



Spatial and temporal dynamics of movements in eastern Atlantic cod

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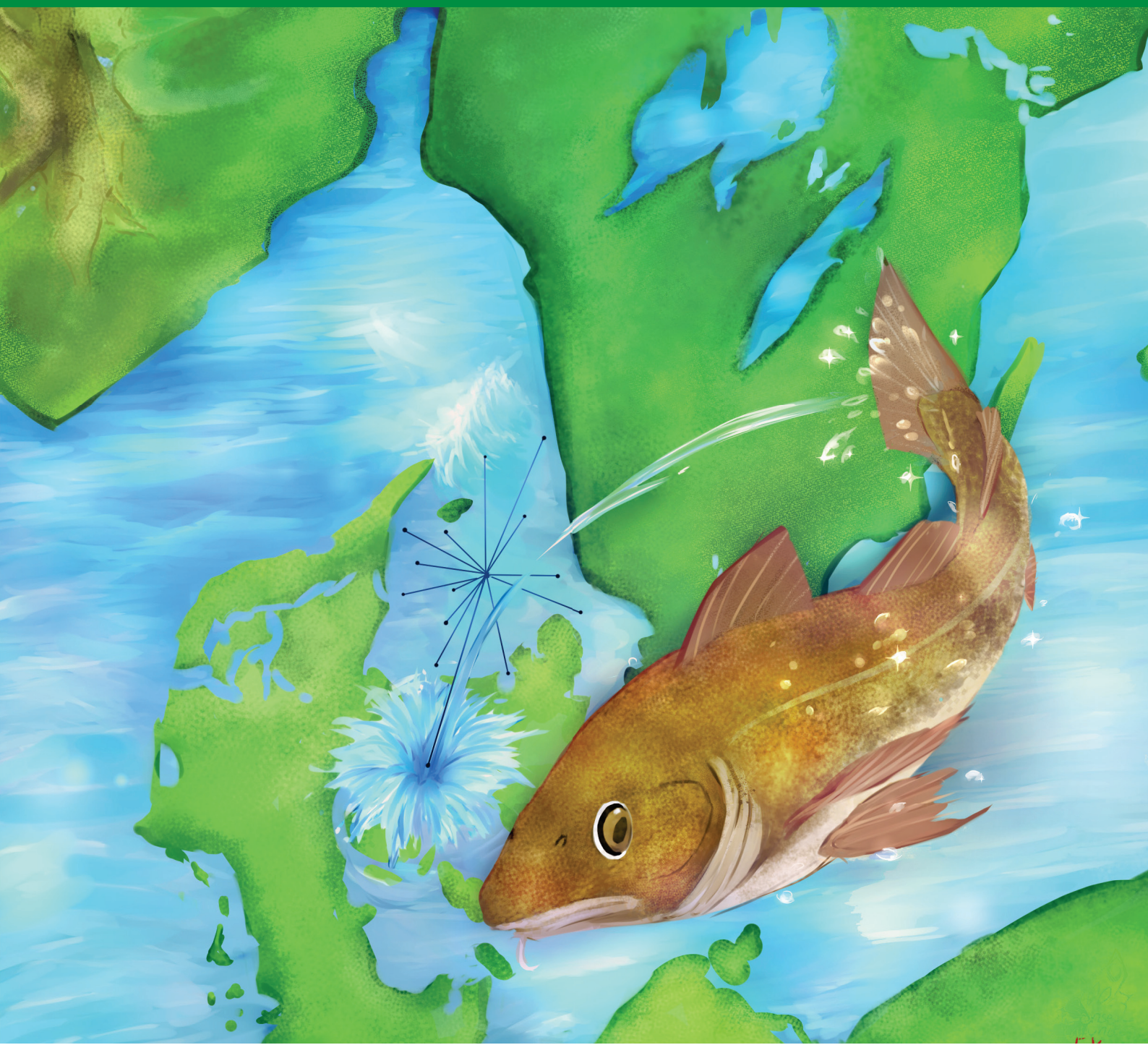
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Spatial and temporal dynamics of movements in eastern Atlantic cod

Regitze Benedicte Carlstedt Lundgreen

PhD Thesis





PhD thesis
Doctor of Philosophy

Spatial and temporal dynamics of movements in eastern Atlantic cod

Regitze Benedicte Carlstedt Lundgreen

Denmark, 2022

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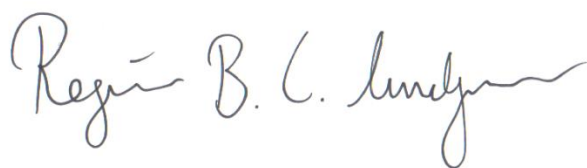
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"Cod are not very good at swimming, that is why they are easily overtaken by trawlers with fishing nets."

From a British report on why the cod is disappearing from the North Sea
(compiled by Leif Eriksson & Kristoffer Lind)

Preface

This PhD dissertation has been submitted in fulfilment of the requirements for the Doctor of Philosophy (PhD) degree at the Technical University of Denmark (DTU). The thesis consists of a literature review, three individual studies, and finally a synthesis and conclusion. The research presented in this thesis was carried out at the Section for Oceans and Arctic under the National Institute of Aquatic Resources (DTU Aqua) between June 2019 and August 2022. The work was supervised by Senior Researcher Karin Hüsey and Professor MSO Anders Nielsen. The PhD was funded by the European Maritime and Fisheries Fund (EMFF) and the Danish Fisheries Agency through the project 'Management of mixed cod stocks in the transition zone between the North Sea and the Baltic Sea: How can this be achieved most efficiently?' (FABBIO). Funding was also provided by BalticSea2020 (<http://balticsea2020.org>) through the project 'Tagging Baltic Cod' (TABACOD). Additional funding for the external stay was covered by the Idella Foundation and the Otto Mønsted Fond.



Regitze Benedicte Carlstedt Lundgreen

August 2022

"The preface is the most important part of a book. Even reviewers read a preface."

