Understanding the spatiotemporal dynamics of demersal fish species in the Baltic Sea

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Cover: *Platichthys flesus* near Vääna-Jõesuu in Estonia (on the left)
    Photo by Tiit Hunt (CC BY-SA 3.0)
    Gadus morhua (on the right)
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Abstract

Species are not homogeneously distributed and the interdependencies between trophic interactions, environmental factors and anthropogenic forcing determine how their distribution changes over time. Hence taking into account both the spatial and temporal components of the dynamics of potentially interacting species is essential in management and conservation.

Cod and flounder are two key fish species of the Baltic Sea, both ecologically and commercially. However, their dynamics and interactions in the offshore demersal habitat have been largely neglected in the past. Therefore, the objective of this thesis was to obtain further knowledge on how their dynamics have changed in space and time in this region. This was achieved by investigating the long-term changes in the horizontal and vertical distribution of cod and flounder, and by quantifying their spatial overlap and potential interactions.

The results show that large changes have occurred in the demersal fish community of the Baltic Sea during the past four decades. Cod collapsed and contracted to the south, while flounder increased both in abundance and extent of distribution in the central Baltic. A contraction in the vertical distribution have been shown for both species from the early 1990s, possibly due to a combination of expanded areas of hypoxia in deep waters and an increase in predation risk in shallow waters. These changes have increased the spatial overlap between life-stages and species, which may have amplified the interaction strength between cod and flounder. The changes in predator-prey and competitive interactions between cod and flounder are hypothesised to have contributed to the low abundances of flounder during the "cod outburst" in the early 1980s, and to the low condition and feeding level of juvenile cod in the last decades.

These results are highly relevant both for fisheries management and marine spatial planning as they can be implemented in multispecies models or directly used to protect important areas and habitats. Moreover, the results could be used in stock assessments and management to take into account more realistically the dynamics of cod and flounder in the Baltic Sea.

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Rumslig och tidsmässig dynamik hos bottenlevande fisk i Östersjön

Sammanfattning

Arter är inte jämnt fördelade i naturen och trofiska interaktioner, miljöfaktorer och mänsklig påverkan styr tillsammans hur utbredningarna förändras över tid. Det är därför viktigt att ta dessa förändringar i tid och rum i beaktande i förvaltningen.

Torsk och skrubbskädda är två nyckelarter i Östersjön både ekologiskt och kommersiellt. Kunskapen om deras dynamik och interaktioner i utsjön har tidigare varit svag. Målsättningen med den här avhandlingen är därför att förbättra kunskapsläget gällande hur dessa arters dynamik förändrats i tid och rum i Östersjön. Arbetet har bestått i att undersöka långtida förändringar i utbredningen av torsk och skrubbskädda både geografiskt och i djupled, samt att kvantifiera deras rumsliga överlapp och möjliga interaktioner.

Resultaten visar att bottenfisksamhället i Östersjön har genomgått stora förändringar under de senaste fyra årtiondena. Samtidigt som torskbeståndet minskat kraftigt och koncentrerats till södra Östersjön så har skrubbskäddan ökat både i antal och geografisk utbredning i centrala Östersjön. Utbredningen i djupled har minskat för båda arterna sedan tidigt 1990-tal, möjligen orsakat av en kombination av ökande syrefattiga bottnar i djupa områden och en ökad predationsrisk i grunda områden. Dessa förändringar har ökat överlappet i utbredning mellan livsstadier och arter, vilket kan ha förstärkt interaktionerna mellan torsk och skrubbskädda. Dessa förändringar i predator-bytesinteraktioner och konkurrens mellan torsk och skrubbskädda kan ha bidragit till den låga abundansen av skrubbskädda under perioden med starkt torskbestånd från slutet av 1970-talet till mitten av 1980-talet, och till den svaga kondition och födonivå som observerats hos ungtorsk de senaste årtiondena.

Dessa resultat är av central betydelse både för fiskförvaltning och havsplanering, exempelvis genom att de kan nyttjas i flerartsmodeller eller direkt användas för skydd av viktiga områden och livsmiljöer. Resultaten kan även användas i beståndsanalyser och förvaltning för att på ett bättre sätt ta hänsyn till dynamiken hos torsk och skrubbskädda i Östersjön.

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Dedication

To my mom and dad

Dovrei chiedere scusa a me stessa per tutte le volte in cui ho creduto di non essere abbastanza.
I should apologize to myself for all the times I believed I was not enough.
    Alda Merini

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I   Orio, A., Florin, A.-B., Bergström, U., Šics, I., Baranova, T. and Casini, M. (2017). Modelling indices of abundance and size-based indicators of cod and flounder stocks in the Baltic Sea using newly standardized trawl survey data. *ICES Journal of Marine Science*, 74 (5), 1322-1333, doi:10.1093/icesjms/fsx005.

II Orio, A., Bergström, U., Florin, A.-B., Lehmann, A., Šics, I. and Casini, M. (2019). Spatial contraction of demersal fish populations in a large marine ecosystem. *Journal of Biogeography,* doi:10.1111/jbi.13510.

III Orio, A., Bergström, U., Casini, M., Erlandsson, M., Eschbaum, R., Hüssy, K., Lehmann, A., Ložys, L., Ustups, D. and Florin, A.-B. (2017). Characterizing and predicting the distribution of Baltic Sea flounder (*Platichthys flesus*) during the spawning season. *Journal of Sea Research*, 126, 46-55, doi:10.1016/j.seares.2017.07.002.

IV Orio, A., Bergström, U., Florin, A.-B., Lehmann, A., Šics, I. and Casini, M. (2019). Long-term changes in spatial overlap between interacting demersal fish: a Baltic Sea case study. (manuscript)

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The contribution of A. Orio to the papers included in this thesis was as follows:

I   Participated in planning and designing the study. Conducted the data standardization and the statistical analyses, primary author of the manuscript and handled the review process.

II Participated in planning and designing the study. Conducted the statistical analyses, primary author of the manuscript and handled the review process.

III Participated in planning and designing the study. Participated in the gillnet survey. Conducted the statistical analyses, primary author of the manuscript and handled the review process.

IV Participated in planning and designing the study. Conducted the statistical analyses, primary author of the manuscript.

1 Introduction

1.1 Spatiotemporal population dynamics in ecology and management

In the natural environment species are not homogeneously distributed. Their spatial distribution is the result of the connections between the intrinsic characteristics of the populations, species interactions, as well as environmental and anthropogenic forcing (Hutchinson 1957; Wisz et al. 2013; Layeghifard et al. 2015 and references therein). This is true in marine (Bonsdorff 2006; Ojaveer et al. 2010; Casini et al. 2014; Romagnoni et al. 2015), as well as in freshwater (Bond et al. 2011; Bond & Jones 2015 and references therein) and terrestrial environments (Van der Putten et al. 2010; Robinson et al. 2011 and references therein). Because of all these interdependencies, the abundance of a species in a determined area is likely changing over time. Hence taking into account both the spatial and temporal components when studying species dynamics is of primary importance for both conservation and management (Marasco et al. 2007; Hsieh et al. 2008). This is particularly true under climate change when large redistributions of species are increasingly recorded (Perry et al. 2005; Loarie et al. 2009; Rijnsdorp et al. 2009; Chen et al. 2011).

Understanding the spatiotemporal dynamics of marine ecosystems is a key element to achieve an Ecosystem-Based Fisheries Management (EBFM) (Eero et al. 2012; Kempf et al. 2013). EBFM is a management strategy whose aims are to "plan, develop, and manage fisheries in a manner that addresses the multiple needs and desires of society without jeopardizing the options for future generations to benefit from the full range of ecosystem goods and services" (Marasco et al. 2007, pp 929-930). To achieve these goals, spatial aspects need to be taken into account, for example, for the designation of marine protected areas but also for the development of spatial harvest strategies (Marasco et al. 2007, Cadrin & Secor 2009). From a fisheries management perspective, in the

latest years increasing effort has been devoted to developing spatially explicit stock assessment as well as multispecies models that can handle information such as the spatial distribution of species (Berger et al. 2017). These models are used to account for the spatial variability of species and their interactions through predator-prey relationships or competition, and to assess the causes and consequences of the changes in their distributions (Ciannelli & Bailey 2005; Neuenfeldt & Beyer 2006; Cadrin & Secor 2009; Romagnoni et al. 2015; Berger et al. 2017). In particular, these models should take into account the environmental variability that fish populations experience in their area of distribution, as well as mechanisms such as density dependence and age- or stage-dependent habitat preference (Bjørnstad & Grenfell 2001; Ciannelli et al. 2007; Ciannelli et al. 2008; Planque et al. 2011). Failing to take into consideration the spatial distribution of species as well as intra- and interspecific interactions can hinder the success of fisheries management as shown for many areas around the world (Cury et al. 2000; Fisher & Frank 2004; Hutchings & Reynolds 2004; Hunsicker et al. 2011; Berger et al. 2017). One of the most well-known examples is the failure in understanding the strong interaction between cod and capelin and the changes in both species' spatial distributions, which was one of the main reasons leading to the collapse (and now to a recent increase) of the Northern cod stock in the northwest Atlantic (Rose & Rowe 2015).

