Bridging the gap between ecosystem modelling and ecosystem-based fisheries management solutions for the Baltic Sea

Nataliia Kulatska

Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Department of Aquatic Resources

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Swedish University of Agricultural Sciences, Department of Aquatic Resources,
Institute of Marine Research, Turistgatan 5, 453 30 Lysekil

E-mail:
nataliia.kulatska@slu.se

Abstract

The Baltic species live on the edge of their tolerance limits. They face environmental challenges, such as temperature and salinity gradients, large hypoxic/anoxic regions, and also human induced eutrophication and high fishing pressure. In my PhD project I want to understand the predator-prey interactions between cod, herring and sprat in the Baltic Sea and how they are framed by a combination of processes: fishing exploitation, climate variability and density dependence. I will address this question with the help of multi-species modelling. Knowledge of study species and system is required to build a good model. This essay covers information on biology of cod, herring and sprat, interaction between them and environment challenges they face. Previous approaches used in studying predator-prey interactions in Baltic are reviewed and analysed.

Keywords: predator-prey interactions, multi-species modelling, Baltic Sea, cod (*Gadus morhua*), herring (*Clupea harengus*), sprat (*Sprattus sprattus*), fisheries.

Table of contents

List of Figures

Glossary

Anoxia is a phenomenon, when oxygen concentration is ≤ 0 ml/l (negative concentration of oxygen, O_2, is used to describe concentration of hydrogen sulfide, H_2S)

Batch spawner – same individual has multiple spawning in one spawning season.

Brackish water – water with salinity less than 24.7 psu, but more than 0.5 psu.

Demersal organisms live close to the bottom.

Equilibrium is a point where the population size is not changing. It might be stable, when after perturbation system return to equilibrium; or unstable, if after perturbation system moves away from equilibrium (population size decrease or increase even more).

Eutrophic environment is rich in nutrients, which promote growth of phytoplankton. As a result organisms in lower layers of a lake or another water body have little access to the oxygen from the surface.

Halocline – cline that separate two water layers with different salinities.

Hypoxia when oxygen concentration is ≤ 2 ml/l.

Normoxia normal oxygen conditions in water.

Oligotrophic environments have very little nutrients.

Otolith – is a hard structure in the inner ear of a fish, used for perception of acceleration including gravity and hearing. Otoliths frequently show daily, seasonal or annual checks, rings or layers which can be used to determine ages.

Pelagic organisms are those that live in a water column.

Pycnocline – cline that separate two water layers of different density

Regime shift is an abrupt reorganization in a food web.

Residence time – time required for the entire water volume to be renewed.

Stock is a group of individuals of the same species, inhabiting the same area and having the same parameters (body growth, recruitment, mortality, etc.)

Thermocline – cline caused by difference in temperature of two water layers.

Whitebait -- immature fry of fish, typically between 25 and 50 mm long.

Abbreviations

BB	Bornholm Basin
GB	Gotland Basin
GD	Gdansk Deep
HELCOM	Helsinki Commission
ICES	The International Council for the Exploration of the Sea
NCE	non-consumptive effect
psu	stands for Practical Salinity Unit, here it is equal to 1 particle of salt per 1000 particles of water (‰)
SD	Subdivision; management area unit used by ICES
SST	sea surface temperature.

1   Introduction

The Baltic species live on the edge of their tolerance limits. They face several environmental challenges, such as temperature and salinity gradients, large *hypoxic/anoxic* regions, as well as human induced eutrophication and high fishing pressure.

Cod (*Gadus morhua*), herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) are key species of the Baltic Sea ecosystem but also a bulk of commercial fisheries catches. The overarching goal of my PhD project is to understand how predator-prey interactions between cod, herring and sprat in the Baltic Sea are framed by a combination of different processes: fishing exploitation, climate variability and density dependence. I will address this question with the help of multi-species modelling.

In order to build a good model, it is important to have a good knowledge about both the study system and the interacting species. For that, I searched in the literature for background information on:

- Environment:
    - general characteristics of the Baltic Sea environment;
    - environmental challenges that cod, sprat and herring have to cope with in the Baltic Sea.
- Biology:
    - specific adaptations required by the cod, herring and sprat to live in the Baltic;
    - dynamics of cod, herring and sprat populations in the Baltic;
    - interactions between cod, herring and sprat.

The aim of this essay is twofold, first to briefly introduce the topic of predator-prey interactions, which is my main scientific interest as well as the core of my PhD project; second to review the research approaches used to study predator-prey interactions between cod, herring and sprat in Baltic.

2 Predator-prey interactions and basics of ecosystem theory

Ecosystems can be regarded as either being bottom-up or top-down driven (McQueen et al., 1986). In the first case changes in the lower links of food web influence changes in all upper links. For example, an increase in the vegetation will cause an increase in the herbivore abundance, which in its turn will increase the predator and the top predator abundances. In the second case, also called a trophic cascade, changes in upper links impact lower links. For example, decrease in the top predator abundance, will release pressure on the predator of the next trophic level and increase its abundance, which will decrease the abundance of the herbivore and increase the vegetation. Many ecosystems (both terrestrial and marine) belong to the first type, however due to strong perturbations, for instance as a result of hunting or overfishing, those ecosystems may turn into top-down driven. This effect is even stronger in ecosystems with low species diversity and strong trophic interactions (Frank et al., 2007), since changes in one trophic level in such systems will affect the whole food web. The Baltic Sea is an example of an ecosystem with few trophic links. That is why, after the crash of some top-predator populations (seals and harbour porpoises) and a decline of others (cod), all trophic levels of the Baltic Sea ecosystem experienced large changes. The biggest consequence of that was a *regime shift*[1] from a cod-dominated to a sprat-dominated system which occurred in late 1980s - early 1990s (Alheit et al., 2005; Möllmann et al., 2004; Casini, 2013).

All ecosystems are affected by gradual changes in environmental conditions, to which they smoothly respond. However recent studies had shown that this smooth response nowadays has been interrupted more often by an abrupt shift to an alternative state. An ecosystem may have several alternative stable states, which are separated by an unstable equilibrium, for the same environmental conditions. A shift between those two states cannot happen smoothly, instead, when a sufficient change happens in the conditions, a "catastrophic" transition to a second state occur. It is not enough to restore the conditions that were prior to the shift, to switch the system back to the first state, but rather the conditions that existed further back in time. This phenomenon, when different critical conditions are required to switch the system from one state to another and then back, is called hysteresis (Scheffer et al., 2001).

Four mechanisms that promote alternative stable states have been suggested by Fauchald (2010):

1. reversal of predator-prey roles (Fauchald, 2010; Walters and Kitchell, 2001). This is a variant of the cultivation-depensation mechanism in Walters and Kitchell (2001) and Gårdmark et al. (2015).

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[1] Here and on, words in italic can be found in glossary.

2. recruitment competition (Casini et al., 2009; Walters and Kitchell, 2001), also called cultivation-depensation (Walters and Kitchell, 2001; Gårdmark et al., 2015).
3. size selective predation and food dependent growth (De Roos and Persson, 2002), also called overcompensation (Gårdmark et al., 2015).
4. risk effects (Willis, 2007).

Reversal of predator-prey roles is when a prey itself predates on its predator eggs and/or larvae. In this way a predator will promote its recruitment success by keeping the prey population low and blocking the system in predator-dominated state. If the prey population becomes more abundant, it will decrease recruitment of the predator and block the system in a prey-dominated state. When this mechanism is in act selective harvesting may push the system from one state to another by switching target species (Fauchald, 2010).

The main principle of the cultivation-depensation mechanism is that young stages of the predator compete with the prey species over food. By controlling the prey abundance the predator creates ("cultivate") an environment for its offspring with low competition with the prey species. Then, if the predator is unable to control its prey, competition of predator juveniles and prey species increases, the population of the predator is not growing, which may prevent the predator from recovery. Another variant of this mechanism is when the prey itself is a predator on its predator's eggs and/or larvae (called predatory cultivation-depensation or reversal of predator-prey roles) (Walters and Kitchell, 2001; Gårdmark et al., 2015).