Philip Guedalla, "The Missing Muse" (1930)

List of publications presented in the dissertation

Paper I	Lundgreen, R.B.C. , Nielsen, A., Krüger-Johnsen, M., Righton, D., Mion, M., Radtke, K., Plikshs, M., Leskelä, A.J., Raitaniemi, J., Griffiths, C.A., Casini, M., Krumme, U., Hüssy, K. 2022. Examining fish movement in terms of advection and diffusion: a case study of northeastern Atlantic cod. Marine Ecology Progress Series, 691, pp.115-129.	Published
Paper II	Lundgreen, R.B.C. , Nielsen, A., van Deurs, M., Olesen, H. J., Mion, M., Haase, S., Casini, M., Krumme, U., Hüssy, K. Stock connectivity patterns and indications of sub-stock component structuring of cod in the Sound.	Submitted
Paper III	Lundgreen, R.B.C. , Nielsen, A., Hinrichsen, H.-H., Mion, M., Hüssy, K. Simulating movement patterns in Baltic cod (<i>Gadus morhua</i>) in response to historical changes in environmental parameters	In prep.

Other publications during PhD study

Lundgreen, R.B.C. , Jaspers, C., Traving, S.J., Ayala, D.J., Lombard, F., Grossart, H.P., Nielsen, T.G., Munk, P. and Riemann, L., 2019. Eukaryotic and cyanobacterial communities associated with marine snow particles in the oligotrophic Sargasso Sea. Scientific reports, 9(1), pp.1-12.
Mion, M., Griffiths, C.A., Bartolino, V., Haase, S., Hilvarsson, A., Hüssy, K., Krüger-Johnsen, M., Krumme, U., Lundgreen, R.B.C. , Lövgren, J. and McQueen, K., 2022. New perspectives on Eastern Baltic cod movement patterns from historical and contemporary tagging data. Marine Ecology Progress Series, 689, pp.109-126.

Conference presentations during PhD study

AquaPhD symposium	Initial exploration of 70 years of Atlantic cod tagging from the Baltic Sea to the North Sea Oral presentation Arranged by Swedish University of Agricultural Sciences, Sweden	May 2021 (online)
Introduction symposium	Movements in Atlantic cod Oral presentation Arranged by the Pacific Community (SPC), New Caledonia	September 2021 (online)

External stay during PhD study

Collaboration with Dr. Simon Nicol, Dr. John Hampton, and Dr. Joe Scutt Phillips on modelling Baltic cod movement patterns	The Pacific Community (SPC), Nouméa, New Caledonia, August-December 2021
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Throughout this journey, I have had the utmost pleasure of being supervised by Karin Hüssy and Anders Nielsen. I would like to thank you both for your tireless guidance and our countless interesting discussions regarding methodology and ways to approach this plethora of tagging data. Karin, thank you for sharing your extensive knowledge on Atlantic cod and providing excellent feedback on my papers. Anders, thank you for introducing me to the interesting world of data analysis and for always being ready to advice when I ran into an analytical issue. Your combined supervision from both a biological and statistical standpoint has been truly inspiring.

I would also like to thank all collaborators in the TABACOD project and all fishermen who have contributed to this massive dataset over the years. In addition, I would like to thank my collaborators (Hans-Harald, Mikael, Hans Jakob, Marie, David, Monica, Krzysztof, Maris, Ari, Jari, Christopher, Michele, Uwe).

One very important aspect of my PhD has similarly been the amazing people I got to share an office with over the years. As such, I would like to thank Marie, Kjetil (or was it Kjertil?), Peter, Søren, Gitte, Rune, Maria, Phillip, Anshul, and all the other amazing people who have been residents of office 255. You have all enriched my work life considerably and it would take too long to list individual contributions, so I just want to say a big thank you to you all!

A special thanks also goes to my amazing officemate Ole who took his time to give me valuable and extensive feedback on the chapters of this thesis.

While COVID-19 sadly put a bit of a shadow over my external stay, I am very grateful to have been able to experience the courtesy of the Pacific Community (SPC). Specifically, I would like to thank the gracious Dr. Simon Nicol for hosting me in his home for almost two months, Dr. John Hampton for always being ready to help (maybe you can teach me some golf moves someday?), and Dr. Joe Scutt Phillips for our long and interesting discussions and aid in building the initial 'TorskSim' movement model in Python. Special thanks also goes to my building mates: Priya, Claudio, and Ed. It was a pleasure and I hope to be back in some function someday (hopefully with fewer cyclones)!

Special thanks, of course, goes to my beloved family and friends who have supported me throughout this long journey. Thank you for always being ready to celebrate my victories and support me in my defeats; I would not have come this far without you. I would also like to extend a special thanks to my mother; our writing symposiums truly helped me pull through in the final stretch. The image that so graciously adorns the cover of my dissertation also needs a special mention; Elisabeth, thank you for your hard work and for giving me the most beautiful of dissertations!

And last, but not least, I would like to thank the four computers that tirelessly worked to finish my simulations in time (especially during the surprise summer heat during the final stretch!).

Regitze Benedicte Carlstedt Lundgreen

August 2022

Summary

Movement in fish species can be incredibly complex. While some species can remain resident throughout most of their life cycle (e.g., the blacktail seabream *Diplodus sargus capensis*), other species exhibit more migratory behaviour with occasional long-distance migrations (e.g., in several species of tuna). Even more interestingly, some species are characterized by a mix of resident and migratory individuals.

The Atlantic cod (*Gadus morhua*) is one such species with complex movement patterns. Both resident, migratory, and stocks and populations with a mix of these two ecotypes have been documented which can cause issues for management. This is exemplified in MPAs (marine protected areas) where seasonal movement outside the MPA can compromise the efficacy of the MPA, such as in the resident Gilbert Bay cod. In addition, larval transport from the North Sea to the Kattegat and the subsequent return migrations of the adult North Sea cod similarly exemplifies this issue. This highlights the need to document cod movement behaviour in detail in order to understand underlying causes and connectivity to surrounding areas in order to ensure efficient management.

The aim of this PhD study was thus to analyse the movement behaviour of Baltic and North Sea cod in detail using tagging data spanning ~70 years. The goal was to clarify the movement through time and, in the case of the Baltic Cod, try to understand the potential effect of the environment due to the significant past and projected changes in the Baltic Sea caused by climate change.

This dissertation consists of an introduction and three papers (Paper I-III) followed by a discussion. The introduction serves to give an extensive background on the Atlantic cod, including movement, ecotypes, and the effect of the environment on the cod physiologically and behaviourally. This also includes a review of the historical tagging projects in the Baltic Sea and surrounding waters to set the stage for the following papers. The first paper (Paper I) outlines general movement in Baltic and North Sea cod through a period of ~70 years, while the second paper dives into a more detailed analysis of connectivity in the Sound cod stock component (Paper II). Finally, the third paper (Paper III) showcases the results of extensive simulations of movement where the resulting distribution patterns are based on Baltic cod following optimal values of oxygen, temperature, and salinity as summarized by a habitat index. Finally, the results of the three papers are discussed and put into perspective.