With an increasing use of the marine environment, spatial aspects in marine management have been increasingly important for not only fisheries related issues, but also for conservation, which is an integral part of marine spatial planning (Mackelworth 2012). A pivotal issue in marine spatial planning is to identify and to produce full-coverage maps of essential fish habitats (EFH) (Valavanis et al. 2008; Thrush & Dayton 2010; Bergström et al. 2013; Le Pape et al. 2014; Janßen et al. 2017). EFH are environments necessary for the fish's existence and reproduction, and include nursery, feeding and spawning areas as well as migratory routes (Rosenberg et al. 2000; Levin & Stunz, 2005). High availability of EFH can sustain large catches per fishing effort, but the limited availability of such habitats can have serious implication on the overall population sizes by acting as population bottlenecks (Halpern 2004). In particular, low availability of EFH with a spawning and/or nursery function can impact the population growth of commercial fish species (Rijnsdorp et al. 1992; Levin & Stunz, 2005; Fodrie & Levin 2008; Sundblad et al. 2014). Therefore, EFH maps are an invaluable tool to assess the impacts of human activities and management measures on the habitats, and to ensure that they are protected to maintain the fish populations that are dependent on specific habitats (Kraufvelin et al. 2018).

1.2 The Baltic Sea

The Baltic Sea (Fig. 1) is one of the largest brackish water areas in the world. It is one of the 66 Large Marine Ecosystems identified and described by the National Oceanic and Atmospheric Administration (NOAA) in terms of bathymetry, hydrography, productivity, and trophic relationships (Sherman & Hempel 2009). The Baltic Sea is a shallow semi-enclosed basin with nearly one third of its extension characterized by depths of less than 25 m (maximum depth of 459 m; average depth of 53 m). The Baltic is non-tidal with a large drainage area, and connects to the North Sea via narrow straits between Denmark and Sweden, acting as thresholds between the brackish and marine systems. Outflow conditions usually dominate the water exchanges with the North Sea resulting in the Baltic Sea in a marked salinity gradient from southwest to northeast and a permanent halocline. The surface salinity in the innermost part of the Baltic is 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 (Vuorinen et al. 2015). The Baltic surface salinity has decreased significantly in the last decades and the forecasted changes in salinity confirm this declining trend (Vuorinen et al. 2015). The declining salinity is one of the crucial drivers of changes in distribution of the different species inhabiting the Baltic Sea, especially since many of these species live close to their physiological limits with respect to salinity and oxygen (Gogina & Zettler 2010 and references therein). The decrease in salinity has also contributed to important quantitative and qualitative changes in the 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 diminishes egg survival (Nissling et al. 2002). Low salinity also means reduced buoyancy of eggs leading to pelagic eggs sinking into the oxygen-depleted deeper water where survival is hindered. Temperature is another key factor shaping the Baltic ecosystem. During the 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 Baltic sea surface temperature has increased significantly over the past century (Philippart et al. 2011) and it is predicted to increase even more by the end of the 2000s due to climate change (Graham et al. 2008). Temperature is particularly important for coastal areas; it impacts the recruitment success, the growth and year-class strength of herring and several freshwater species (Cardinale et al. 2009a; Olsson et al. 2012). Short-term changes in water temperature may also have a significant effect on the species composition of coastal zones (HELCOM 2006; Olsson et al. 2012).
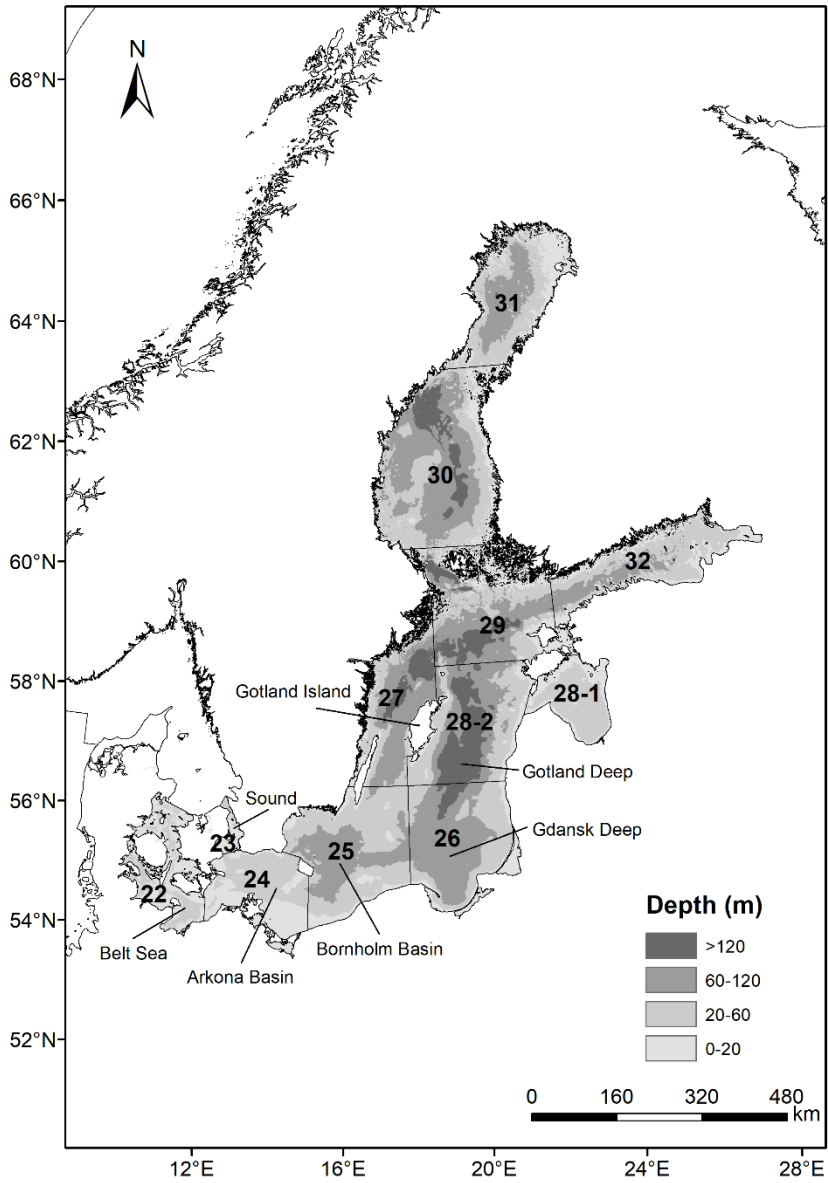
Figure 1. Map of the Baltic Sea divided in ICES subdivisions.

The temperature in the surface and subsurface layers is also important in open waters since it can affect the reproductive success of species, such as sprat (MacKenzie et al. 2007). The temperature in the deep water has also increased in the past century by 2 and 4 °C, depending on the different areas (Carstensen et al. 2014).

Salinity in the deep waters of the Baltic Sea is regulated by the estuarine water circulation regime of the basin, consisting of inflows of saline and oxygenated bottom water and outflow of superficial brackish currents. The bottom water salinity has fluctuated considerably in the last century, but appears to be increasing since the beginning of the 1990s (Carstensen et al. 2014; Mohrholz 2018). 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 (i.e. large scale downwelling of saline and oxygenated waters; Döös et al. 2004), make the Baltic Sea prone to hypoxia (defined as oxygen concentrations below 2 mL L^{-1}) (Carstensen et al. 2014). The ventilation of the deep water is governed by irregular large inflows from the North Sea, called Major Baltic Inflows (MBIs) that are caused by both 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 around one MBI per decade has been recorded thereafter (but see Mohrholz 2018), causing a progressive decrease in dissolved oxygen (Mohrholz et al. 2015). However, the decrease in dissolved oxygen in the bottom waters is also due to increased eutrophication, as also confirmed by Meier et al. (2018). Hypoxic areas have expanded from 5000 km^2 to 70000 km^2 over the past century, increasing fivefold during the last two decades (Hansson et al. 2013; Carstensen et al. 2014; Meier et al. 2018). The areas especially affected by hypoxia and anoxia are the Bornholm Basin, the Gdansk Deep, the Gotland Deep and the deep areas around Gotland Island (Carstensen et al. 2014; Fig. 1). The bottom water hypoxia is one of the main factors shaping the benthic community in the Baltic, causing a lack of macrofaunal biomass on large areas of the sea bottom, with repercussion on all trophic levels of the Baltic Sea ecosystem (Karlson et al. 2002; Conley et al. 2009; Villnäs et al. 2013). For example, the degradation or elimination of the benthic communities over vast areas of the Baltic has been proposed as one of the triggers of negative density-dependence effects, such as increased cannibalism and decrease in growth, on cod population (Eero et al. 2012). The

bottom water hypoxia, together with the bottom salinity conditions, are also affecting the reproduction and recruitment success of many fish species spawning in the deeper parts of the Baltic, whose eggs need a minimum oxygen concentration to survive, and a salinity concentration high enough to float (Ustups et al. 2013; Hinrichsen et al. 2017a).

Eutrophication in the Baltic has increased significantly from the 1950s (Elmgren 2001), mainly due to an increase in nutrient loads (Carstensen et al. 2014). All the open-sea areas of the Baltic are currently classified as affected by eutrophication (HELCOM 2014; Andersen et al. 2017). Future projections are also showing a potential increase in eutrophication due to increased precipitation that will result in higher nutrient inputs from land-based sources further worsening the Baltic condition (Philippart et al. 2011; Ryabchenko et al. 2016). The effects of eutrophication in the Baltic are several, such as enhanced primary production in coastal and open waters, leading to decreased Secchi depth, and decreased oxygen concentrations in the deep waters (Snickars et al. 2015). These phenomena have had important impacts on the species inhabiting the Baltic and in particular the one dwelling in the coastal and in the deepest areas (Snickars et al. 2015 and references therein). It is also worth mentioning that the increase in productivity of the Baltic due to eutrophication can also lead to an increase in fish production as already suggested by Ojaveer & Lehtonen (2001).

