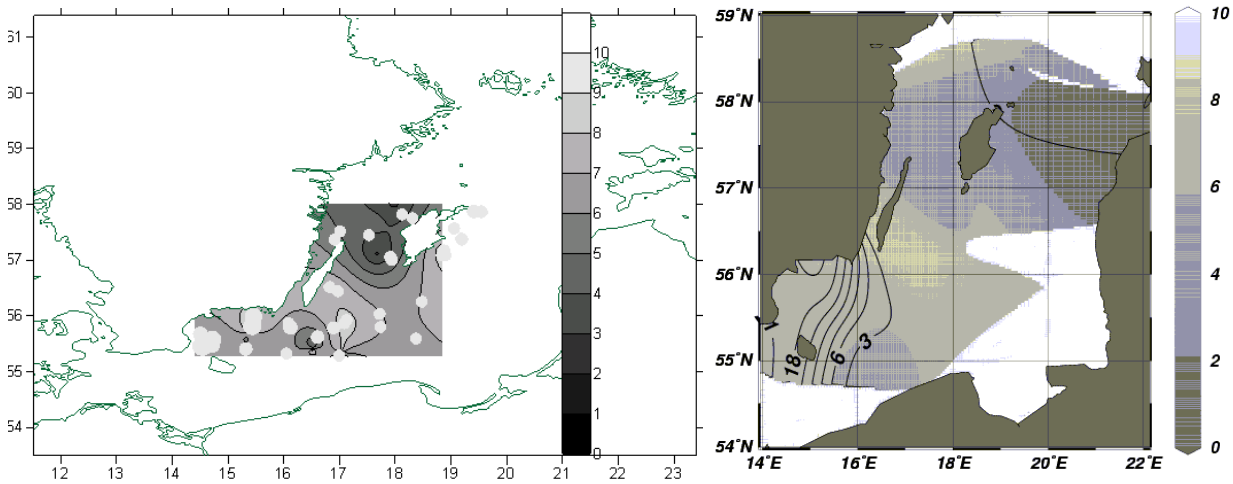
Figure 4.

a)



61
60
59
58
57
56
55
54
12 13 14 15 16 17 18 19 20 21 22 23
10
9
8
7
6
5
4
3
2
1
0
59°N
58°N
57°N
56°N
55°N
14°E 16°E 18°E 20°E 22°E
150
100
75
50
10
8
6
4
2
0

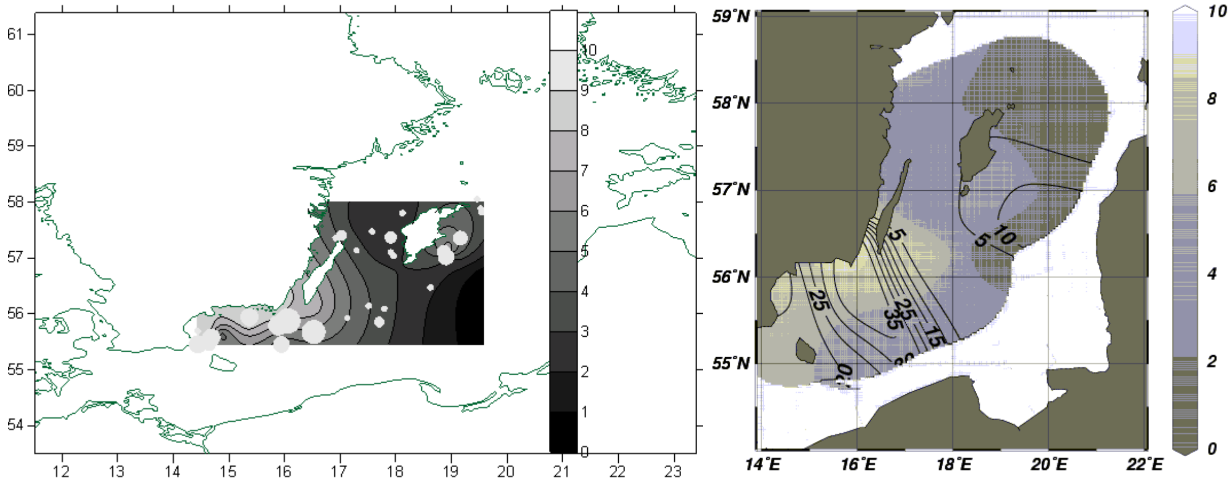
b)



