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5–8 November 2013

Riga, Latvia



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Executive summary

The ICES Study Group on Spatial Analyses for the Baltic Sea (SGSPATIAL) met in Riga, Latvia, 5–8 November 2013 (Chairs: Michele Casini, Sweden, and Stefan Neuenfeldt, Denmark), with nine participants and four countries represented.

The objectives of SGSPATIAL 2013 were to i) continue the analyses of the drivers of species spatial distribution; ii) quantify the spatial overlap between interacting species; iii) analyse the connectivity between open sea and coastal waters; iv) update the spatial indicators suggested in SGSPATIAL 2012.

The report contains an introductory chapter about the relevance of the SGSPATIAL for fisheries management and ecosystem-based management within the Marine Strategy Framework Directive (MSFD). A schematic representation of the envisaged role of the SGSPATIAL within ICES structure, and the link with other external activities was provided. The report continues with information on the current distribution of fish stocks, four chapters addressing the ToRs, and a final paragraph presenting ideas on the future developments of the SGSPATIAL.

Spatially disaggregated data of spawning-stock biomass (SSB) and reproductive volume (RV, hydrological conditions necessary for successful cod recruitment) were treated in a novel way to try finding a better fitting of the stock–recruitment relationship for the Eastern Baltic cod stock. The area-specific SSB were weighted by the correspondent reproductive volume to provide a general fit to the S-R for the whole stock. The results are promising and showed that the use of combined spatially disaggregated data, analysed with this method, can provide a better fit of the data than their simple addition. Preliminary analyses for the Bothnian Sea (SD 30) herring stock showed a negative spatio-temporal relation between the abundance of adult herring and the abundance of sprat in October, suggesting the potential for interspecific competition in this area.

Changes in prey–predator and predator–prey overlap have been estimated between 1999–2012. A decrease has been observed in the overlap between cod and its prey herring and sprat in the Bornholm Basin (SD 25), whereas the overlap between adult cod and juvenile cod has increased in the same area indicating increasing cannibalism.

Changes in spatial connectivity between coastal and offshore areas have been shown for Eastern Baltic cod and sticklebacks. The two species, as consequences of variations in their population sizes, may connect or disconnect adjacent ecosystems, as different sub-basins or coast-offshore habitats.

Indicators of the spatial distribution of cod, sprat and herring, from ICES-coordinated international surveys, using the centre of gravity, were updated. The indicators provided also new information of the age-specific changes in distribution. The indices evidenced that the Eastern Baltic cod has concentrated in the southwestern Baltic since the late 1970s, whereas the sprat recruits and adults became concentrated in the northeastern Baltic Proper after the early 1990s. Herring recruits have shown a high degree of spatial oscillation, whereas the adult part of the population showed a lower degree of change. In 2012, herring and sprat recruits and sprat adults were concentrated in the northern part of the Baltic Proper, whereas the herring adults were homogeneously distributed.

The following key recommendations were put forward: 1) WGSAM (Working Group on Multispecies Assessment Methods) is recommended to account for the changes in species distributions in the estimation of predation mortalities and multispecies reference points; 2) ACOM/SCICOM is recommended to include information on fish spatial distribution for the Ecosystem Overview of the Baltic Sea.

1 Opening of the meeting

The Co-Chairs Michele Casini (Sweden) and Stefan Neuenfeldt (Denmark) welcomed the participants (Annex 1) of the meeting. The Co-Chairs introduced the goals and focus of the meeting (see Introduction) and the state of the different tasks to be conducted by the group.

The meeting has been given the following Terms of References (ToRs):

- a) Continue the analyses on the drivers of change in spatial distribution of commercially and ecologically important fish species
- b) Analyse and quantify the spatial overlap of main fish predators and preys, in both open sea and coastal areas
- c) Investigate and quantify the connectivity between open sea and coastal areas of commercially and ecologically important fish species
- d) Further develop the fish spatial indicators proposed during the SGSPATIAL 2012

2 Adoption of the agenda

The Co-Chairs introduced the agenda which was shortly discussed, adjusted and finally adopted by the participants. However, a flexible agenda was adopted.

3 Introduction

The SGSPATIAL is a forum where the following main issues are addressed: 1) improve the knowledge of the processes shaping populations' spatial distribution, with the aim to increase the ecological understanding on ecosystem functioning in general, but also to provide information to be used in stock assessment and the management of the exploited resources in particular; 2) provide quantitative information on the spatial overlap between interacting species (ex. predator-prey or competitors) to be used to estimate predation mortalities in both single-species and multispecies stock assessments; 3) provide indicators of the changes in populations' spatial distribution that can be directly used in fisheries advice and in the production of the ICES regional ecosystem overviews; 4) provide indicators of ecosystem state and pressure to aid the implementation of the Marine Strategy Framework Directive (MSFD, EC 2010). The work done in SGSPATIAL is seen as tightly linked with the work done in HELCOM and the new BONUS project INSPIRE running 2014–2017 (Figure 3.1).

Multispecies and ecosystem Advice

The Baltic Sea is in the front line in terms of ecosystem assessment (see work done in WGIAB, ICES, 2012d) and ecosystem analyses to be used in stock assessment and management (ICES, 2012a,b,c,d). The integration of spatial consideration would add a missing dimension to this process and is therefore of fundamental importance, as also stressed by the ICES Baltic Fisheries Assessment Working Group (WGBFAS, ICES, 2012d), and the European Commission (EC, 2012).

In June 2012, ICES has provided for the first time an example of multispecies advice for the Baltic Sea to the EU Commission (ICES, 2012b). This means that the fisheries opportunities (ex. fishing quotas) for one species can be set considering the implications for, and the effect of, the other species co-occurring in the system. This consti-

tutes a tremendous step forward in the management of exploited resources and ecosystem, and in this the Baltic Sea has been the pioneer in Europe. However, ecologically and commercially key fish species have recently changed their spatial distribution in the Baltic Sea, and therefore the interactions between them (in terms of competition, predation, etc.) have also changed. Hence, both ICES and the EU Commission have pointed out that a sound multispecies fisheries management should consider the changes in spatial distribution of the interacting species (ICES, 2012b,c; EC, 2012). Currently, however, spatial considerations cannot be incorporated in the ICES multispecies advice because of the lack of sufficient and robust knowledge of the fish populations' spatial patterns and the driving mechanisms of their spatial distribution (ICES, 2012c, EC, 2012).

Therefore, three aspects have been identified as being crucial for the development of a more robust Multispecies Advice: a) quantification of the changes in spatial overlap between predator and prey species to be implemented in the multispecies assessment models; b) better understanding of the mechanisms leading to the changes in spatial distribution of fish species, which would forecast future changes in species distributions to be implemented in the simulations on multispecies reference points (ICES, 2012b; EC, 2012); c) better understanding of the ecosystem consequences of the changes in spatial distribution of fish species.

Marine Strategy Framework Directive

Information about the changes in the spatial distribution of fish populations is also important for an ecosystem approach to the management of human activities, as directly specified in the new EU Marine Strategy Framework Directive (EC, 2010). Species distribution has been identified as key biodiversity criteria for evaluating environmental status. The Baltic Sea is one of the four marine regions at focus in the Directive, together with the Northeast Atlantic, the Mediterranean Sea and the Black Sea. However, at the moment there is no international coordination among the Member States to deal with motile fish species which occur across the boundary of national waters. SGSPATIAL could serve as platform for an international coordination in the MSFD, using the existing spatially explicit data from international surveys and commercial vessels.

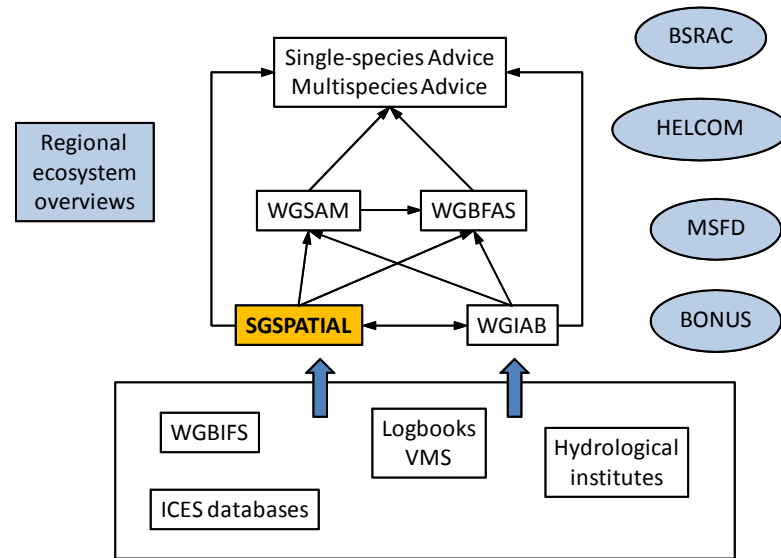


Figure 3.1. Schematic representation of the envisaged linkages between SGSPATIAL and other activities within and outside ICES.

4 Historical and current distribution of fish stocks

The relative distributions of predator (cod) and clupeid prey (herring and sprat) have changed over the recent decades, and for the time being most herring and sprat are outside the predatory reach of cod, at least for parts of the year. Since 2007, after a period of 20 years of a very low biomass, the eastern Baltic cod stock has rapidly increased. However, the stock has not re-occupied its former central Baltic wide distribution range, but remains concentrated in a limited area in the southern Baltic Sea, i.e. in SD 25. In contrast, most of the clupeid biomass is currently found in northeastern Baltic Sea (Casini *et al.*, 2011). Consequently, at present spatial distribution of the stocks, the overlap between cod and clupeids is to a large extent limited to SD 25; with less interaction in SD 26 and almost no overlap between cod and clupeids in the northeastern areas (SD 28–32). Due to these changes in distribution of the three stocks in the Baltic Sea, it might be appropriate to develop spatially explicit management targets for the Baltic stocks (WKMULTBAL, ICES, 2012c).

The most recent acoustic surveys performed in the Baltic Sea in October 2012 show that age-1 sprat is mainly concentrated in the northeastern part of the Baltic Proper, with the highest concentrations inside and just outside the Gulf of Finland (SD 32). Older sprat (age 2+) have a more homogeneous distribution, but they also show the highest concentrations in the Gulf of Finland (Figure 4.1).

Age-1 herring present the highest concentrations in the northern part of the Baltic Proper (north SD 27 and SD 29) and Bothnian Sea (SD 30). Older herring (age 2+) are more uniformly distributed in the Baltic Proper and Bothnian Sea, with lesser abundances in the Gulf of Finland (SD 32) and Western Baltic (SD 22–24; Figure 4.2).

Cod in Quarter 4 2012 showed highest abundances in SD 25, with isolated peaks in the eastern part of SD 26. In Quarter 1 2013 the situation was similar, but with the highest concentration of small fish (age 1) occurring in SD 24 (Figures 4.3 and 4.4).

The patterns of distribution of sprat, herring and cod confirm the situation of the past 10-15 years with high concentrations of pelagic fish in the northern Baltic and high concentrations of cod in the southern Baltic. See Chapter 8 on Spatial Indicators for a time-series of the changes in distribution of the stocks.

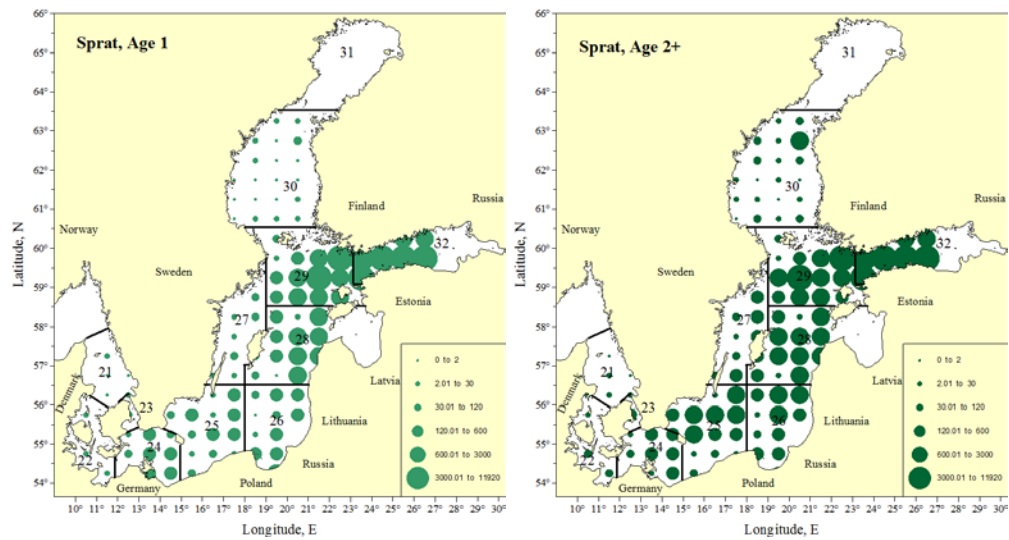


Figure 4.1. Spatial distribution of sprat in Quarter 4 2012 (BIAS survey).

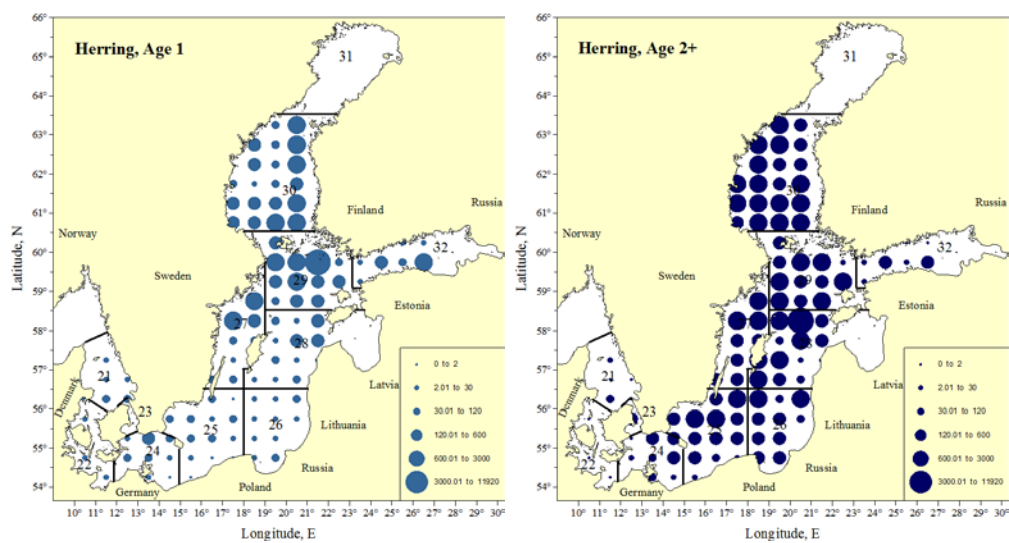


Figure 4.2. Spatial distribution of herring in Quarter 4 2012 (BIAS survey). Three different stocks are represented: Western Baltic (SDs 22–24), Central Baltic (SDs 25–29, 32) and Bothnian Sea (SD 30).

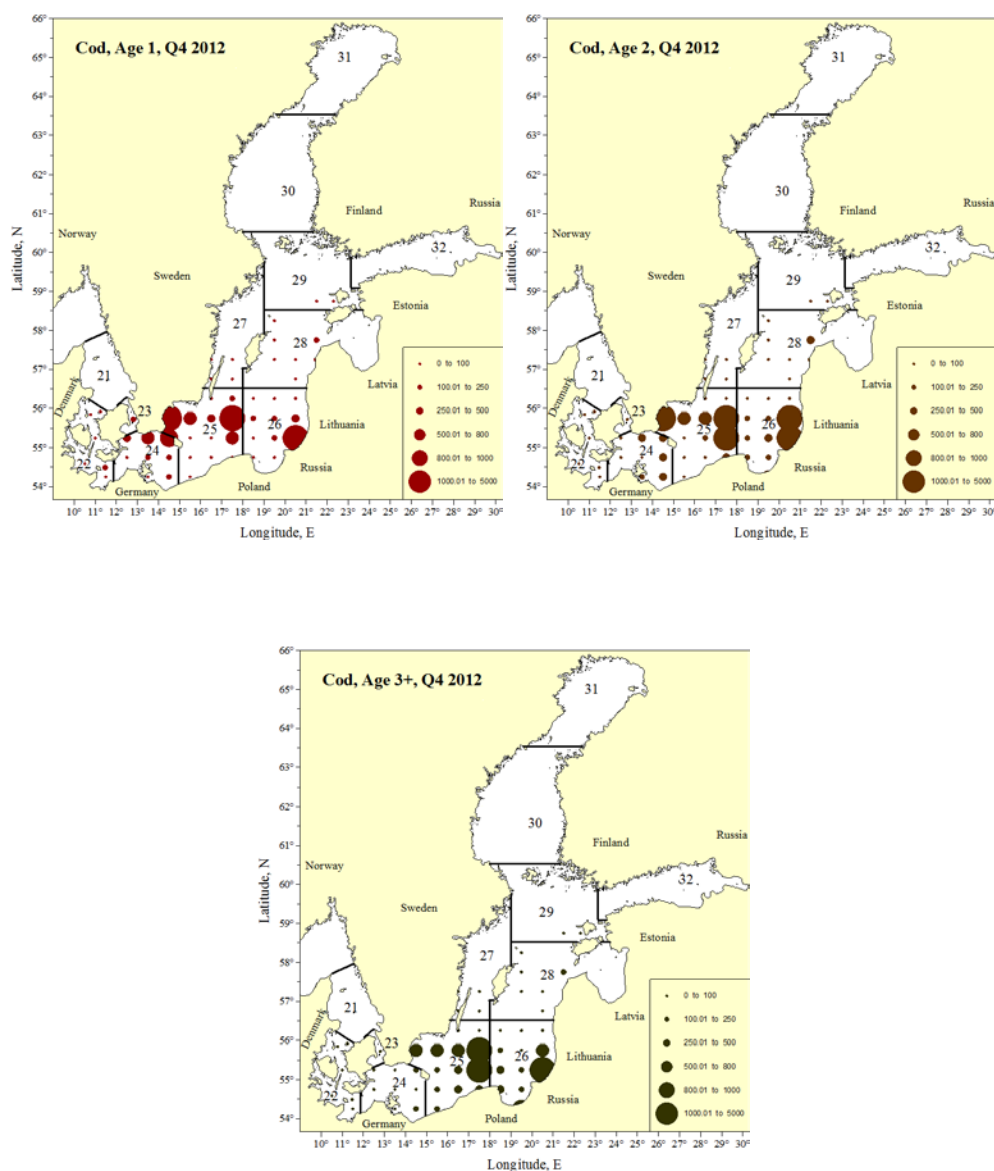


Figure 4.3. Spatial distribution of cod in Quarter 4 2012 (BITS survey). Two different stocks are represented: Western Baltic cod (SDs 22–24), and eastern Baltic cod (SDs 25–32).