Resumé

Bevægelsesmønstre hos fisk kan være utroligt komplekse. Dette kan ses i, at nogle arter kan være stationære igennem størstedelen af deres livscyklus (f.eks. sorthalen *Diplodus sargus capensis*), hvorimod andre arter udviser langt mere vandrende adfærd, til tider i form af udførlige langdistance migrationer (f.eks. i mange arter af tun). Derudover er der nogle arter, hvori der kan forefindes både en stationær og vandrende adfærd blandt individer.

Den atlantiske torsk (*Gadus morhua*) er en af disse arter, som udviser komplekse bevægelsesmønstre. Både stationære, vandrende, samt bestande og populationer med begge disse "økotyper" er blevet dokumenteret, hvilket er problematisk for forvaltningen af torsk. Dette kan f.eks. ses i beskyttede havområder, hvor sæsonbestemte vandringer udenfor områderne kan besværliggøre forvaltningen, hvilket er tilfældet for de stationære Gilbert Bay torsk. Derudover er der også situationer som transport af torskelarver fra Nordsøen ind i Kattegat, hvor de voksne Nordsøtorsk senere hen vender tilbage til Nordsøen. Disse eksempler illustrerer, hvor vigtigt det er at dokumentere bevægelsesmønstre i torsk for at forstå de underliggende grunde, samt sammenhængen med omkringliggende områder for at opnå god og effektiv forvaltning af torsken. Hovedformålet med dette ph.d.-studie var at analysere bevægelsesmønstre i Østersø- og Nordsøtorsk i detaljer ved brug af en mærkningsdatabase, som strækker sig over ~70 år. Målet var at dokumentere bevægelsesmønstre igennem tiden, samt, i forhold til Østersøtorsk, at forstå de potentielle effekter af miljøet grundet de store forandringer i Østersøen, som er forekommet igennem tiden grundet klimaforandringerne.

Denne afhandling består af en introduktion og tre artikler (Paper I-III) efterfulgt af en diskussion. Introduktionen giver et overblik over den atlantiske torsk, inklusiv bevægelsesmønstre, økotyper, samt effekten af miljøet på torskens fysiologi og adfærd. Dette inkluderer også et overblik over de historiske mærkningsprojekter i Østersøen og omkringliggende vande for at give en god baggrund til de efterfølgende artikler. Den første artikel (Paper I) beskriver generel bevægelse i Østersøen og Nordsøen gennem ~70 år, hvor den næste artikel (Paper II) giver et mere detaljeret indblik i sammenhængen mellem Øresundstorsken og de omkringliggende vande i en bevægelsesmæssig forstand. Til sidst viser artikel III (Paper III) resultaterne af et simulationsstudie, hvor bevægelse blev simuleret ift. hvis torskene bevægede sig efter optimale værdier af oxygen, temperatur og salinitet (summeret i form af et habitat index). Afhandlingen slutter af med en diskussion og perspektivering af resultaterne fra ph.d.-studiet.

Chapter I

General introduction



Setting the stage

The Atlantic cod (*Gadus morhua*) is one of the most overfished fish species in the world. The cod fisheries have a great historical importance, such as being the centre of both the Cod Wars in the 20th century disputes between Iceland and the United Kingdom over fishing rights; furthermore, the infamous fisheries stock collapse in 1992 of the Newfoundland cod has commonly been highlighted as an example of overfishing. Today, several Atlantic cod stocks in the world have collapsed or are currently in a poor state. For example, the cod stocks in the eastern Atlantic have been harvested unsustainably for decades. In the North Sea, cod stocks have decreased greatly in abundance since a peak in the 1970s, while the western and eastern Baltic cod stocks, which have historically been commercially important, are now faring so poorly that essentially only small bycatch quotas are currently allowed. Due to the poor status of many cod stocks in the North Atlantic, it is vital to ensure efficient and sustainable management if the cod stocks are to recover.

Fish are usually managed as separate stock units which are generally defined as spatially isolated subpopulations which are self-sustaining, meaning immigration and emigration are negligible, with separate spawning grounds from other stocks. In general, a smaller unit of a stock can be referred to as a stock component, e.g., the Belt Seas stock component of the western Baltic cod stock. The status of a stock is determined by an analytical stock assessment where the current population state is estimated based on data from surveys and fisheries catches which are used to advice management and regulate fishing activities. A key element of stock management is knowing when and where fish are in time and space. This is highly important as the temporal and spatial dynamics of fish can complicate assessments, such as in the Arkona Sea in the Baltic Sea which represents a mixing zone for western and eastern Baltic cod stocks. Thus, if movement and connectivity between areas are not properly accounted for, the uncertainty of the stock assessments will increase and potentially introduce bias that may affect the perception of stock status and sensitivity.

The overall aim of this PhD thesis is to clarify and analyse the movement behaviour of the eastern Atlantic cod. To accomplish this, I utilize a large historical database with tagging experiments in the Baltic and North Sea which stretch back to the 1950s. Additionally, I create a simple toy model to test whether the patterns I have observed can be linked to changes in environmental conditions in the Baltic Sea. The upcoming chapters will outline the background for my thesis, including a brief introduction to the historical and current status of the relevant stocks. This will be followed by an introduction to movement, including biological aspects such as ecotypes, and tools for analysis, and finally the scope and hypotheses of the PhD thesis.

1. The eastern Atlantic cod stocks

In the eastern Atlantic, the cod stocks are assessed by the International Council for the Exploration of the Sea (ICES) which provides advice to managers. The advice is divided by ecoregions which are based on scientific (biogeography and oceanography) and societal considerations (e.g., exclusive economic zones and management areas). Of particular interest for this thesis is the Greater North Sea and Baltic Sea ecoregions (**Figure 1**). Out of the 17 cod stocks recognized by ICES, two of the relevant stocks are located in the Greater North Sea region (North Sea (ICES subarea 4.a-c), eastern English Channel (ICES division 7.d), Skagerrak (ICES subdivision (SD) 20; Kattegat (SD 21)) and two in the Baltic Sea (western (SD 22-24) and eastern Baltic Sea (SD 24-32), respectively). While the Skagerrak and Kattegat are not traditionally viewed as an extension of the North Sea, they will be considered as part of the North Sea stock structure in the following chapters due to the ICES ecoregions.