1.3 Cod

Cod (*Gadus morhua*) is a key species in the North Atlantic both ecologically and commercially (Hamilton & Butler 2001; Frank et al. 2007). In the Baltic Sea it is the main fish top predator (Casini et al. 2012). Cod can live in waters with temperatures ranging from near 0 °C up to 20 °C, although individuals are usually found in waters with temperatures between 0-12 °C, and salinities ranging from almost fresh to full oceanic water (Cohen et al. 1990; Drinkwater 2005). This species resides in a great variety of habitats, from shallow rocky bottoms down to muddy seabed at over 600 m depth. The preferred depth range of adult cod in the Atlantic is considered to be between 150 and 200 m (but significantly shallower in the Baltic, see ICES 2014), while the juveniles generally prefer coastal shallower waters (Cohen et al. 1990). Cod is considered a demersal species, even if it becomes pelagic under certain hydrographic conditions when feeding or spawning (Godø & Wespestad 1993; Strand & Huse 2007 and references therein). In the Baltic Sea, for example, this pelagic behaviour is enhanced because of the hypoxic bottom waters (Schaber et al. 2009; Casini et al. 2019).

Cod changes its diet with ontogeny. Larvae and post larvae feed on plankton, while juvenile cod feeds mainly on crustacean and other invertebrates. Fish consumption, especially on clupeids, increases in adult cod, but crustaceans and other invertebrates are still present in its diet (Cohen et al. 1990; Bagge et al. 1994; Hüssy et al. 1997; Huwer et al. 2014). In the Baltic, its main invertebrate prey is *Saduria entomon*, a large isopod whose proportion in numbers in the diet of small cod is up to 40%, while its main fish prey are sprat and herring, whose proportions in numbers in the diet of cod between around 30 and 80 cm can reach 40% (ICES 2016). Large cod also predate on flounder and other cod (ICES 2016). Cannibalism is considered to be an important factor controlling recruitment success in cod stocks (Neuenfeldt & Köster 2000). The main feeding period of cod in the Baltic is after spawning (i.e. late summer to early winter) (Wieland et al. 2000).

The migratory behaviour and the distribution patterns of cod can vary markedly with respect to area, season and with the strength of major environmental factors (Pálsson & Thorsteinsson 2003). Some cod individuals are relatively stationary, while others can perform migrations of over 1000 km (Aro 1989; Cohen et al. 1990).

The estimation of age at maturity of cod varies between studies but is generally in the range 2-10 years (Curry-Lindahl & Nyström 1985; Jonsson & 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 & Grygiel 2013). The spawning period of cod varies between populations, but generally occurs between December and June. However, in the Baltic Sea, the spawning period in the Eastern areas (ICES subdivisions 25-32; Fig. 1) occurs from April to August (Bagge et al. 1994). In the last few decades a delay in the spawning period, with the peak spawning by the end of July, has been recorded, possibly due to a change in the age distributions towards younger fishes (Wieland et al. 2000). In the Western areas (ICES subdivisions 22-24) cod spawns earlier in the year (between January and April), with the peak spawning taking place in March (Bagge et al. 1994).

In the Baltic, the egg survival rate primarily depends on the salinity and oxygen content of the water. The minimum salinity concentration required for the eggs to float is 11 PSU and the minimum oxygen content for eggs' survival is 2 mL L^{-1} (Hinrichsen et al. 2017a). 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 effects are also important, since the eggs produced by larger females have a higher buoyancy and thus a better survival rate (Vallin & Nissling 2000; Hixon et al. 2014; Mion et al. 2018).

The spawning grounds in the Baltic Sea are the Sound, the Belt Sea, the Arkona Basin, the Bornholm Basin, the Gdansk Deep and the Gotland Deep (Bagge et al. 1994; Hinrichsen et al. 2011; Fig. 1). However, in the last decades, the required conditions for successful cod egg development have changed in the Gdansk Deep and Gotland Deep areas. These areas are not available anymore as spawning grounds, or contribute only to a minor extent (MacKenzie et al. 2000).

In the Baltic Sea, two cod stocks have been identified using genetics and tagging experiments, the Western Baltic cod in ICES subdivisions (SDs) 22-24 and the Eastern Baltic cod (EBC) in SDs 25-32 (Aro 1989; Bagge et al. 1994; Fig. 1). The Eastern Baltic cod stock has experienced a dramatic change in abundance and distribution throughout the last century. At the beginning of the last century EBC abundance was low and mainly controlled by marine mammal top-predators (seals and harbour porpoises), the cod main predators, and probably by low ecosystem productivity due to a low nutrient availability (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 (Eero et al. 2011). In the late 1970s and beginning of the 1980s, the favourable water conditions for cod spawning, the high abundance of cod larval prey (*Pseudocalanus acuspes*, a pelagic copepod), and a decrease in fishing mortality, produced the 1980s "cod outburst" resulting in enormous commercial landings (Köster et al. 2005; Casini 2013). The subsequent period, characterized by overfishing in combination with the hypoxia intensification, caused a 10-fold decline in cod biomass.

During the "cod outburst" EBC was distributed all over the Baltic Sea with spillover in areas where cod normally do not occur, such as the Gulf of Riga (SD 28-1) and the Bothnian Sea (SD 30) (Casini et al. 2012; Casini 2013). Instead, after the EBC stock collapsed, the distribution contracted and is now limited to the southern part of the Baltic and in particular in SD 25 (Eero et al. 2012; Casini et al. 2012). In the same period, the stocks of cod pelagic prey species, herring and sprat, have become concentrated in the Northern Baltic, mainly outside the spatial distribution of EBC (Casini et al. 2011; 2014). Only a small fraction of the biomass of sprat and herring is concentrated in SD 25, and it has been hypothesised that this contributed to the decline in the proportion of full stomachs, as well as in the mean weight at age and condition of adult cod (Eero et al. 2012; Casini et al. 2016). Moreover, since the end of the 1980s, cod has also experienced a decrease in the extent of suitable habitat due to decrease in oxygen conditions, as well as a decline in mean size at maturity and a change in the length distribution with a shift toward smaller sizes (Eero et al. 2015; Casini et al. 2016; Köster et al. 2016).

1.4 Flounder

The European flounder (*Platichthys flesus*) is distributed along the northeastern Atlantic coast, from the Mediterranean and Black Sea to the White Sea (Skerritt 2010; www.fishbase.org). Flounder in the Baltic Sea have two different spawning strategies: offshore spawning of pelagic eggs, and coastal spawning of demersal eggs (Nissling et al. 2002; Florin 2005). Momigliano et al. (2017) showed that these two strategies were not characteristic of two ecotypes but instead two species, and the flounder with demersal eggs have been described as a new species, the Baltic flounder, *Platichthys solemdali* (Momigliano et al. 2018a). In the rest of the thesis, I will refer to the species complex *P. flesus* and *P. solemdali* as flounder and the two species will be referred to as two ecotypes. The demersal spawning flounder is present only in the Northern and Central areas of the Baltic (SDs 25-32). The two flounder ecotypes distributions overlap in southern areas like, for example, in the eastern part of Gotland Deep but also in the southern coast of Sweden (Nissling et al. 2002; Florin & Höglund 2008; Momigliano et al. 2018a). Flounder is the most commercially important flatfish in the Baltic (Florin & Höglund 2008). This species inhabit primarily coastal and brackish waters, but it can enter into estuaries and live for long periods in freshwater habitats, although it is unable to spawn there (Hemmer-Hanson et al. 2007). In general, flounder prefer sandy and muddy substrates from 1 to 100 m depth, but are mostly found at depths shallower than 50 m (Skerritt 2010; www.fishbase.org).

In general, information on flounder diet comes predominantly from coastal and shallow areas. 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 (Aarnio et al. 1996; Florin 2005; Skerritt 2010). The main feeding period of flounder occurs during summer and there are indications that the feeding activity is reduced during spawning in spring (Florin 2005).

Flounder have 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 & Steffensen 1989; Skerritt 2010; ICES 2010). This species usually moves out from coastal waters to deeper areas in winter and spawns in the same areas during spring. The demersal spawning flounder, on the other hand, spawn close to the coast or in shallow offshore banks (Florin 2005).

In general, sexual maturity is reached around the second or third year and the spawning period occurs between February and June (Skerritt 2010). The flounder is a broadcast spawner typically with floating eggs that sink as development occurs. Its "Reproductive Volume" in the Baltic is defined by salinity > 10.7 PSU and oxygen concentrations > 1 mL L^{-1} (Ustups et al. 2013).

The demersal spawning flounder has 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 & Höglund 2008). Fertilization of demersal spawning flounder eggs is successful at salinities down to 5-7 PSU (Nissling et al. 2002). The pelagic larvae of both ecotypes will end up in shallow water nursery areas where they will metamorphose into benthic small flatfish (Florin 2005).

In the Baltic Sea, flounder is currently managed as four stocks (SDs 22-23, 24-25, 26+28 and 27+29-32; Fig. 1); three stocks with pelagic eggs and one stock with demersal eggs (ICES 2018). Flounder in the Baltic became one of the dominant demersal fish species in the Eastern Baltic Sea after the cod stock collapsed in the late 1980s (Ustups et al. 2013). In the years preceding the collapse however, the flounder in SD 28 reached an extremely low level of abundance and a fishing ban on the specialized flounder fishery was enforced by the Soviet Union (D. Ustups, pers. comm.). Another study 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 particularly important for eggs abundance. For larval production, instead, both environmental factors and stock size are particularly important. Interestingly, Ustups et al. (2013) show that there is no correlation between the larval production and the recruitment estimates derived from the extended survivor analysis (XSA) performed on the Eastern Gotland stock (Gårdmark et al. 2007; Ustups et al. 2013). Explanations for this could be that recruitment is regulated during a post-settlement phase, or that a mix of juveniles of the two flounder ecotypes in the recruitment areas is obscuring a potential coupling between pelagic larvae and juveniles.