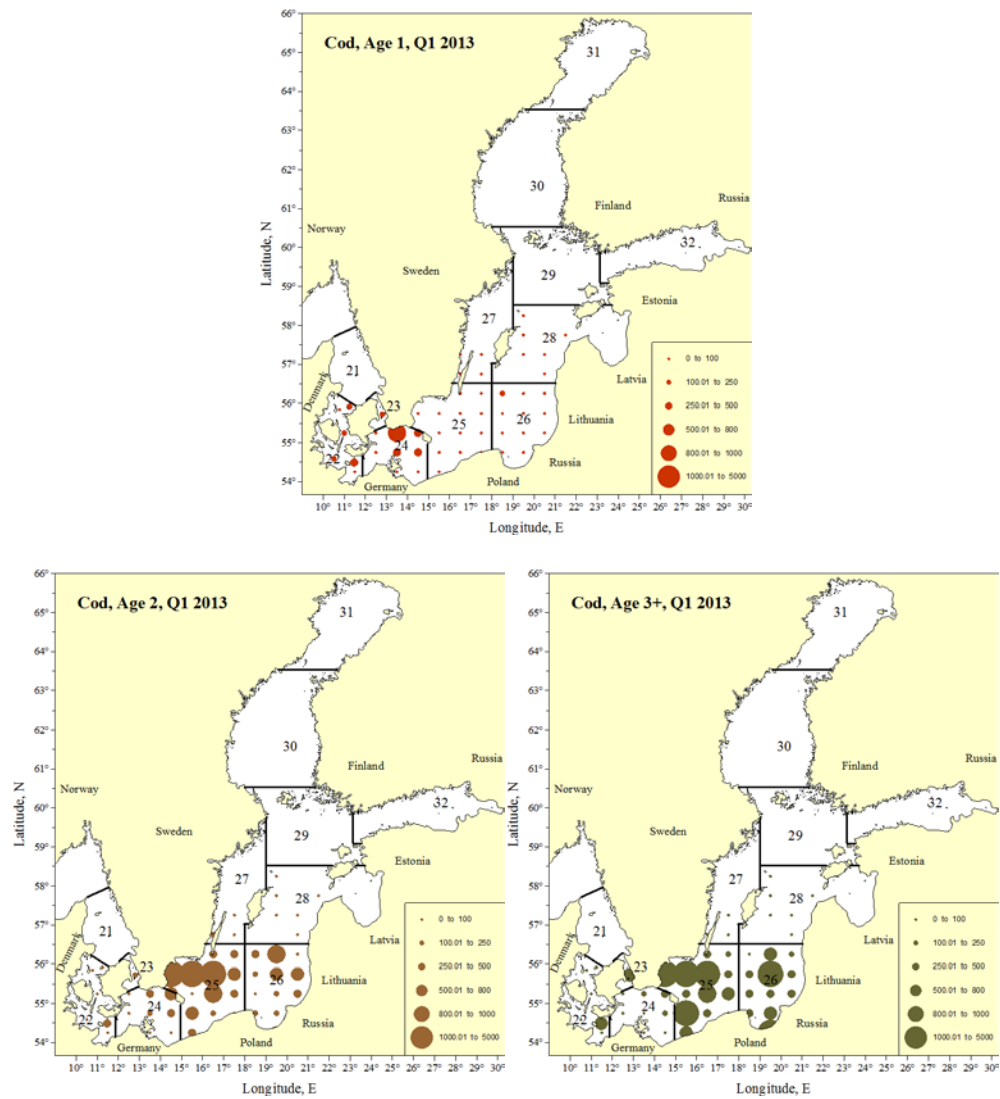


Figure 4.4. Spatial distribution of cod in Quarter 1 2013 (BITS survey). Two different stocks are represented: Western Baltic cod (SDs 22–24), and Eastern Baltic cod (SDs 25–32).

5 ToR a) Continue the analyses on the drivers of change in spatial distribution of commercially and ecologically important fish species

5.1 Stock–recruitment relationships in the eastern Baltic cod and the relevance of local environmental conditions to the contribution of the different spawning components

Understanding which processes regulate recruitment of fish populations and ultimately predicting the intensity of recruitment in exploited stocks is crucial part of fishery assessment and a necessary step towards a sustainable management of fish resources.

Environmental variability and the internal structure of fish populations have major effects on the quantitative relationship that exists between the recruits and the mature population (Beaugrand and Kirby, 2010).

Recently, environmentally driven stock–recruitment relationships have been proposed (Chen and Irvine, 2001; Fiksen and Slotte, 2002; Cardinale *et al.*, 2009) to incorporate the effect of environmental variability, providing considerable improvement to the explanation of recruitment variability for a number fish stocks including cod (Stige *et al.*, 2006; Olsen *et al.*, 2011; Margonski *et al.*, 2010).

The structures of adult fish populations are rarely homogeneous and invariant. Demographic and spatial structure of the spawning part of populations has been found to have direct implications for their recruitment, but their incorporation into stock–recruitment relationships has been limited.

The main drivers of Eastern Baltic cod recruitment have been found in literature to be salinity and oxygen. Specifically, the reproductive volume (RV, volume of water characterized by oxygen levels >2 ml/L and salinity >11 psu), affecting cod reproduction and egg survival, is considered the most powerful parameter to explain the variation in cod recruitment.

Beside the large number of studies aimed to disentangle the multiple factors affecting the recruitment of eastern Baltic cod, a satisfactory stock–recruitment relationship that could be used for operative purposes is still lacking. The Bornholm Basin, the Gdańsk Deep and the Gotland Basin are the main spawning grounds for the eastern Baltic cod. However, the contribution of the different sub-basins to cod recruitment varies depending on the local abiotic conditions, which can largely differ between years. For example, in stagnation periods (i.e. low inflow of salty and oxygen-rich waters from the North Sea), only the Bornholm basin has the favourable abiotic conditions for successful cod recruitment. When, on the other hand there are strong water inflows from the North Sea, cod recruitment can be successful also in the other sub-basins. However, the successfulness of the recruitment depends also on the spawning biomass present in each sub-basin each year.

We used the output of Stochastic Multi-Species (SMS) models run separately for the Bornholm Basin, the Gdańsk Deep and the Gotland Basin (represented by the ICES Subdivisions 25, 26, 28 respectively) to fit SR models for each sub-basin. Age 0 fish in quarter 3 and the biomass of mature fish in quarter 2 are selected from SMS as recruits and spawners, respectively. The main assumption of fitting SR models at a basin level is that spawners and recruits estimated from SMS runs are resident in the same subdivision during the spawning period in quarter 2 and across the quarter 3.

Two different SR models were fitted, the classic Ricker model and a modified Ricker model to include the effect of environmental variability, according to Chen and Irvine (2001). The reproductive volume (RV) for each sub-basin was included in the model as environmental descriptor of the suitable habitat needed for the successful reproduction of cod. The two competing models were formulated as follows:

$$1) R = aSe^{-bS}$$

$$2) R = aSe^{-bS+cRV}$$

where R is recruitment, S is the spawning-stock biomass and a, b and c are parameters to be estimated. Both model formulations have been transformed on a logarithmic scale before the actual fitting to better meet the assumption of normality of the error distribution.

From personal observations in a number of sampling occasions, cod has been observed spawning also under unsuitable conditions, for instance in very low salinity levels, where the survival of eggs would have been certainly compromised. These observations suggested an alternative approach where the contribution of different spawning components to the whole stock recruitment was first weighted by the available RV in the different sub-basins. A classic Ricker SR model was fitted using the weighted spawning-stock biomass (S_{adj}) that was computed as:

$$3) S_{adj} = \sum S_{SD} RV_{SD}$$

where SD is the ICES Subdivision and RV is the relative reproductive volume (i.e. scaled to a maximum of 1).

Results

The reproductive volume (RV) shows high variability within and across the different ICES Subdivisions. Subdivision 28, and in minor extent Subdivision 26, show numerous observations with very small or even 0 RV. On the other hand, although the high fluctuations, the RV in Subdivision 25 is never zero suggesting the key role of the Bornholm Basin for the recruitment of the stock.

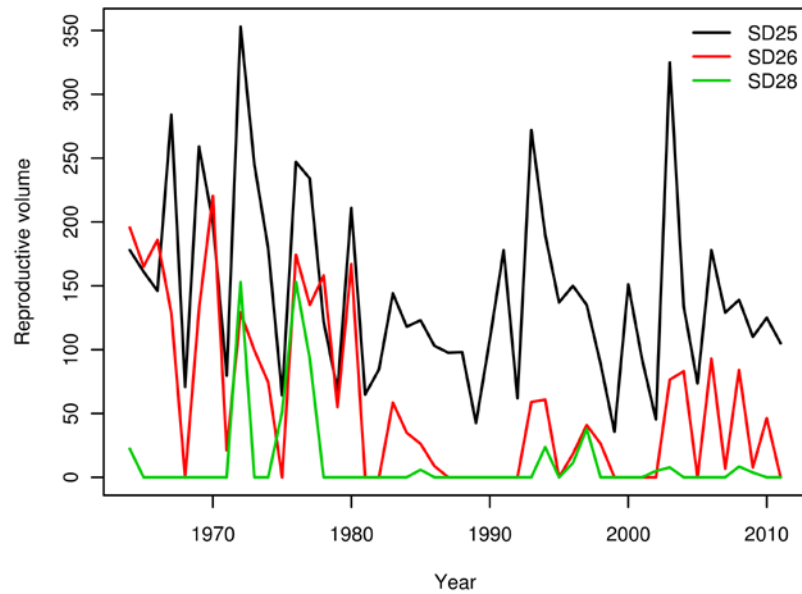


Figure 5.1.1. Reproductive volume calculated separately for the Subdivisions 25, 26, 28 for the time period 1964–2011.

In most cases the fitted stock–recruitment (SR) models were not significant with the exception of sub-division 26 where inspection of the SR curve suggests that the Ricker model could be inappropriate to supporting the relationship as no sign of density-dependence is observed in the data. Although poor or lack of statistical fitting, qualitative considerations can be drawn. The SR model for Subdivision 25 is the poorest one in reconstructing the recruitment dynamics and none of the formulations adopted is able to capture the large recruitment levels that characterize the second half of the 1970s. In the case of both Subdivision 26 and 28 the models appear able to capture the general pattern in the recruitment with some improvement in the formulation including the effects of the RV.

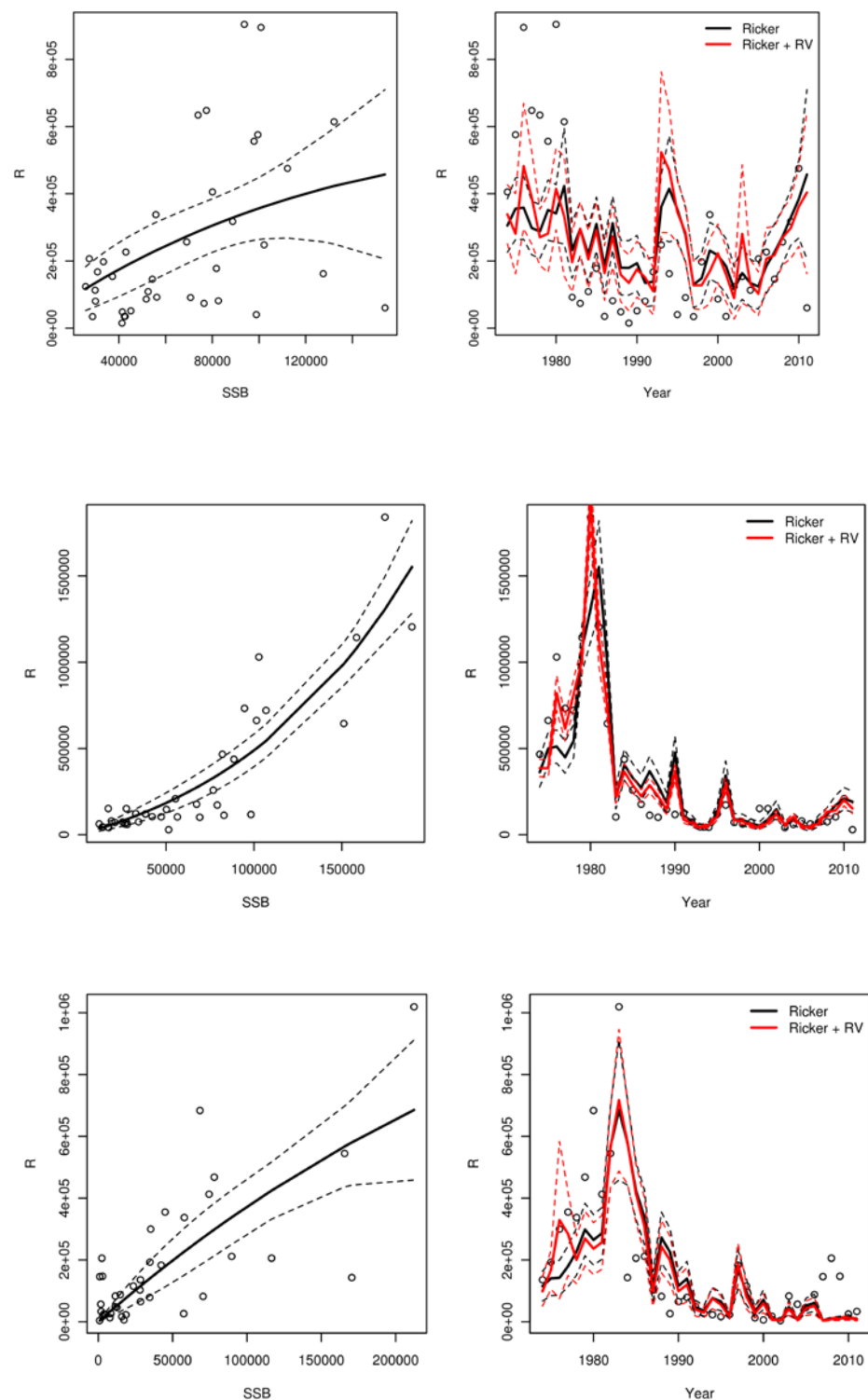


Figure 5.1.2. From top to bottom stock–recruitment relationships for eastern Baltic cod in Subdivision 25, 26 and 28 for the time period 1974–2011. On the left panels the SR curve (continuous line) with 95% CI (dotted line) fitted using the classical Ricker model. On the right panels the estimated recruitment (continuous line) with 95% CI using the classical (black) and the environmentally driven Ricker model. Points are observations (i.e. subdivision specific SMS outputs).

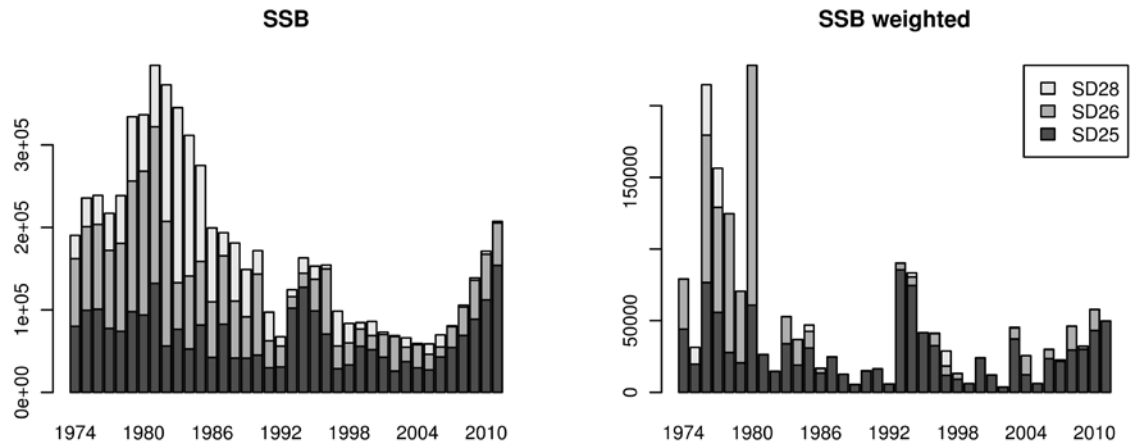


Figure 5.1.3. Baltic cod SSB time-series with the contribution by ICES Subdivision. On the left the non-adjusted SSB, and on the right the SSB adjusted for the relative size of the RV by subdivision.