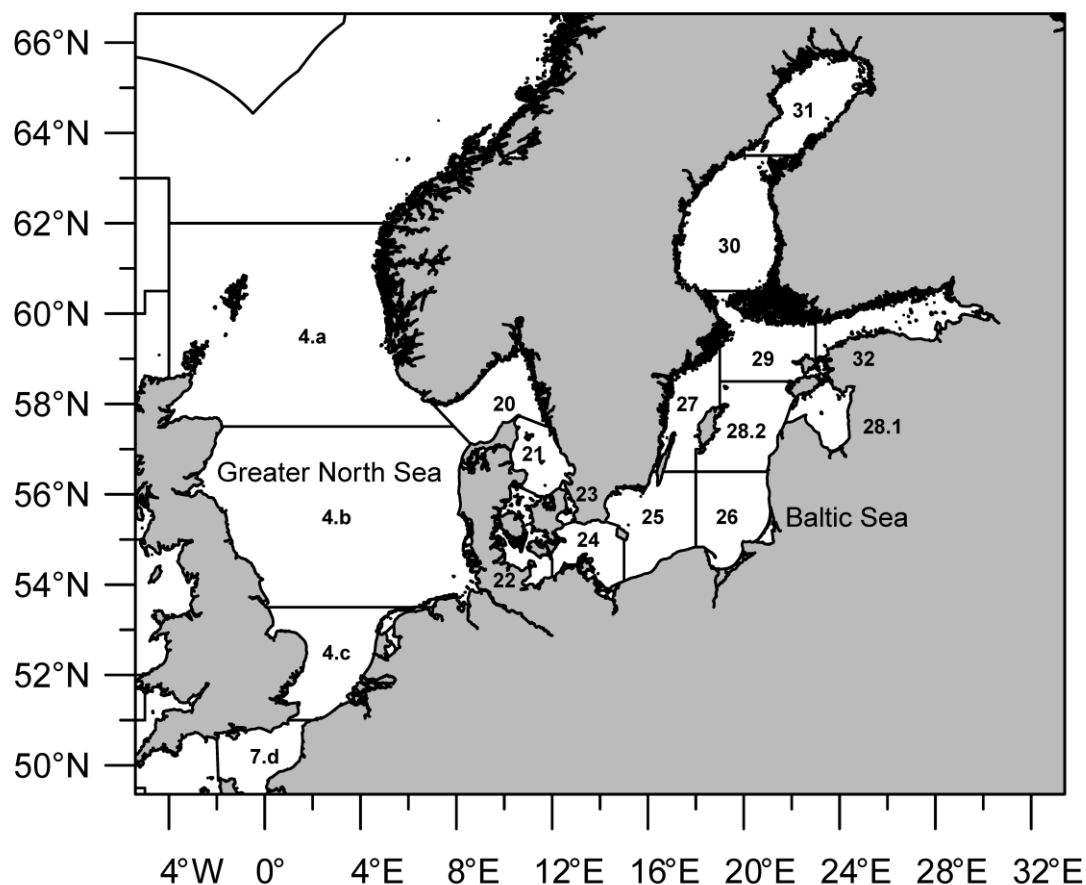


Figure 1. Map of the North Sea and Baltic Sea showing ICES ecoregions. For this thesis, the relevant areas in the Greater North Sea include the North Sea (subarea 4.a-c), Skagerrak (SD 20), and Kattegat (SD 21). The relevant areas in the Baltic Sea include the western Baltic Sea (SD 22-24) and the eastern Baltic Sea (SD 25-32).

1.1 The North Sea stock status

The North Sea is an inland sea located in the eastern Atlantic and borders the United Kingdom, Denmark, Norway, France, Germany, the Netherlands, and France. It connects to the Baltic Sea through Skagerrak and Kattegat to the east, the Norwegian Sea to the north and to the rest of the Atlantic Ocean through the English Channel in the southern region (**Figure 1**).

The gadoid stocks (cod, haddock, whiting) in the North Sea have been commercially important throughout the 20th century (Pope & Macer 1996). In the case of cod, stock assessments, i.e. Virtual Population Analysis (VPA) estimations, have suggested high spawning stock biomass and low levels of recruits in the early 20th century until the gadoid outburst in the 1960s and 1970s (**Figure 2**; Pope & Macer 1996, ICES 2019) which has been suggested to be caused by a delay in *Calanus* production (Cushing 1984). This has been followed by a fishing mortality (F) around 0.5 prior to the gadoid outburst which steadily increased until the stock declined significantly in the early 2000s (Engelhard et al. 2014). While the cod stock started to recover in the late 2000s, the majority of the biomass has been centred in the deeper northern and north-eastern North Sea (Engelhard et al. 2014). In comparison, the shallow southern North Sea has experienced low recruitment, possibly due to changes in distributions of prey zooplankton and climate change (Beaugrand & Kirby 2010, Engelhard et al. 2014, Núñez-Riboni et al. 2019).

In the Skagerrak and Kattegat areas, the cod stocks are considered depleted (**Figure 2**; Svedäng 2003, Svedäng & Bardon 2003, Jørgensen et al. 2011). Historical reports have shown annual catches of 400-600 tonnes between 1920-1960 for inshore cod landings and a continuous decline in the coastal cod fisheries until they disappeared in the late 1990s (Svedäng et al., 2019 and references therein). However, evidence of local spawning (Svedäng et al. 2019) and transport of North Sea larvae in years with higher inflow of North Sea water (André et al. 2004, Hemmer-Hansen et al. 2020) may indicate the potential for recovery in these areas in the future.

However, despite a brief recovery in the 2010s, the spawning stock biomass for the North Sea stock has since decreased and recruitment has remained low since the late 1990s, possibly due to high fishing pressure for the same period which has only recently started to decrease to below overfishing levels (ICES 2022a). As a result, ICES currently advises that, if the maximum sustainable yield concept is followed, catches can only be up to ~23,000 tonnes in 2023 (ICES 2022a). Similarly, ICES considers the continuous decline in spawning stock biomass for the Kattegat stock to be below biomass reference points and currently advises zero catch for 2023 (ICES 2022b). As it stands, it is currently unknown if the stocks will ever recover in biomass as prior to the declines, possibly mirroring the fate of the Newfoundland cod stock which has not yet recovered from overfishing (Schijns et al. 2021).

