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Understanding the spatio-temporal dynamics of demersal fish species in the Baltic Sea

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Front cover: Cod. Photo: Pauline Snoeijs Leijonmalm
Back cover: Flounder. Photo: Pauline Snoeijs Leijonmalm

Abstract

The Baltic Sea is one of the largest brackish areas in the world with mixed salt and fresh water. The particular hydrological characteristics of this sea, such as the temperature and salinity gradients from the Danish Straits to the northernmost part of the Gulf of Bothnia as well as the hypoxia of its deep waters, make it a unique ecosystem. During the last century the Baltic Sea has undergone major structural changes not only in its physical characteristics but also in the biological communities inhabiting it.

Cod (*Gadus morhua*) and flounder (*Platichthys flesus*) are two key species of the Baltic Sea ecosystem. Cod in the Baltic has experienced huge changes in spatial distribution, variations in growth, mortality and abundance in the last 40 years, but still the environmental and the biological drivers that have caused these modifications are unclear. Much less is known for flounder even though it is predated by cod and could potentially compete with it for benthic resources.

All these changes have caused and are causing problems to the fishing industry and the consequent management.

The present situation of the Baltic Sea illustrates the importance of understanding on the processes causing spatial heterogeneity and changes in the fish population dynamics. Such knowledge is crucial in order to work out a better management of the resources.

This essay has the aim of reviewing the state of the knowledge on the spatio-temporal dynamics of cod and flounder in the Baltic Sea and to point out the knowledge gaps that need to be filled.

Keywords: cod, flounder, Baltic Sea, spatio-temporal dynamics.

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1 Introduction

Ecosystem based approach to fisheries management has been widely recognized as one of the main tools for achieving a sustainable use of resources and ultimately healthy marine ecosystems (Pikitch *et al.,* 2004). The basis of this approach is an ecologically sound resource conservation that responds to the reality of ecosystem processes (Marasco *et al.*, 2007).

Taking into account species distribution when developing an ecosystem based fisheries management strategy has been increasingly recognized as essential (Eero *et al.,* 2012b). The distribution of a marine species is the result of the connections between the intrinsic characteristics of the populations, trophic interactions, environmental and anthropogenic factors (Bonsdorff, 2006; Ojaveer *et al.,* 2010; Casini *et al.,* 2014). Because of all these interdependencies, the abundance of a species in a determined area is likely changing over time. Hence taking into account not only the spatial component but even the temporal one of these dynamics is of primary importance (Marasco *et al.*, 2007; Hsieh *et al.*, 2008). From a management perspective the spatial distribution of the species, especially in the case of competitors or prey-predator interactions, could give valuable information that can be used, for example, to estimate predation mortality and estimate reference points in order to better manage one or more stocks (STECF, 2012; ICES, 2013).

Cod (*Gadus morhua*) and flounder (*Platichthys flesus*) are two key species of the demersal Baltic Sea ecosystem both ecologically and commercially. According to Begg *et al.* (1999) a stock describes characteristics of semi-discrete groups of fish with some definable attributes which are of interest to fishery managers. In the Baltic Sea cod and flounder are managed and assessed as two different stocks, in the case of cod, and four stocks, in the case of flounder (ICES, 2014a).

This essay has the aim of reviewing the current knowledge on the spatio-temporal dynamics of cod and flounder in the Baltic Sea and identifying main gaps in knowledge.

Since hydrological characteristics, such as salinity, temperature and oxygen are central factors determining the distribution of marine species in the Baltic, a small introduction of the Baltic Sea hydrology is firstly presented.

Subsequently I will give a short outline of the biology of the two study species, since understanding it is essential for having a clear picture of the biological background of the species distribution.

Finally in the last section of this essay, the spatio-temporal dynamics of cod and flounder are reviewed and a brief analysis of the main gaps in knowledge is also given, together with an assessment of studies needed to fill these gaps.

2 Baltic Sea hydrology

The Baltic Sea is one of the largest brackish areas in the world with a mix of salt and fresh water. The maximum depth of the Baltic is 459 m while the average depth is 53 m; nearly one third of its extension is characterized by depths of less than 25 m. The fresh water inputs come from precipitation and a number of large and small rivers while the salt water inputs come from the North Sea trough the straits between Denmark and Sweden (ICES, 2008). This results in a marked salinity gradient from southwest to northeast and a permanent halocline. The surface salinity in the innermost part of the Baltic is of less than 3 psu (Practical Salinity Unit). It then increases gradually moving towards southwest reaching values between 10 and 15 psu in proximity of the straits between Denmark and Sweden. The time series of surface salinity shows a decrease (Figure 1) and the forecasted changes in salinity confirm this declining trend (ICES, 2014a; Vuorinen *et al.*, 2015).

The change in salinity is one of the crucial drivers of changes in distribution of the different species inhabiting the Baltic Sea. The decrease in salinity is also the cause of important quantitative and qualitative changes in fish fauna such as, for example, a decrease in growth and condition of herring with a related decline of approximately 50% of herring Spawning Stock Biomass (SSB) (Casini *et al.*, 2010; Vuorinen *et al.*, 2015). Salinity is also a limiting factor for successful reproduction of marine species in the brackish Baltic Sea. Low salinity immobilizes sperm and also diminishes egg survival (Nissling *et al.*, 2002). Low salinity also means reduced buoyancy of eggs leading to pelagic eggs sinking into the more oxygen-depleted deeper water where survival is not possible.