The adjusted and non-adjusted SSB time-series show substantial differences in the overall patterns. Also the relative contribution of the subdivisions to the overall SSB is highly variable during the time-series as a consequence of different dynamics of the RV in the different sub-basins. In particular, the high SSB levels observed at the beginning of the 1980s are down-weighted by the poor reproductive volume that characterized most of the cod spawning grounds. Although the poor statistical support to prefer any of the two models, it is interesting to observe how the use of SSB adjusted for the availability of the suitable reproductive habitat allows to capture the high variability that characterizes the beginning of the recruitment time-series up to 1980. On the contrary, from mid 1980s onwards this model appears to have worse estimates than the model based on non-adjusted SSB. In the mid-1990s the combination of on-average SSB levels and elevated RV, especially in the Subdivision 25, produced an overestimation of recruitment, and in the 2000s the use of non-adjusted SSB produces more stable recruitment estimates closer to the fitted data.

Table 5.1.1. Parameters estimated for the classic (1) and environmentally driven (2) stock–recruitment Ricker models. * $P < 0.05$; ** $P < 0.01$.

Area	Model	SSB	a	b ($\times 10^{-6}$)	c ($\times 10^{-3}$)
25	1		4.950*	3.370	
25	2		3.339	3.559	2.911
26	1		2.762**	-5.715**	
26	2		2.266**	-5.093**	4.221**
28	1		4.222**	1.265	
28	2		3.498**	0.168	6.457*
25,26,28	1	non-adjusted	2.802**	-2.066	
25,26,28	1	adjusted	15.830**	0.912	

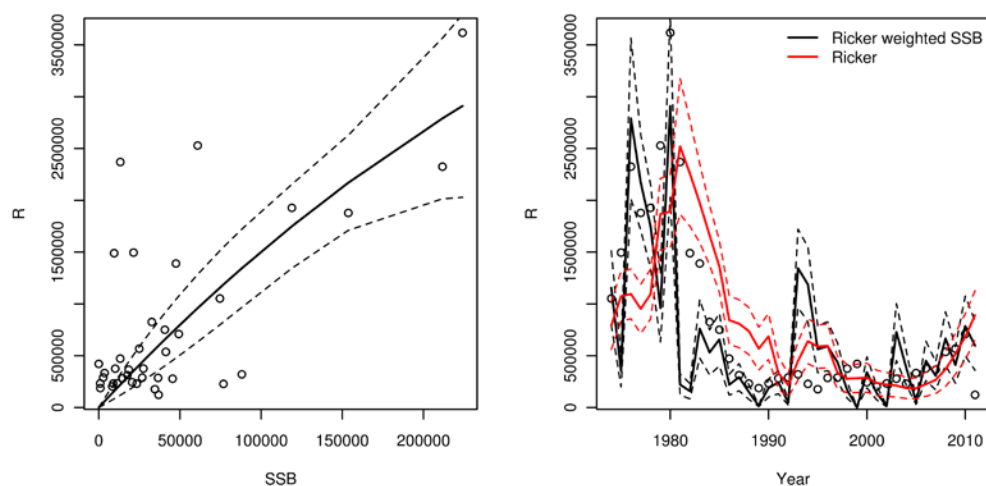


Figure 5.1.4. Stock–recruitment relationship for eastern Baltic cod for the time period 1974–2011. On the left panels the SR curve (continuous line) with 95% CI (dotted line) fitted using the classical Ricker model. On the right panels the estimated recruitment (continuous line) with 95% CI using the classical (black) and the environmentally driven Ricker model. Points are observations (i.e. subdivision specific SMS outputs).

Further improvements of the current analysis would include a correction of the RV by accounting for its quality (e.g. positive correlation between eggs survival and oxygen up to 4–5 ml/L), and fitting the SR model on observational data (eventually age 1 fish if the abundance of age 0 fish is poorly sampled) rather than SMS outputs.

5.2 The potential effect of environmental variability and species interactions on the spatio-temporal abundance of herring in the Bothnian Sea (SD 30)

The extent at which environmental variability and species interactions may explain the spatial distribution of the Bothnian Sea (SD30) herring was studied using Generalized Additive Models (GAMs). The analysis was based on fish abundance data from October BIAS surveys (per rectangle) covering the entire SD30 and the years 2007–2012, and the corresponding hydrological data that were provided by SMHI.

More specifically the combined, and potentially non-additive, effects of surface water (10m) salinity, temperature on the spatial distribution of 1-year old, 2-year old and older herring (ages 3+) were studied. In addition, the effect of sprat abundance (ages 1+) on the different age groups of herring was analysed. The GAM analysis was carried out using the *mgcv* package of the R software. In the approach chosen, all explaining variables were first included in the model. Then the non-significant variables were excluded one by one starting from the least significant relationship. The sprat data included a few very high abundances, which were excluded from the final analysis.

The results for herring age 2 and 3+ showed statistically significant relationships between the herring abundance and salinity, as well as the abundance of sprat (Figures 5.2.1 and 5.2.2). For the older herring (3+), the relationship with salinity was negative (Figure 5.2.1a). Also, at higher sprat abundances (approx. $>300 \times 10^6$) a negative relationship was detected between herring age 3+ and sprat (Figure 5.2.1b). Together, variability of salinity and sprat abundance explained 24.1% of the deviation of herring age 3+. Younger herring (age 2), on the other hand, displayed a positive correlation with salinity across the salinity range tested (Figure 5.2.2a). The relationship between herring age 2 and sprat abundance was positive up to the abundance of approx. 600×10^6 after which it turned into a negative one (Figure 5.2.2b). Together, salinity and sprat abundance explained 19.3% of the spatial deviation of herring age 2.

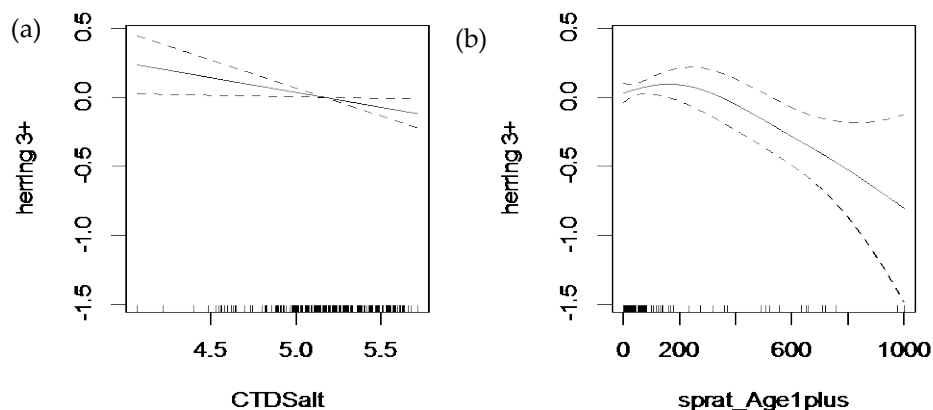


Figure 5.2.1. The relationship between herring age 3+ abundance and (a) near surface (10 m) salinity and (b) sprat age 1+ (abundance) in SD 30 in October 2007-2012. 24.1 percent of the spatial deviance of herring age 3+ was explained by salinity (*) and sprat age 1+ (**).

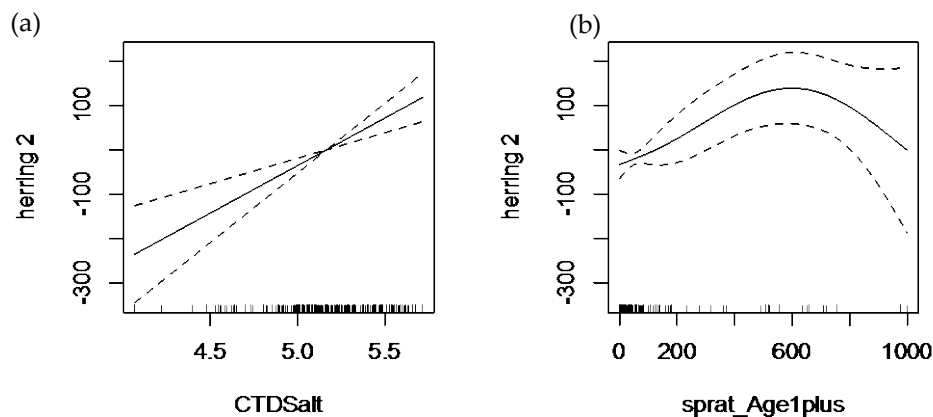


Figure 5.2.2. The relationship between herring age 2 abundance and (a) near surface (10m) salinity and (b) sprat age 1+ (abundance) in SD 30 in October 2007-2012. 19.3 percent of the spatial deviance of herring age 2 was explained by salinity (***) and sprat age 1+ (**) abundance.

The youngest herring (age 1) abundance showed a statistically significant relationship with near-surface temperature in addition to salinity and sprat abundance (Figure 5.2.3). The results suggest that herring prefers salinities below and above 5 psu (Figure 5.2.3a), as well as has a positive relationships with sprat abundance (Figure 5.2.3b). Also some preference for intermediate temperatures (around 10 °C) is suggested (Figure 5.2.3c). The GAM model including the three explanatory variables explained 40.6% of the spatial deviation of herring age 1.

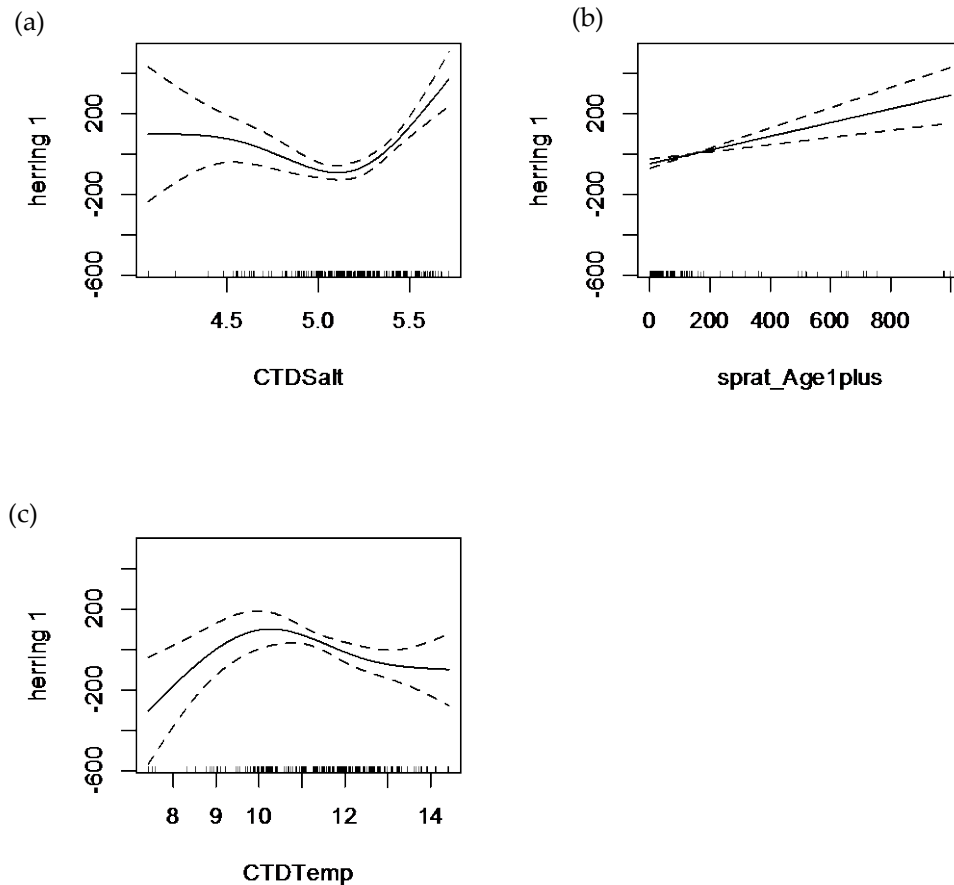


Figure 5.2.3. The relationship between herring age 1 abundance and (a) near-surface (10m) salinity, (b) sprat age 1+ (abundance) and (c) near surface temperature in SD 30 in October 2007-2012. 40.6 percent of the spatial deviance of herring age 1 was explained by salinity (***), sprat age 1+ abundance (***) and temperature (*).

The work done in this meeting is the first attempt by the SGSPATIAL to study the relationship between the spatial distribution of Bothnian Sea herring and environmental variability, as well as herring co-occurrence with sprat. The results from the above GAM models alone, would suggest that different age groups of herring have a different response to environmental variability, as well as to interaction with sprat. For example, salinity had a negative relationship with herring age 3+, but a positive one with herring age 2. In the case of herring age 3+, the higher concentration of herring in the low salinity areas may reflect the adaptation of Bothnian Sea herring to low salinity conditions and/or reflect the sprat avoidance behaviour in case sprat does not occupy the northernmost low-saline areas. The negative relationships between the older herring (age 2 and 3+) and sprat 1+, when sprat is at high abundances, may be indicative of competition or avoidance behaviour between the two fish species that occupy a rather similar niche in the Baltic Sea ecosystem. The positive correlation between herring and sprat abundance, when herring is young (age 1) or the sprat abundance is low (for herring age 2), may indicate that there are factors that make some areas preferential for both species, at least until the competition becomes too strong for older herring.

These analyses are snapshots of the potential effects of environmental variables and species interactions on the herring abundance, as all data are collected in connection

to the BIAS surveys. Thus, e.g. the environmental effects on recruitment success or other processes where the species response is delayed are not explicitly accounted for. Furthermore, the outcome of the used GAM models should be studied further and complemented with alternative methods and biological data capable of explaining the observed relationships, and thus providing the ecological mechanisms behind the observed patterns.

6 ToR b) Analyse and quantify the spatial overlap of main fish predators and preys, in both open sea and coastal areas

Predator–prey overlap

There are a number of niche overlap measures in ecological literature (see Krebs, 1989 for a review; Williamson 1993; Garrison 2000). Although spatial distribution can be interpreted as an ecological niche, most of these measures cannot be used as weighting factors for local predator densities, because predator and prey densities are combined to an ambivalent measure. Focusing on incomplete predator–prey overlaps, prey abundance has to be weighted according to the proportion of the prey population available to the predator, and predator population has to be weighted according to the presence of predators in the prey habitat in order to derive population level predation pressure.

With the term PEV_i indicating the potential encounter volume, *i.e.* the water volume where prey i and the predator co-occur (Neuenfeldt, 2002), there are hence two operational ways to formulate predator–prey habitat overlap for integration into food selection and functional response models, both from the predator and from the prey perspective:

$$O_i = \frac{N_{i,j}}{N_i} \quad ; \quad Q_k = \frac{P_{k,j}}{P_k} \quad (1)$$

The predator–prey overlap O_i defines the fraction of the prey i population N in sub-area j (for example an ICES Subdivision, or the Eastern Baltic Sea as assessment unit). O_i is used when determining the prey-specific availability in the average predator functional response.

The prey–predator overlap Q_i (henceforth termed occupation) defines the fraction of the predator population k in subarea j . Q_k is applied as weighting factor when raising the average functional response to the population level to determine predation rates.

Functional response and food selection

'Functional response' (Solomon 1949) is any function that describes the change in the per capita rate of food intake at changing prey density. Holling (1959) defined type 1 (linear), type 2 (hyperbolic due to handling time) and type 3 (sigmoidal due to learning and handling time) functional responses of an individual predator for 1 single prey type (Figure 6.1). The type 2 response is based on the disk model (Holling, 1959), which is mathematically similar to the Michaelis–Menten equation (1913) based on enzyme kinetics and the Monod equation (1942) based on bacterial population growth. The handling time h and successful attack rate a of the type 2 response (Holling, 1959, *cf.* eq. (2) with $k=1$) are expressed in terms of maximum rate m and half saturation constant k of M.-M. and Monod equations by $m=h^{-1}$ and $k=(ah)^{-1}$ (Gentleman *et al.*, 2003).

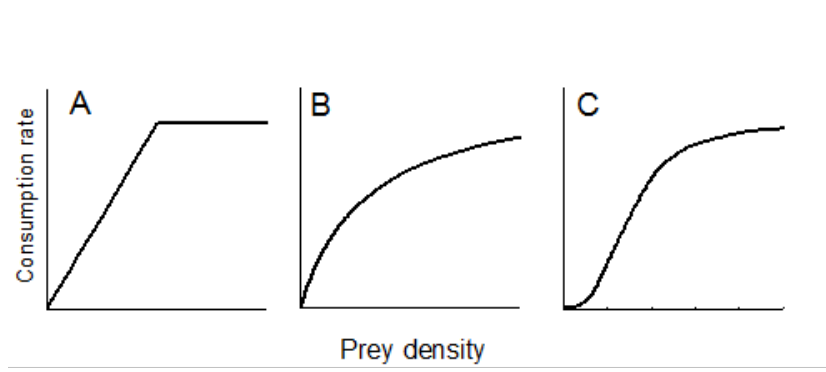


Figure 6.1. Functional response types suggested by Holling (1959); A: Type 1, B: Type 2, and C: Type 3 (redrawn from Holling 1959).