58
57
56
55
54
12 13 14 15 16 17 18 19 20 21 22 23
10
9
8
7
6
5
4
3
2
1
0
59°N
58°N
57°N
56°N
55°N
54°N
14°E 16°E 18°E 20°E 22°E
18
6
3
10
8
6
4
2
0

Figure 5.

a)



b)

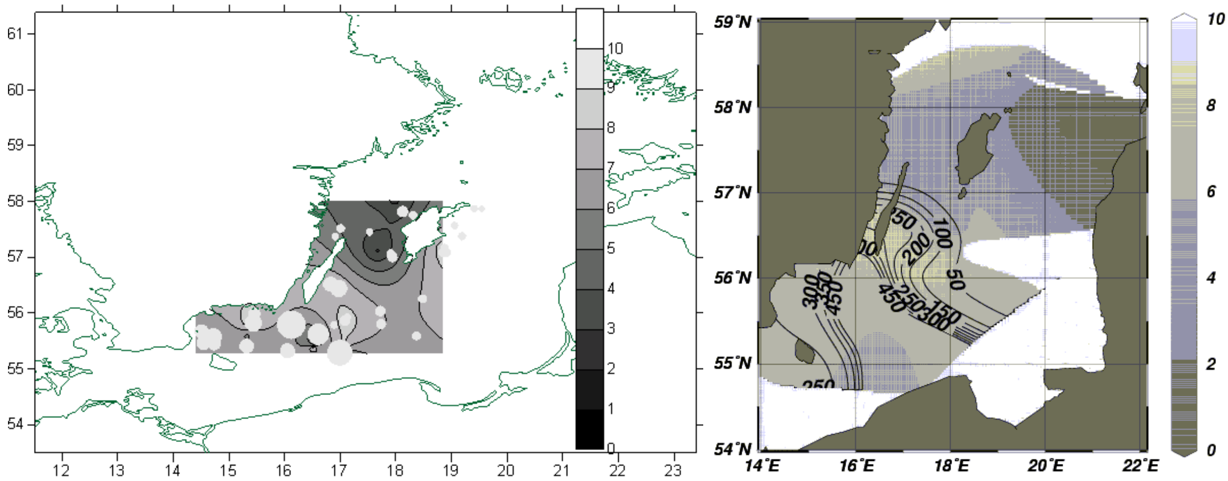
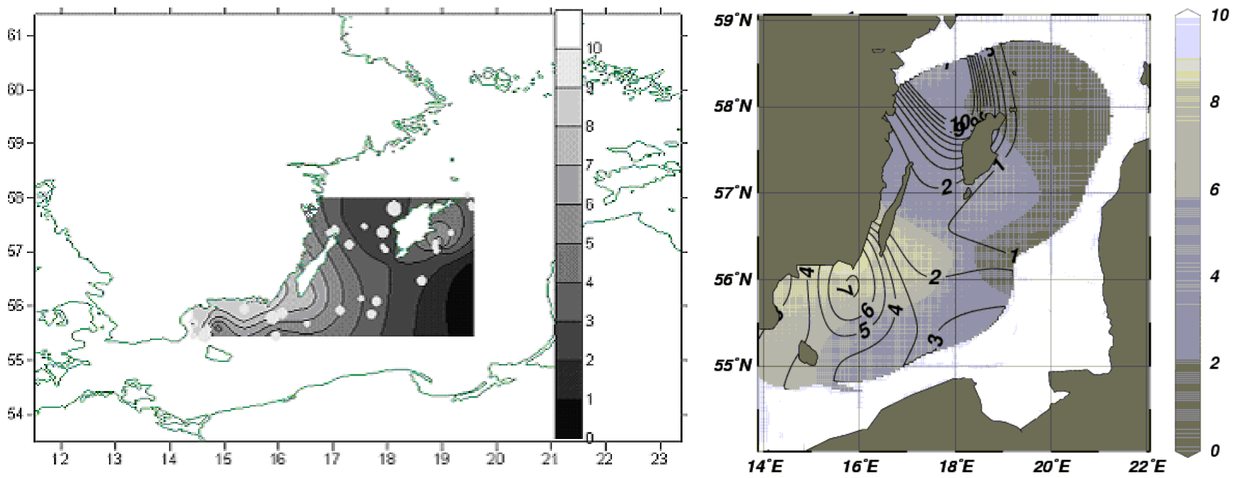