Since predation in fishes is often size-dependent (a certain length group of fish eats prey of specific length ranges), by eating smaller prey, predators decrease intraspecific competition for remaining larger individuals. Then they have higher fecundity and their population grow ("overcompensation", since recruitment is then even higher than the loss due to predation). Moreover recruitment then includes suitable sizes of prey again. If a predator is unable to control a prey population, intraspecific competition of the prey increase, fecundity decrease and as a result there is little amount of the prey of suitable sizes for the predator. A variant of this mechanism is when a predator affect condition of a prey rather than its abundance (De Roos and Persson, 2002; Gårdmark et al., 2015).

Risk effects. A predator creates risk zones for prey. The area where the predator is present constitutes a high-risk zone, and reversed; if the predator is absent the risk is low. If the predator is removed then the zone, that formerly was high-risk, becomes low-risk. If new predators arrive to the former low-risk zone this area will now become a high risk. If the prey now choose the new low-risk area (which might be of lower quality), to avoid predators from the new high-risk zone, it become less

abundant (growth and fecundity decrease) despite the fact that the main predator was removed (Willis, 2007).

The listed mechanisms and their variants are not all strictly exclusive and they may act simultaneously (Fauchald, 2010).

Researchers studying predator-prey interactions should also keep in mind non-consumptive effects (NCE) of predators, which are important part of predator-prey interactions (Peckarsky et al., 2008). Prey may develop anti-predator techniques, alter their behaviour in order to not be seen, caught or eaten (Lima, 1998). For example prey that can move try to avoid predators and escape from them, not to be eaten (Rose and Leggett, 1990). It is not only the behaviour that might change, but also the development or growth of prey can be alternated by the presence of predators. NCE can act in the same or opposite direction as effect of consumption so ignoring them can result in underestimating the effect of predator on prey or lead to the wrong conclusions about this effect. NCE can also be misinterpreted as bottom-up effects (Peckarsky et al., 2008).

Another important aspect, when interpreting species interactions, is the scales. Rose and Leggett (1990) provided a good example of that. Their study species cod and its prey capelin (*Mallotus villosus*) differ in thermal preferences. This allows capelin to use areas which are outside of cod preference zone as refugees. Positive spatial correlation (prey and predator in the same place) between cod and capelin occur only on scales greater than prey refuges and also greater than aggregation sizes of both the predator and the prey. Negative correlation (avoidance of predator by prey) occurs, when scales are smaller than predator and prey aggregations (Rose and Leggett, 1990). By choosing one or the other scale we would come to totally different conclusions.

3 The Baltic Sea

3.1 General overview
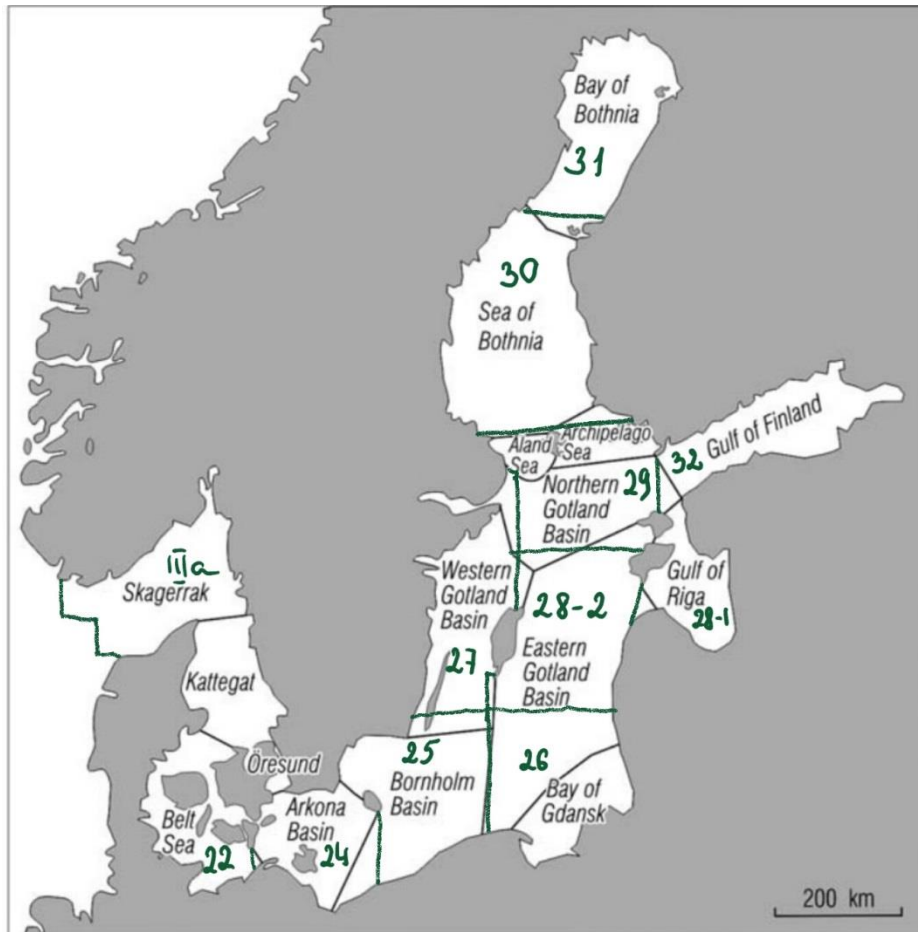
Figure 1. The Baltic Sea and its basins, including ICES Sub-Divisions. Modified after Fonselius, 1995.

The Baltic Sea (Figure 1.) differs a lot from other seas in the World Ocean. It consists of a series of basins, which are connected to the Atlantic Ocean via the Danish Straits. The Baltic Sea is small, shallow and with *brackish water*. Besides the Baltic Sea, there are only three other major *brackish* basins in the world: the Black Sea, Gulf of Ob and Chesapeake Bay (Leppäranta and Myrberg, 2009).
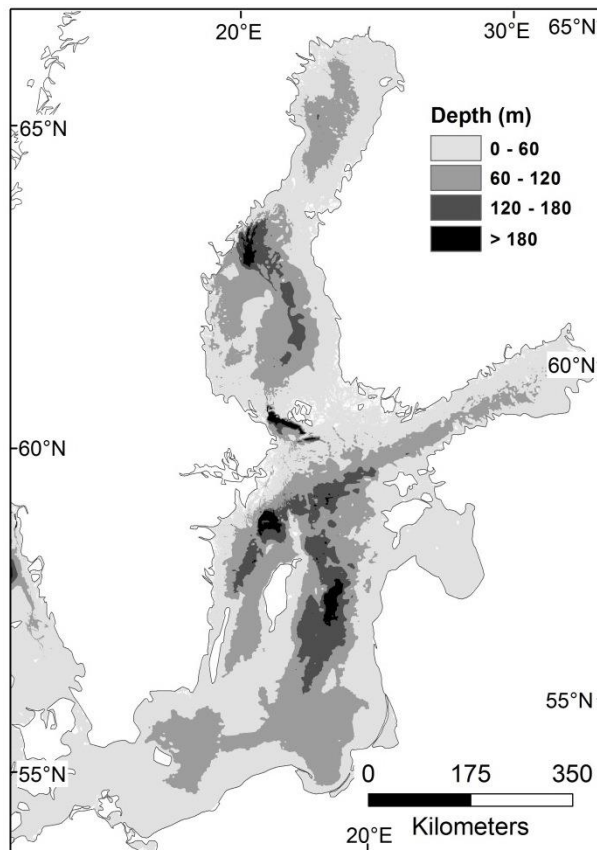
The average depth of the Baltic Sea is 54 meters (Figure 2.) and its fundamental feature is the permanent salinity stratification (Figure 3.). This is the reason for limited vertical convection and weak oxygenation of deep waters. Salinity is decreasing from areas near the North Sea boundary to areas near river mouths. The renewal of water is slow (i.e. long *residence time*). It takes about 50 years before all water is renewed according to Leppäranta and Myrberg (2009). According to other sources (Matthäus and Schinke, 1999), *residence time* in the Baltic is 25-35 years.