The experiments that yielded results like those in figure 10 have lasted a short time relative to the lifespan of the predator (generally a few hours, Murdoch, 1973). So the term functional response in general usage describes a short-term behavioural phenomenon (Murdoch 1973).

The majority of functional response occurring in nature can statistically be allocated to one of the three Holling types. However, alternative formulations exist which cannot be separated statistically, but have different bases and implications due to their different details of formulation (Gentleman *et al.*, 2003 and references herein). This makes it difficult to identify an appropriate functional response empirically.

Furthermore, basic knowledge of the effect of prey densities on the abundance of a prey species in the predator diet has been derived on the individual scale through experimental manipulations of homogeneous fine-scale systems (for example Holling, 1959, Murdoch, 1969). This experimentally derived knowledge cannot be scaled to derive population level predation rates without at least accounting for (i) multiple prey types, and (ii) spatial heterogeneity in predator prey overlap (not considering variable predators, long-term predator learning, interference between predator individuals, or prey-density-dependent changes in predator condition modifying attack rates).

Multiple prey species

In the presence of multiple prey species, the individual predator's functional responses for each of the prey types cannot be investigated without simultaneously considering prey-specific attack rates, handling times and changes in density. Hollig's disc equation (*cf.* Figure 1 B) for k species was first specified by Murdoch (1973):

$$f_i(\rho_1, \dots, \rho_k) = \frac{a_i \rho_i}{1 + \sum_{j=1}^k a_j h_j \rho_j} \quad (2)$$

The ratio $a_i \left(\sum_{j=1}^k a_j \right)^{-1} = \alpha_i$ was in the case of the multispecies disc equation thought

of as a measure of the predator's preference for species i , when the relative frequency of prey eaten is their relative frequency in the environment, modified by a preference which is constant (Manly *et al.*, 1972, Chesson, 1978; 1983). More general, preference was interpreted as the attack rate a on food type i relative to the attack rates on the other food types (Chesson, 1983). In functional responses where attack rate depends

for example on prey density ρ (such as Holling-type III, Figure 1 C) preference will depend on density, too.

When two prey species have densities q_1 and q_2 with an individual predator's functional responses $f_1(q_1, q_2)$ and $f_2(q_1, q_2)$, and α_1 is a increasing function of relative density $q_1 q_2^{-1}$, then positive switching (apostatic selection when different morphs of the same prey species are involved) occurs (Murdoch, 1969; Murdoch and Oaten, 1975; Chesson, 1984). On the other hand, when α_1 is a decreasing function of relative density, the negative switching (anti-apostatic selection) arises (Chesson, 1984 reanalysing Murdoch *et al.*'s 1975 data, Greenwood *et al.*, 1984a, b). Actually, frequency-dependent selection of food is likely to be common (Greenwood *et al.*, 1984b), and to assume frequency independence may hence often be misleading.

One possible cause for individual predator switching is that the predator remains in one distinguishable subarea of its habitat unless the reward rate falls below a certain threshold, when the predator will spend time leaving one subarea to go to another (Murdoch *et al.*, 1975). This notion leads to the next feature in scaling individual base knowledge to the population scale: spatial heterogeneity.

Spatial heterogeneity

Functional responses with multiple prey types as considered so far make the basic assumption that all prey individuals have equal probability of being encountered during the time interval over which predator consumption is measured. In order to fulfill this basic requirement, predator and prey have to be randomly distributed (e.g. according to a Poisson point process) and move at random (Gerritsen and Strickler, 1976). For such 'well mixed' systems, the encounter rate for a single predator depends on prey density only. However, aquatic systems are rarely 'well mixed', and a crucial refinement required for functional responses in heterogeneous systems is that the spatial dispersion of predators and prey (Cosner *et al.*, 1999) must be carefully considered on different spatial scales:

On the spatial scale of a single predator's encounter radius (*i.e.* cm to m), predators of the species *Caranx ignobilis* were relatively unsuccessful in capturing individuals in schools of *Stolephorus purpureus*, while grouped predators were more successful to capture schooled prey within an enclosure in the field (Major, 1978), one of the very few experimental studies with large marine predators under natural conditions.

On a spatial scale larger than the predator's encounter radius, but not larger than the distance a predator can move during the time unit for consumption measurement (oftentimes m to km), sequential encounter of food patches with different prey can lead to the appearance of switching without a stabilizing functional response (Murdoch *et al.*, 1975). The choice of which patch type to feed in, the optimal allocation of time in different patch types in relation to maximizing the net energy gain, and the related optimal patterns of speed and movement inside and between patches are matters to optimal foraging theory (Emlen, 1966; MacArthur and Pianka, 1966; Schoener, 1971), all of which affect predator prey encounter rates and predator food selection, ultimately modifying the predator's functional response. Also the predators have to avoid being eaten by other predators. When foraging, it is advantageous to minimize the ratio of mortality risk to energy intake rate. Juvenile bluegill sunfish (*Lepomis macrochirus*) chose patches according to this simple rule in laboratory experiments (Gotceitas, 1990). On the other hand, simple adaptations of the prey, e.g. avoiding patches with high risk of being eaten, affects occurrence and sign of predator switching (Abrams and Matsuda, 1993).

For spatial scales larger than the individual predator range during a time unit of consumption measurement up to the ecosystem scale, van Valen (1965) hypothesized that variation in diet among individuals is common within a population, and reflects the adaptation of individuals to different micro-environments. Variability of the diet compositions of tiger salamander larvae (*Ambystoma tigrinum nebulosum*) occurred due to site-dependent differences in prey availability (Zerba and Collins, 1992). The predator diet appears consequently variable, when individuals from different patches are sampled and the data are explored disregarding the heterogeneous spatial structure of the predator population habitat. Such variability can, together with individual functional responses showing no switching behaviour and sufficiently abundant food, lead to apparent negative switching on the population level (Chesson, 1984).

Overlap and population level functional response

Disregarding spatial heterogeneity on scales smaller than the population dispersion scale, and considering the simplified Baltic case with one predator (cod) and two prey species (herring and sprat, the *per capita* aggregate functional response f_i^* with respect to prey species i ($i = 1, 2$ for herring and sprat) can be calculated, considering the available data on ICES Subdivision level, as weighted average of the individual functional responses f_i in the different ICES Subdivisions (with different prey fields) with the relative predator abundances n_j / n in the subdivisions as weighting factors (Neuenfeldt and Beyer, 2006). Here, $O_j N_i$ denotes the subdivision specific prey abundances, P the total predator abundance, and $Q_j P$ the predator abundance in subdivision j (available data for Subdivisions 25, 26 and 28, therefore j is from 1 to 3):

$$f_i^* = \sum_{j=1}^3 Q_j P f_i(O_j N_1, O_j N_2), \quad (3)$$

The same concept of using local densities as weights is used in Chesson (2000) and Hassel *et al.* (1991) to determine population dynamics in spatially varying environments.

Time-series of predator prey overlap

Distribution data for calculating O and Q have been derived from the Baltic International trawl survey for cod, and the acoustic survey for herring and sprat (WKMULTBAL ICES, 2012). However, not all quarters have been covered, and the data substitution is detailed in Table 6.1. Total abundance data are available at ICES (WGSAM ICES, 2012e).

Table 6.1. Usage of survey data to calculate the relative distributions of cod, herring and sprat in the Central Baltic Sea.

	Cod	Herring	Sprat
Quarter 1	<i>Before 2000:</i> BITS Feb/Mar <i>After 2000:</i> BITS Feb/Mar	Acoustics Oct/Nov	<i>Before 1999:</i> Acoustics Oct/Nov <i>After 1999:</i> Acoustics May
Quarter 2	<i>Before 2000:</i> BITS Feb/March <i>After 2000:</i> BITS Feb/Mar		<i>Before 1999:</i> Acoustics Nov <i>After 1999:</i> Acoustics May
Quarter 3	<i>Before 2000:</i> BITS Feb/March <i>After 2000:</i> BITS Nov		Acoustics Oct/Nov
Quarter 4	<i>Before 2000:</i> BITS Feb/March <i>After 2000:</i> BITS Nov		Acoustics Oct/Nov

Overlap and occupation have been calculated for the 4th quarter from 2000 onwards. The data are presented in Figure 6.2 A-C. In Subdivision 25, the Bornholm Basin, there is a clear trend from the mid-2000s showing decrease in herring and sprat overlap in the subdivision (Figure 6.2 A). This trend is not as clear in Subdivision 26, the Gdańsk deep (Figure 6.2 B). In contrast to the decreasing overlap with clupeids, large cod (ages 4+ shown in the figure) still have rather constant overlaps to small cod (ages 0 and 1) in sub-div. 25 (Figure 6.2 A). Subdivision 28 differs from 25 and 26, because the part of the cod stock present here has been much smaller than in the other subdivisions. Cod occupation in Subdivision 26 decreased further in the late 2000s to a historical minimum.

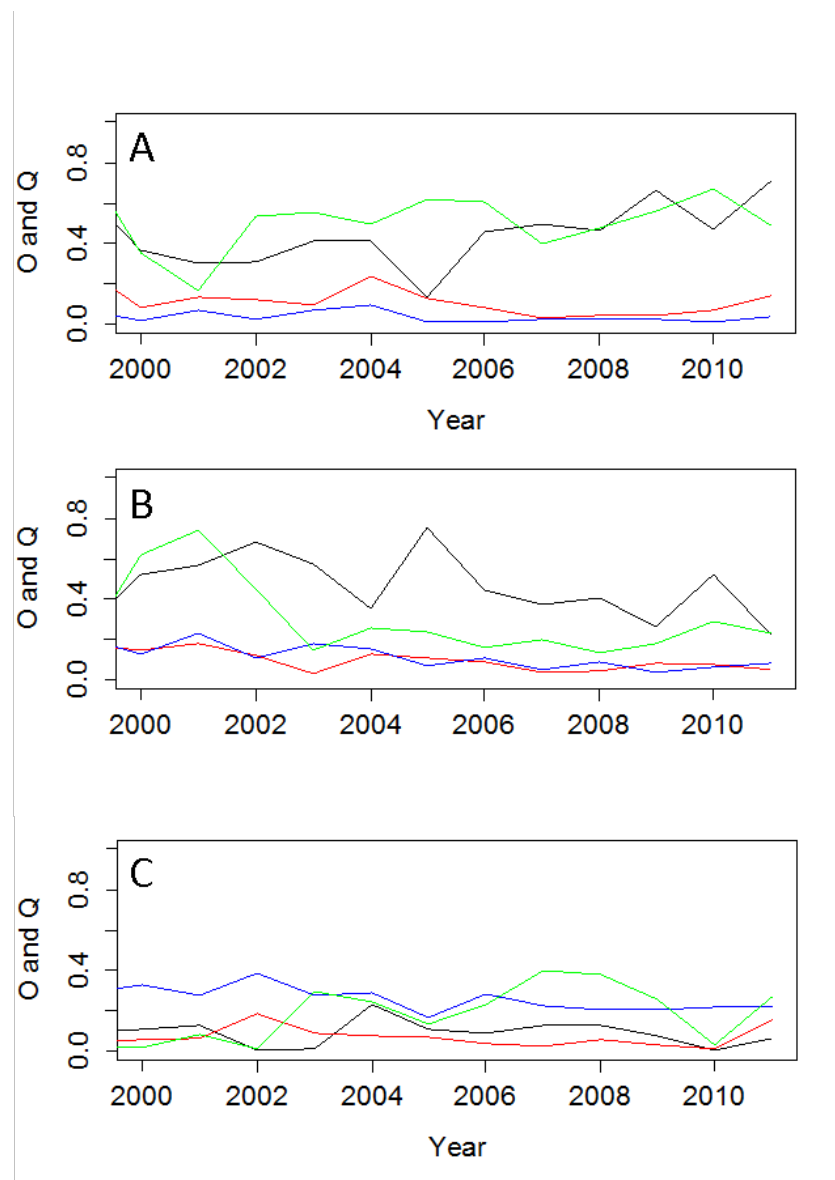


Figure 6.2. Overlap and Occupation time-series. Panel A Subdivision 25, Panel B Subdivision 26, and Panel C Subdivision 28. Black line: $Q(\text{cod})$, ratio of the cod (predator) ages 4+ stock present in the subdivision; red line: $O(\text{her})$, ratio of the age 0 and 1 herring stock present in the subdivision; blue line: $O(\text{spr})$, ratio of the sprat ages 3+ stock present in the subdivision; green line: (ration of small cod subjected to cannibalism present in the subdivision).

7 ToR c) Investigate and quantify the connectivity between open sea and coastal areas of commercially and ecologically important fish species

In the Baltic Sea, migrating fish may constitute an important link connecting coastal and offshore ecosystems, transporting energy and nutrients between systems and affecting foodweb interactions. Three-spined stickleback (Bergström *et al.*, 2013) and herring (Parmanne *et al.*, 1994) both utilize shallow coastal areas as spawning and nursery areas and thus make seasonal migrations between the systems. Cod, on the other hand, is an important species in coastal areas of the central and northern Baltic Sea during periods of high cod abundance, while when the spawning stock decreases the densities in coastal areas become very low (Casini *et al.*, 2012; Olsson *et al.*, 2012a).

While the effects of these fish migrations on energy and nutrient cycling is not known, there is some recent information on the potential effects of stickleback and cod migrations on the coastal foodwebs.

Stickleback

The three-spined stickleback (*Gasterosteus aculeatus* L.) spends a large part of its life cycle in the open sea, but reproduces in shallow coastal habitats. Stickleback might hence play a role in both offshore and coastal ecosystems. Stickleback has increased sharply in offshore areas of the Swedish part of the Baltic Proper and in the Bothnian Sea during the last decades, as seen by the trawl haul data from the Baltic International Acoustic Survey. Data from the surveillance programmes of the nuclear power plants at Forsmark and Oskarshamn show that a similar increase is also evident in two coastal areas of the two basins (Bergström *et al.*, 2013, in preparation).

Sticklebacks in coastal areas have been shown to have a large influence on the production of filamentous algae through a trophic cascade via invertebrate grazers (Eriksson *et al.*, 2011). High densities of sticklebacks give rise to a high production of filamentous algae, which may have negative effects on large-growing plants and give rise to oxygen deficiency on shallow bottoms. Furthermore, sticklebacks have also been shown to have negative effects on the reproduction of pike and perch, most likely through a combination of direct predation on eggs and larvae and competition for zooplankton prey with larvae of pike and perch (Ljunggren *et al.*, 2010; Bergström *et al.*, 2013).

While the impact of sticklebacks on the dynamics of the coastal ecosystem is clear, it is not yet known what factors regulate the dynamics of sticklebacks and what has caused the recent expansion of this species. Potentially a decrease in predation pressure (Eriksson *et al.*, 2011) in combination with increasing temperatures (Lefebure *et al.*, 2013) may be involved. The increase in stickleback means that it currently constitutes a considerable proportion also of the biomass of pelagic fish in offshore areas of the Baltic Sea. The potential impact of this increase is not known.

Cod

Gillnet survey data on cod in the coastal area Kvädöfjärden at the Swedish Central Baltic Sea coast and in Forsmark at the southern Bothnian Sea coast show that cod densities are much higher at the Central Baltic Sea coast than at the Bothnian Sea coast. Furthermore, the temporal development shows that the decrease in cod catches at the coast starts earlier in the 1980s in the Bothnian Sea area than at the Central Bal-

tic Sea area (Figure 7.1), which in turn appears earlier than in the offshore BITS survey. This shows how changes in population sizes may be seen earlier in regions outside the core of the distribution area.

The effects of cod on coastal systems have been demonstrated also in the Gulf of Riga by Casini *et al.* (2012). When cod stock size increased at the beginning of the 1980s, cod expanded its area of distribution northward and spilled over into the Gulf of Riga, while when the stock size dropped in the late 1980s cod disappeared again from the Gulf of Riga and became concentrated in its focal area, the southern Baltic Sea (Figure 7.2). The appearance and then disappearance of cod in the Gulf of Riga caused large multi-level changes in the Gulf of Riga ecosystem (herring, zooplankton and phytoplankton), showing the importance of studying the spatial connectivity between regions.

In Kattegat, the effects of cod on the coastal ecosystem are pronounced. Here, cod populations have decreased dramatically during the last decades. This decrease has given rise to a pronounced increase in mesopredators (Eriksson *et al.*, 2011). This has, together with effects of eutrophication, lead to an increase in growth of filamentous algae, which in turn has had detrimental effects on eelgrass populations (Baden *et al.*, 2012).