Differently from cod, less is known about the spatial dynamics of flounder in the Baltic. A study on the regional distribution of juveniles in the Northern Baltic Proper found that 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). Erlandsson et al. (2017) have shown that flounder in the Baltic exhibit spatial differences in growth, with higher growth, length-at-age and maturation in the southern areas (SDs 25-26), compared to the more northern ones (SD 28). One of the hypotheses suggested to explain this trend is the higher extent of hypoxic areas in SD 28, which is known to affect growth in flatfish species (Stierhoff et al. 2006). Spatial studies using hydrodynamic models have been performed by Hinrichsen et al. (2017b; 2018), to investigate

the survival and dispersal of eggs and larvae of flounder. Their result demonstrated that the highest survival probabilities are in SDs 26 and 25, while the lower probabilities in SD 28, mainly due to low salinity and oxygen concentration (Hinrichsen et al. 2017b). Another interesting result is that larval drift does not seem to be a major bottleneck in recruitment, since the majority of the larvae after drifting end up close to suitable nursery habitats in coastal areas (Hinrichsen et al. 2018).

2   Goals of the thesis

Despite the Baltic being one of the most intensively studied marine area of the world, the understanding of the spatiotemporal dynamics of cod and flounder was before the work of this thesis largely missing. Some general information on the spatial distribution of adult cod was available, while knowledge on the distribution of juvenile cod and of flounder was lacking. Moreover, no information was available on the long-term changes in the depth distribution of these species in the Baltic and their potential causes and consequences. In the case of flounder, little was also known about habitat preferences as well as the distribution of the spawning areas of the two ecotypes.

Cod-flounder interactions in the Baltic had not been studied before and only Persson (1981) suggested that high competition between cod and flatfishes at the beginning of the 20th century could have been the cause of low cod abundances. Therefore, it was of particular interest to understand how the spatial overlap between different size classes of cod and flounder changed over time and how this could be related to the known spatial and temporal dynamics of these species in the Baltic. Filling these gaps in knowledge would represent a significant advancement towards an Ecosystem Based Fisheries Management in the Baltic Sea, as well as a step forward in the collection of key information to be used in species conservation and marine spatial planning.

Given the reasons above, the objective of this thesis was to achieve further understanding of how the demersal fish community of the Baltic Sea has changed its dynamics in space and time.

Specifically, the main focuses were to:

➢ Investigate the trends in abundance and maximum length of different cod and flounder stocks in the Baltic (**Paper I**).
➢ Study the long-term changes in the horizontal and vertical distribution of both cod and flounder in the Baltic Sea (**Paper II**).

➢   Characterize the spatial distribution of flounder during spawning time and its spawning habitats (**Paper III**).

➢   Quantify the spatial overlap between cod and flounder to explore the potential interactions between the two species (**Paper IV**).

3   Material and Methods

3.1 Trawl survey data

Catch and individual data for cod and flounder, collected during the Baltic International Trawl Survey (BITS; ICES 2014), were combined together with historical trawl survey carried out by the former Swedish Board of Fisheries (currently the Swedish University of Agricultural Sciences, Department of Aquatic Resources) and the former Baltic Fisheries Research institute (BaltNIIRH; currently the Latvian Institute of Food Safety, Animal Health and Environment).

Catch per unit of effort (CPUE) data were standardized following the approach of Cardinale et al. (2009b). A full description of the standardization method can be found in **Paper I**. A total of 14565 hauls from 1928 to 2016 in SDs 22-32 were standardized (Fig. 2). Smaller datasets were used to study changes in indices of abundance and maximum length of different stocks (**Paper I**), changes in horizontal and vertical spatial distribution (**Paper II**) and changes in the spatial overlap between cod and flounder (**Paper IV**).
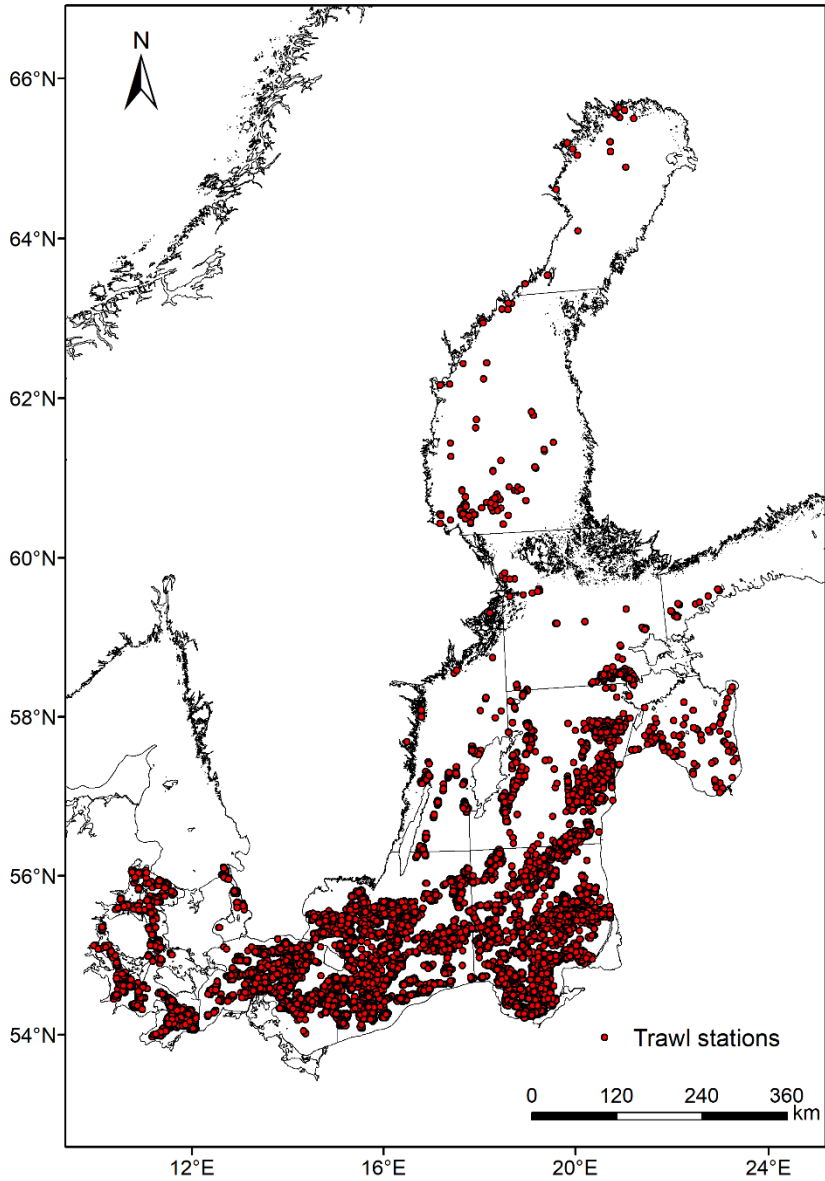
Figure 2. Map of the trawl survey stations.

3.2 Gillnet survey data

Gillnet surveys were conducted in the southern and central Baltic Sea in the spring of 2014 and 2015, as part of the BONUS INSPIRE project (http://www.bonus-inspire.org/). Depth strata between 5 and 70 m were fished with a modified coastal multi-mesh net. Catch and individual data for flounder were collected together with hydrographic data (temperature, salinity and oxygen) and underwater video recordings, in order to estimate a set of habitat variables. The full description of the survey can be found in **Paper III**. A total of 427 fished stations were used to study the spawning distribution of flounder and to characterize their spawning habitat (**Paper III**, Fig. 3).
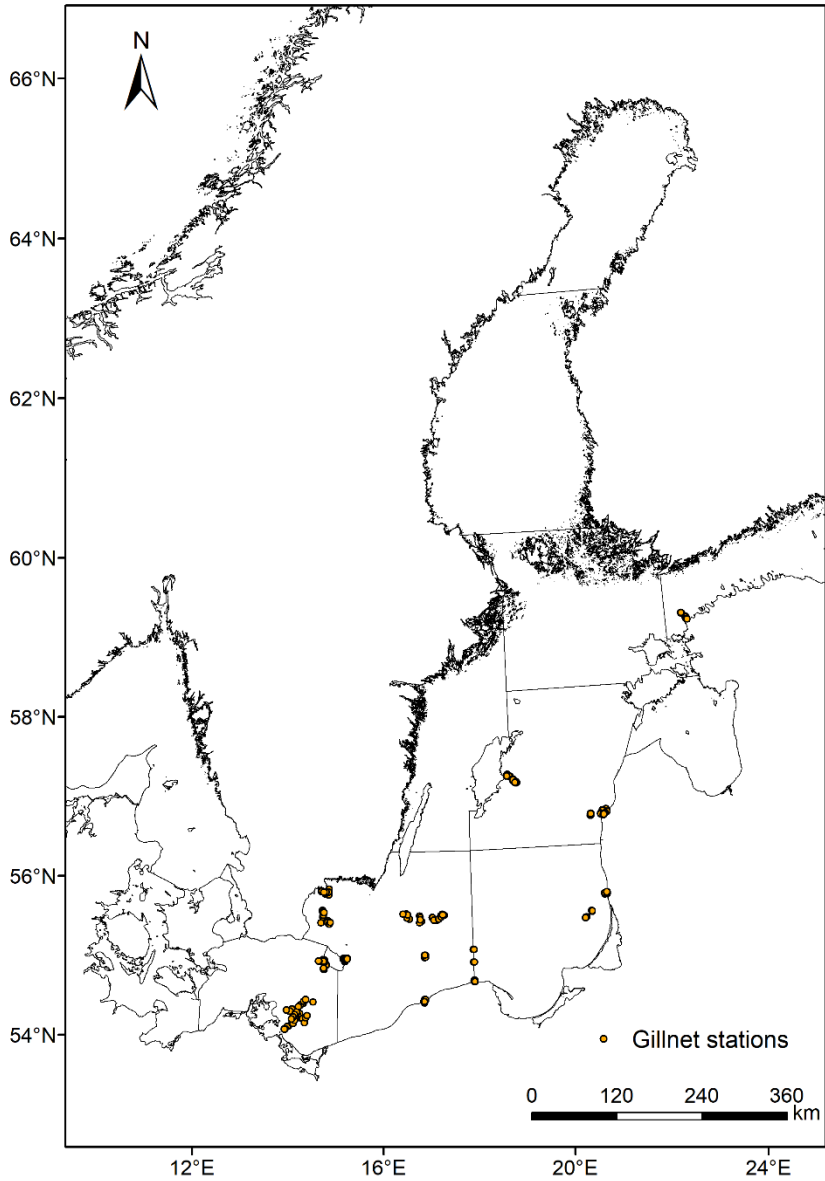
Figure 3. Map of the INSPIRE gillnet survey stations.