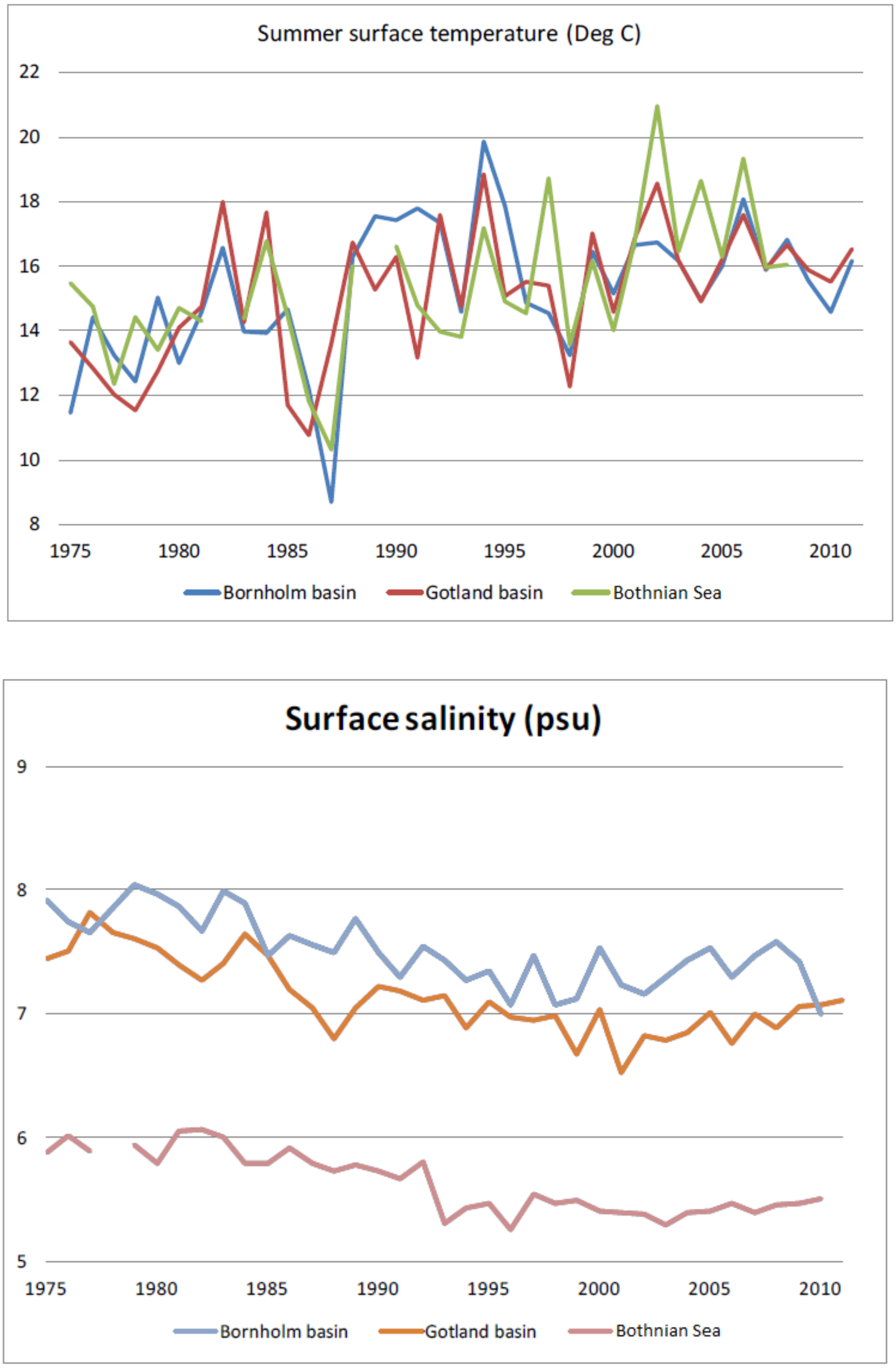

Figure 1. Time series in summer surface temperature and salinity in the Bornholm Basin, Gotland Basin and in the Bothnian Sea (modified from ICES, 2014a).

Temperature is another key factor shaping the Baltic ecosystem. During winter part of the Baltic is covered by ice and the water temperature can get down to -2 °C while in summer it can reach 25 °C. The summer surface temperature shows a increase over the past 40 years (Figure 1). Temperature is particularly important for coastal areas; it impacts the recruitment success, the growth and year class strength of fresh-water species like *Perca fluviatilis* and even short term changes in water temperature may have a significant effect on the species composition of coastal zones (HELCOM, 2006; Olsson *et al.,* 2012).

The Baltic Sea has an estuarine water circulation regime consisting of inflows of saline and oxygenated bottom water and superficial brackish currents flowing out of the area. The scarce water exchange between this area and the North Sea, a water residence time of about 25-30 years and the lack of deep water production (Döös *et al.,* 2004) make the Baltic Sea prone to hypoxia (defined as oxygen concentrations below 2 mg L^{-1}) (Carstensen *et al.*, 2014).