Figure 2. Bathymetry of the Baltic Sea. From MareFrame Baltic Sea D5.1 General description of the ecosystem.

The Baltic Sea is among the most actively and systematically investigated seas in the world. It has been known for a long time that the Baltic Sea is a very fragile environment. That was the reason for a close co-operation between coastal countries to monitor the state of it in order to protect it. In 1902 The International Council for the Exploration of the Sea (ICES) was founded. Baltic countries played an important role in its foundation. Then, in 1974, coastal countries of the Baltic Sea signed the Baltic Sea Protection Agreement, according to which each country is responsible for carrying national monitoring program, loading data into a common database and strengthening the protection of the Baltic Sea. As a consequence of that agreement,

the Baltic Marine Environment Protection Commission or Helsinki Commission (HELCOM) was founded in the same year (Leppäranta and Myrberg, 2009).
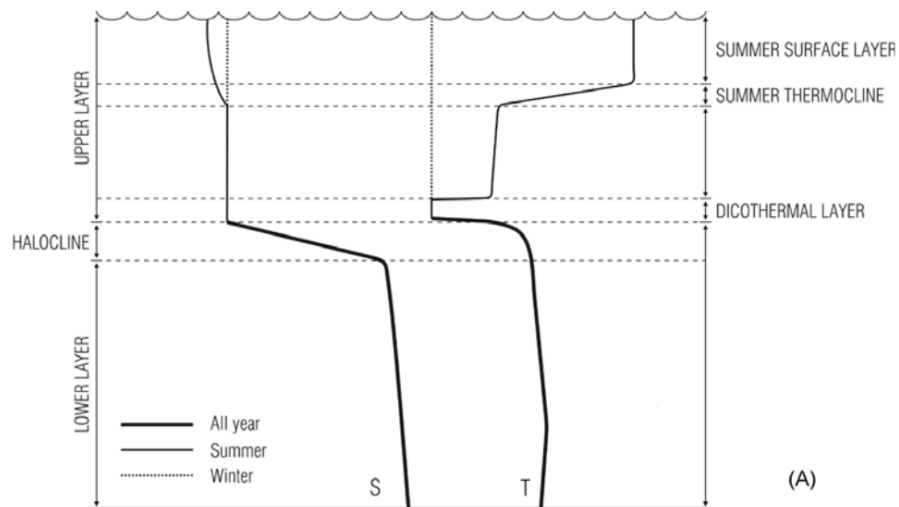
Figure 3. Water stratification in the Baltic Sea. From Leppäranta and Myberg, 2009.

3.2   Brackish water

Brackish water has salinity level between those of fresh and oceanic waters. Mean salinity of the Baltic Sea is 7.5 psu. Often 24.7 psu is used as salinity of inflow water into the Baltic Sea (Brogmus, 1952). Physical properties of *brackish waters* differ from those of fresh and ocean waters. The difference in electromagnetic properties is quite large (Apel, 1987), while mechanical and thermal properties differ within a few percent (Dietrich et al., 1963). However, in stratified waters even small differences in density is critical for horizontal and vertical motion (Leppäranta and Myrberg, 2009).

The osmotic pressure of sea water depends on salinity. Freshwater and marine species cope with differences between osmotic pressure in their cells and in the water, but *brackish water* is much more difficult to adapt to and many species are not able to do that (Leppäranta and Myrberg, 2009).

3.3   Oceanic water inflows

The origin of deep waters in the Baltic Sea is the North Sea, but they are more diluted further from Kattegat. Inflows of water from the North Sea renew lower layers of water, keep salinity stratification and are extremely important for the oxygen amount in the bottom layer. Inflows are repeated and have moderate salinity.

14

However, from time to time, inflows are strong and bring water with high salinity. Then they are called Major Baltic Inflows. These inflows are crucial for the Baltic Sea ecosystem, since they influence conditions in the Baltic Sea by being the only force that can renew water in the bottom layer. Time intervals between major inflows are called stagnation periods and are characterized by low oxygen amount in bottom water (Leppäranta and Myrberg, 2009).

Major inflows

Recently, major inflows happen on average every 10th year and bring dense and salty water with high amount of oxygen. As a result, oxygen conditions improve and *anoxic* areas decrease or disappear. Major inflows do not happen very often, since specific conditions are required for them, which are rare to occur. Sea level and water density should differ between Kattegat and Arkona Basin. The water densities in these two basins differ nearly always, but in order to cause differences in sea water levels, specific wind conditions are needed. Major inflows always happened in September-April, with 60% of the cases in November-January (Matthäus et al., 1994). Winter inflows bring cold waters into the Baltic Sea (Leppäranta and Myrberg, 2009).

The major inflows differ in strength. They can be very strong (e.g. one in 1951, 1922, 1993), strong (e.g. 1965, 1976, 2003) and moderate (e.g. 1964, 1925, 1948). Two recent inflows happened in 1993 and 2003. They are very well studied and documented. In 1993, for example, salinity in the bottom waters of the Bornholm Basin changed from 15 psu to 20 psu and the oxygen concentration from 1 ml/l to 7.5 ml/l in October 1992 and March 1993 respectively. That year it took about 4.5 months before the inflow water renewed the water column between 200 m and the bottom in the Gotland deep (Leppäranta and Myrberg, 2009).

The most recent major inflow happened in December 2014 and has been ranked as the third largest inflow in modern time It brought about 320 km^3 of water into the Baltic, of which 198 km^3 had high salinity. The total amount of salt transported is estimated to be 4×10^9 t and oxygen about 2.04×10^6 t. It is predicted that the inflow of 2014 will finish the stagnation period, which has lasted for 10 years, and turn the entire deep waters of the Baltic into oxic conditions (Mohrholz et al., 2015). There is an ongoing research on the effects of this inflow.

Other inflows.

Except for major inflows, there are also inflows of warm water and small- or medium size inflows.

Warm water inflows happen regularly in late summer and early autumn. They bring saline, warm, but usually oxygen-deficient water. They can improve or worsen oxygen conditions in the Baltic. From one side, they bring water with a low amount

of oxygen and high temperature (which increases the rate of oxygen consumption and hydrogen sulfide formation, Matthäus, 2006). On the other hand, they may ventilate the intermediate water layer, so the oxygen will arrive from the surface layer. Inflows in 2002 and 2003 were exceptionally warm. The effects of those inflows lasted until 2005. Temperature and salinity of water increased to the highest of a period from the 1970s and high concentration of hydrogen sulfide turned into high oxygen concentrations (Feistel et al., 2006). For example the temperature became 7.2°C and the salinity 13.2 psu in near-bottom water of the Gotland Deep in February 2004 compare to less than 4°C and 12.5 psu prior to the effect of the inflow in 2003 (Feistel et al., 2006; Leppäranta and Myrberg, 2009).

Small- and medium-size inflows occur a few times per year. They ventilate a part of the intermediate layer water, increase oxygen amount there, but are not sufficient to renew the water in the bottom layer (contrary to major inflows) (Leppäranta and Myrberg, 2009). The effect of inflows on the central Baltic deep water depends on the volume and density of the saline water. Water from small- and medium-size inflows, but also some major inflows, fills only the Bornholm Basin and does not reach the Gotland Basin (Matthäus et al., 2008).

3.4   Environmental factors

3.4.1   Light

As a measurement of water transparency, Secchi depth is used. That is the depth at which a white disk with a diameter of 30 cm can be seen from the surface. At present, the Secchi depth is about 5-10 m in the Baltic Sea, with some spatiotemporal differences (Laanemets et al., 2004). In coastal areas, the Secchi depth is lower compare to the central basins. Mean Secchi depth of the Baltic has decreased over the last 100 years, which can be explained by decreased water transparency due to eutrophication (Leppäranta and Myrberg, 2009).