3.3 Modelling framework

In this thesis, cod and flounder data were modelled using Generalized Additive Models (GAMs; Hastie & Tibshirani 1990). The decision was based on the assumption that characters such as abundance, probability of occurrence and maximum length of cod and flounder would be better described by non-linear functions of space, time and environmental variables. GAMs have been shown to fit non-linear relationships with lower prediction errors compared to generalized linear models, to have less issues with autocorrelation, and to have greater predictive power (Potts & Rose 2018 and references therein).

Different GAM setups were used to address the goals of this thesis. Standard GAMs, with different data distributions, were used to analyse the changes in maximum length of different stocks of cod and flounder (**Paper I**), the relationship between habitat and abundance of the two flounder ecotypes (now species) during spawning time (**Paper III**), and the changes in probability of occurrence of cod and flounder (**Paper IV**). A different approach was needed to study the abundance trends (**Paper I**) and the changes in the spatial distribution of cod and flounder (**Paper II**). The CPUE data derived from the trawl survey contained a large amount of zero catches that could not be handled by a standard GAM. Therefore, GAMs in a delta modelling approach framework were applied to these data. This approach has previously been used to analyse zero-inflated data (Stefansson 1996; Barry & Welsh 2002; Maunder & Punt 2004), to estimate the spatial distribution of marine organisms at large spatial scales (Loots et al. 2010; Lauria et al. 2011; Grüss et al. 2014; Parra et al. 2016), and to standardize CPUE data and indices of abundance (Cosgrove et al. 2014; Thorson & Ward 2014). This modelling approach allows the separation of the model into two ecologically distinct components (Thorson & Ward 2013): the first estimates the probability of encountering the target species and the second estimates the population density within its range of distribution. The total abundance is then the product of the probability of encounter and the population density. The two components are essential because both the distribution range and the densities are likely to change over time. A full description of the Delta-GAMs can be found in **Papers I** and **II**.

4   Results and Discussion

4.1   Geographical distribution

The results of this thesis are in line with the literature (e.g. Eero et al. 2012; Casini 2013; Bartolino et al. 2017) showing, for the Eastern Baltic cod, high widespread abundances of adult cod in the mid-1980s and a subsequent decrease and contraction of its distribution to the southern part of the Baltic Sea (**Papers I** and **II**). In both **Papers I** and **II** the models of adult cod reveal a recent increase in abundance in the southern areas and confirm the lack of re-expansion in the north. Several hypotheses have been formulated to explain such pattern. 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 Eastern Baltic 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; Hinrichsen et al. 2016). This is also supported by the fact that those areas are still severely affected by bottom water hypoxia (Carstensen et al. 2014; Casini et al. 2016).

   Another factor possibly linked to the contraction of the Eastern Baltic cod stock to the south and the absence of expansion in the north is the natal homing behaviour of cod. In recent years, natal homing behaviour of cod has been suggested as one of the primary causes of segregation between different sub-populations, instead of environmental forcing (Svedäng et al. 2010). Indeed the natal homing behaviour does not exclude the presence of opportunistic recruitment, but highlights the importance of this behavioural trait as a structuring mechanism of the population. The contraction of the Eastern Baltic cod could be linked to the eradication of potential sub-populations spawning in SDs 26 and 28 that, due to the natal homing behaviour, are unlikely to be

replaced even if hydrographic condition improves in the Gotland and Gdansk Deep (Cardinale & Svedäng 2011).

The lack of re-expansion in the northern areas could also be linked to changes in the migratory behaviour of cod. Even if cod is known to perform long distance migrations in the Baltic (Aro 1989) there are some factors potentially limiting its ability to perform such migrations in recent times. **Paper I** has shown a significant decrease in the maximum length of cod. Previous works have shown that bigger individuals can perform longer migrations due to higher energy reserves (Roff 1988 and references therein), also in the case of cod (Jørgensen et al. 2008). Therefore, the changes in the size distribution of Eastern Baltic cod could limit the migration and re-establishment of the stock in the northern areas. This hypothesis is also supported by the low body condition of cod (Casini et al. 2016), which again is indicative of low energy reserve potentially hindering the ability to migrate. 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 prey for cod and cod's feeding efficiency especially in SDs 26-32 causing the migration into SD 25 (Eero et al. 2012).

In **Paper II** we discuss the "ideal free distribution" theory and "density-dependent habitat selection" (Fretwell & Lucas 1969; Rosenzweig 1991; Shepherd & Litvak 2004), which have been linked to the spatiotemporal dynamics of cod in the Baltic (Bartolino et al. 2011). According to these theories, cod should expand/contract its distribution area during periods of high/low abundance, respectively, to maximize its fitness. Of particular interest is the apparent shift that happened between the end of the 1980s and the beginning of the 1990s in concomitance with the regime shift occurring in the Baltic (Möllmann et al. 2009). Before the regime shift, the changes in spatial distribution of cod seem to follow the "basin model", according to which there is an expansion in the distribution when total abundance increases and all the different areas show an increase in local abundances (Petitgas 1998). After the regime shift, on the other hand, cod abundances show an increase only in the most suitable southern areas and the "proportional density model" thus seems to better reflect the recent dynamics of cod (Petitgas 1998). This result allows the formulation of a new hypothesis according to which the Baltic regime shift has disrupted the relationships between local density, total abundance and the distribution area that were governing the spatial dynamics of cod. The mechanisms that can potentially explain this change in behaviour are several, from the extensive decrease of available spawning areas in the eastern part of the Baltic due to the decrease in bottom oxygen (Hinrichsen et al. 2016), to the low body condition of cod (Casini et al. 2016) that could hinder the migration to more favourable environments due to a lack of energy. Therefore, it is possible

that cod, in the current ecosystem state, will not be able to re-expand into the northern areas even if its abundance will further increase.

This thesis has provided for the first time information on the long-term changes in the distribution of juvenile cod (**Paper II**). The main trends are similar to the one of adult cod, although with a clear preference for shallower waters compared to the adult. Moreover, differently from the adult dynamics, juvenile cod has shown signs of re-expansion in the northern areas during the mid-2000s in line with the work of Plikshs et al. (2015), who related this temporary increase in juvenile cod abundance in the Gotland Basin with favourable environmental conditions for the development of eggs.

All the results from this thesis regarding the spatial dynamics of flounder are novel and fill a large gap in the knowledge of one of the most important demersal Baltic fish species. **Paper II** shows that flounder at the end of the 1970s and during the first half of 1980s was not as widely distributed as in recent times and its abundance was relatively low. From the end of the 1980s its distribution and abundance have increased all over the central and southern Baltic, with particularly high abundances in SDs 24 and 25 in the most recent years, as also shown in **Paper I**. This increase could be partly explained by the results of **Paper III** that show an increase in availability of high quality spawning habitat between the 1990s and the mid-2010s. The increase in flounder abundance in the northern areas (i.e. SD 28) on the other hand, could potentially be explained by a shift in the dominance between the two ecotypes (now species), with an increase of the demersal ecotype and a decrease of the pelagic one. This hypothesis is in accordance with the recent work of Momigliano et al. (2018b) who show that between the 1980s and the 1990s a complete shift in dominance between flounder ecotypes occurred in the Gulf of Finland. In the 1980s, the flounder assemblage was dominated by the pelagic ecotype and later by the demersal one. In the Gulf of Finland case the main explanation of this shift is the cessation of either larval supply or juvenile spillover from southern populations (Momigliano et al. 2018b), which could imply also a decrease in abundance of pelagic flounder and an increase in the demersal one in SD 28. Another potential explanation for the increase in the abundance of flounder in the northern areas could be predation release from large cod and a decrease in competition for benthic resources as suggested by the results of **Paper IV**.