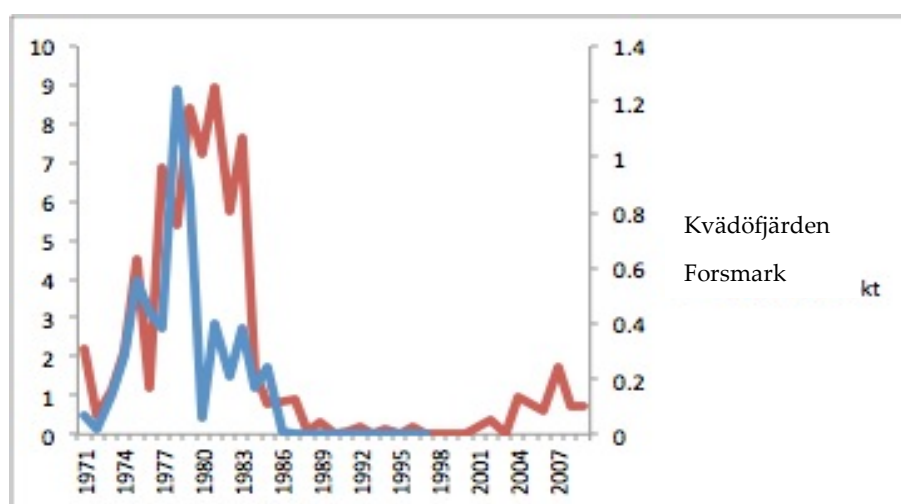


Figure 7.1. CPUE of cod in gillnet catches in Kvädöfjärden at the Swedish coast in the Central Baltic Sea and at Forsmark in the southern Bothnian Sea in 1971–2009. Data from Olsson *et al.* 2012b.

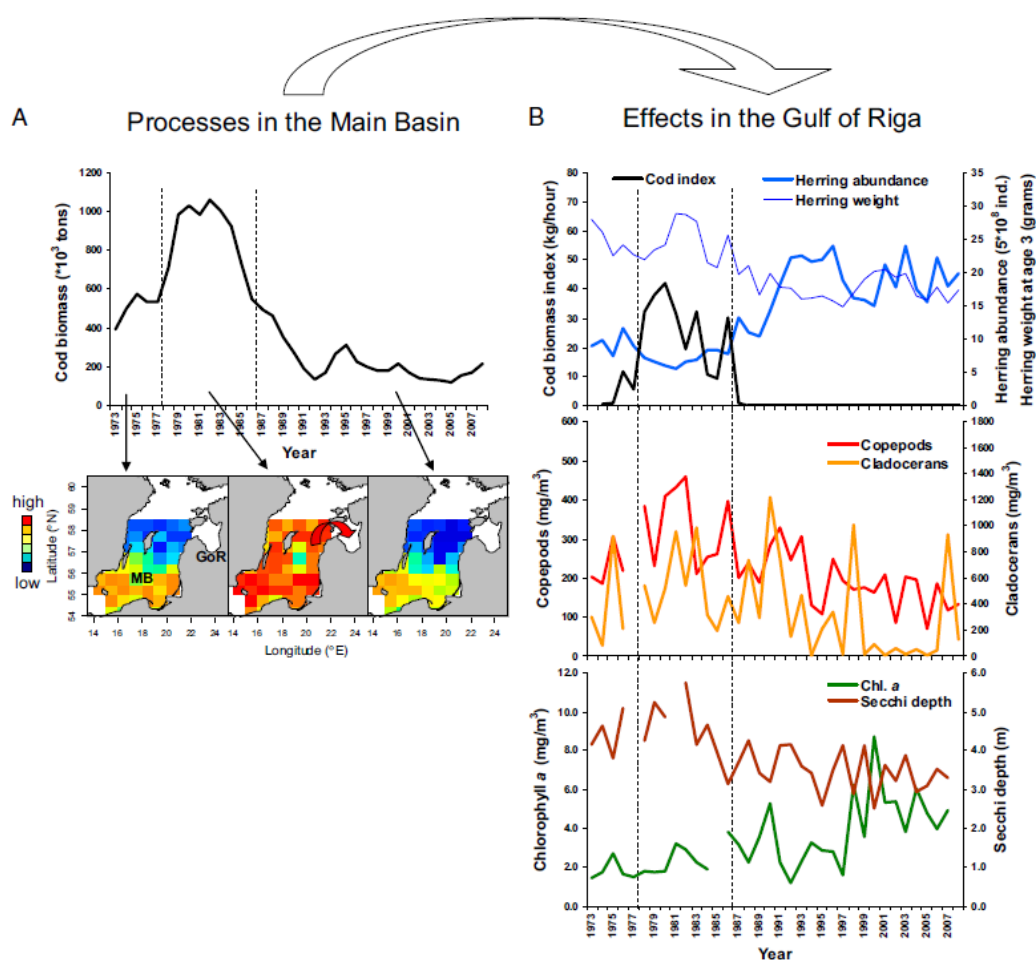


Figure 7.2. Structural changes in the MB and GoR ecosystems during the past 35 y. (A) Changes in cod biomass and spatial distribution in the MB (source habitat for cod). (B) Changes in the food-web of the GoR (sink habitat for cod), as indicated by time-series of cod biomass index, herring abundance, zooplankton, and phytoplankton. The vertical dashed lines indicate the period of maximum cod population size and range of distribution in the MB that triggered the spillover into the GoR. The scale bar next to the distribution maps is in relative values.

8 ToR d) Further develop the fish spatial indicators for offshore species

Distributional range, distributional patterns within the latter, and area covered (for sessile and benthic species) are the three indicators suggested in the MSFD for the Criterion “Species distribution” for the Descriptor 1 (Biodiversity in the MSFD). For the main commercial fish species cod, herring and sprat this can be achieved using bottom trawl and acoustic survey estimates. A first attempt to provide indices of distribution pattern was made during the SGSPATIAL 2012 for Eastern Baltic cod, Central Baltic herring and Baltic sprat. SGSPATIAL considers these indicators of outermost importance, to be usable directly in ICES Advice, but also providing the first step to estimate spatial overlaps between species to be used in predation mortality estimates used in both single-species and multispecies assessment.

SGSPATIAL 2012 started to work on indicators of spatial patterns using the centers of gravity. This was estimated by averaging the position (lat and long) weighted by the local total density. This metric is very simple and has the ability to track the mean geographic location of the population. However, care must be taken in its interpretation since the position of the center of gravity does not necessarily provide information on hot spots or areas of major concentrations. In SGSPATIAL 2013 this index was separately produced for juveniles and adults, and including for the first time the Bothnian Sea herring.

Our analyses show that the Eastern Baltic cod has shifted its center of gravity towards southwestern areas since the early 1980s. This is likely due to the strong decrease in stock size and decrease in salinity (SGSPATIAL 2012). After the early 1990s, corresponding to enduring low stock size, the cod distribution has not changed markedly (Figure. 8.1 and 8.2).

Sprat shows an opposite spatial trend than cod. The center of gravity of both juveniles and adults was located in the middle of the Baltic Proper in the 1980s, whereas afterwards a progressive movement to the northeastern Baltic Proper has occurred (Figures 8.3 and 8.4). Central Baltic Herring, on the other hand, has not shown clear temporal changes in the center of gravity (Figures 8.5 and 8.6), although Age 1 seems to have generally shifted towards the northeast during the past decade.

For the Bothnian Sea, herring seems to have slightly shifted its distribution to the south, whereas sprat to the north (Figures 8.7 and 8.8). However, the acoustic time-series for the Bothnian Sea is short and with a big jump from 2000 to 2007, and therefore it is not possible to infer if the patterns are just annual fluctuations or part of a long-time change.

The patterns of Eastern Baltic cod, sprat and Central Baltic herring conform to the previous knowledge of the changes in spatial distribution of the three species. Therefore, the center of gravity could be used as indicator of the shifts in distribution patterns. It should be accompanied by other more specific metrics of spatial patterns, as indices of hot spots or aggregation.

The indices provided here can be used in the currently ongoing process in ICES to provide ecosystem overviews (e.g. WKECOVER ICES, 2013, and WKDECOVER 2013). Especially for the Baltic Sea, large changes in species distribution have occurred during the past 40 years, and these should be integral part of the Baltic ecosystem overview. The indices suggested here also address directly the MSFD, providing clear and simple information on the changes in stocks’ spatial patterns.

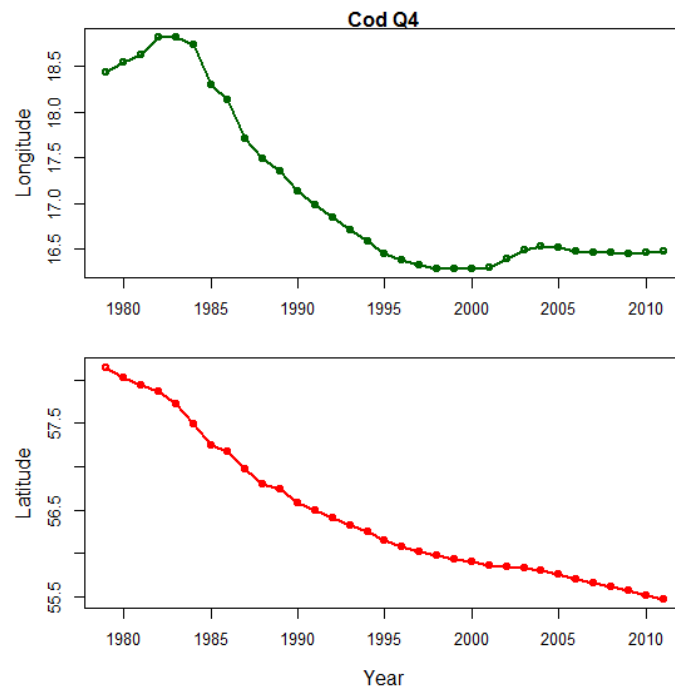


Figure 8.1. Time-series of Eastern Baltic cod center of gravity, from BIAS Quarter 4 (data modelled with GAMs).

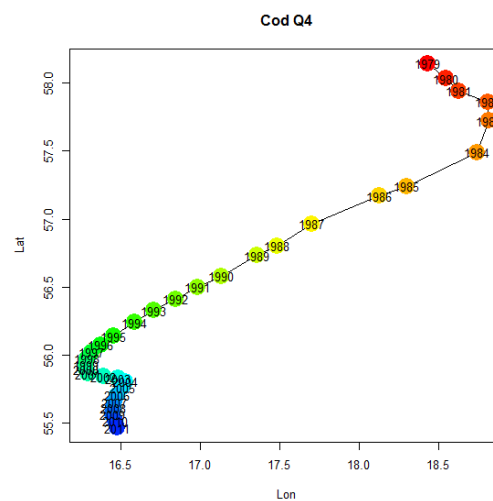


Figure 8.2. Plot of the changes in the position of the Eastern Baltic cod center of gravity, from BIAS Quarter 4. Colors from dark red to dark blue were used to better illustrate the temporal changes of the center of gravity (data modelled with GAMs).

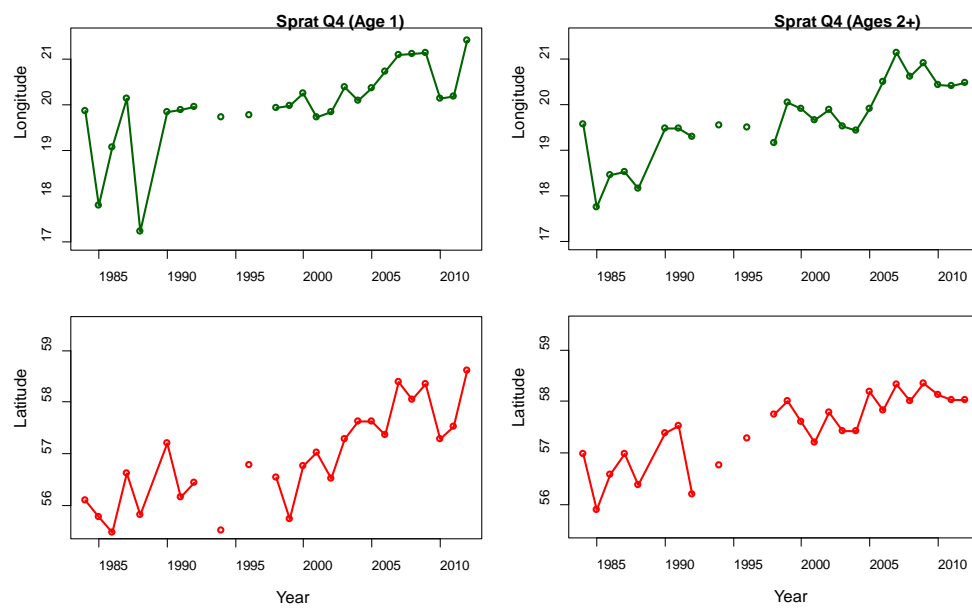


Figure 8.3. Time-series of sprat center of gravity, for age 1 (juveniles, left panel) and ages 2+ (adults, right panels), from BIAS Quarter 4. Only data for Subdivisions 25–29 are included in the analysis.

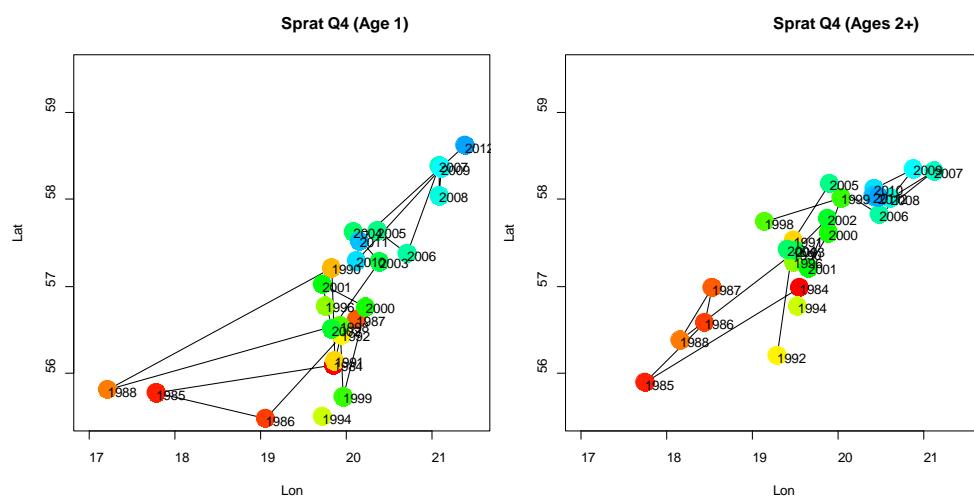


Figure 8.4. Plot of the changes in the position of sprat center of gravity, for age 1 (juveniles) and ages 2+ (adults), from BIAS Quarter 4. Only data for Subdivisions 25–29 are included in the analysis.

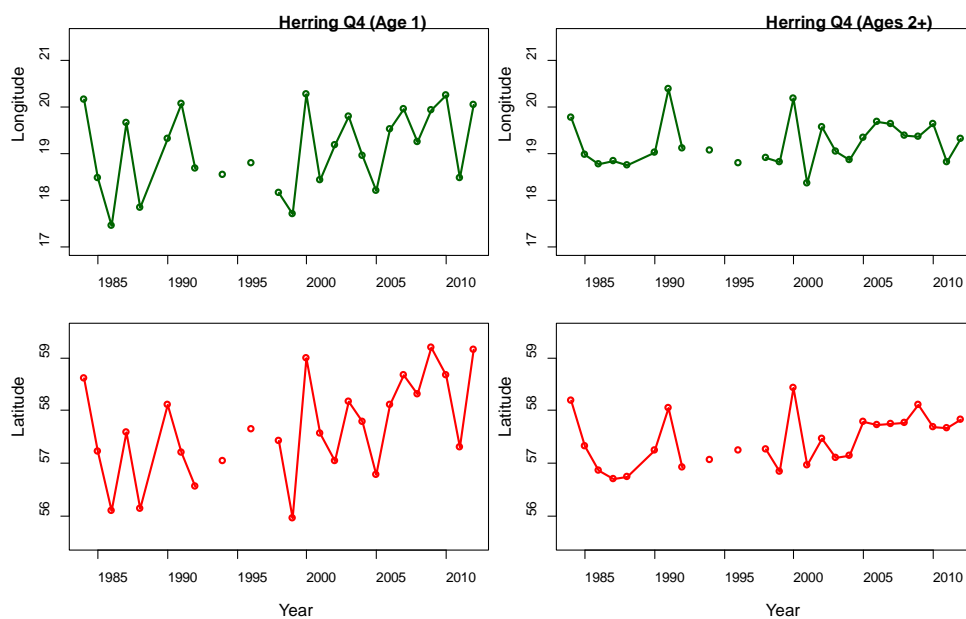


Figure 8.5. Time-series of Central Baltic herring center of gravity, for age 1 (juveniles) and ages 2+ (adults), from BIAS Quarter 4. Only data for Subdivisions 25–29 are included in the analysis.