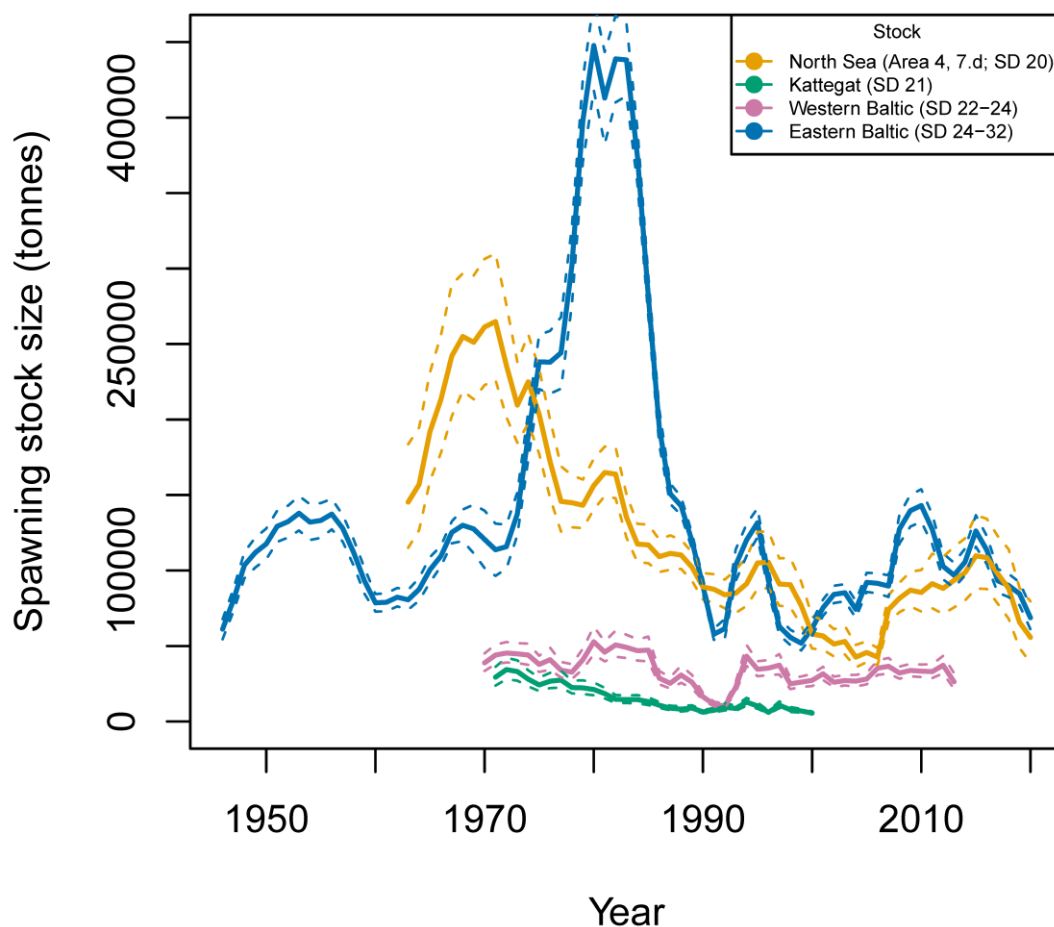


Figure 2. Historical spawning stock sizes (tonnes) for the North Sea-eastern English-Channel Skagerrak (subarea 4, division 7.d, SD 20), Kattegat (SD 21), western Baltic (SD 22-24), and eastern Baltic (SD 24-32) cod stocks. Data taken from ICES assessments and working group reports (Jørgensen et al., 2011; Storr-Paulsen et al., 2014; ICES, 2019, 2020). Dashed lines indicate 95% confidence intervals.

1.2 The Baltic Sea stock status

The Baltic Sea is an inland sea connected to the North Sea through Skagerrak and Kattegat which are straits located between Norway, Sweden, and Denmark (**Figure 1**). A sharp decline in salinity occurs from Skagerrak and Kattegat through the narrow Danish inner straits and to the easternmost part of the Baltic where a low salinity is generally observed (Bendtsen et al. 2007) due to increasing freshwater inflow from rivers.

The western and eastern Baltic cod stocks live in remarkably different environments mainly driven by differences in hydrography, such as bathymetry (Jakobsson et al. 2019) and salinity (Bendtsen et al. 2007). Spawning grounds for the western Baltic cod stock are mainly found in Kattegat, the Sound (also called Øresund), and the Belt Sea (Bleil et al. 2009, Hüsey 2011) while the spawning grounds for the eastern Baltic cod stock have traditionally been in the southern Baltic Sea (i.e., Bornholm Basin, Gdansk Basin, Gotland Basin; Bleil et al. 2009). Additionally, the two stocks are

known to spawn in the Arkona Sea (Bleil et al. 2009). Currently, otolith shape analyses and genetics aid in splitting stocks for stock assessments (Schade et al. 2019, ICES 2022c d).

Spawning stock sizes have been relatively high for the eastern Baltic cod prior to a sharp increase in the late 1970s and early 1980s which was followed by a sharp drop (**Figure 2**; Anonymous, 1993). Despite fluctuations over time in spawning stock biomass that have been driven by differences in mainly year class strength and variations in fishing pressure (Thurow 1974, Anonymous 1988, 1991, 1993), the spawning stock has not been able to reach previous levels of high abundances of almost 500,000 tonnes but has remained around or below 100,000 tonnes (ICES 2020, 2022d). In comparison, the spawning stock biomass for the western Baltic cod stock has remained relatively low throughout the same period with a peak around 50,000 tonnes (**Figure 2**; Storr-Paulsen et al. 2014, ICES 2022c). Despite regulations that limit the fisheries pressure, recruitment has remained low for decades (ICES 2022c). ICES currently advises a minor catch of ~900 tonnes in 2023 which is in sharp contrast to previous peaks of ~50,000 tonnes in the mid-1990s (ICES 2022c). In comparison, ICES advises zero catch in 2023 for the eastern Baltic cod stock (ICES 2022d). While cod in the Sound are considered to be in a relatively healthy shape (Lindegren et al. 2013), cod in the rest of the Baltic are in poor condition (e.g., see Casini et al. 2021) and it is unknown if any recovery is possible. Currently a marine National Park for the Sound is being discussed which is promising regarding conservation of the Sound stock component.