Paper III focuses mainly on understanding flounder distribution during spawning time in order to map the changes in the extent of spawning habitats of the two different flounder ecotypes present in the Baltic. The models produced in this paper reflect the dual depth distribution and dual salinity preference of flounder at spawning time known from the literature (Nissling et al. 2002; Ustups et al. 2013). Furthermore, the models show a negative relation between

the abundance of demersal flounder and the abundance of the invasive round goby (*Neogobius melanostomus*). The round goby is becoming increasingly more common and abundant in the coastal waters of the Baltic Sea in the last decade and especially in SDs 26 and 28 (Puntila et al. 2018). The round goby is known to have a strong predation impact on invertebrate communities (Kuhns & Berg 1999; Lederer et al. 2008, Skabeikis & Lesutienė 2015), it can actively predate on young flounder (Schrandt et al. 2016) and aggressively protect its nest (Charlebois et al. 1997; Kornis et al. 2012; Wickett & Corkum 1998). Because of all these known characteristics it is possible that demersal flounder is currently suffering from an increase in competition for both food and space with this invasive species, while the pelagic flounder is potentially less affected, residing in coastal areas only during feeding time and not during spawning. This can be a potential explanation of the decreasing abundance trend observed in the last decade for the flounder stock in SDs 26 and 28 (**Paper I**). This negative influence of round goby revealed by the model, however, cannot be seen in the changes in the distribution and quality of potential spawning areas for demersal flounder (**Paper III**). This is because those predictions do not take into account the round goby, due to the absence of round goby abundance maps for our study area. Therefore, the predicted high availability of demersal spawning areas in the whole Baltic and the increase in high quality spawning habitat in SDs 26 and 28 could be much lower in reality in local areas with high abundances of round goby. The analyses on the pelagic flounder reveal a considerable reduction in the availability of spawning areas in the eastern part of the Baltic in line with the worsening oxygen condition in the deep areas related to the ongoing climate change (Hinrichsen et al. 2011; Lehmann et al. 2014; Carstensen et al. 2014). This result is supported by both the work of Ustups et al. (2013), which show a decrease in the reproductive volume for pelagic flounder, and by Hinrichsen et al. (2017b), who show a large decrease in the survival probability of pelagic flounder's eggs and larvae especially in SD 28. This reduction in spawning habitat could be one of the causes of the switch in the dominance in the different flounder ecotypes in the Gulf of Finland (Momigliano et al. 2018b) as well as the decreasing trend in the stock abundance in SDs 26 and 28 (**Paper I**).

The model of the pelagic flounder (**Paper III**) also shows a positive effect of salinity on the abundance of flounder, similar to the flounder model of **Paper II**. On the other hand, both oxygen and temperature show different patterns. In **Paper III** both the effects of oxygen concentration (between 4 and 10 mL L^{-1} i.e. the common range between the two studies) and of temperature (between 3 and 8 °C) are negative while in **Paper II** are positive. This contrasting result can be explained by the physiological limits for successful spawning of the pelagic flounder. This ecotype needs salinities > 10.7 PSU (Ustups et al. 2013) in order

for the eggs to float and survive. Therefore, during spawning, flounder needs to migrate towards the deep area of the Baltic that are also characterized by lower oxygen concentrations (but still > 1 mL L^{-1} needed for egg survival) and temperature compared to shallower areas as reflected by the pelagic model in **Paper III**.

4.2 Vertical distribution

One of the most interesting results of **Paper II** is the change in depth distribution of cod and flounder that happened in the last 40 years. This change has resulted in the current situation in which the three species/life-stages became concentrated in the same depths (Fig. 4).
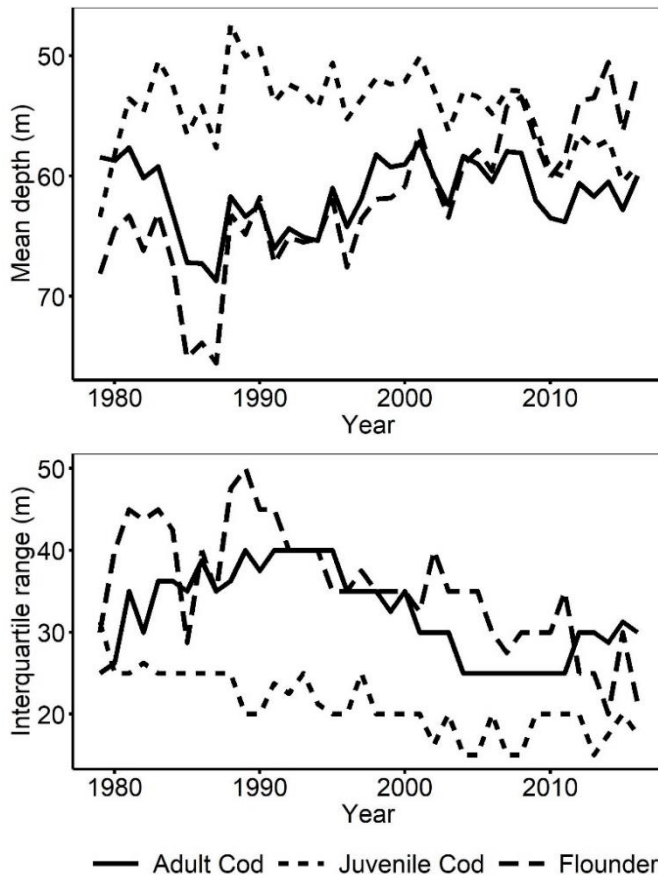

Figure 4. Time series of mean depth and depth range (calculated as the interquartile range of each predicted depth distribution) of adult cod, juvenile cod and flounder in the Baltic Sea in the first quarter of the year. Modified from **Paper II**.

In the past, adult cod and flounder depth distributions were considerably different compared to their distributions in recent years. The highest densities of adult cod and flounder between the mid-1980 and the beginning of the 1990s were at depths around 70-80 m (but see **Paper II** for the differences depending on the SDs), while in recent years they are concentrating at depths around 60 m. Furthermore, in the same period the range of their distribution dropped from around 40-50 m to 20-30. These are clear signals of habitat contraction, which could be related to the increase in hypoxic and anoxic areas in the Baltic in the same period (Carstensen et al. 2014). Anoxic and hypoxic waters can have severe effects on organisms that span from increased natural mortality and susceptibility to predation, alteration of metabolism and growth, to forced migration and habitat contraction (Bijma et al. 2013; Chu & Tunnicliffe 2015). However, the more common effects that can be observed on mobile organisms such as fishes are usually related to habitat contraction and changes in spatial distribution, as it has been shown for many marine organisms (Eby & Crowder 2002; Craig & Crowder 2005; Eby et al. 2005; McClatchie et al. 2010; Stramma et al. 2012; Mislan et al. 2017). Similar vertical shifts (i.e. elevational range shifts) in animal distribution in terrestrial environment caused by climate change have been reported for insects (Colwell et al. 2008; Chen et al. 2011), birds (Sekercioglu et al. 2008; Chen et al. 2011) and mammals (Chen et al. 2011; Büntgen et al. 2017).

Signs of habitat contraction can also be seen in the changes in depth distribution of juvenile cod. However, differently from adult cod and flounder, the shift in depth distribution is less pronounced and towards slightly deeper areas, resulting in a similar average depth in recent years as the adult part of the population. In this case, the increase in hypoxic areas in the Baltic cannot explain such a shift. A possible explanation of this trend could be an active risk avoidance from seal and cormorant predation in the shallower waters. Both these marine top predators have increased their abundance exponentially in the Baltic Sea in the last decades, causing an increase in predation on fishes (Hansson et al. 2017). Seals and cormorants are known to feed in shallow waters down to around 50 and 30 m respectively (Nelson 2005; Oksanen et al. 2014). An active movement of juvenile cod to deeper waters could therefore decrease the predation risk. Comparable changes in spatial distributions of cod and other fishes to avoid seal predation have been reported for the Gulf of St. Lawrence after a large increase in the seal population (Swain et al. 2015).

4.3 Species overlap

Species distribution models are used to relate species distribution data (occurrence or abundance) to environmental explanatory variables (Elith & Leathwick 2009). The study of species interactions by means of species distribution models (e.g. GAMs) and overlap indices allows ecologists to estimate population level effects of heterogeneously distributed species. It also offers an essential set of complementary data to the more common information on species interaction based on dietary analyses since, particularly in marine systems, the direct observations of interactions are rare (Williams et al. 2004; Kuhn et al. 2009; Barnett & Semmens 2012).

The CPUE trends obtained from **Paper I** for cod in SDs 25-28 and flounder in SDs 26 and 28 gave an indication of a potential negative link between the dynamics of the two stocks, since the flounder stock decreased during the cod outburst in the late 1970s and beginning of the 1980s, and then increased when the cod stock collapsed. A similar potential negative relation was revealed by the results of **Paper II** showing almost opposite spatial trends in abundance of cod and flounder. Moreover, studies focusing on diet analyses have shown predation of large cod on flounder (Almqvist et al. 2010; ICES 2016), potential competition for benthic prey, and also significant diet overlap between small cod and flounder (Arntz & Finger 1981; Haase 2018).

The results from **Paper IV** support the previous findings and reveal pronounced changes in the spatial overlap and in the potential competition and predation between different size classes of cod and flounder (Fig. 5). Of particular interest are the trends in the percentage of area with a potential competition between cod and flounder, from the cod perspective (i.e. % of areas where cod is present and also flounder occurs; Fig. 5a). These trends show low potential competition in the 1980s and then a steep increase at the beginning of the 1990s. These changes in potential competition between cod and flounder are supported by the known population dynamics of both cod and flounder. In the beginning of the 1980s, cod in the Baltic experienced a massive increase in abundance and it was widely distributed also in areas where cod is usually not present (Casini et al. 2012; Casini 2013; **Paper II**). On the contrary, flounder abundance was low and its distribution was concentrated in a smaller portion of the Baltic (**Paper II**). Furthermore, from the beginning of the 1990s, both the body condition (Casini et al. 2016) and the feeding level of small cod dropped (Neuenfeldt et al. in preparation), and the most frequently used explanation for this has been the decrease in benthic prey availability due to the increasing bottom hypoxia. However, the results of my thesis suggest that both the drop in condition and the low feeding level of cod could be due to the increased competition for benthic food with flounder.
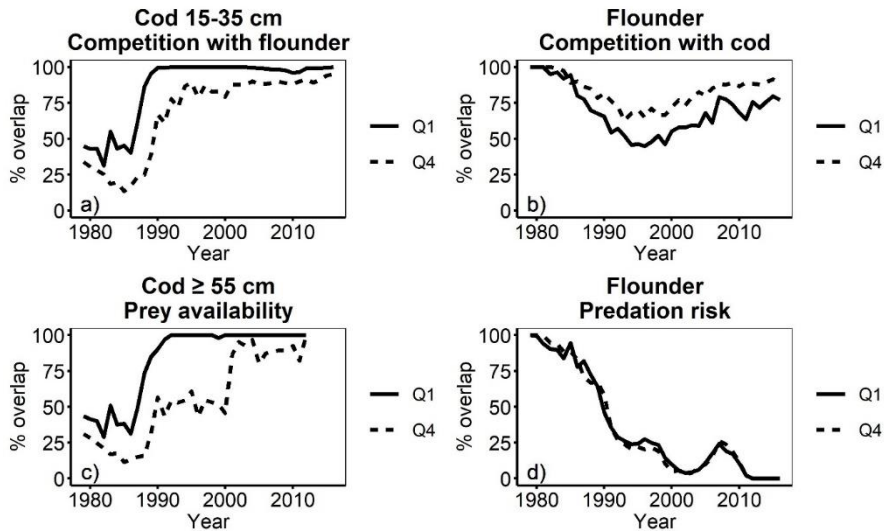
Figure 5. Time-series of percentage of area in which there is potential competition between cod 15-35 cm and flounder (a, b) and predator-prey interactions between cod ≥ 55 cm and flounder (c, d), from both cod (a, c) and flounder (b, d) perspectives, in the different SDs in the first and fourth quarter. Missing values correspond to years when either cod (a, c) or flounder (b, d) probability of occurrence was < 0.75. Modified from **Paper IV**.