The ventilation of the deep water is governed by irregular large inflows called Major Baltic Inflows (MBIs) that are caused by large-scale and local meteorological forcing (occurring mostly between October and April), and have large variations in frequency and magnitude over time-scales of decades (Döös *et al.,* 2004; Matthäus *et al.*, 2008; Reissmann *et al.,* 2009). Although the MBIs may improve the oxygen conditions in the bottom waters in the short term, they also enhance the stratifications of the water column that could lead to a reduction of vertical mixing and oxygen fluxes in the long term (HELCOM, 2013). Before the mid-1970s the water inflows were frequent while only four MBAs were recorded thereafter, in 1976, 1983, 1993 and 2003, causing a progressive decrease in salinity and dissolved oxygen (ICES, 2008).

The area of hypoxia in the Bornholm and Gotland basins has increased from around 5,000 km^2 to over 60,000 km^2 over the past 115 years (Figure 2) (Carstensen *et al.,* 2014). The bottom water hypoxia is a main factor shaping the benthic community in the Baltic Proper causing a lack of macrofaunal biomass (the missing biomass is estimated as 1.7 million tons) on huge extensions of the sea bottom with repercussion on all trophic levels of the Baltic Sea ecosystem (Karlson *et al.*, 2002; Villnäs *et al.,* 2013). For example the lack of benthos could have been one of the causes triggering density-dependence effects such as increased cannibalism and decrease in growth on cod populations (Eero *et al.*, 2012b).

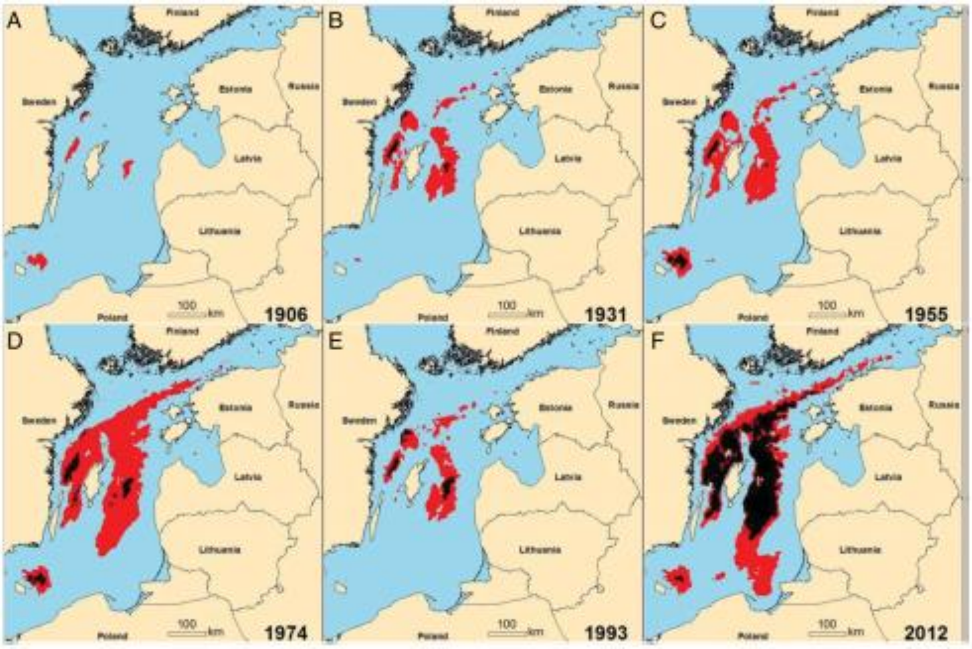

Figure 2. Spatial distributions of bottom hypoxia and anoxia over time. Estimated bottom oxygen concentrations <2 mg L^{-1} are shown in red, and concentrations <0 mg L^{-1} are shown in black for 1906 (A), 1931 (B), 1955 (C), 1974 (D), 1993 (E), and 2012 (F). The spatial distributions represent means across all months (January to December) (from Carstensen *et al.,* 2014).

3 Biology

3.1 Atlantic cod

The Atlantic cod (*Gadus morhua* Linnaeus, 1758) is generally considered as a demersal species even if it could become pelagic under certain hydrographic conditions when feeding or spawning. In the Baltic Sea, for example, this behavior is enhanced because of the hypoxic bottom waters (Schaber *et al.,* 2009). This species is distributed along the east coast of North America, east and west coasts of Greenland, around Iceland and from the Bay of Biscay up to the Barents Sea. It can live up to 20 years and reach a maximum size of almost 2 m (Cohen *et al.*, 1990).

The cod is a species that can live in waters with temperature ranging from near 0°C up to 20°C, although individuals are usually found in waters with temperature between 0-12°C, and salinity ranging from almost fresh to full oceanic water (Cohen *et al.,* 1990; Drinkwater, 2005).

This species is generalist inhabiting a great variety of habitats from shallow rocky bottoms down to muddy seabeds at over 600 m depth; the preferred depth range of adult cod in the Atlantic is considered to be between 150 and 200 m while the juveniles generally prefer coastal shallower waters (Cohen *et al.,* 1990).

Cod is an omnivorous fish; larvae and post larvae feed on plankton, juvenile cods feed mainly on crustacean and other invertebrates. Fish consumption, especially clupeids, increases in adult cods but crustaceans and other invertebrates are still present in their diets (Cohen *et al.,* 1990; Bagge *et al.,* 1994; Hüssy *et al.*, 1997). The shift in the diet reduces the competition between different life-stages. Cannibalism is considered to be important in controlling recruitment success in cod stocks, especially for the two Baltic stocks (Neuenfeldt and Köster, 2000).