Figure 6.

a)


59°N
58°N
57°N
56°N
55°N
14°E
16°E
18°E
20°E
22°E

b)

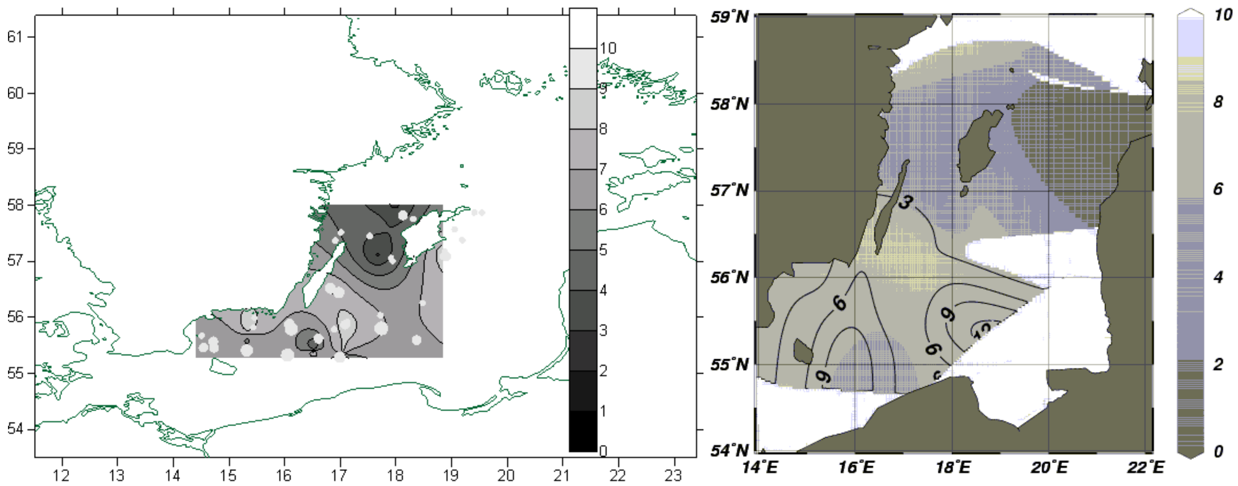
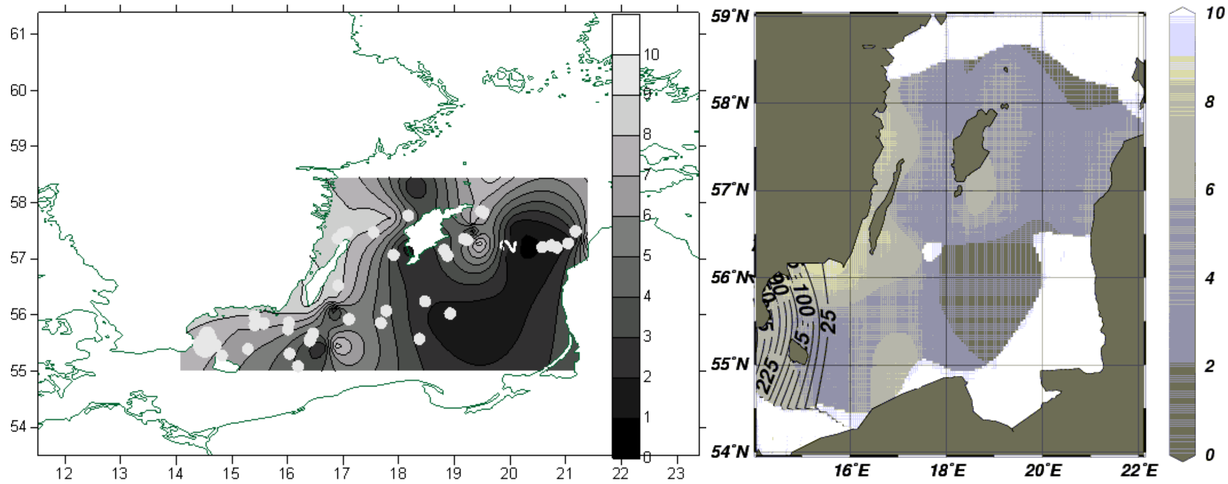