This hypothesis also seems to be supported by the temporal negative correlation (r = -0.57) between the trend in potential competition from the cod perspective (as estimated in **Paper IV**) and the body condition of cod 20-30 cm in the fourth quarter (as from Casini et al. 2016). All these results suggest that flounder, due to the increased spatial overlap with cod, could have enhanced the decrease in benthic prey available for cod through competition. The trend of percentage of area with a potential competition between cod and flounder, from the flounder perspective (i.e. % of areas where flounder is present and also cod occurs; Fig. 5b) instead, is U-shaped with high values at the beginning and end of the time-series and lower values in the mid-1990s, concomitant with the cod stock collapse. Differently from cod, there are no studies concerning condition and feeding level of flounder giving insights into whether competition with cod could affect flounder. The decreasing trend in the maximum length of the flounder stock inhabiting SDs 26 and 28 (Fig. 6d), concomitant with the increase in potential competition from the flounder perspective, is probably not a direct result of the competition for benthic food with cod, since the low abundance of cod in those areas. Nonetheless, this decrease in maximum length could be related to other factors, for example intraspecific competition due to the increase of flounder abundance in the area (**Paper II**), or changes in the dominance

between the two flounder ecotypes with an increase of the demersal ecotype and a decrease of the pelagic one, which is known to grow faster (Nissling & Dalman 2010).
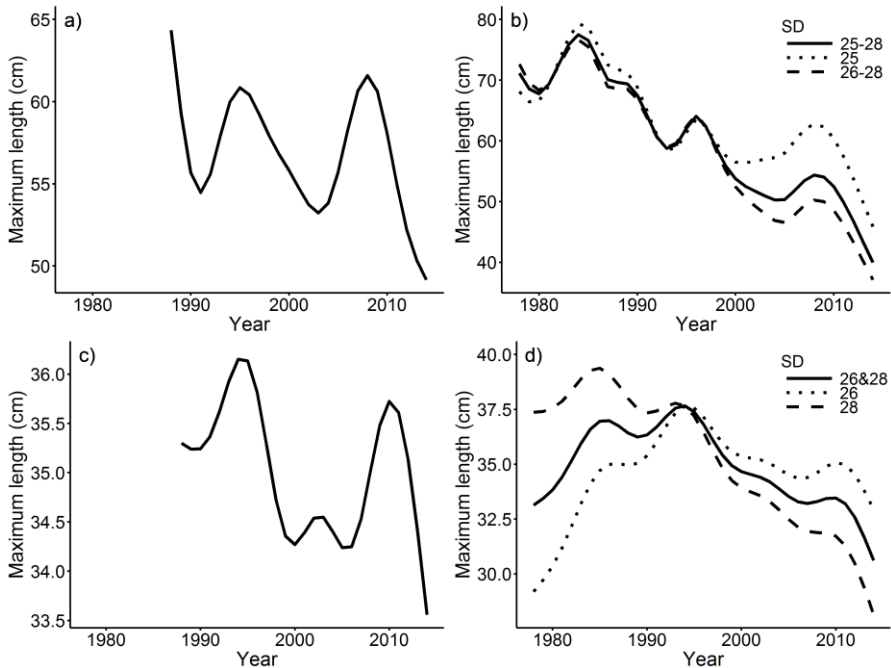

Figure 6. Estimated average yearly maximum length (cm) for (a) cod in SD 24, (b) cod in SDs 25–28, (c) flounder in SDs 24–25 and (d) flounder in SDs 26 & 28. Reproduced from **Paper I**.

The results of **Paper IV** about cod predation on flounder revealed a striking decrease in flounder predation risk (i.e. the % of areas where flounder is present and also large cod occurs; Fig. 5d). In fact, the time-series of percentage of area with potential predation risk show values close to 100% at the beginning of the time-series, then declining sharply to values close to 0% in the northern SDs and less sharply in the southern ones (SDs 24-26). These trends are produced considering only predation from cod ≥ 55 cm since from around this length cod can predate on flounder bigger than ~ 20 cm in the Baltic Sea (ICES 2016). Such a declining trend in the potential predation risk is supported by the results of **Papers I** and **II**, which show a contraction of cod to the southern part of the study area and a drastic decrease in its maximum length (Fig. 6a, 6b) that can explain the extremely low values in the recent decades. This result could also indicate a predation release on flounder that could have contributed to the increase in abundance of flounder populations as well as to the extent of their distribution (**Papers I** and **II**). Similar dynamics of predation release have

already been shown for small pelagic species in the Baltic (Casini et al. 2009) and in other areas where cod stocks have collapsed (Frank et al. 2005). From the cod perspective, the trend revealed by the time-series of percentage of area with prey availability (i.e. the % of areas where large cod is present and flounder also occurs; Fig. 5c) is increasing from the beginning of the 1990s. This increased food availability is supported by the work of Neuenfeldt et al. (in preparation) who calculated feeding levels of cod of different lengths from the 1960s to recent years, and found that from the mid-1990s the feeding levels of cod $\geq$ 55 cm have increased and are the highest recorded from the 1960s. However, the high feeding levels do not correspond to high body condition as shown by Casini et al. (2016) and this could be caused by a combination of different processes, other than food availability, affecting cod condition. One of these processes could be represented by the increased intensity and prevalence of parasite infection in cod, (ICES 2017) especially large individuals, that could affect energy conversion (Horbowy et al. 2016). Also, it is known that hypoxia can affect organisms by altering their metabolism and growth (Diaz & Rosenberg 2011; Levin 2018). Therefore, cod living in areas with low oxygen concentrations could experience physiological stress affecting its conditions even if its feeding level is high. Another possible explanation is that, due to the decrease in benthic preys because of increasing hypoxic areas, cod is predating relatively more often on pelagic species, which requires higher energy, contributing to explain the low body condition of cod. It is also important to consider that the abundance of cod $\geq$ 55 cm has decreased drastically from the mid-1990s, and in the most recent year cod $\geq$ 55 cm are very seldom caught. Therefore, it is hard to draw a strong conclusion on what drives the feeding level of such a poorly represented length class of cod.

5 Conclusions

The studies of this thesis show that large changes have occurred in the demersal fish community of the Baltic Sea in the last four decades. The cod stock collapsed and contracted to the south, while flounder increased both in abundance and distribution in the entire central Baltic from the early 1990s. At the same time, habitat contraction, especially concerning the vertical distribution, have been shown for both cod and flounder, possibly caused by a combination of the increase in the extent of hypoxic areas and increased abundance of marine top-predators, such as seals and cormorants, resulting in higher predation risk in shallow coastal areas. The net effect of this habitat contraction is that adult cod, juvenile cod and flounder overlap more and are concentrated at more similar depths, which may increase the intra- and inter-specific interactions. The changes in the strength of interactions between cod and flounder are hypothesised to be the reason of the low abundances of flounder during the "cod outburst" (and high abundances after the cod stock collapsed), and of the low condition and feeding level of juvenile cod in the last decades. The results of this thesis has also shown a progressive decline of maximum length of both cod and flounder, pointing at the fact that the demersal fish community is becoming dominated by small individuals, as have already been shown for the pelagic community (Oesterwind et al. 2013). Such structural changes in the Baltic fish communities are indicative of changes in the trophic interactions and, on a population level, of a decrease in the potential resilience of cod and flounder due to the loss of large and old fishes.

The results of this thesis are highly relevant both for ecosystem-based fisheries management and for marine spatial planning. They can be implemented in, for example, multispecies models, which at the moment neglect flounder populations, or used as they are to protect important spawning areas for flounder, or areas with high abundances of both species. In addition to that, the results can be used in order to move from stock assessments that consider homogenous and "spaceless" populations to ones that can take into account more realistically the

dynamics of heterogeneously distributed species. This transition to spatially explicit stock assessment is already occurring for some stocks (Quinn et al. 2011; Berger et al. 2017 and references therein), and spatial distribution maps, like the one produced in **Paper II**, can be used to produce area disaggregated indices of abundance or to inform the assessment model about the movement of the stock between different areas. Moreover, from a pure management perspective, such distribution maps can also be helpful in setting a Total Allowable Catch (TAC) apportioned spatially, in order to take into consideration the spatial distribution of the stock or, for example, to protect specific areas (e.g. hotspot area, spawning aggregations or areas with high concentrations of small fish).