The migratory behavior and the distribution patterns of cod can vary markedly with respect to area, season and the strength of major environmental factors (Pálsson *et al.*, 2003). Some groups of cod are relatively stationary while others can perform migrations of over 1000 km (Cohen *et al.,* 1990).

For the Atlantic cod the estimation of age at maturity seems to vary between authors but mostly in the range 2-10 years (Curry-Lindahl,1985; Jonsson and Semb-Johansson, 1992); in the Baltic it reaches maturity after around 3 or 4 years but the earliest reported maturity is at age 2 (Radtke and Grygiel, 2013). The spawning period of Atlantic cod varies among different populations but most cod spawns between December and June; in the Baltic Sea the spawning period for the Eastern Baltic cod is mostly from April to August with a tendency of late spawning by the end of July possibly due to a change of the age distributions towards younger fishes while the Western Baltic cod spawns earlier in the year (between January and April) with the peak spawning in March (Bagge *et al.,* 1994; Wieland *et al,* 2000).

The average egg production is around 1 million eggs per female but the maximum registered was 9 million (Cohen *et al.,* 1990).

In the Baltic the egg survival rate primarily depends on the salinity and oxygen content of the water; the minimum salinity that allows the egg to float is 11 psu and the minimum oxygen content that allows eggs' survival is 2 mg L^{-1}. The volume of water, comprised by these two limits, suitable for survival and development of eggs is called "Reproductive Volume" (MacKenzie *et al.,* 2000; Plikshs, 2014). Maternal effect is also important since the eggs produced by larger females have higher buoyancy and thus a better survival rate (Vallin and Nissling, 2000)

The spawning grounds in the western part of the Baltic Sea are the Sound, the Belt Sea and the Arkona Basin, while in the eastern part are the Bornholm Basin, the Gdansk Deep and the Gotland Deep (Bagge *et al.,* 1994; Hinrichsen *et al.,* 2011).

3.2 European flounder

The European flounder (*Platichthys flesus* Linnaeus, 1758) is a demersal species distributed along the northeastern Atlantic coast, from the Mediterranean and Black Sea to the White Sea. It can live up to 15 years and reach a maximum size of 60 cm (Skerritt, 2010; www.fishbase.org).

This species inhabits primarily coastal and brackish waters but can enter into estuaries and live for long periods in freshwater habitats although unable to spawn there (Hemmer-Hanson *et al.,* 2007). It prefers sandy and muddy substrate from 1 to 100 m depth but it is mostly found at depths shallower than 50 m.

Juvenile flounder feed mostly on meiofauna (animal size between 0.1 and 1 mm), especially on copepods, ostracods and small larvae, while the adult predominantly on macrofauna, especially on bivalves, polychaetes and crustaceans. This shift in the diet composition reduces the competition between individuals in different life-stages (Aarnio *et al.,* 1996; Florin, 2005; Skerritt, 2010).

P. flesus has been recorded to migrate over vast distances to reach the spawning grounds but the annual average migration distances are around 30 km (Aro, 1989; Bagge and Steffensen 1989; Skerritt, 2010; ICES, 2010).

Normally flounder feeds in shallow, coastal areas during summer, moves out to deeper areas in winter and spawns in the same areas during spring. In some parts of the Baltic Sea, however, some populations are known to spawn close to the coast or in shallow offshore banks instead of spawning in the deep sea (Florin, 2005). These flounders are referred to as "coastal spawning flounders" while the regular type is referred to as "offshore spawning flounder". The pelagic larvae of both those spawned at sea and those spawned in coastal areas will end up in shallow water nursery areas where they will metamorphose into benthic small flatfish (Florin, 2005).

The sexual maturity is reached around the second or third year and the spawning period occurs between February and June (Skerritt, 2010). The European flounder is a broadcast spawner typically with floating eggs that sinks as development occurs. In the Baltic Sea the coastal spawning flounders have adapted to the brackish environment, spawning smaller and denser benthic eggs instead of pelagic ones usually laid offshore. This could be an adaptation in order to avoid the anoxic conditions present in the deeper areas of the Baltic (Florin, 2005; Hemmer-Hanson *et al.*, 2007; Florin and Höglund, 2008).The coastal spawning flounder ecotype is occurring in the northern, less saline areas of the Baltic Sea but there is overlap with the offshore spawning flounder ecotype in southern areas like, for example, in the eastern part of Gotland Deep (Nissling *et al.,* 2002; Florin and Höglund, 2008; ICES, 2014a).

In the Baltic Sea, the "Reproductive Volume" for offshore spawning flounder is defined by salinity between 10.7 and 12 psu and oxygen concentrations > 1 mg L^{-1} (Ustups, et al 2013).

4 Spatio-temporal dynamics of cod and flounder

Understanding the spatio-temporal dynamics of fish stocks and the mechanisms linking physical and biological processes in the marine ecosystems is crucial for an effective spatial management of marine resources (Botsford *et al.,* 1997; Embling *et al.*, 2012). Fisheries management relies mostly on stock assessment methods based on aggregated catches, fecundity and mortality estimates averaged for an entire stock. It is thus overlooked that fish stocks are part of an ecosystem, that they are not uniformly distributed and often composed of different sub-populations with life history parameters that can differ over time and space (Wilen, 2004; Pauly, 2009; Norse, 2010).