3.4.2   Temperature

The Baltic Sea has colder and warmer phases. The first warming phase in last 100 years started in about 1920-1930 and reached maximum in the 1940s (Tinz, 2000). It was followed by a cold phase until the 1970s, when the new warming phase started. That warm phase last until today (with some breaks in the early 1980s). Since the 1990s, the warming seems to progress. In the period 1990-2005 the seven warmest summers for the past 60 years were registered (Siegel et al., 2008).

Water temperatures reach minimum values in February-March and maximum in August. The northern Baltic usually has lower temperature than the southern, especially in May-June and September-October due to slower warming in spring and

faster cooling in autumn there. However, in the past years this difference has decreased (Siegel et al., 2008).

Due to the salinity stratification (Figure 3), the temperature in the Baltic Sea has a two-layered structure. The summer *thermocline* is at about 15-30 m depth in all basins of the Baltic Sea (Leppäranta and Myrberg, 2009). The ice cover in the northern part lasts for 6 months, and the productive period is 4-5 months. In the South the ice cover is only present during the coldest winters, while the productive period is 8-9 months (Elmgren, 1984).

3.4.3 Salinity

The Baltic Sea salinity decreases the further you move from the Danish Straits (Leppäranta and Myrberg, 2009). It also differs between water layers. Salinity has values from 2-3 psu at the surface (Bothnian Bay) up to about 20 psu in bottom waters (Danish Sounds and Kiel Bight). Most of the Baltic surface has salinity of 5-8 psu. The *halocline* is at about 50-70 m and below it the water is a little warmer and more saline (Elmgren, 1984).

As an example we may look at the Gotland basin. It contains about half of the Baltic Sea water. A permanent *halocline* is at a depth of 60-80 m. Salinity in the upper layer is 6.5-8 psu. Below the *halocline* it linearly increases to 9-12 psu at 100 m depth and 11.5-13 psu at 200 m. Only Major Baltic inflows ventilate water in the deepest basins.

3.4.4 Oxygen

Oxygen condition of water has three states: *normoxia*, *hypoxia* (Diaz and Rosenberg, 1995, 2008), and *anoxia* (Diaz and Rosenberg, 1995). In the areas where the oxygen level is low due to natural processes, benthic biota is able to adapt even to 0.1 ml/l of O_2, however in anthropogenic influenced habitats a usual consequence of *hypoxia* is an increase in mortality of benthic organisms. Oxygen decline is time-lagged by about 10 years from the enrichment of water by fertilizers. Most often *hypoxia* occurs once a year from summer to autumn after spring algal blooms (Diaz and Rosenberg, 2008). An increase in temperature decreases the solubility of oxygen in water as well as it increases the respiration of organic matter. The current increase in temperature has caused about 0.5mg/l decrease in oxygen saturation over past 115 years. However, in the Baltic Sea the main driver of deoxygenation is anthropogenic nutrient discharges (Carstensen et al., 2014). Because of persistent stratification of the Baltic Sea, *hypoxia* is also persistent there. The Baltic Sea became the largest dead zone in the world (Diaz and Rosenberg, 2008). Over the past 115 years *hypoxic* areas (Figure 4.) in Bornholm and Gotland Basins increased from 5 000 km^2 to 60 000 km^2 (Carstensen et al., 2014). This 10-fold increase in *hypoxic*

areas corresponds to about $1.7x10^6$ t of macrofauna biomass, which would inhabit the Baltic otherwise (Karlson et al., 2002).
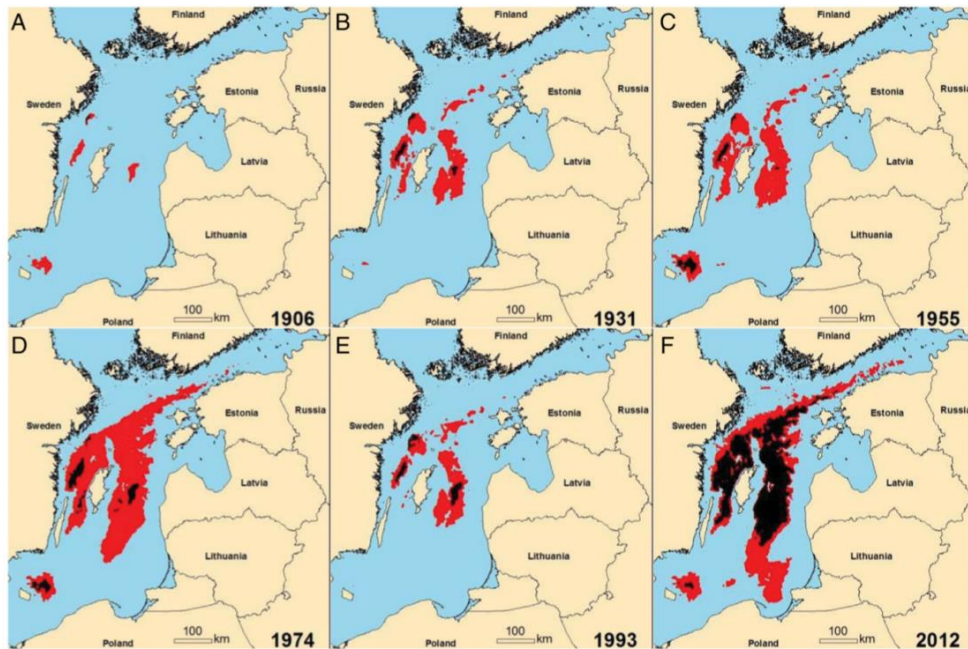
Figure 4. Change in Baltic hypoxic (red) and anoxic (black) areas over a 100 years. From Carstensen et al. 2014.

3.4.5 Eutrophication

Discharges of nutrients into the Baltic Sea increased a lot during the 20th century: N increased from 9 600 t/year to 77 700 t/year and P from 300 000 t/year to 1 189 700 t/year. As a result, the Baltic Sea turned from *oligotrophic* into *eutrophic* (Larsson et al., 1985). Consequently, blue-green algae blooms explode, some of which produce toxins (Larsson et al., 1985; Jansson, 1980; Hansson and Rudstam, 1990; Karlson et al., 2002). Another drawback of eutrophication is that geochemical cycles, which include P and N, consume a lot of O_2 creating or increasing *hypoxic* regions near the bottom (Larsson et al., 1985; Hansson and Rudstam, 1990).

4 The Baltic fauna

In order to stay *brackish*, the Baltic Sea needs a stable balance between fresh and marine water inflows. However, the probability that this balance can be maintained for long periods is low, which is why there is not enough time in evolutionary terms for large amount of species to adapt to *brackish* waters (Elmgren, 1984). According to Elmgren (1984) there were 4 groups of animals that naturally immigrated into the Baltic:

– euryhaline marine and brackish-water organisms, that are native to northwest European estuaries;
– freshwater fauna from continental Europe;
– glacial relicts, that migrated via the ice-dammed lakes from Siberia;
– glacial organisms that migrated from the west via the sea (cannot survive in fresh water).

The first two groups are poorly adapted to cold waters (it's the reason of low benthic diversity in deep waters of the Baltic), while the last two groups are typical cold water organisms.

4.1 European sprat

European sprat, *Sprattus sprattus* (Linnaeus, 1758), belongs to the family Clupeidae. Sprat has a quite wide geographic distribution (Baltic Sea, northeastern North Sea, northern Mediterranean Sea and Black Sea), which shows its high adaptivity (Parmanne et al., 1994). It is a small fish with a maximum length of about 14-20 cm (Havs- och vattenmyndigheten, 2012). Sprat is a pelagic fish. Sprat matures at an age of 2-3 years, but with some individuals maturing at 1 or 4 years (Veldre, 1974; Havs - och vattenmyndigheten, 2012). The maximum age of sprat in the northern Baltic is 18 years, but 9 years in the southern (Ojaveer, 1981). Sprat form wintering shoals, which winter below the *halocline*, in waters with temperature ≥ 4 °C and sufficient oxygen content (Parmanne et al., 1994). After wintering, sprat migrates to spawning grounds for spawning (Parmanne et al., 1994). Sprat is a warm-water species (Ojaveer and Kalejs, 2010).