Some of the results of this thesis, in fact, are already being used both in assessment and in marine spatial planning. A slightly modified version of the historical abundance trend of Eastern Baltic cod presented in **Paper I** will be used as a survey index in this year (2019) new stock assessment model. The spatial predictions of the potential spawning areas of flounder in the Baltic Sea presented in **Paper III**, instead, have been presented at the HELCOM PanBaltic Scope meeting and are going to be used as one out of several Essential Fish Habitat maps for marine spatial planning.

6   Future perspectives

Although Eastern Baltic cod is probably one of the most studied fish stock around the world, it appears that the more research studies are made, the more questions remain open for answers. Of particular interest would be to further study the dynamics of juvenile cod and especially the spatial distribution of the smallest individuals (e.g. <15 cm), because there are no conclusive answers to where these individuals are dwelling. Considering the large increase in abundance and density of cod <30 cm in the southern Baltic, the smallest individuals should have increased even more and yet no trawl or gillnet survey seem to be able to catch them, and identify the characteristics of the habitats they are living in. Studying the spatial distribution and the abundance dynamics of these small cod individuals would be important, for example, for the estimation of reliable recruitment indices for stock assessment, for understanding the connectivity between habitats utilized by cod during different life stages, and for the inclusion of essential fish habitats important for small cod into marine spatial planning.

Flounder has been an understudied and "underestimated" species in terms of its dynamics and impacts on the ecosystem. The reasons for this are several, such as low commercial values in many Baltic countries and for not being a charismatic species as cod. However, in recent years, the research on flounder in the Baltic has increased substantially and many knowledge gaps have been filled. Further studies are needed, however, in order to shed light on the dynamics characterising this species complex. In particular, due to the description of the new flounder species (Momigliano et al. 2018a), flounder research will be essential in order to manage this species complex in the Baltic. Specific topics that should be further investigated are stock identification and the distribution and overlap between the different species, which are going to be fundamental in order to revise the current management of flounder in the Baltic. In addition, studying the impacts of flounder on benthic communities, and especially in areas with increasing risk of hypoxia, would help quantifying the

potential effects of flounder competition on other demersal and benthic species in areas where the benthic resources are limited. Moreover, further research on the biology, ecology and habitat occupation of the new flounder species, with particular focus on conservation issues, will be needed since the Baltic flounder is one of very few endemic Baltic species.

In general, more research is needed to fully understand the nature and dynamics of cod-flounder interactions. Many experts have been reluctant in accepting the idea of a potential competition between cod and flounder mainly because those two species have never been studied in relation to each other, and because diet studies have not indicated potential interactions. This is mainly due to the fact that diet studies in the Baltic for cod and flounder are usually not comparable due to differences in the sampling areas, periods and depths. Therefore, synchronized sampling of cod and flounder diet in different seasons and areas is required before ruling out the possibility of interactions between them a priori. Using stomach content data could allow researchers to quantify the impacts of this potential competition on both cod and flounder and to provide quantitative estimates of competition, which could be used as input in multispecies models that include also flounder. A similar research question could be addressed to infer on the potential effects that predation of cod on flounder could have had in the past, especially during the "cod outburst", by combining the existing cod stomach database with time-series of abundance of both cod and flounder. In addition, proxies similar to the one produced in **Paper IV** could be further developed. Such information about the interactions between cod and flounder could also be valuable for management. For example, in the case of a confirmed and quantified effect of flounder abundance on the body condition of cod, management could favour the development of a specialized fishery in order to thin out the flounder population in areas where cod condition appears to be particularly low due to high competition for benthic resources.

The Baltic Sea is an area where an incredible amount of research has been done and data have been collected for more than a century. New and improved statistical methods are capable of overcoming many of the problems encountered when using long time-series of data coming from different sources, or discontinuous datasets, but still most of the old data are kept in dusty closets and unavailable for further research. Trying to make use of the knowledge that researchers before us have built is definitely a way to move forward in our understanding of the complex dynamics of the Baltic ecosystem. In particular, longer time-series of indices of abundance, as well as age- and size-based indicators and life history parameters, could be implemented as historical baselines in stock assessment and management, reducing the risk of overly optimistic or misleading results on the status of fished populations in the Baltic.

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Popular science summary

By investigating long-term trends in distribution of cod and flounder I show that the two species have changed both their geographical and depth distribution in the last four decades. In particular, in the southern Baltic they are now concentrated in the same areas, thus potentially competing for the same food. This increased interaction may have contributed to the low condition of small cod observed in the last decades.

In nature species are not homogeneously distributed. Their distribution depends on many different factors such as the biology of the species itself, but also the interactions with other species, with the environment and with human activities. Because of these factors, the abundance of a species in a determined area is likely changing over time. Hence, for the success of both conservation and management, it is very important to take into account both time and space when studying species dynamics.

The Baltic Sea is one of the most studied marine areas of the world. Cod and flounder are two key species, both commercially and ecologically, inhabiting this region. At the beginning of this thesis, some general information on the spatial distribution of adult cod was available, while knowledge on the distribution of juvenile cod and of flounder was lacking. Moreover, their dynamics and potential interactions (competition for food and predation of cod on flounder) have been largely neglected in the past. Therefore, the objective of this thesis was to understand better how the dynamics of cod and flounder, and their potential interactions, have changed in space and time in the last four decades. Thus, I investigated the long-term changes in the spatial and in the depth distribution of cod and flounder, with particular attention at the potential interactions between them.

Both cod and flounder spatial distribution changed in the last four decades. The cod population suffered a massive decrease in abundance at the beginning of the 1990s and became more concentrated in the southern areas of the Baltic. The abundance of flounder, instead, increased and its spatial distribution

expanded massively in the central Baltic. At the same time, the depth distribution of both species have contracted. This contraction is possibly due to a combination of the expansion of areas in deep waters where oxygen concentration is extremely low and an increasing risk of being predated by seals and cormorants in shallow waters. These changes in their distribution have increased the extent of areas where cod and flounder can be found together. Sharing the same areas may have amplified the interactions between the two species. In particular, in this thesis I hypothesised that when cod and flounder co-occur in the same area they compete for food, especially for saduria, a crustacean living on the sea floor. This food competition can be one of the reasons of the low condition of small cod observed in the last decades. Moreover, the results of this thesis suggest that the increase in abundance and in the distribution area of flounder could have been favoured by the decrease in abundance of large cod diminishing the predation pressure on flounder.

The results of this thesis are highly relevant both for fisheries management and for conservation. For example, the results can be used as input data in the models that are performed yearly in order to assess the status of the fished populations of cod and flounder in the Baltic and to manage the fisheries targeting them. Additionally, the distribution maps produced in this thesis can be used to plan the protection and conservation of determined areas important for reproduction or because of high abundances of cod and/or flounder.

Populärvetenskaplig sammanfattning

Genom att undersöka de långsiktiga trenderna i utbredning hos torsk och skrubbskädda visar jag att både den geografiska fördelningen och utbredningen i djupled har förändrats under de senaste fyra årtiondena. I södra Östersjön är arterna idag koncentrerade till samma områden, vilket kan göra att konkurrensen om föda ökar. Detta kan ha bidragit till den låga kondition man sett hos torsk de senaste årtiondena.

I naturen bestäms arters utbredning av många olika faktorer, som exempelvis deras biologi, interaktioner med andra arter och den omgivande miljön, och påverkan från mänskliga aktiviteter. Förändringar i dessa faktorer gör att utbredningen av arterna ändras över tid. För att bevara och förvalta arter på ett bra sätt är det därför viktigt att ta hänsyn till den här typen av förändringar.

Östersjön är ett av de bäst studerade havsområdena i världen. Torsk och skrubbskädda är två nyckelarter i regionen, både kommersiellt och ekologiskt. Tidigare hade man viss kunskap om utbredningen av vuxen torsk, men inte om ungtorsk och skrubbskädda. De här arternas dynamik och interaktioner mellan dem, genom konkurrens om föda och predation från torsk på skrubbskädda, hade till stora delar försummats. Målsättningen med den här avhandlingen var därför att öka förståelsen för förändringar i tid och rum hos bestånden av torsk och skrubbskädda under de senaste fyra årtiondena. Jag har undersökt de långtida förändringarna i utbredning hos arterna både geografiskt och i djupled, och hur detta kan påverka interaktionerna mellan dem.

Utbredningen av både torsk och skrubbskädda har ändrat påtagligt de senaste fyra årtiondena. Torskbeståndet minskade kraftigt i början av 1990-talet och koncentrerades till södra Östersjön. Skrubbskäddan å andra sidan ökade i antal och spred sig över stora delar av centrala Östersjön. På samma gång har djuputbredningen av båda arterna minskat, möjligen orsakad av en kombination av ökande syrefattiga bottnar i djupa områden och en ökad risk för predation från säl och skarv i grunda områden. De här förändringarna har gjort att de områden där torsk och skrubbskädda lever tillsammans har ökat, vilket kan ha

förstärkt interaktionerna mellan arterna. I avhandlingen undersöker jag om torsk och skrubbskädda konkurrerar om föda, i synnerhet det bottenlevande kräftdjuret skorv. Resultaten visar att konkurrensen om föda kan vara en orsak till den svaga kondition som setts hos ungtorsk de senaste årtiondena. Samtidigt kan ökningen i antal och utbredning av skrubbskädda hänga samman med att de storvuxna torskarna blivit färre och att predationen därmed minskat.

Resultaten som presenteras i avhandlingen är viktiga både för fiskförvaltning och naturvård. Till exempel kan resultaten nyttjas för att bedöma statusen hos bestånd av torsk och skrubbskädda i Östersjön och förvalta fisket på dessa arter. De kartor över arternas utbredning som tagits fram i arbetet med avhandlingen kan dessutom användas inom havsplanering, exempelvis för att skydda områden som är viktiga för arternas.

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