Stock assessments attempts to predict the behavior and dynamics of a fictional homogeneous and "spaceless" population are likely to be compromised by the heterogeneity and complexity of real ecosystems (Wilen, 2004). Moreover there is a huge discrepancy between stock assessment, the leading management tool, and fishers' behavior. In fact the fishers, taking into account that the populations are spatially structured, focus the fishing effort on the largest concentrations of, usually, largest fishes (Norse, 2010).

In the latest years increasing importance has been given to the implementation of ecosystem-based approach to fisheries management. There is also a growing trend in exploring the possibility of using spatially explicit stock assessment models as well as multispecies models. These models are used in order to account for the spatial patterns of the different species, their interactions through predator-prey relationships or competition and assess the causes and consequences of the changes in their distributions (Ciannelli and Bailey, 2005; Neuenfeldt and Beyer, 2006; Cadrin and Secor, 2009; STECF, 2012; ICES, 2013).

In the Baltic Sea the four species that form more than 95% of the commercial catches are cod, flounder, herring and sprat. In the next sections I will review the spatio-temporal dynamics of cod and flounder.

4.1 Baltic cod

In the Baltic Sea, two cod stocks have been identified using genetics and tagging experiments, the Western Baltic cod in ICES Sub-Division 22-24 and the Eastern Baltic cod in ICES SD 25-32 (Aro, 1989; Bagge *et al.*, 1994). In this section I will mostly focus on the Eastern Baltic cod stock.

The Eastern Baltic cod stock has experienced a dramatic change in abundance and distribution throughout the last century. A recent work from Eero *et al,* (2011) has analyzed the temporal variation of the abundance of this stock in relation to four main key forcing factors: fishing pressure, seals predation, nutrient concentration and climate-driven hydrographic conditions (Figure 3).

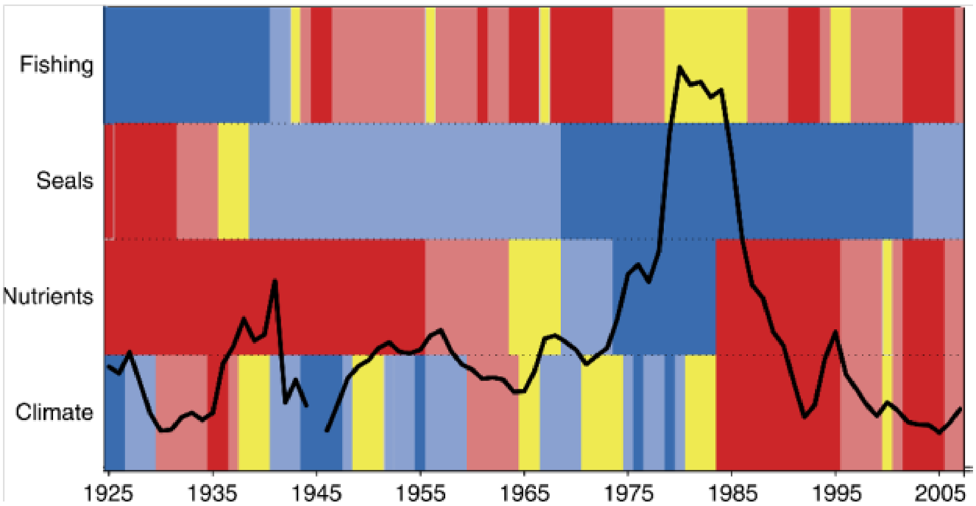

Figure 3. Changes in climate-driven hydrographic conditions, nutrient concentration, seal abundance, and fishing mortality compared to trends in SSB of the eastern Baltic cod (shown as a line) during 1925–2007. The data for climate and fishing variables are lagged in relation to SSB to represent their potential impacts on age groups 3–7 in SSB in a given year. The values of the parameters shown by the five color categories represent 20 percent intervals of the range of observed values (from minimum to maximum) for each variable during the analyzed period. The colors represent beneficial and detrimental effects on cod, coded from red (detrimental) to yellow (neutral or moderate) to blue (beneficial) (from Eero *et al.*, 2011).

At the beginning of the last century this stock's abundance was low and mainly controlled by the marine mammal dominant top-predators such as seals and harbour porpoises and probably by low nutrient availability causing a decrease in the biological productivity of the ecosystem (Österblom *et al.*, 2007; Eero *et al.*, 2011; Casini, 2013). When, due to human activities (especially hunting), the abundance of marine mammals decreased, the cod was released from marine mammal predation but the abundance remained low due to the high fishing mortality. In the mid 80s the cod stocks experienced a massive increase in abundance. This increase was mainly explained by the favorable water conditions for cod spawning, the high abundance of cod larvae prey (*Pseudocalanus acuspes,* a pelagic copepod) and a decrease in fishing mortality (Casini, 2013). In the late 80s a 10-fold decline in cod biomass was caused by heavy fishing pressure and unfavorable climate conditions which led to reduced productivity of the stocks. In the latest years the cod has shown a slightly increasing abundance trend corresponding to a strong decrease in fishing mortality (Cardinale and Svedäng, 2011; Eero *et al.,* 2012a).