59°N
58°N
57°N
56°N
55°N
54°N
14°E
16°E
18°E
20°E
22°E

Figure 7.

a)



b)

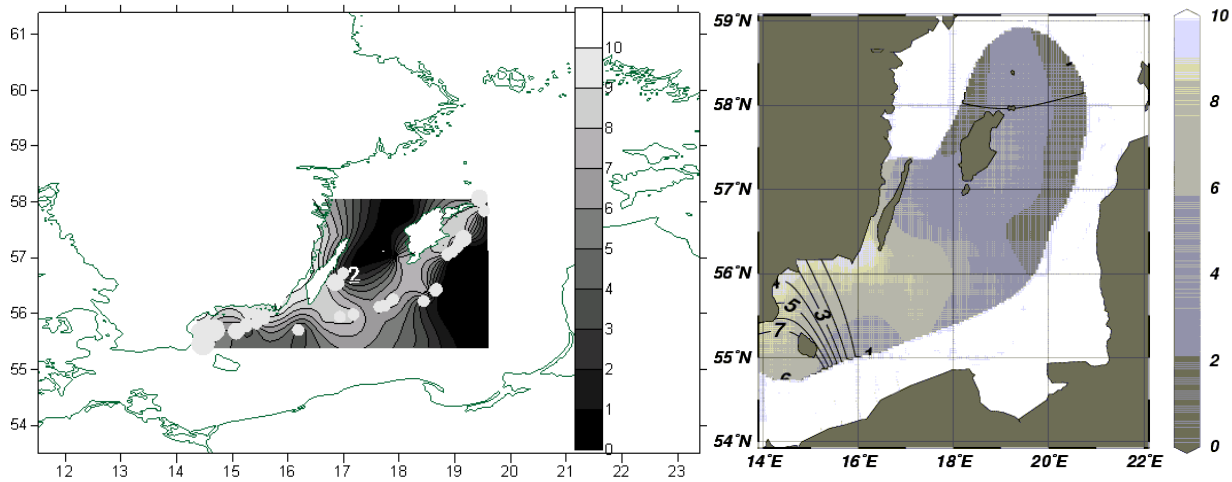
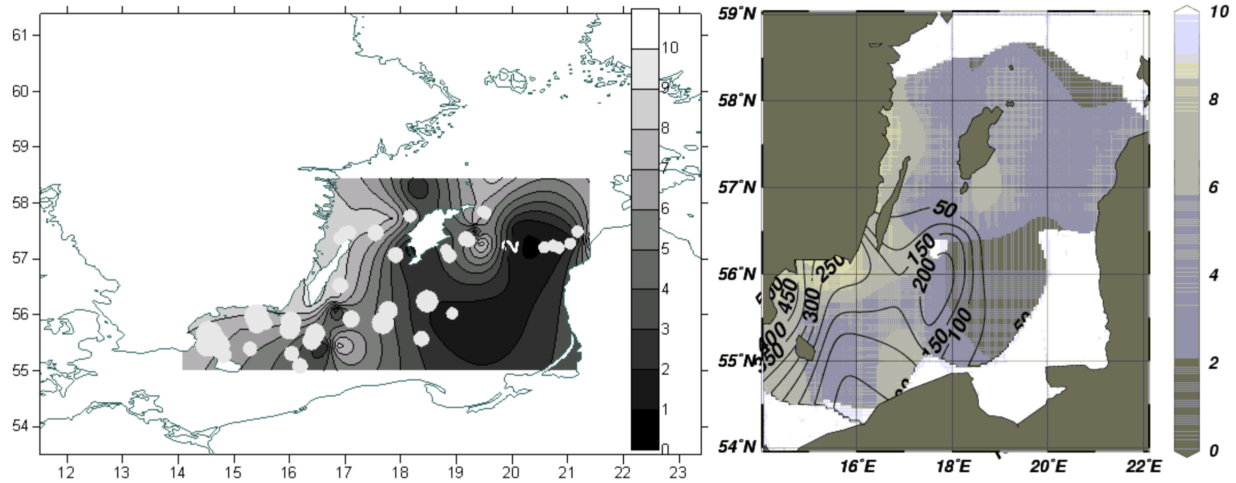