Stocks and their dynamics

Sprat from different regions of the Baltic Sea differ in morphology, growth rate, and other biological parameters (Lindquist, 1971), which might indicate local populations. However, they mix in spawning and wintering grounds (Rechlin, 1986), making it difficult or even impossible to separate them into different *stocks*. Therefore, the Baltic sprat is managed as one *stock*. Big part of sprat catches comes from mixed

spratherring fishery with large spatiotemporal fluctuations in species composition (ICES, 2013).

The sprat *stock* is the largest *stock* assessed in the Baltic. SSB was low in the 1980s, then it rapidly increased, reaching maximum SSB of 1.7×10^6 tons. This is explained by strong recruitment, caused by mild spring temperatures (MacKenzie and Köster, 2004), and declining natural mortality, caused by a decline in the cod population. Then the *stock* declined as a result of increased fishing mortality and a recovery in the cod population.

Reproduction and development

Sprat is a *batch spawner* (Parmanne et al., 1994). It spawns 8-10 times in a season in the Southern Baltic and 6-9 in the Northern, with intervals of about 8-10 days (Veldre, 1974). Spawning starts in deep waters of about 90-110 m, and then continues in warmer surface waters (Parmanne et al., 1994; Ojaveer and Kalejs, 2010). Sprat spawns in salinity of at least 5 psu and temperature of 4-14°C. In the southern part of the sea spawning last from March-April to July-August, in the northern -- in June- August. Larvae hatch in about 3-4 days at a length of 2-3.6 mm. Sprat metamorphoses in 6-8 weeks after hatching at a length of about 30-40 mm (Ojaveer, 1981). Difference in time intervals of spawning in the southern and the northern parts may be due to different environmental conditions there: spring temperature gets higher earlier in the south.

Food

Sprat larvae feed on algae (diatoms and flagellates) and eggs and young stages of copepods (Ojaveer, 1981). *Whitebait* feed mainly on molluscs and young copepods (Veldre, 1974). Clupeoids have two types of feeding: biting or capturing (particulate-feeding) or filtering food from water (Blaxter, 1982). Sprat prefers the oldest stages of copepods, even if there are other stages available, which indicates that sprat is a more particulate feeder (Möllmann et al., 2004). Adult sprat feeds mainly on larger copepods (*Temora, Acartia, Pseudocalanus* etc.) (Ojaveer, 1981). Sprat actively selects its prey, since the abundance of prey in the sea and stomachs of sprat differ. (Casini et al., 2004). It preys on cod eggs and larvae (Köster and Schnack, 1994; Köster and Möllmann, 2000), but cases of cannibalism on sprat eggs and larvae have also been reported (Karaseva et al., 2013). Sprat feeding decreases a lot during spawning and is the most intensive after spawning (Ojaveer, 1981).

20

4.2   Atlantic herring

Atlantic herring, *Clupea harrengus* (Linnaeus, 1758), also belongs to the Clupeidae family. It is a pelagic fish which is in the Least Concern (LC) category of the HELCOM Red List (HELCOM, 2013a). Two groups of herring occur in the Baltic: spring and autumn spawners (Parmanne et al., 1994; Ojaveer, 1981). It is possible to distinguish between them by the *otoliths* (Ojaveer, 1981), and also by vertebrae number and timing of gonads development (Parmanne et al., 1994). Sometimes, in the northern part of the Baltic Sea, spawning of spring spawners is prolonged. Then, there may be some spatial and temporal overlap of spawning of autumn- and spring-spawners. In that case, even their hybrids may appear, however, survival probability of them is low (Ojaveer, 1981). Herring perform diurnal feeding migrations, spending the daytime mainly near the bottom, but raises up to the surface during the night (HELCOM, 2013a). Herring in the Baltic Sea is generally smaller than in other parts of its distribution (Ojaveer, 1981). It is usually 23-30 cm in Skagerrak and Kattegat and 15-24 cm in the Baltic Sea. Body weight is usually 40-200 g, but can be smaller. Herring might reach the age of 25 years, but it is rarely above 10 years (Havs- och vattenmyndigheten, 2012). The maximum age of herring differs between different areas of the Baltic, but generally it increases towards the north. The maximum age of the spring spawning herring in the north is 20 years, in the south 12 years, while for the autumn spawning herring it is 15 and 12 years respectively (Ojaveer, 1981). Herring matures earlier in the Baltic Sea (at 2-3 years old), than in Skagerrak and Kattegat (at 3-4 years old) (Havs- och vattenmyndigheten, 2012), but some spring spawners may mature even at the age of 1 year (Ojaveer, 1981). Central and Southern Baltic proper is a mixing zone where different *stocks* migrate for feeding. There herring form shoals, when migrating northward for wintering. Next spring they separately migrate to different spawning sites. Western Baltic spring-spawning herring migrate to the North Sea for feeding in summer and then in autumn or winter they migrate back to the Baltic for spawning (Parmanne et al., 1994). Both salinity and sprat abundance influence the herring growth, i.e. condition and biomass, but sprat abundance affects the growth to a higher degree (Casini et al., 2010). Herring has a high ability to adapt (Rönkkönen et al., 2004), therefore it was able to form five local populations in the Baltic (Ojaveer and Kalejs, 2010)

Stocks and their dynamics

Herring in the Baltic Sea is managed as five *stocks*: Central Baltic herring (SD 25-29 and 32, Figure 1), Gulf of Riga herring, herring in SD 30, herring in SD 31 (ICES, 2013, ICES, 2014a) and Western Baltic herring (SD 22-24).

Central Baltic herring is one of the largest herring *stocks*. It was large in 1970s, but then declined (ICES, 2013). This was caused by a combination of different fac-

tors. First of all, fishing pressure was too high (above safe reference points). Secondly, spawning grounds degraded because of eutrophication of coastal areas (Casini, 2013). Finally, competition with sprat over main herring prey, *Pseudocalanus acuspes* (whose abundance decreased because of low salinity), increased (Casini et al., 2010). The *stock* consists of a number of spawning components. Southern component, which includes relatively larger fishes, has declined in recent years, while northern component (herring, which is up to 18-20 cm) is dominant in landings nowadays. There is a decreasing trend in SSB since the 1990s (ICES, 2013, 2014) (ICES, 2013, ICES, 2014a).

Gulf of Riga herring is a stable *stock*. Its year-class abundance is highly influenced by environmental conditions (for ex. winter temperatures) (ICES, 2013).

SSB of herring in SD 30 was relatively low until 1980, followed by a three-fold increase until 1994. Then it declined by 40%, increased again and is stable now. The highest values were reached in 2012 (ICES, 2013).

Herring in SD 31 is one of the smallest assessed *stocks* in the Baltic. *Stock* dynamics is highly determined by environmental conditions (ICES, 2013).

In the Western Baltic herring both *stock* size and recruitment decreased in the 2000s, however, there might be some signs of recovery (Ices, 2014).

Reproduction and development

Spring spawning herring spawns in March-June (there is variability in spawning time between *stocks*) (Ojaveer, 1981). They spawn in coastal waters with relatively low salinity (Parmanne et al., 1994; Ojaveer, 1981). Spawning starts in shallow waters with about 2-4°C and ends in waters of 6-20 m depth. Older and larger herring spawn earlier. Embryo development depends on temperature. Hatchlings are 5.5-8 mm long. Herring larvae live close to the surface. They metamorphose after 2-2.5 months, at a length of about 25-30 mm. At the *whitebait* stage herring lives close to the coast above or in the *thermocline* (Ojaveer, 1981).

Autumn spawning herring spawns offshore (Ojaveer, 1981; Parmanne et al., 1994) at depths of about 3-25 m. Contrary to spring spawners, spawning begins in deeper grounds and shifts to shallower. Older fish spawn later. Size at hatching is the same as in spring spawners, about 5.5-8 mm. Eggs of autumn spawning herring can develop parthenogenitically (without sperm) and give viable offspring. Larvae of autumn spawning herring develop at bigger depth than spring herring (up to 62 m). Metamorphosis takes place in shallow waters, in about 8-9 month after hatching and at a length of 40-44 mm (Ojaveer, 1981).