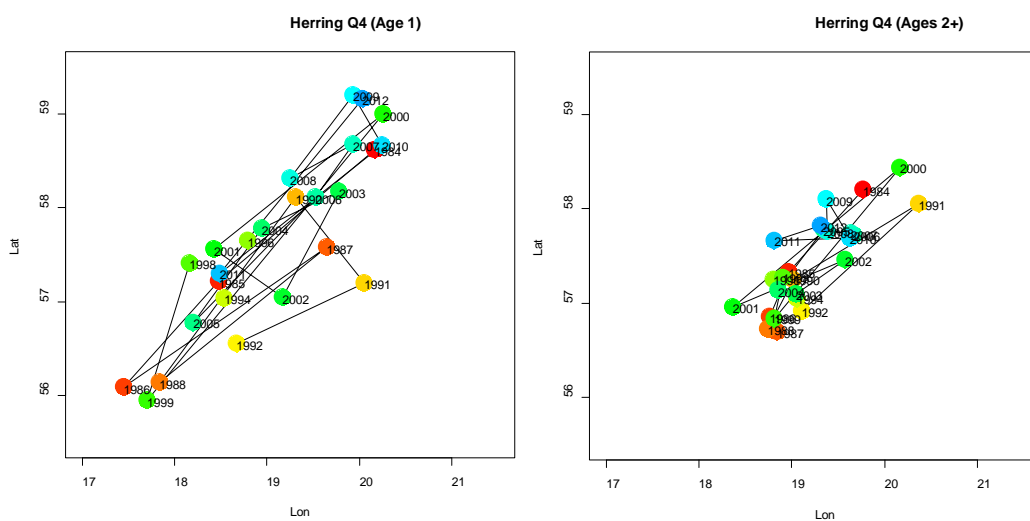


Figure 8.6. Plot of the changes in the position of Central Baltic herring center of gravity, for age 1 (juveniles) and ages 2+ (adults), from BIAS Quarter 4. Only data for Subdivisions 25–29 are included in the analysis.

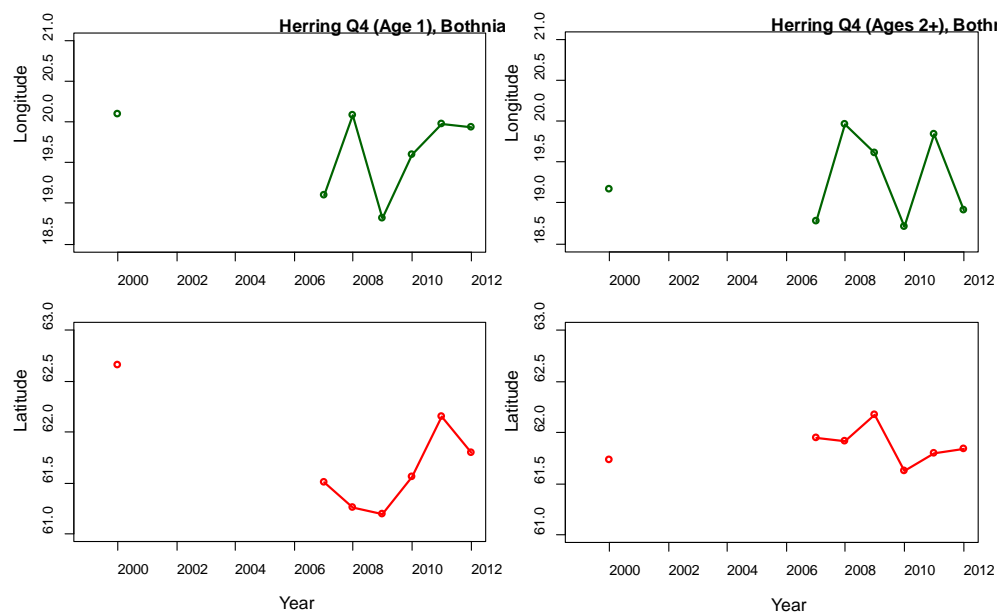


Figure 8.7. Time-series of Bothnian Sea herring center of gravity from BIAS Quarter 4.

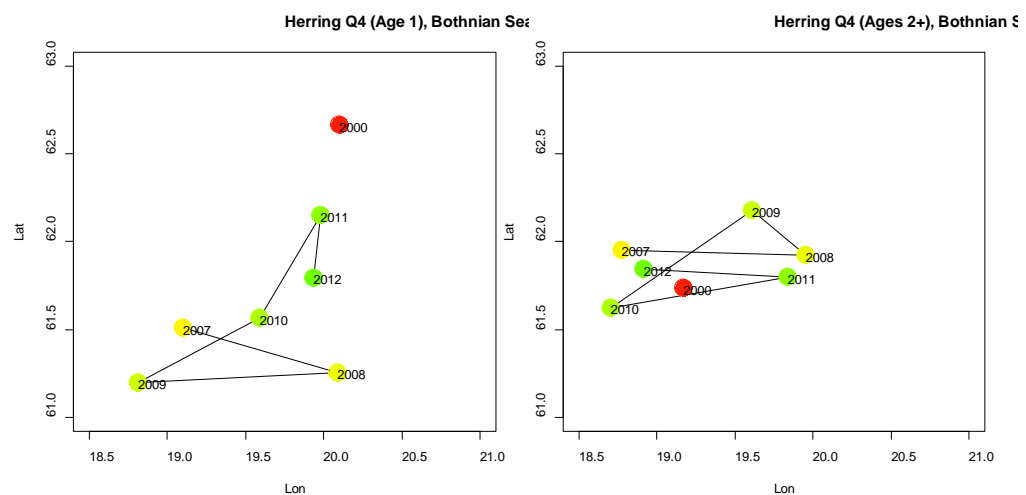


Figure 8.8. Plot of the changes in the position of Bothnian Sea herring center of gravity, from BIAS Quarter 4.

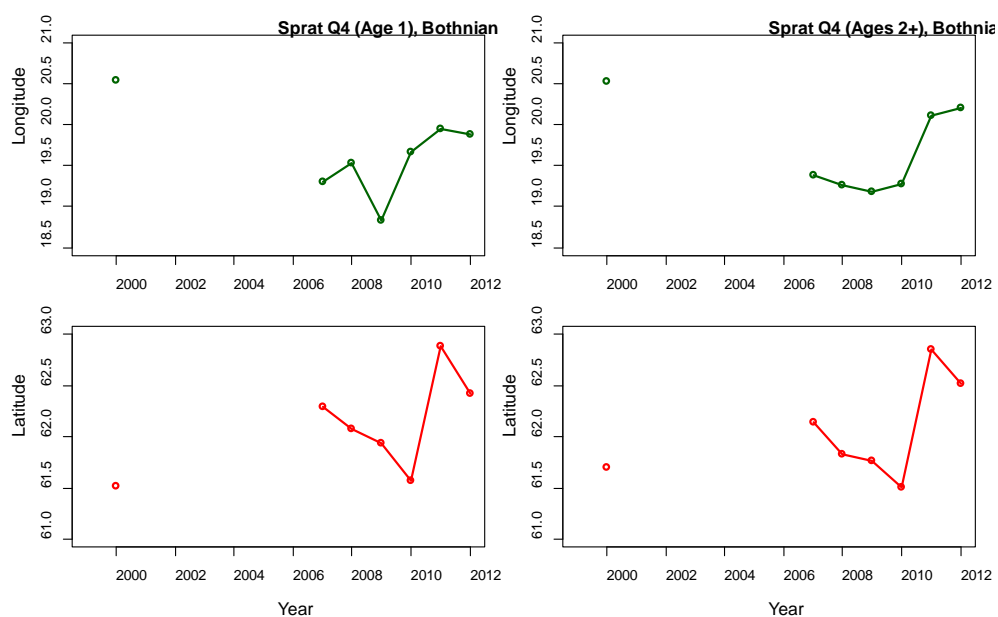


Figure 8.9. Time-series of sprat center of gravity in the Bothnian Sea, from BIAS Quarter 4.

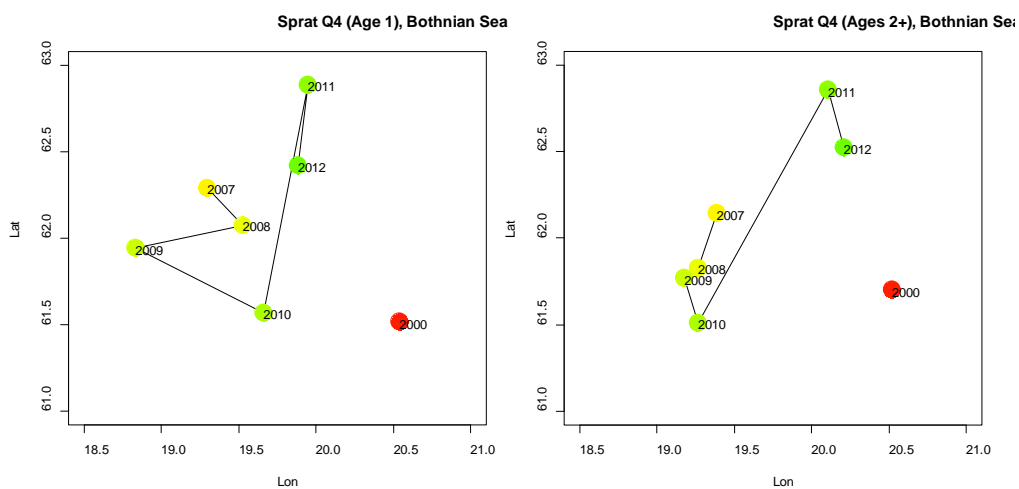


Figure 8.10. Plot of the changes in the position of sprat center of gravity in the Bothnian Sea, from BIAS Quarter 4.

9 Future development of SGSPATIAL

The Baltic has to face a largely modified spatial ecosystem set-up affecting the biological interactions among species. At the present distribution of the fish stocks in the Baltic Sea, intensive predator–prey and competitive interactions are taking place in limited areas in the southwestern and northeastern Baltic Sea, respectively. The present ecosystem setup may not be any longer structured to sustain large cod stocks (Frank *et al.*, 2005). At the same time, fisheries are competing with cod for the limited resources of sprat and herring in the southern area, which results in a substantially greater mortality on these local stock components of pelagic fish compared to the abundant resources distributed in the northern Baltic Proper.

The present situation in the Baltic Sea calls hence for a spatially explicit assessment and management of these resources. For example, a relatively higher fishing pressure on clupeids in the north could release clupeid competition in these areas (Casini *et al.*, 2011), and at the same time release prey-to-predator feedback loops (Bakun and Weeks, 2006) favoring cod recruitment in the north and a re-expansion of the stock distribution into northern areas. However, before such a management can be designed and implemented, more knowledge is needed on the processes generating spatial heterogeneity (ICES 2012c; EC 2012), i.e. to be able to identify processes which operate on a local scale, but potentially have wider ecosystem consequences. Especially, the basic ecological processes of recruitment, predation, migration and exploitation have to be re-interpreted in their spatial context in order to create the knowledge-base necessary to implement a spatially explicit ecosystem-based fisheries management. The Baltic Sea is currently chosen as a pilot case for taking into account biological interactions in the new fisheries management plans being under development in the European Commission (ICES, 2012c; EC, 2012). Thus, the experiences from the Baltic Sea can serve as a basis for similar developments elsewhere.

SGSPATIAL will continue to focus on the fish distributions and their properties at different points in time, including environmental (habitat) impact factors, trophic interactions and fisheries. Dynamics of the distributions due to passive movements or active migrations, together with environmental or anthropogenic obstructions to such movements or migrations are going to be treated as well.

Besides modelling the distributions, SGSPATIAL will also aim at quantifying movements at different temporal and spatial scales and in different life-stages. Besides quantifying these movements, emphasis is put on the characterization of obstacles for the transport or movement between nursery and feeding habitats, between feeding and spawning habitat, and (closing the life cycle) between early life stages habitats and nursery grounds. This includes the assessment-relevant movements between ICES Subdivisions.

SGSPATIAL will furthermore aim at quantifying the impact of individual scale movements on population scale spatial distributions. Besides the scaling from individuals' movement to populations' dispersion in space, focus will be on local scale mortality, for example hazards due to hot spot fisheries, predation on aggregations of juveniles, or climatic extremes such as severe winter storms. The question to be addressed is whether such local events shape larger, regional scale population abundance and recruitment strength and thus spatial distribution patterns.

SGSPATIAL will aid in including knowledge of the processes shaping heterogeneity in spatial distribution of exploited species in the existing analytical assessments for cod, herring and sprat. Besides the traditional single- and multispecies stock assess-

ments, input is generated to estimate indicators of good environmental status according to the Marine Strategy Framework Directive.

SGSPATIAL will critically revise the existing management for Baltic cod, herring and sprat, taking into account possible modifications and extensions when spatial heterogeneity is accounted for. Modification may include changes in maximum sustainable yield due to different perception of predation mortality and recruitment. Extensions may include regionalization of management measures due to local extremes in exploitation of fish biomass. Furthermore, the implementation of the Marine Strategy framework Directive will be supported by linking MSFD indicators in a spatially explicit context.

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Annex 1: List of participants – Study Group on Spatial Analyses for the Baltic Sea 5 – 8 November 2013

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Annex 2: Agenda

ICES SGSPATIAL 5 – 8 November 2013 – BIOR, Riga, Latvia

Coffee 10.30 and 15.30

Lunch 13:00-14:00

Tuesday 5 November (10 am – 18 pm)

Morning

Arrival

Afternoon

1. Welcome and practical information (Michele, Stefan and Georgs)
2. Round table introduction
3. Introduction to the meeting (Michele and Stefan)
4. ToRs and duties, adoption of the agenda, setup of the report (Michele and Stefan)
5. Work in subgroups, addressing the ToRs
6. Presentations
 - Impact of the spatial variability of cod distribution patterns on the BITS indices (Svetlana)
 - Spatial Ecopath (Susa and Caterina)
 - Predator–prey overlaps and the aggregate functional response by Baltic cod (Stefan)

Wednesday 6 November (9 am – 18 pm)

Morning

1. Presentations
 - Spatial variability of cod reproductive volume (Maris)
 - Patterns of trawling exploitation and the occurrence of hypoxia in the Bornholm Basin (Valerio)
2. Work in subgroups, addressing the ToRs
3. Presentations of results and discussion of the analyses

Afternoon

4. Presentations
 - Connectivity open sea-coast (Michele, figures from Ulf)
5. Work in subgroups, addressing ToRs
6. Presentations of results and discussion of the analyses

Thursday 7 November (9 am – 18 pm)

Morning

1. Work in subgroups, addressing the ToRs
2. Presentations of results and discussion of the analyses
3. Report writing

Afternoon

4. Work in subgroups, addressing ToRs
5. Presentations of results and discussion of the analyses

6. Report writing

Friday 8 November (9 am – 16 pm)

Morning

1. Presentations of results and discussion of the analyses
2. Report writing

Afternoon

1. Others
 - Report writing
 - Discussion on how to move on
 - ToRs for next year
 - Venue for next year

Annex 3: SGSPATIAL terms of reference for the next meeting (preliminary)

The **Study Group on Spatial Analyses for the Baltic Sea** (SGSPATIAL), chaired by Michele Casini, Sweden, and Stefan Neuenfeldt, Denmark, will meet in XXX, XXX, XXX 2014 to:

- a) Continue the analyses on the drivers of change in spatial distribution of commercially and ecologically important fish stocks (populations) in open sea and coastal areas, including connectivity between open sea and coastal areas, and between adjacent basins
- b) Further develop the fish spatial indicators of commercially and ecologically important fish species, specifically addressing the MSFD
- c) Develop process models and update existing spatially explicit models for the population dynamics of commercial fish and major ecosystem components
- d) Quantify the horizontal and vertical small-scale properties in the spatial distributions of commercially and ecologically important species, such as schools size and inter-schools distance, different types of aggregation in relation to environmental parameters, and individual vertical and horizontal movements

SGSPATIAL will report by XXX (via SSGRSP) for the attention of SCICOM and ACOM.

Supporting information

Priority	The work of this SG will support the current ICES initiative to provide multispecies advice and the EU Marine Strategy Framework Directive (MSFD). This will provide a step forward, and add the spatial dimension, to the implementation of an integrated advice and ecosystem approach in the Baltic Sea. Consequently, these activities are considered to have a very high priority.
Scientific justification	<p>The Baltic Sea is in the front line in terms of ecosystem analyses to be used in stock assessment and management. The integration of spatial consideration in this process would add a further dimension and is therefore of fundamental importance.</p> <p>In June 2012, ICES has provided for the first time an example of multispecies advice for the Baltic Sea to the EU Commission. However, both ICES and the EU Commission have pointed out that a sound multispecies fisheries management should consider the changes in spatial distribution of the interacting species. Currently, spatial considerations cannot be incorporated in the ICES multispecies advice because of the lack of sufficient and robust knowledge of the fish populations' spatial patterns and the driving mechanisms of their spatial distribution.</p> <p>Information about the changes in the spatial distribution of fish populations is also important for an ecosystem approach to the management of human activities, as directly specified in the MSFD. SGSPATIAL could serve as platform for an international coordination among the Member States to deal with motile fish species which have wide distribution and occur across the boundary of national waters, using the existing spatially explicit data from ICES-coordinated international surveys and commercial vessels.</p> <p>SGSPATIAL is specifically intended to provide the stock assessment</p>

	<p>working groups and ICES with information on the changes in spatial distribution of exploited stocks that can be directly used in single-species and multispecies assessment and fisheries advice.</p> <p>It is intended, during the life period of the SGSPATIAL, to deal also with non-commercial species to further fulfil the goal of an ecosystem approach.</p>
Resource requirements	Assistance of the ICES Data Centre in the extraction and management of the data. One Data Centre expert from ICES would be beneficial to the SG, before and during the meeting.
Participants	The Group is expected to be attended by some 15-20 members and guests.
Secretariat facilities	None.
Financial	No financial implications.
Linkages to advisory committees	Relevant to the work of ACOM and SCICOM
Linkages to other committees or groups	SSGSRP, all SG/WGs related to Baltic Sea issues (as WGBFAS, WGBIFS, WGIAB, SGEH, WGSAM), SIASM, WGINOSE, WGNARS, WGISDAA, WGISUR
Linkages to other organizations	The work of this group is closely aligned with the priorities and work of HELCOM and OSPAR, BONUS and MSFD.