Figure 8.

a)



61
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55
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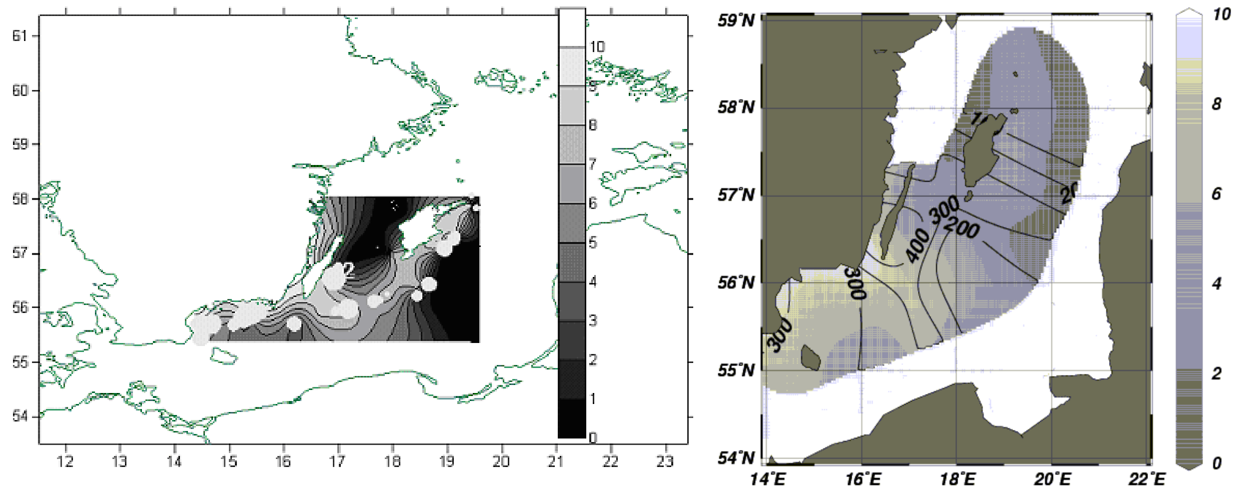
12 13 14 15 16 17 18 19 20 21 22 23
10 9 8 7 6 5 4 3 2 1 0
59˚N
58˚N
57˚N
56˚N
55˚N
54˚N
16˚E 18˚E 20˚E 22˚E
50
150
200
250
300
450
100
10 8 6 4 2 0

b)