Food

During the first year, herring feeds mainly on plankton (Popiel, 1951). Later the proportion of large crustaceans (e.g. *Mysidae, Amphipoda*), fish eggs and larvae increases in the diet (Ojaveer, 1981). The main prey of adult herring is copepods (*Temora, Pseudocalanus, Acartia*, etc.) (Ojaveer, 1981; Möllmann et al., 2004; Casini et al., 2004), but larger herring feed on nektobenthos, like *Mysis mixta*, amphipods and polychaetes (Casini et al., 2004). Even though herring prefers older stages of prey, it might switch to filtering if the availability of older and bigger copepods is low (Möllmann et al., 2004). Herring also predates on eggs and larvae of sprat and cod, as well as on herring larvae (Köster and Schnack, 1994; Köster and Möllmann, 2000; Karaseva et al., 2013). Medium and large herring select mysids, which are larger and have higher nutrition value than copepods, in autumn and winter (Möllmann et al., 2004). Herring, like sprat, actively selects their prey, since the abundance of prey in the sea and stomachs of both herring and sprat differ (Casini et al., 2004), however herring has a higher ability to change their prey composition than sprat does (Popiel, 1951).

4.3 Atlantic cod

Atlantic cod, *Gadus morhua* (Linnaeus, 1758), belongs to the Gadidae family. In the red list of both HELCOM and IUCN cod is listed as vulnerable (HELCOM, 2013; Sobel, 1996). Cod is a *demersal* marine coastal fish (HELCOM, 2013). It is a cold-water species (Ojaveer and Kalejs, 2010) with a generation length of about 13.5 years (HELCOM, 2013). The maximum age of a caught Baltic cod was about 40 years, weight -- 50 kg and length -- 150 cm (Havs- och vattenmyndigheten, 2012, Figure 5.), nevertheless, after 1980's few individuals older than 10 years old were caught (Bagge, 1981). Cod reach maturity at 2-6 years old (Havs- och vattenmyndigheten, 2012, HELCOM, 2013) and at length about 31-74 cm (HELCOM, 2013). Eastern Baltic cod usually reaches maturity earlier, at about 2-3 years old, while western Baltic cod matures at 3-4 years (Bagge et al., 1994). Although cod is distributed in the whole Baltic, the reproduction is limited to the zones with highest salinity (HELCOM, 2013). After spawning cod migrates to feeding grounds and the following spring they return to spawning grounds (Bagge, 1981). The biggest individuals perform migrations most frequently (Bagge, 1981).

Figure 5. Large cod in late 1980s. Photo of Eero Aro from HELCOM, 2013.

Age reading problems.

Age reading on *otolith* from eastern cod older than 3 years is difficult. The contrast of seasonal growth zones is low, probably due to the fact that some cod stay most of the time below the pycnoline, where the temperature is stable (Bagge et al., 1994). Also, the results of *otolith* readings differ between different countries, some consistently tend to age cod as older, while others as younger (ICES, 2013, 2014)

Stocks and their dynamics

Three cod *stocks* are managed in the Baltic: eastern *stock* (ICES subdivision 25-32, Figure 1), western (SD 22-24) and Kattegat (SD 21) (HELCOM, 2013, ICES, 2013). Despite the fact that there is not much of a spatial overlap between them (Bagge et al., 1994), there is some migration of cod between eastern and western *stocks* (ICES, 2013).

Eastern Baltic cod is the biggest *stock*. The cod *stock* in the Baltic was quite small until the 1970s, but due to low fishing pressure and favourable environmental conditions for egg and larvae survival (high salinity, oxygen amount and abundance of prey copepods), it rapidly grew (Eero et al., 2011). In the late 1980s, *stock* size declined again (Casini, 2013; ICES, 2013). The reasons for that was a combination of overfishing and degradation of spawning areas (decreased oxygen amount in the deeper zones of the Eastern Baltic, HELCOM, 2013). In addition to that, the condition of cod become extremely bad (Figure 6.), which may indicate that cod *stock* in

24

SD 25 reached carrying capacity (Eero et al., 2012). However more causes of low cod condition, like parasites, low prey availability, size-selective fisheries etc., have been suggested (see Eero et al., 2015 for more details). Lately, the eastern cod *stock* has increased, as a result of managed fishing from 2007 (HELCOM, 2013, ICES, 2013). Even though the *stock* is assessed in SD 25-32, catches in recent years (ICES, 2013, 2014) are mainly in SD 25-26, which indicate that cod is concentrated mainly there.

Figure 6. Difference in cod condition. Courtesy of: Bastian Huwer, DTU Aqua

Western Baltic cod is biologically different from eastern Baltic cod. It is a highly reproductive *stock*, which maintained itself despite the high fishing pressure. The *stock* size is highly determined by the strength of incoming year-classes (ICES, 2013). Western *stock* has been decreasing but levelled out after management of fishing from 2007 (HELCOM, 2013).

The Kattegat *stock* is declining heavily: from 15 000 ton of reported catches in the 1970s, it first decreased to less than 7-8 000 ton in the 1990s and then to less than 500 tons in recent years (ICES, 2013). A drastic decrease of SSB, together with reduction of spawning areas and overfishing, has caused a critical situation in the *stock*. A management plan was adapted one year later than in other *stocks*, in 2008. Sweden ban fishing during the spawning period (1st of January--31st of March). In

2010 an MPA was established for protection and recovery of Kattegat cod. Fishing is prohibited in central part of this area (HELCOM, 2013).

Food

Prey species and their proportions in the diet slightly differ between subdivisions. But in general, small young cod (15-24 cm) eats mainly invertebrates: crustaceans (*Mysis sp* and *Pontoporeia sp.*) and polychaete (*Antinoella sarsi*); middle size cod prefers the isopod *Saduria entomon*, but predates also on small sprat and herring; larger cod feeds mainly on sprat and herring, but also *S. entomon* (Bagge et al., 1994; Rudstam et al., 1994). Eastern Baltic cod eats more sprat than herring, probably because some herring migrate to Kattegat and Skagerak. Invertebrates also comprise part of cod's diet (Bagge et al., 1994), as well as cod eggs, larvae and juveniles (Jensen and Sparholt, 1992). Sprat and herring comprise 80% of bigger (>30 cm) cod stomach content (Røjbek et al., 2014). Before 1980, *S. entomon* was more frequent in the cod diet than afterwards (Uzars, 1994). Cod feeds during the whole year, except for very severe winters (Bagge, 1981).
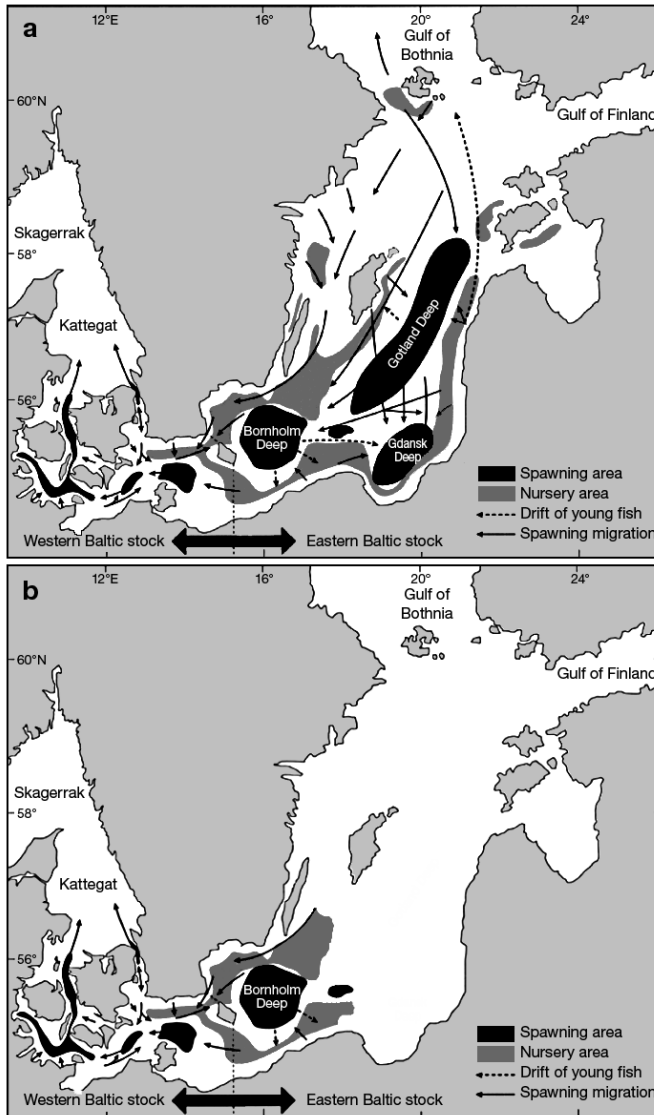
Figure 7. Spawning grounds of Eastern and Western Baltic cod stocks before (a) and after (b) mid 1980s. From Cardinale and Svedäng (2011), a) redrawn from Bagge (1994)