Annex 4: Recommendations

Recommendation	Adressed to
1. WGSAM (Working Group on Multispecies Assessment Methods) is recommended to account for the changes in cod, sprat and herring spatial distributions in the estimation of predation mortalities and multispecies reference points.	WGSAM
2. WGIAB is recommended to include information on fish spatial distribution for the Baltic Sea Ecosystem Overview, and to consider the use of the spatial indicators suggested by SGSPATIAL.	WGIAB

Annex 5: Working Documents

WD 1

Impact of the spatial variability of cod distribution patterns on the BITS indices

Svetlana Kasatkina and Pavel Gasyukov

Atlantic Research Institute of Marine Fisheries and Oceanography (AtlantNIRO), Kaliningrad, Russia.

Introduction

The long-term bottom trawl surveys in the Baltic Sea (BITS) provide the cod abundance indices being the important component for stock assessment and management. The consideration of changes in cod spatial distribution is not involved in survey processing. However, existence of these changes is known fact (ICES, 2012).

The BITS are carried out annually by the Baltic countries in the first quarter (spring survey) and in the fourth quarter (autumn survey). The small standard trawl type TV-3#520 (TVS: distance between upper wings-ends is 13.5–14.5m, height of headline is 2.2–2.5m) and the larger standard trawl type TV-3#930 (TVL: distance between upper wings-ends is 26–27m, height of headline is 5.5–6.5 m) are used during the BITS since 2001 as standard fishing gears for vessels with different towing power. The conversion factors (CF) among two types of standard fishing gear have been estimated from data of inter-calibration experiments 2000, 2003. All observations from the small trawl TVS have been recalculated into those as if they were obtained by larger trawl TVL using these conversion factors as constant value for spring and autumn surveys by years (ICES, 2005; Lewy *et al.*, 2004). In this approach, the fish spatial distribution is assumed homogenous and constant between the years.

The authors analyzed whether the variability of cod spatial distribution should impact on estimates of BITS indices. A spatial-temporal variability of CFs efficiency was used as the indicator of this impact. Results of this analysis is shown for the Baltic eastern cod as the example

Material and Methods

The BITS abundance indices by age groups for each trawl station presented in the ICES database DATRAS by abundance indices from TVL and abundance indices from TVS recalculated with using conversion factor were used. The GLM regression (generalized linear models with robust quasi-likelihood estimation and power link functions) and PCA (Principal Component Analysis) were applied to analyze this information (Gasyukov and Kasatkina, 2010, Kasatkina *et al.*, 2013). Acoustic observations on cod distribution in the near-bottom layers of 2.5 m and 6m with using the Simrad EK60 echosounder (38 kHz) were also analyzed. These data were obtained during the Russian spring bottom trawl surveys carried out as part of BITS spring surveys. Spatial patterns of acoustic density indices (NASC values, $m^2 / mile^2$) were analyzed.

Results and Discussion

Application of GLM for analysis of cod abundance indices from BITS data revealed that efficiency of CFs may significantly change by age groups (Figure1): CFs provid-

ed acceptable estimating abundance indices for 1 age group and underestimate recruitment (Age 2) and older age groups in the all cases of BITS 2001–2012. The evidence that efficiency of CFs varies considerably by years, ICES subdivisions for spring and autumn surveys has been also obtained. Obtained changes in CFs efficiency allow assuming the existence of significant inter-annual variability of cod spatial distribution and their impact on observations with different fishing gears (TVL and TVS). Results of PCA and acoustic observations provide information for understanding changes in efficiency of CFs.

PCA revealed significant inter-annual variability of eastern cod spatial distributions by age groups (Figure 2). High estimates and high variability of recruitment abundance (age group 2) and abundance of age-groups 3–4 are peculiar to subdivisions 25 and 26 and associate with the depth strata 41–60m and 61–80m. Fish abundance of these age-groups in subdivision 25 considerably exceeds fish abundance in subdivision 26. The spatial distribution of the older age-groups (5–7) differs from the distribution of age-groups 2–4 with considerable reduction of cod abundance with age increase.

Acoustic observations revealed significant inter-annual variability of cod spatial distribution in the near-bottom layers investigated by trawl surveys (Table 1, Figure 3). It was shown that heterogeneity of fish density vertical distribution provided significant differences between fish density in the near bottom layers corresponded to the vertical openings of TVL and TVS. It was also revealed the heterogeneity of fish horizontal distribution in the near-bottom layer: the coefficient of variation of the acoustic density between the trawl stations may exceed 100%. Acoustic observations provide the evidence that trawl survey results are often of random nature and depend on the location of trawl stations as well as on the trawl effective zone parameters.

Thus, BITS indices are great extent determined by the conformity of sampling design and data processing methods with fish distribution patterns. The consideration of changes in cod spatial distribution should be incorporated into survey processing. Revealed cod spatial-temporal variability is one of key sources of uncertainty in BITS results. The impact of cod spatial distribution on BITS results is clearly demonstrated by variability of CFs efficiency which has random nature depending on the location of trawl stations and varying by years and subdivisions. Traditional practice of using the Conversion Factors (CFs) as constant value for spring and autumn surveys by years is not the solution for fitting observation with several standard fishing gears during bottom surveys. One of approach to reveal information on cod spatial distribution is accompanying trawl surveys by acoustic observations.

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Table 1. Statistical characteristics of the Ratio of $NASC_{6m} / NASC_{2.5m}$ obtained during the Russian spring bottom trawl surveys carried out as part of BITS spring surveys (data were collected on trawl stations and between trawl stations)

	Min	1st Qu	Median	Mean	3st Qu	Max
2010	1.0	1.31	1.49	1.72	2.0	4.67
2013	1.0	1.0	1.18	1.61	2.1	4.96

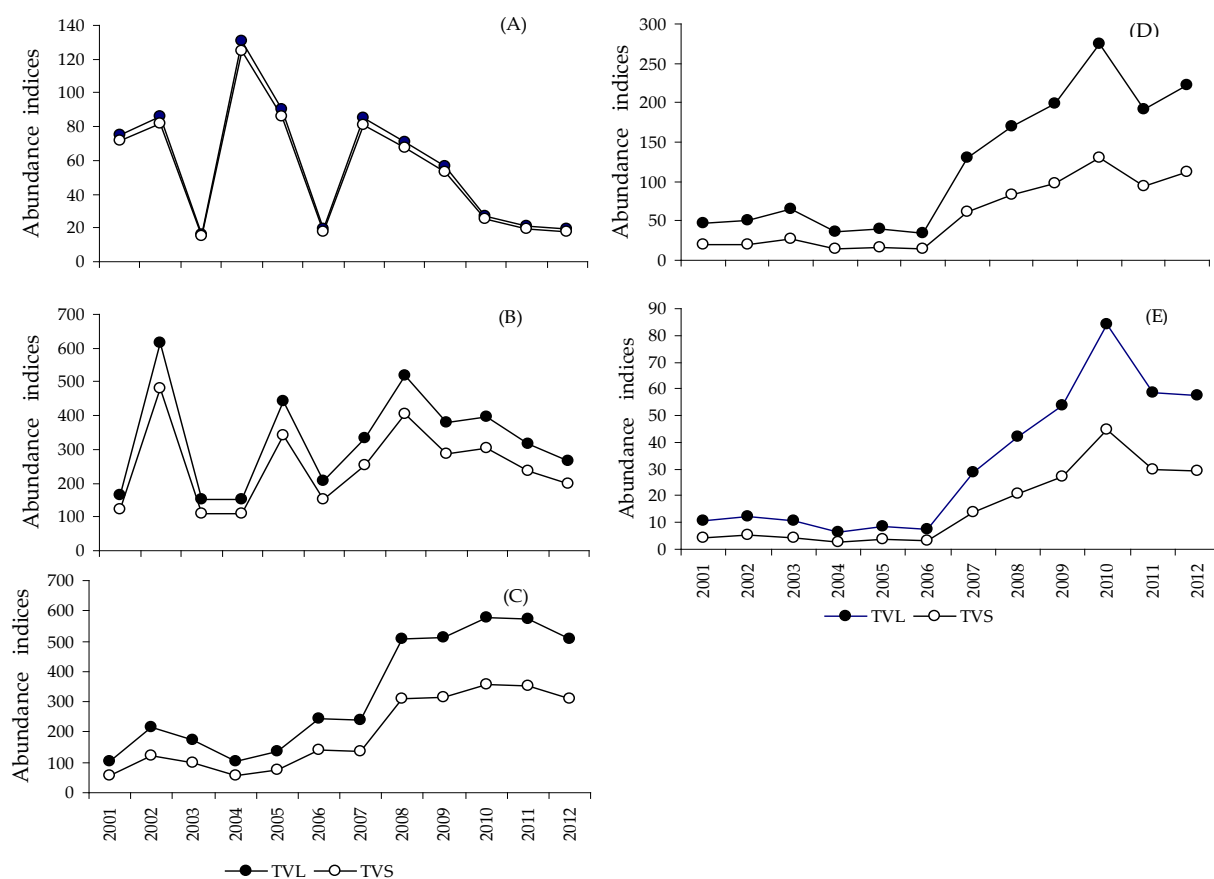


Figure 1. Predictions from GLM model for eastern cod abundance indices by years and age groups from BITS spring survey as the example.: age 1 (A), age 2 (B), age 3 (C), age 4 (D) and age 5 (E).

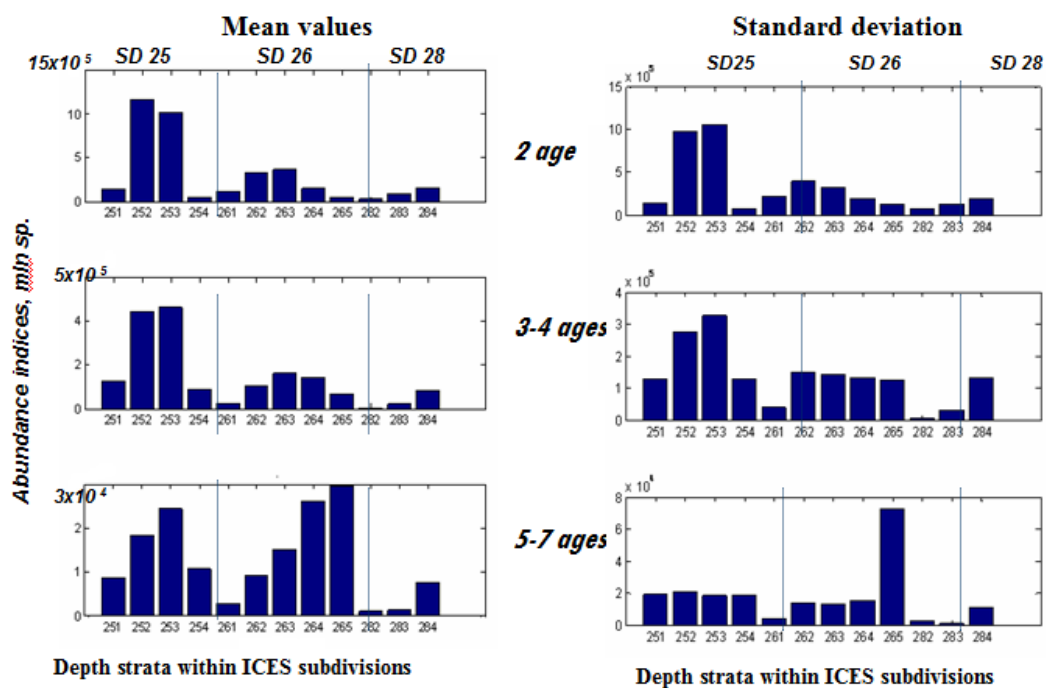


Figure 2. The long-term abundance indices of the Baltic eastern cod. The data of the International trawl surveys (BITS) carried out by the Baltic countries in the Baltic Sea during 1991–2009 (spring surveys, first quarter) were used in the PCA study.

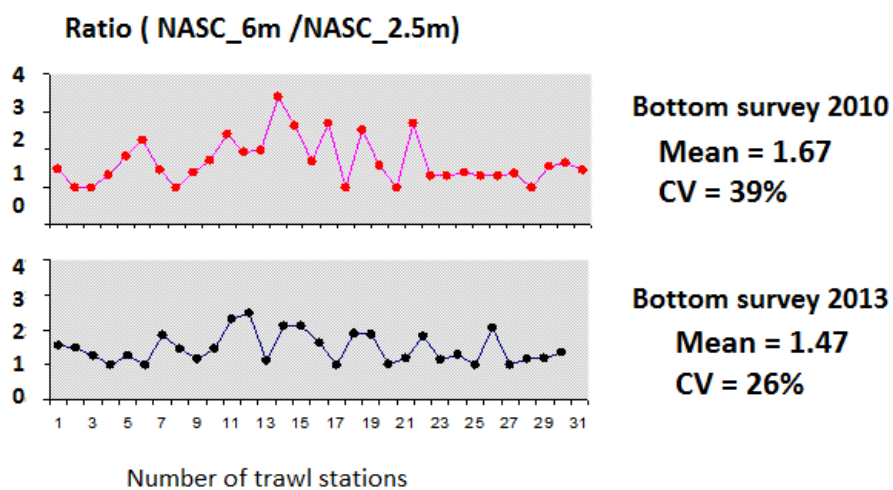


Figure 3. Variability of the Ratio of $NASC_{6m} / NASC_{2.5m}$ obtained on trawl stations during the Russian spring bottom trawl surveys carried out as part of BITS spring surveys.

WD 2

Patterns of trawling exploitation and the occurrence of hypoxia in the Baltic Sea

Valerio Bartolino et al.

The Baltic Sea is characterized by high environmental variability. Seasonal and inter-annual variability in the river run-off and inflow of Atlantic waters are among the main drivers which determine the hydrography of the Baltic environment.

Hypoxia is a natural phenomenon in the Baltic Sea. However, anthropogenic activities are likely a major driver of the increased oxygen deficiency in the Baltic over the past half century, as larger nutrient loads have increased algal production and hence sedimentation of organic matter to the deep water.

Atlantic cod generally show avoidance behaviour for hypoxia. However, experimental studies showed that it can tolerate low oxygen levels for several hours and it has the ability to spend short periods of time in extreme hypoxic conditions if well oxygenated waters are available and accessible. Recently, electronic archival tags showed that cod in the Bornholm Basin does "hypoxic diving" to feed on zoobenthos for short periods of time, likely taking the advantage of increased vulnerability of burrowing species during hypoxia.

Despite the large number of studies on the effects of hypoxia on the physiology, behaviour, and reproductive success of cod, to our knowledge there is no study on how the occurrence of hypoxia may affect fish exploitation patterns. It would be of primary importance for the management of cod in the Baltic to understand if fish behavioural responses to rapid hydrographic changes and oxygen deficiencies may affect its catchability to the fisheries. We are currently investigating changes in the distributional pattern of effort and catches of the Swedish cod fisheries in the Bornholm Basin to variations in the hydrographic properties in the area.

Preliminary results show marked differences in the seasonal patterns of exploitation of the bottom (OTB) and mid-water (OTM) trawl fisheries, particularly in relation to the distribution and dynamics of the hypoxic areas in the central part of the Bornholm Basin. Due to the presence of a fishing closed area during the summer period, two main fishing seasons characterize the exploitation pattern. The OTM fishery targeting cod is operative during a limited period of time that in most years is restricted to March-June, while the OTB fishery operates during most of the years (with the exception of the summer closure). Comparison of the effort distribution of the two fisheries during the first half of the year shows a high concentration of the OTB activity within few kilometres around the boundaries of the hypoxic areas. On the contrary, the OTM activity largely concentrates in the water column above hypoxic areas.

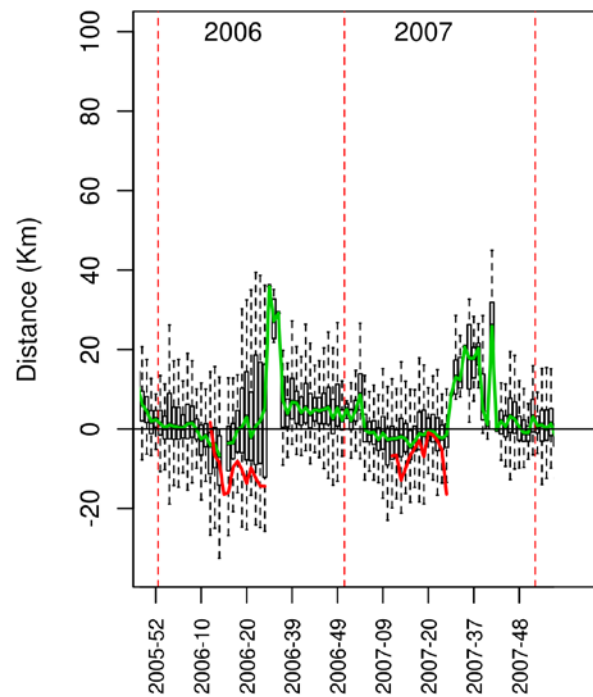


Figure 1. Average distance between VMS pings of the Swedish cod fisheries and the boundary of the oxycline at 2 ml/L for bottom (OTB, green) and mid-water (OTM, red) trawlers for each week during the time period 2004-2010.