During the high abundance period the cod was distributed all over the Baltic Sea while after the cod collapse the distribution contracted and is now limited to the southern part of the Baltic (Eero *et al.,* 2007; Casini *et al.,* 2012). In fact, although the current abundance of adult cod is estimated to be around 30% of the maximum abundance registered in the 1980s, in SD 25 the density of cod is close to the highest values since the 1970s. In this area the number of cod has been increasing continuously in recent years while in the SDs 26-32 the abundance has remained low since the 1990s (Eero *et al.,* 2012b). On the contrary the stocks of cod pelagic prey species, herring and sprat, have become concentrated in the Northern Baltic, mainly outside the spatial distribution of the cod stock (Casini *et al.,* 2011a and 2014). Only a small fraction of the biomass of sprat and herring is concentrated in SD 25, possibly explaining the huge decline in the proportion of full stomachs as well as in the mean weight at age and condition of adult cod (Eero *et al.,* 2012b).

There are many hypotheses on why the Eastern Baltic cod stock has contracted to SD 25. One of these is that the hydrographic conditions in the Gdansk Deep (SD 26) and the Gotland Deep (SD 28) have not been suitable for cod spawning since the last part of the 1980s and the only spawning ground available for successful cod reproduction is the Bornholm Basin in SD 25 (Vallin *et al.,* 1999; Köster *et al.,* 2009).

Another factor possibly linked to the contraction of the Eastern Baltic cod stock is the natal homing behavior of cod. In recent years there is increasing evidence of a natal homing behavior of cod as one of the primary causes of segregation between different sub-populations instead of environmental forcing (Svedäng *et al.,* 2010). Indeed the natal homing behavior does not exclude the presence of opportunistic recruitment but highlights the importance of this behavioral trait in the structuring mechanisms of the population. The contraction of the Eastern Baltic cod could be linked to the eradication of the sub-population spawning in SD 26 and 28 that due to the natal homing behavior will hardly be replaced even if hydrographic condition will improve in the Gotland and Gdansk Deep (Cardinale and Svedäng, 2011).

More explanations to the contraction have been formulated; for example lower salinity and dissolved oxygen in the deep waters have reduced the amount of benthic preys for cod and cod's feeding efficiency especially in SDs 26-32 causing the migration in SD 25 (Eero *et al.,* 2012b).

If we look at what happened in the Baltic Sea in the last 40 years from a broader perspective it is clear that the ecosystem has undergone some major structural changes that have been described as regime shifts (Österblom *et al.*, 2007). A regime shift describes the transition between two different states and is characterized by infrequent and abrupt changes in ecosystem structure and function propagating through multiple trophic levels and on large geographic scales (Collie *et al.*, 2004; Möllmann *et al.*, 2009). In the Baltic two different states (1974-87 and 1994-present) separated by a transition period (1988-93) have been identified in the last 40 years described by the alternative predominance of cod in the first one and of sprat in the second (Möllmann *et al.*, 2009; Casini *et al.*, 2011b) (Figure 4).

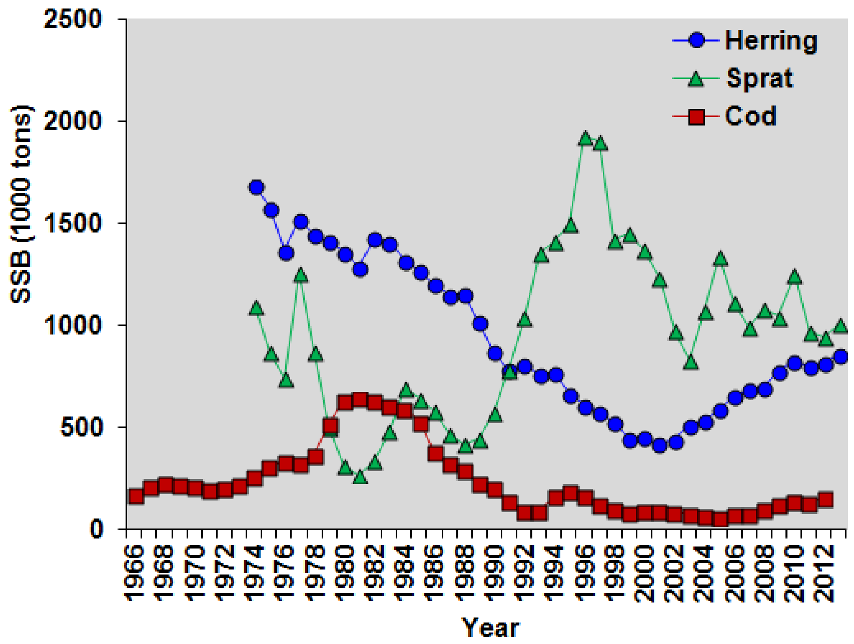

Figure 4. Time-series of cod (SDs 25-32), sprat (SDs 22-32) and herring (SDs 25-29, 32 excluding the Gulf of Riga) spawning stock biomass (SSB). Data from ICES (2014a).

The shift between the two states occurred in a period in which the Baltic Sea water was characterized by low salinity and low levels of dissolved oxygen as well as high temperature and nutrients load (Möllmann *et al.*, 2009). Moreover a high fishing pressure on cod caused the dramatic collapse in the 1990s triggered a trophic cascade and contributed to the regime shift (Casini *et al.*, 2009; 2011b). The sprat stock during the cod collapse period experienced an inverse trend increasing its abundance to the highest level recorded in the last 40 years (Casini, 2013); this was mainly due to the release from cod predation and the increase in water temperature (Casini *et al.*, 2014). Before the regime shift the high cod abundance was able to control the sprat population via predation while on the contrary, after the shift, the high sprat population could probably control the cod one through competition for food resources (*P. acuspes*) and predation on cod eggs and larvae (Österblom *et al.*, 2007; Möllmann *et al.*, 2009; Casini, 2013). These are typical examples of prey-to-predator feedback loops that seem to stabilize the present regime, hindering the cod recovery (Bakun and Weeks, 2006; Möllmann *et al.*, 2009; Casini *et al.*, 2011b).