2. Movement in Atlantic cod

Differences in spatial distributions within a fish species are usually explained by three related concepts: ecotypes, homing behaviour, and site fidelity. While 'ecotypes' as a term is used differently within ecology (e.g., see Turesson 1922, Rijnsdorp et al. 2009), it is used here to denote the separation of individual movement behaviour into either migratory or non-migratory/resident (e.g., see Grabowski et al. 2011, Berg et al. 2017). Similarly, homing behaviour indicates a tendency to return to the same area annually, e.g. for spawning or feeding purposes, while cod lacking homing behaviour would be characterized by high site fidelity which indicates a limited home range (Robichaud & Rose 2004). Based on extensive reviews of the available literature, Robichaud & Rose (2004) further classified migratory behaviour into the following categories: resident (high site fidelity), accurate homers (homing to a small area around the original tagging position), inaccurate homers (homing to a large area around the original tagging position), and finally dispersers (moving to seemingly random locations to spawn). In the coming chapters, these concepts will be explained more clearly as exemplified through cod stocks in the North Atlantic. In addition, historical and recent analytical tools of estimating movement behaviour will be presented with the eastern Atlantic cod stocks as the focus, including descriptions of methodology. Due to the nature of the tagging data used in this PhD thesis, only horizontal movement will be considered.

2.1 Ecotypes and migratory behaviour within Atlantic cod

Both the migratory and resident ecotypes are common within populations of Atlantic cod which are distributed from the western to the eastern North Atlantic (**Figure 3**). Genetic analyses have shown ecotype divergence caused by genetic differentiation in both northwest Atlantic cod (Berg et al. 2017) and northeast Atlantic cod (Karlsen et al. 2013, Berg et al. 2016, Kirubakaran et al. 2016). The continuous persistence of the ecotypes on both sides of the North Atlantic furthermore suggests selection on specific genomic regions that might originate from a shared common ancestor (Berg et al. 2017). In addition, it is also possible for ecotypes to co-exist in the same area, such as in nursery areas or spawning grounds (Grabowski et al. 2011, Knutsen et al. 2018, Jørgensen et al. 2020). While these cases only concern cod stocks from sympatric populations, they are still interesting as they illustrate that some isolating mechanisms must occur to keep the populations separate.

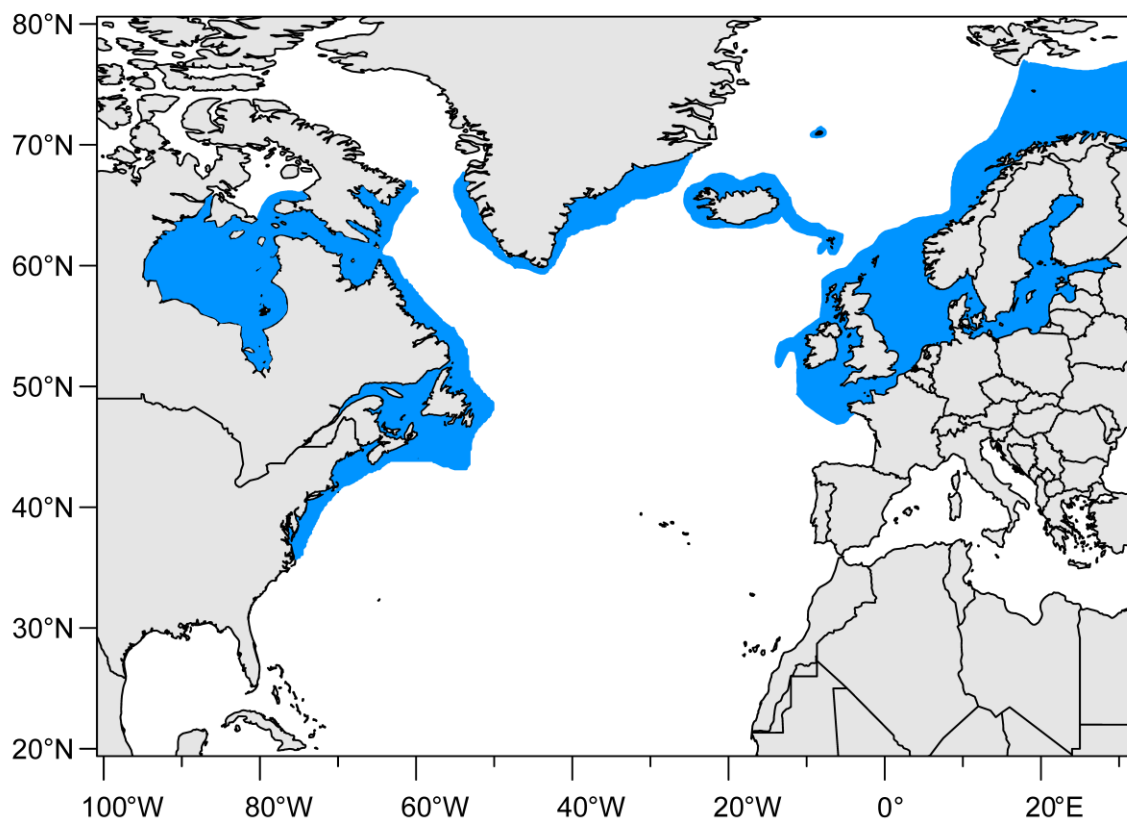


Figure 3. Approximate geographical distribution of Atlantic cod according to the Food and Agriculture Organization (FAO).

2.1.1 North-western Atlantic cod

In the north-west Atlantic (**Figure 3-4**), the northern cod are generally managed as a stock complex known as the Newfoundland–Labrador northern cod stock which constitutes several major and minor cod stocks (Lear & Green 1984). In this area, resident groups of cod have been found in inshore areas, such as around Newfoundland and Labrador (Templeman & Fleming 1962), and specifically in the Gilbert Bay in Labrador (Green & Wroblewski 2000, Morris & Green 2002).