61
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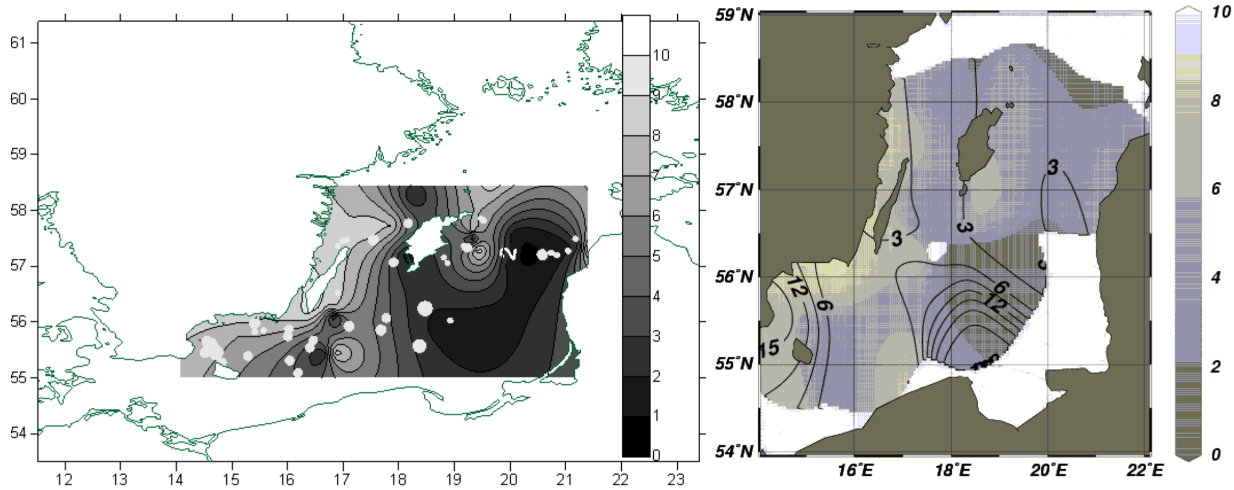
12 13 14 15 16 17 18 19 20 21 22 23
10 9 8 7 6 5 4 3 2 1 0
59˚N
58˚N
57˚N
56˚N
55˚N
54˚N
14˚E 16˚E 18˚E 20˚E 22˚E
300
200
400
10 8 6 4 2 0

Figure 9.

a)


61
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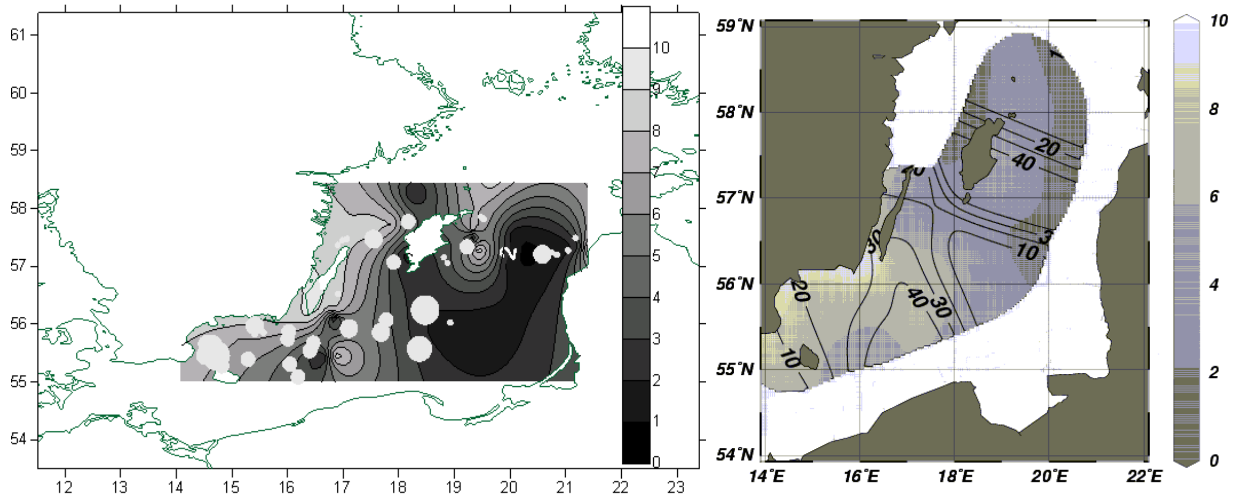
12 13 14 15 16 17 18 19 20 21 22 23
0 1 2 3 4 5 6 7 8 9 10
59°N
58°N
57°N
56°N
55°N
54°N
16°E 18°E 20°E 22°E
0 2 4 6 8 10
3
3
3
12
6
15
6
12

b)


61
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12 13 14 15 16 17 18 19 20 21 22 23
0 1 2 3 4 5 6 7 8 9 10
59°N
58°N
57°N
56°N
55°N
54°N
14°E 16°E 18°E 20°E 22°E
0 2 4 6 8 10
20
40
3
10
20
40
30
10