The stock of herring (SDs 25-29, 32 excluding the Gulf of Riga), the second most important forage fish for cod, has had a constant decrease in terms of spawning stock biomass with a slight recovery in the last few years. The causes of this could be linked to high fishing pressure coupled with eutrophication, low salinity levels and increased competition with sprat for the main prey item *P. acuspes* (Casini *et al.*, 2010; Casini, 2013).

4.2 Baltic flounder

In the Baltic Sea two flounder populations differing in their spawning habitat and egg characteristics have been described (Florin and Höglund, 2008; Ustups *et al.*, 2013). The separation between the two populations seems to be in the region of the Bornholm Island (Figure 5). North of that the flounder population is characterized by coastal spawners with demersal eggs adapted to the lower salinity level while south of Bornholm the population of flounder is characterized by deep-water migratory spawners with pelagic eggs (Florin and Höglund, 2008). The management stocks are more than two. By the end of the 1990s on the basis of tagging studies 15 potential stocks were identified (Aro, 1989; Florin, 2005; Florin and Höglund, 2008). However, during the last WKBALFLAT (ICES, 2014b) the experts came to the conclusion that there was evidence of only three stocks with pelagic eggs and one stock with demersal one. The definition of the management units is made more difficult by the fact that although the two populations are genetically distinct and during spawning they segregate in different habitats, they probably mix in some areas during the feeding season; at least the eastern Gotland basin SD 28 is known to contain both types of flounder (Florin and Höglund, 2008, ICES, 2014b).

After the cod stock collapsed in the late 1980s, flounder became one of the dominant demersal fish species in the Eastern Baltic Sea (Ustups *et al.*, 2013). However, little information is available on the spatio-temporal dynamics of this species in the Baltic.

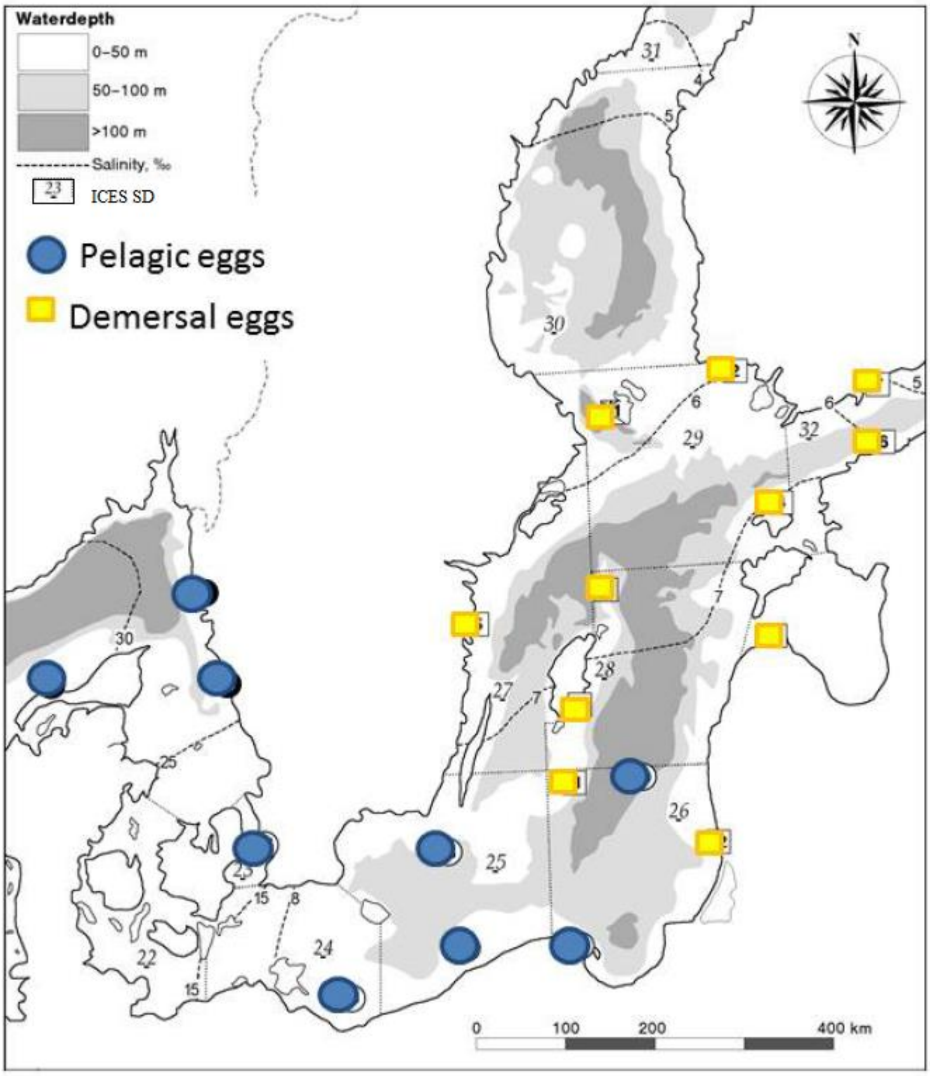

Figure 5. Map of sampling locations and identified populations according to microsatellite variation. The two distinct populations of flounder in the Baltic Sea correspond to distribution of flounder with demersal or pelagic eggs (from ICES, 2014b).