The cod in Gilbert Bay exhibit high site fidelity (home range within ~40 km of overwintering and spawning sites), although individual cod may move outside of the bay area in the summer (within a ~270 km² area outside Gilbert Bay; Morris et al. 2014). This movement behaviour has complicated efforts to protect the cod, and abundances have continued to decline despite the designation of Gilbert Bay as a Marine Protected Area (MPA) in 2005 because of ongoing catches outside the MPA (Morris et al. 2014). In addition, concerns have been raised in regard to managing the Gilbert Bay stock component as part of the Newfoundland–Labrador northern cod stock due to local adaptations and biological characteristics, such as smaller length-at-age (Morris & Green 2002). Transplantations have further showed the importance of local conditions for homing behaviour, such as previous experience with the migration route, as only a low amount of individuals returned to the capture site within a year after relocation outside of the home range while all individuals released close to the capture site within their home range managed to return (Morris et al. 2014). This indicates a high degree of accurate homing within this population.

In comparison, migratory cod populations can be found offshore of Newfoundland and Labrador which undertake long distance migrations between spawning and feeding grounds and exhibit inaccurate homing behaviour (Robichaud & Rose 2004). Indeed, genetic differentiation has been shown between inshore and offshore cod in Newfoundland based on studies of microsatellites (Ruzzante et al. 1996), most likely helping to drive the differences in ecotypes. Annual migrations occur from offshore overwintering grounds to inshore areas along Labrador and Newfoundland to feed on mainly capelin (Templeman 1966, Rose 1993). Spawning migrations occur to offshore areas on the continental shelf in the fall and early winter, and spawning commences in early spring (Templeman 1979, Hutchings et al. 1993). In contrast, the more resident cod found in Labrador and Newfoundland overwinter in inshore areas, such as Trinity Bay (Thompson 1943, Wroblewski et al. 1994, Ruzzante et al. 1996).

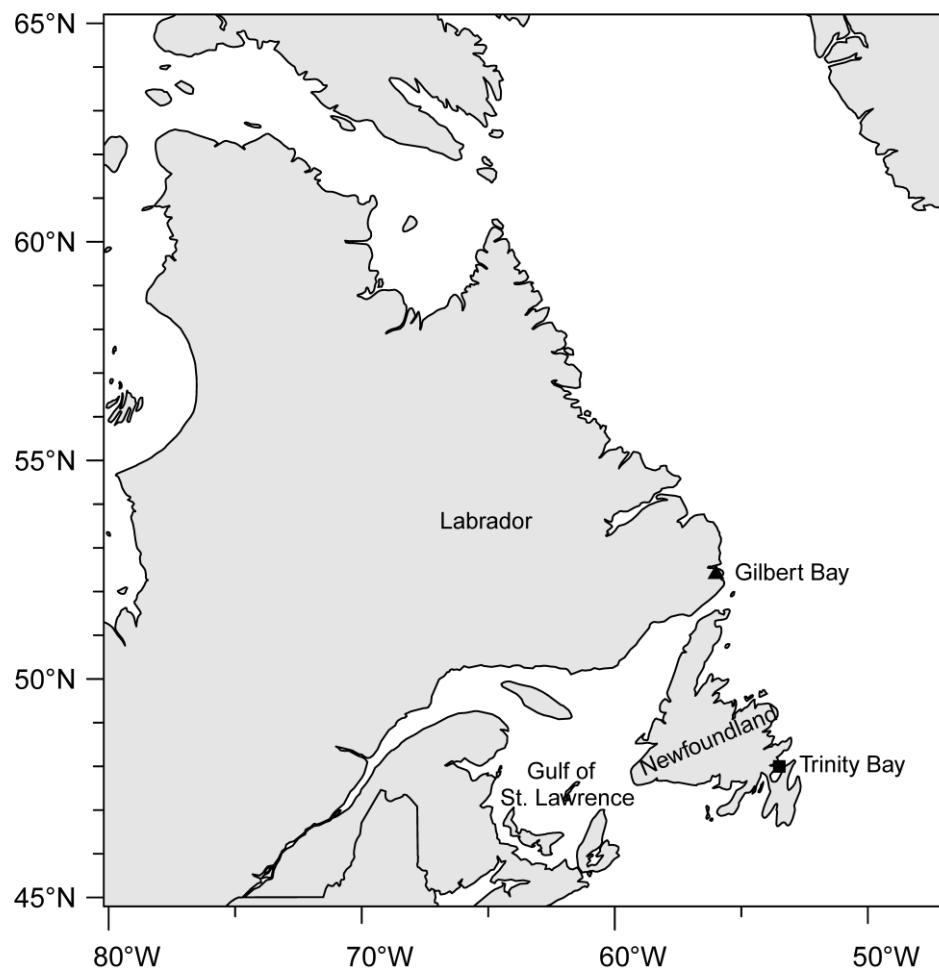


Figure 4. Map of Newfoundland-Labrador in the north-west Atlantic. Noteworthy locations have been marked.

2.1.2 North-eastern Atlantic cod

The north-east Atlantic is similarly characterised by populations of both ecotypes (**Figure 3, 5**). The resident type is commonly found in Norway, and there are countless examples of resident fjord populations along the Norwegian coast (e.g. see Bergstad et al. 2008, Skjæraasen et al. 2011). In general, northeast Atlantic cod are divided into two stocks: the resident NCC (Norwegian coastal cod) and migratory NEAC cod (north-east Arctic cod; Nordeide et al. 2011), respectively.

NCC utilize coastal spawning and nursing areas and can be further divided into more stationary and more migratory components where stationary NCC primarily stay within their respective fjords to both feed and spawn, and migratory NCC migrate short distances along the coast to feed and spawn (Myksvoll et al. 2014). However, overall they appear to be relatively resident (Robichaud & Rose 2004). Along the southern Norwegian coast in Skagerrak, low genetic differentiation seems to occur at a local scale among the NCC ecotype, possibly due to passive transport in the egg or larval stage rather than adult migrations (Knutsen et al. 2003). Some genetic differentiation similarly seems to occur between (Fevolden & Pogson 1997) and within (Jørstad & Nævdal 1989) individual fjords in northern Norway. Not surprisingly, high genetic differentiation separates the NEAC and NCC cod (Fevolden & Pogson 1997), and NCC favour a demersal life style compared to the pelagic NEAC (Pethon 1985).

NEAC migrate from north to south to utilize spawning grounds along the Norwegian coast which are divided into four spawning districts: Møre, Lofoten, Tromms, and Finnmark (**Figure 5**; Sundby & Nakken 2008, Jørgensen et al. 2008). Following spawning, eggs and larvae are transported by the Norwegian Coastal Current to the feeding and nursing areas in the Barents Sea (Myksvoll et al. 2014). The NEAC are most likely homing but it is unclear whether they are accurate or inaccurate homers (Godø 1984, Robichaud & Rose 2004).