Reproduction and development

There were 3 major spawning grounds for the Eastern Baltic cod: Bornholm Basin, Gotland Basin and the Gdansk deep (Figure 7 a), and of minor importance Slupsk Furrow (Bagge et al., 1994). But since the 1980s the Bornholm Basin is the only spawning ground (Figure 7 b) for the Eastern Baltic cod (Hinrichsen et al., 2003). For the western Baltic cod the major spawning grounds are Kiel Bay and Fehmerh Bay, minor -- Arkona Basin (Bagge et al., 1994). The western Baltic cod spawns during spring, the eastern -- during summer and cod in the Kattegat-- in late winter-early spring (Bagge et al., 1994, HELCOM, 2013). Main threats to recruitment success are egg mortality caused by low oxygen concentration in water (minimum required is 2.3 ml/l) (Bagge et al., 1994), low salinity (the eggs require at least 10.5-11 psu for oating) (Bagge et al., 1994, HELCOM, 2013) and egg predation by sprat and herring (Köster and Möllmann, 2000). Cod spawning in water with lower salinity produce larger eggs than those spawning in 'ordinary' sea water (Bagge, 1981).

Both cod eggs and larvae are pelagic (HELCOM, 2013). Eggs hatch after 18 days at +5°C (Bagge, 1981). After hatching, cod larvae start vertical migration for feeding (Hinrichsen et al., 2003; Bagge et al., 1994). They stay at about 30--40 m depth (Gronkjær et al., 1997), close to the *pycnocline* (Bagge et al., 1994). Their survival is highly dependent on size and species composition of available prey. Retention and dispersion from spawning grounds into optimal feeding grounds is also crucial. If *Pseudocalanus elongatus* is abundant, it is better for larvae to stay in deep waters, while if it's not, it is more beneficial to disperse into shallower regions with high abundance of other copepods (Hinrichsen et al., 2003). There is still a knowledge gap about biology and dynamics of 0-1 year old cod. However, the smallest juvenile cod is observed in deep waters of spawning grounds, mainly in the 4th quarter. Settled juvenile cod don't form schools. The highest concentration of them is close to the *pycnocline*. Vertical distribution seem to follow the one of the prey (mysids) (Nielsen et al., 2013). Juvenile cod live in shallow waters at a depth of 10-70m, for the first 2 years before they join the spawning *stock* (Bagge, 1981).

4.4 Species interactions and influence on each other's population dynamics

To summarize the interactions between the three study species (Figure 8):

- Baltic herring and sprat compete over food resources (Möllmann et al., 2004);
- cod is a main predator of both herring and sprat (Rudstam et al., 1994);
- both herring and sprat may predate on cod eggs and larvae. At the same time, there is cannibalism in cod, herring and sprat, as it is known that they

can predate on their own eggs and larvae. Herring may also predate on sprat
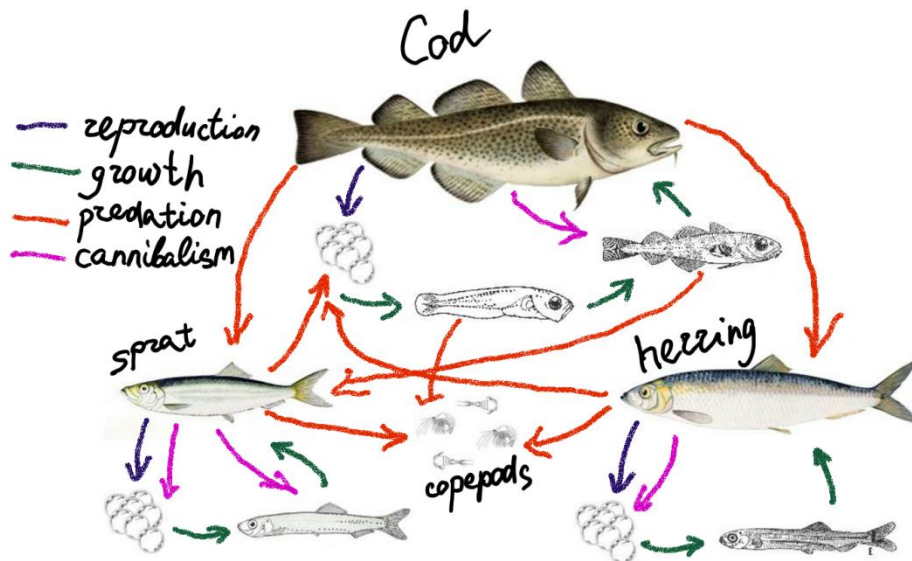larvae and eggs.

Figure 8. Schematic view of the interactions between herring, sprat and cod in the Baltic Sea.

However interactions between cod, herring and sprat is only possible, when
there is spatiotemporal overlap between their populations (Neuenfeldt, 2002), but it
is small now (ICES, 2013; Eero et al., 2012; Casini et al., 2011). Most of the adults
of the cod *stock* are in SD 25, but only about 10-15 % of herring and sprat are in the
same SD. The highest abundances of sprat and herring are in SDs 28-32, where there
is none or very few cod nowadays (Eero et al., 2012).

Ecosystem shifts in the Baltic have a trend: cod dominates, when water salinity
is high; when salinity is low, sprat dominates (Ojaveer and Kalejs, 2010). Following
the collapse of cod population in the late 1980s, sprat abundance increased (Figure
9). As a consequence zooplankton abundance decreased (esp. cladocerans), which
is an evidence for top-down control. Cod-dominated and sprat-dominated regimes
can be separated by a threshold abundance of sprat, which is 17×10^{10} individuals.
After a regime shift favourable conditions for cod didn't translate into it is reproduc-
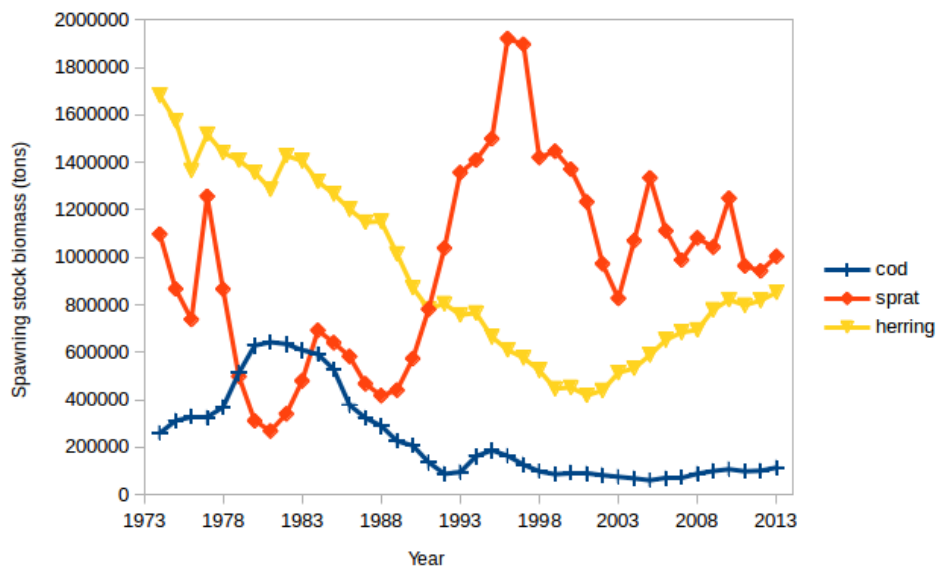tive success which is an evidence for system hysteresis (Casini et al., 2009).