A study of the regional distribution of juveniles in the Northern Baltic Proper in order to identify the characteristics of nursery areas for flounder and turbot (*Psetta maxima*) was published in 2009 (Florin *et al.*, 2009). Juvenile flounder seems to prefer habitats characterized by sand or gravel substrate, salinity > 5.8 psu, presence of structurally complex object on the substrate (as vegetation or large rocks), intermediate wave exposure and low filamentous algae coverage that probably reduce their feeding efficiency (Florin *et al.*, 2009).

A recent work of Ustups *et al.* (2013) demonstrates that flounder SSB and Reproductive Volume are key factors in determining the abundance of eggs and larvae in the Central Baltic, with SSB being the only factor retained in the egg model. For the larval production, instead, both environmental factors and stock size are involved. Interestingly, their work show that there is no correlation between the larval production and the recruitment estimates coming from the extended survivor analysis (XSA) performed on the Eastern Gotland stock (Gårdmark *et al.,* 2007; Ustups *et al.,* 2013). Explanations to this result could be that recruitment is regulated during a post-settlement phase or it is possible that a mix of juveniles of the two ecotypes in the recruitment areas is obscuring a potential coupling between pelagic larvae and juveniles.

4.3 Knowledge gaps

In order to obtain a clearer picture of the cod situation in the Baltic Sea more studies aimed at resolving the causes of the spatial changes in the fish distributions are needed.

It is known that mixing between the Eastern and Western Baltic cod stock is happening in the Arkona Basin and that this phenomenon is increasing in recent years (ICES, 2014c). A better understanding of the spatial distribution of the two stocks and their overlap will help defining the stock limits to better manage the two units and will give more insights on the reasons that are causing the migration of the Eastern Baltic cod towards west.

The causes of the dramatic drop in weight-at-age and condition of cod are another interesting problem to further analyze especially in the light of some new hypotheses about the possible influence of nematode parasitoids in cod, the increase in seal abundance in recent years, and the increasing extent of anoxic areas. The decrease in growth have been associated also to scarce food availability for cod but more studies focusing on analyzing the area specific size matching of cod and clupeids (presence of clupeids of a size that can be eaten by cods present in the same area) are needed in order to better understand the present predator-prey relation between them in the different areas (ICES, 2014c).

In the last SGSPATIAL meeting analyses of stomach contents were performed and the results showed that in areas with larger extent of hypoxic waters, the frequency of occurrence of all prey groups in the stomachs decreased, meaning that the feeding of cod was at a low rate, both upon pelagic and benthic preys. In the same areas the relative proportion of benthic prey in the stomach diminished probably because of decreased availability of benthic preys in correspondence of areas with hypoxic waters, decreased feeding rate at low oxygen levels, or a change in the behavior of cod that under these circumstances would become more pelagic

(ICES, 2014d). More analyses are needed in order to clearly identify the role of the hypoxic areas on the change in growth and condition of cod.

Nematode parasitoids and the increase in seal abundance have been also listed as possible causes of changes in the mortality of cod. Parasite infection could in fact alter cod's behavior as well as cod's metabolic efficiency (ICES, 2014c).

The abundance of grey seal at the beginning of the 1900s was estimated to be around 100000 individuals, then it has been low since the 1930s-40s because of intensive hunting and the increase of toxic pollutants (e.g. PCB). However, the seal population has lately been increasing, reaching in recent years 40000 individuals (Lundström *et al.*, 2007; ICES, 2014c). Seals are not only the final host for the cod worm and liver worm parasites but feed mainly on fish at a rate of 4.4 kg per day (ICES, 2014c). Seal predation on cod was important in the early 1900s and was probably able to control the cod stock. The increase in seals abundance should be further studied and taken into consideration when analyzing the changes in the cod stock dynamics.

There are gaps in our understanding of the long-term spatial distribution of the flounder. The problems of stock identification, stock separation and the mechanisms that regulate the recruitment of this species are of primary importance to develop a sustainable management. With the increasing phenomenon of eutrophication a better understanding of the essential habitats for the different life stages of flounder could offer the basic knowledge to start the implementation of a management plan with the aim of protecting key areas for flounder recruitment, feeding and spawning.

Very little is known about the interactions between cod and flounder, both being important species in the demersal community of the Baltic Sea. Predation of flounder by adult cod has been documented but no studies have been conducted to investigate the possibility of competition for food resources between the two species, especially during the early life stages when both species feed almost exclusively on benthos. Studying the diet overlap between cod and flounder could help identifying possible restrictions in habitat utilization and in food availability for the two species when they both occupy the same area.

Improving the knowledge on their spatial distributions and the intensity of their interactions during different life stages could help in implementing a spatially-explicit ecosystem-based fisheries management. In fact currently flounder is not taken into consideration in the food-web model used for multispecies assessment and advice; the models are based solely on cod, herring and sprat (STECF, 2012; ICES, 2013).

In December 2014 the largest saltwater inflow of the last 60 years has been recorded. This inflow has brought oxygen rich saltwater into the Baltic. It is assumed that this water will spread in the Central Baltic and decrease the distribution of anoxic and hypoxic bottoms of the Bornholm and Gotland Basins. Further studies on how and if this inflow will affect cod abundance, distribution and reproduction could bring new insights important for a better understanding of the Baltic cod population dynamics.

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