WD 3

Reproduction volume of Eastern Baltic cod*Maris Plikshs*

The concept of reproduction volume (RV) of Eastern Baltic cod is based on limiting hydrological parameters that is required for normal spawned cod egg development. In experimental studies was found that a salinity of at least 11 psu is necessary for spermatozoa motility (Westin and Nissling, 1991) Minimum dissolved oxygen requirement for egg development was found to be 2.0 ml/l (Wieland *et al.*, 1994). Therefore the limits of the RV were taken as salinity >11 psu and dissolved oxygen concentration >2.0 ml/l. If any of spawning grounds water volume with such conditions was not observed the RV was taken equal to 0. These volume estimates also should be considered as approximations because they assume 100 and 0% egg survival inside or outside RV.

Calculations of Baltic cod RV were based on standard oceanographic stations from sampling in February, May and August (cod spawning time) in the central parts of the main spawning deeps (Figure 1):

- Bornholm Deep -station BY5A (55°15'E and 15°59'N, depth 90m);
- Gdansk Deep -station P1 (55°05'E, 19°15'N, 105m);
- Gotland Deep -stations BY9A (56°05'E, 19°10'N, 125m);
-station 43 (56°42', 19°52', 153 m) and
-station BY15A (75°18'E, 20°04'N 240m.)

The positions of the salinity (11 psu) and oxygen (2.0 ml/l) depth limits of the RV were calculated with the precision of 1 m. These values were then applied to the bathymetry of the Baltic Sea using the contouring software “BathypsoGraph” (Wulf and Anderson, University of Stockholm) to evaluate the volume in a given area. The contouring software used for the volume estimations employs the hypsographic function for the Baltic proper derived from a gridded 5' x 5' bathymetric database by Stigebrandt (1987) and Stigebrandt and Wulff (1987). This function quantifies the volumes of water below horizontal surfaces at given depth levels. The depth levels at which horizontal surfaces are chosen for calculating water volumes are defined by the vertical profile of hydrographic data collected at the station in the basin. Hence, the volume of water between any 2 surfaces (e.g. those represented by the 11 psu and 2 ml/l oxygen levels) can be derived by assuming horizontal homogeneity on a basin-wide scale. (MacKenzie *et al.*, 2000). This involves some simplifications and assumptions and only the three largest cod spawning grounds were covered.

During recent 20 years the cod spawning timing has gradually changed from late spring to summer (Wieland *et al.*, 2003) hence the RV is adjusted for such change in our analysis e.g. RV in May is used for the time period 1952–1990 and RV in August for 1991–2011.

The Baltic cod RV has shown great inter-annual variation during the last 59 years with a maximum of 635.2 km³ in 1972 and a minimum of 35.8 km³ in 1999 (Figure 2). Only the Bornholm Deep sustained possible successful spawning conditions throughout the sampling period. RV presence in the south-eastern Baltic spawning

grounds (Gdansk and Southern Gotland) was sporadic, after major inflows (Matthäus, 2006).

On the basis of RV distribution between the different spawning grounds it is possible to distinguish three typical situations or years:

- 1) Aeration years, when RV is observed in all the spawning grounds and volume within each area is large. The near bottom layers are characterised by high dissolved oxygen concentrations, 3-4 ml/l (17 cases from 59);
- 2) Intermediate years, when RV has been observed in Bornholm and in one of south-east spawning grounds - Gdansk or Southern Gotland (16 cases);
- 3) Stagnation years, when RV is only present in the Bornholm spawning ground. (26 cases, 16 of which occurred after 1981).

Analysing the RV anomalies during 1952–2011 it can be seen that significant change has occurred in 1981 when negative anomalies started to prevail in all spawning grounds (Figure 3). Obviously it is related to the decrease of North Sea/Kattegat water inflow intensity (Matthäus and Naush, 2003; Matthäus, 2006). This suggests that cod reproduction in the Baltic substantially worsened after 1981 in all spawning grounds. Exceptional situations are observed only after 1993 and 2003 inflows. Baltic integrated assessment that is based on principal component analyses and take into account 52 environmental parameters (Möllman *et al.*, 2009) identify regime shift in the central Baltic around 1986. Obviously eastern Baltic cod reacted much earlier on the ecosystem changes that in great extent were associated with Baltic – North Sea water exchange. Thus it can be stated that cod recruitment and corresponding stock abundance decreased due to exclusion of the eastern spawning grounds from successful reproduction.

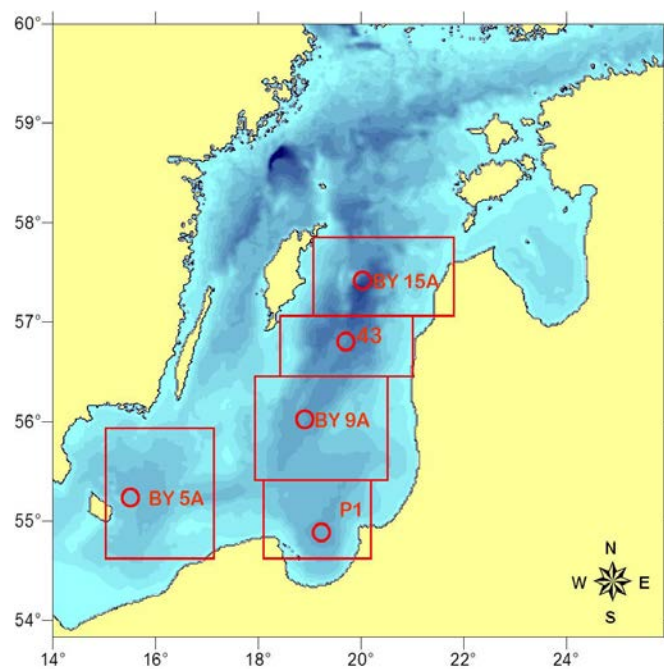


Figure 1. Standard oceanographic stations in the central Baltic deeps. Squares indicate area for which the Reproduction volume was calculated.

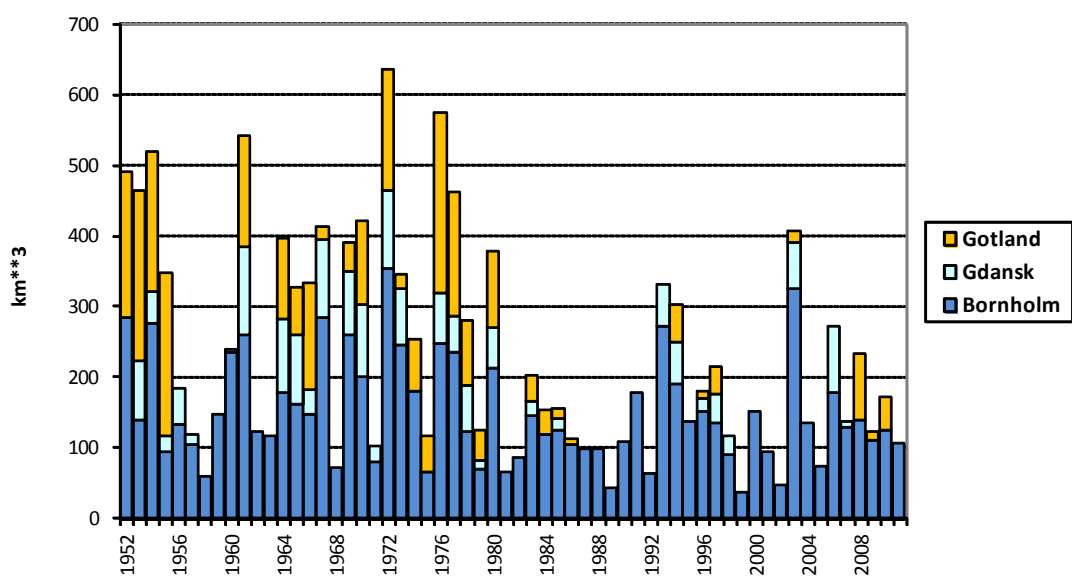


Figure 2. Cumulative potential Reproduction volume of eastern Baltic cod in the main principal spawning grounds (km³).

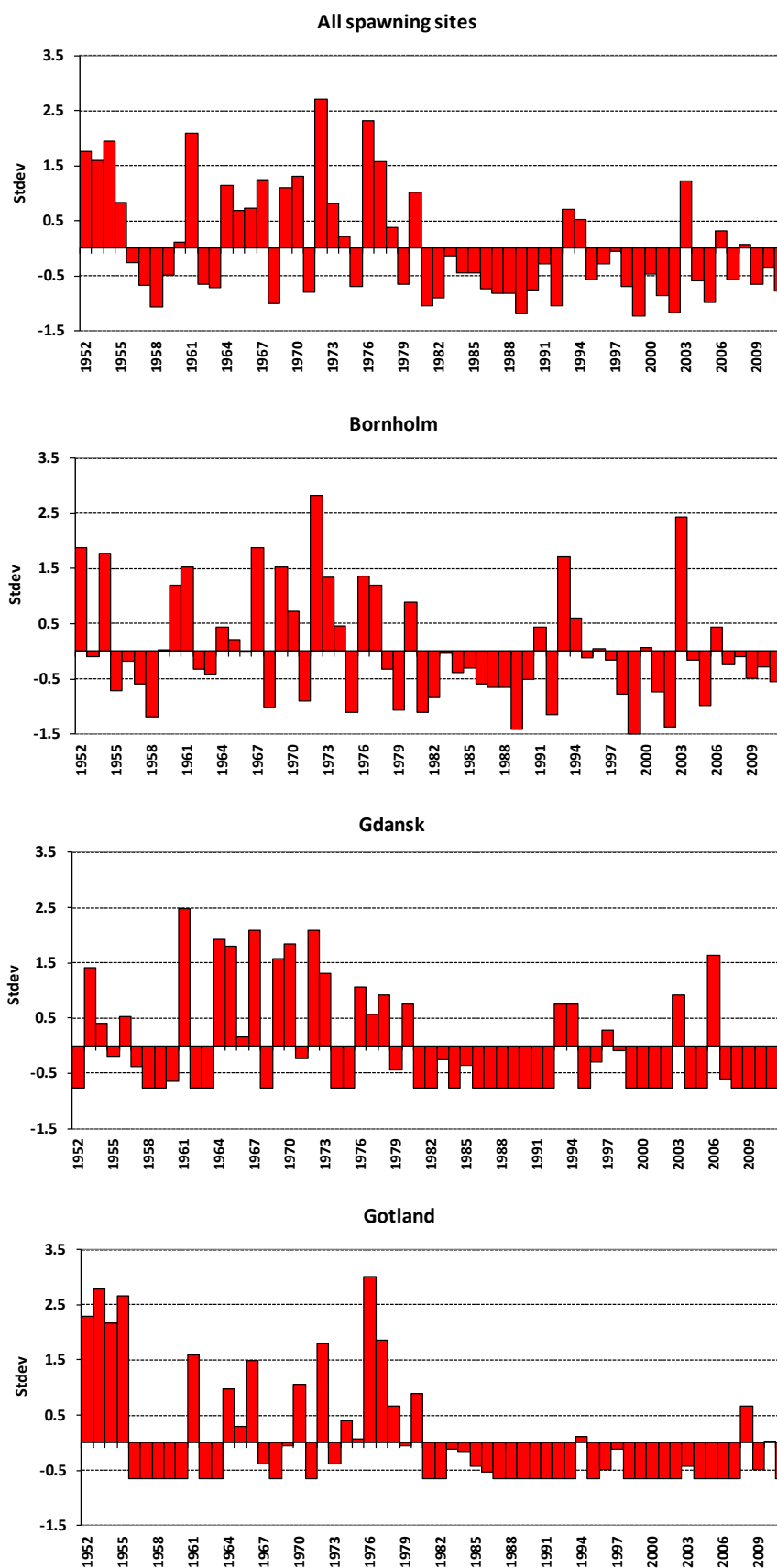


Figure 3. Anomalies of Eastern Baltic cod reproduction volume by principal spawning grounds.

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WD 4**Ecospace – the spatial-temporal module of Ecopath with Ecosim modelling framework**

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Ecopath with Ecosim (EwE, Christensen and Pauly 1992) is worldwide the most extensively applied approach to describe trophic flows in aquatic food webs (Fulton 2010). In the Baltic Sea, the mass-balance (Ecopath) and time-dynamic (Ecosim) modules of EwE have been used to simulate both the past (e.g., Harvey *et al.*, 2003, Sandberg *et al.*, 2007, Tomczak *et al.*, 2012) and future (up to 2098, Niiranen *et al.*, 2013) food web dynamics. However, these models are not suited to resolve the spatial food web dynamics, such as the degree of spatial overlap between predators and their prey, e.g., due to heterogeneous habitat or localized fishing.

The spatial-temporal module of EwE modelling framework (Ecospace) (Walters *et al.* 1999) is yet to be applied in the Baltic Sea. However, Ecospace models have been built for several other marine areas, e.g., the North Sea (Mackinson and Daskalov, 2007), Adriatic (Fouzai *et al.*, 2012) and South-East Pacific (Ortiz 2010). Ecospace is an Eulerian-type 2D temporal model, where biomass is distributed and moves between water cells across a user defined grid-map (Figure 1a). The biomass in each spatial cell is calculated at every time-step (monthly) following the Ecosim differential equations, including the temporal changes in fishing. However, Ecospace does not inherit the external Ecosim forcing functions on productivity (i.e., environmental forcing) assuming that only little information is available about how it should be distributed spatially (Walters *et al.*, 1999). The user assigns a habitat type (e.g., depth (Figure 1a), bottom-type or level of hypoxia) for each cell of the base-map and must then for every functional group define whether this habitat is favoured or disfavoured by them. Relatedly, the level of movement between cells (Figure 1b) is defined according to the habitat preference of functional groups, as well as the functional group biomass and the availability of prey in the cell of origin. The movement is faster out of non-preferred than preferred habitats. Additionally to the parameters inherited from the Ecopath and Ecosim modules, the user needs to define functional group-specific (i) base dispersal rate in the preferred habitats, as well as (ii) relative dispersal and (iii) feeding rates in the non-preferred habitats.

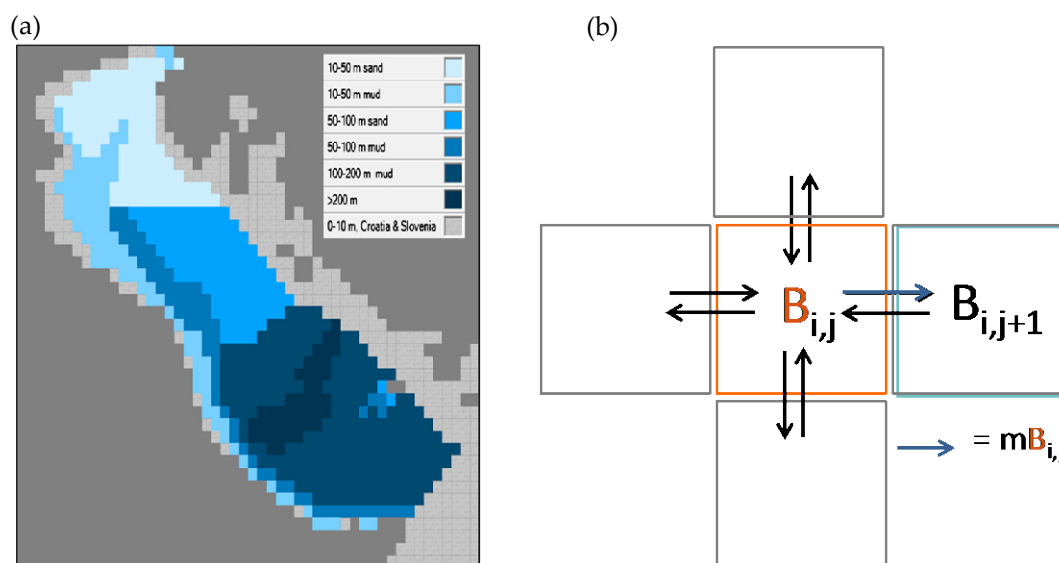


Figure 1. (a) An example of an Ecospace base-map (Adriatic Sea, Fouzai *et al.* 2011), where habitats have been defined according to depth; (b) movement between the adjacent Ecospace grid cells, where B:biomass and m:rate of movement out of the cell of origin.

One of the potential weaknesses of the current Ecospace models is that the extent and quality of the habitats defined cannot change in time (Steenbeek, 2012). Also, downloading the base and habitat maps from, e.g., GIS, has not been a default property in Ecospace. Recently, however, Steenbeek *et al.* (2013) described, using monthly fields of primary production as an example, how GIS formatted data can be uploaded to an Ecospace model and also updated at each time-step. Furthermore, the updated Ecospace module will introduce a concept of “habitat foraging capacity” (Steenbeek, 2012), in which several environmental/habitat characteristics can be applied on a single cell and their combined effects will define the total favourability of the cell as a habitat.

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