Figure 9. Population dynamics of Baltic herring, sprat and cod. Data from WGBFAS report (ICES,2014a)

5 Different approaches to study interactions between cod, herring and sprat in Baltic

A number of different multispecies and ecosystem models have been used to investigate the interaction between cod, herring and sprat. However, because each of them was built to answer certain specific question, they are lacking some important aspects in order to be more realistic or to describe more facets of predator-prey interactions.

<u>Mass-balanced ecosystem model (Ecopath with Ecosim; EwE)</u>

The Ecopath model is a mass-balanced model that estimates allocations of production, consumption and fishing into food-web. These estimates are used to initialize the Ecosim, which simulates dynamics of each biomass pool, which is a species or a group of species that represents an ecological guild, based on different processes (i.e. fishing, recruitment, predator-prey interactions, abiotic factors, etc.). EwE allows to investigate responses of the food-web to various perturbations, but also feedbacks between different trophic levels, impact of bottom-up control and effect of fishery on non-target species (Harvey et al., 2003).

Österblom et al. (2007) built a EwE model, which constitutes of 15 functional groups (from primary producers to top predators). Fishes are represented there by sprat, herring and cod, each separated into juvenile and adult groups.

A model by Tomczak et al. (2012) includes 22 functional groups of the Baltic Proper (SD 25-29, without Gulf of Riga). Fishes are represented there by sprat, herring and cod. Herring and sprat constitutes of two groups each (i.e., juveniles and adults), whereas cod consists of four groups (i.e., larvae, juvenile, small adult, big adult). Groups were designed to describe differences between diet compositions of ontogenetic stages.

Pros:
- the species are in an ecosystem context;
- takes diet differences between ontogenetic stages into account;
- includes several environmental drivers (SST, reproductive volume, *hypoxia*, etc.)

Cons:
- does not take into account spatial or seasonal variations;
- predator-prey interactions are described only by the proportion of functional group in the diet of a predator known from literature;
- population demography is neglected.

<u>Multivariate autoregressive model (BALMAR)</u>

Lindegren et al. (2010) modelled a food-web that consists of cod, herring and sprat. For each species a separate linear regression is run, however they are solved simultaneously in order to get the most parsimonious estimates for the total model. A matrix of interactions between species as well as a matrix of effect of fisheries, climate (salinity for cod, SST for sprat) and zooplankton availability on each species are parts of the model.

Benefits of the model is that it is able to accurately capture the existing interaction between species (predation of cod on sprat and herring, density-dependence for cod, herring and sprat, etc.), as well as it includes impact of fisheries and climate on the species. However, interactions between species are represented by an index, the sign of which represent a direction (negative or positive effect) and the value -- strength of interactions. In my opinion, this is a too simplistic representation of interactions. The model also doesn't take into account differences between ontogenetic stages of fishes, spatial variation of distribution of populations and seasonal variability (only annual variability is included), it lacks demographic structure and it is a purely statistical model (it is not based on a process approach).

Dynamic model

The model by Heikinheimo (2011) includes separate submodels of sprat, herring and cod linked together through predation. Dynamic of each species is simulated with 0.0156 years' time step. Recruits are added to a system at the specific time point by pulse function and at the beginning of each year fishes are moved to the next age class. Clupeoids had Age 0, Age 1 and Adult group, while cod had Age 0-3, and 3+ group.

Pros:
- using small time step allows for studying seasonal variation;
- populations include different age groups;
- effect of environment (salinity) is used for cod recruitment estimation;
- population dynamics is taken into account.

Cons:
- spatial variability is not included;
- except for age differences individuals are biologically identical;
- sprat and herring are combined in one group as a prey for cod;
- effect of fishing is represented only as a part of total mortality.

Physiologically structured model

Van Leeuwen et al. (2008) studied the dynamics and *equilibrium* biomass densities of cod and sprat, by building stage-structured predator-prey-resource model. Both species had juveniles, small and large adult stages. Impact of fisheries was investigated via modelling fisheries mortalities.

Benefits of the model are the division of fishes into ontogenetic groups, which has shared as well as alternative resources; biomass production and maturation are weight specific. However the spatial variation is not included, interactions between species are represented by a fraction of time spent foraging on a specific resource and a maximum ingestion rate, which is a big simplification.

Spatially disaggregated statistical food-web model

Lindegren et al. (2014) modelled a spatially disaggregated food web of the Baltic. This model, based on a multivariate autoregressive platform, included interactions between cod, herring and sprat in SD 25 (Bornholm Basin), 26 (Gdansk Deep) and 28 (Gotland Basin) with the effect of fisheries and climate change on them. Like in previous version described above (Lindegren et al., 2010), the model includes a matrix of interactions between species, but is now basin-specific.

Pros:

- spatial variability is included;
- data used in the model is abundance indices from surveys;
- effects of fisheries and climate (temperature, salinity, O2) are included. Moreover it's on basin-scale.

Cons:

- no seasonal variability (only annual; mismatch in seasonal scales of data: indices of abundance of cod are from spring survey, whereas clupeoids are from autumn survey);
- no ontogenetic stages;
- interactions between species are simplified, they are represented only by direction and strength of effect and spatial overlap between species (possibility of interactions instead of interactions).

My models of cod (Eastern Baltic), herring (Central Baltic) and sprat will be built in Gadget (Globally applicable Area Disaggregated General Ecosystem Toolbox). It is a modelling platform that allows to model marine ecosystems including interactions between species but also the impact of fisheries and environmental variability on the species. Gadget offers a process-oriented framework to model a number of ecological processes that regulate population dynamics including maturation, growth, reproduction, recruitment, predation, and more (Begley and Howell, 2004). Typical implementation of a complex multispecies Gadget model starts with the development of a simple single species models. Accordingly, I will start with the implementation of simple independent models for each population considered in my research project and based on these initial runs I will add complexity. My models will be built separately for each species on a subdivision-scale (or some close approximation of SD) and linked together by cod predation and for herring and sprat

by a common fishery. Models will include mature and immature fish as distinct *stocks*. The models will be fitted to multiple datasets which include information from biological sampling of both commercial fisheries and research surveys, catch statistics of the fisheries and cod stomach data.

6   Research questions

To fulfil the overarching goal of my research project "understand how predator-prey interactions in the Baltic Sea are framed by a combination of processes: fishing exploitation, climate variability and density dependence" I have decomposed the problem into the following questions which I would like to answer during my PhD studies:

- Effects of predator on prey:
    - how is dynamics of prey (demography and abundance) is affected by predation?
    - how does variability in the demographic composition and spatial distribution of study species affect interaction between them?
- Effect of prey on predator:
    - how does condition (size) of cod relate to the availability of prey and amount of prey eaten (and/or frequency of prey species in the stomachs)?
    - extent of the spatio-temporal overlap between herring, cod and sprat
    - how does spatial overlap between species relates to prey eaten by cod?
    - switch from benthic to pelagic prey (and vice versa) as a function of ontogeny, prey availability, *hypoxia/anoxia*
- Ecosystem effects of predator-prey interactions:
    - how can we identify different regimes (i.e. cod-dominated vs. sprat-dominated regime)?
    - is ecosystem shift back to cod-dominated system possible? What does it require? When can this shift happen?
    - is there an *equilibrium* state (specific for each regime) between herring, sprat and cod populations? How and when can it be reached?
    - what is the trade-off between herring and sprat as a food source for cod and a resource for fisheries?
    - what is the trade-off between clupeoids and cod as a resource for fisheries?

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