Interestingly, it has been suggested based on otolith analyses that NEAC from the Barents Sea have established resident populations in fjords in northern Norway, despite NEAC cod not known to be migrating into fjords (Larsen et al. 1997). Akin to NCC in southern fjords of Norway, this may be due to passive drift of larvae and may differ depending on the local conditions. As an example, larvae are more likely to be retained in areas with a high exchange, such as at the open Malangen fjord in Norway compared to silled fjords such as Balsfjord (Larsen et al. 1997). Curiously these cod do not seem to employ a migratory lifestyle despite originating from migratory populations. This may be because they appear to be in the process of differentiation, as gene frequencies in Malangen cod have not been found to resemble NEAC ecotypes (Jørstad & Nævdal 1989). Model simulations have similarly shown the importance of local retention of eggs and larvae in coastal systems on recruitment in fjords and the low possibility of eggs to be transported out of the fjords (Myksvoll et al. 2011, 2014). As such, it is likely that differentiation among fjord cod might be driven by local retention in addition to site fidelity and homing behaviour exhibited by adults (Skjæraasen et al. 2011).

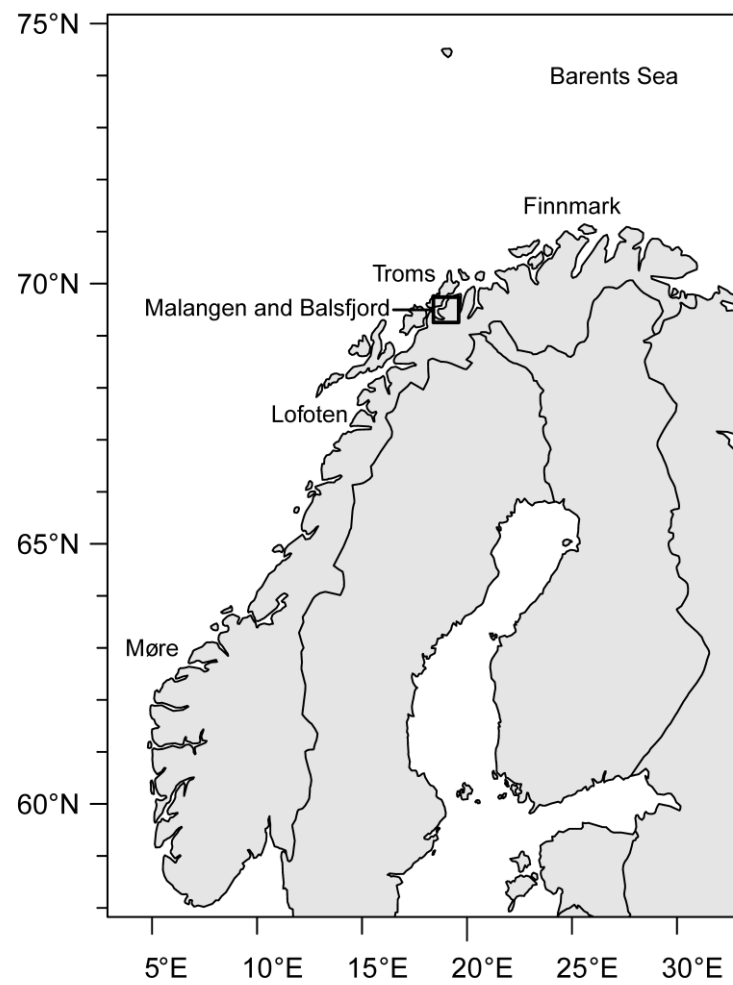


Figure 5. Map of Norway in the north-east Atlantic. Noteworthy locations have been marked. Modified from Sundby & Nakken (2008).

2.2 Why do cod display different migratory strategies?

From the presented examples in the previous chapters, it is interesting to note substantial variation in movement behaviour from even within a population, e.g., the presence of both migratory individuals in resident populations (e.g., Gilbert Bay cod) and resident individuals from migratory populations (e.g., NEAC in Malangen fjord). This most likely infers an evolutionary advantage; if local conditions change, populations resistant to adapting to new conditions would be in danger of extinction. As several Atlantic cod populations are known to contain both ecotypes of migratory and resident individuals (Robichaud & Rose 2004), several attempts have been made to try to understand how and why this occurs. As such, two explanations have gained attention in the literature: **partial migration and metapopulation structure**.

2.2.1 The partial migration concept

The coexistence of both migratory and resident individuals within a population is generally referred to as partial migration but varies from the metapopulation theory in that it focuses on the migration properties of individuals (Shaw et al. 2011), often in panmictic populations, i.e. populations that are not reproductively isolated (Le Bris et al. 2013). This means that throughout the year, resident and migratory individuals might share some habitats during a season, such as spawning or overwintering grounds, but move to separate habitats during other seasons. Shaw et al. (2011) outlined three different types of partial migration (see **Figure 6** for an example of a type of partial migration):

- 1) Outside the spawning season, resident and migratory individuals inhabit different habitats (e.g., different overwintering grounds) but share spawning grounds during the spawning season
- 2) Outside the spawning season, resident and migratory individuals inhabit the same habitat but utilize different spawning grounds during the spawning season
- 3) Outside the spawning season, resident and migratory individuals inhabit the same habitat but only migratory individuals migrate to reproduce during the spawning season

While the majority of studies of partial migration in fish seem to focus on anadromous and freshwater species (e.g., see Chapman et al. 2012a b and references therein), most likely due to the lower difficulty of keeping track of migrants compared to marine systems, the causes of partial migration are likely to be similar or comparable to in marine species.

2.2.2 What causes partial migration?

Several factors have been proposed to explain the cause of partial migration (see Chapman et al. 2012a and references therein). One is the risk of predation, as smaller-sized fish are likely to be subjected to a higher predation mortality depending on the distribution of larger-sized predators

(e.g., see Skov et al. 2011). Indeed, even apex predators would be at risk as juveniles especially if the species practices cannibalism or other higher trophic piscivorous predators are present in the ecosystem.

Another potential cause is differences in body sizes between migratory and resident individuals. This phenomenon has been observed in several fish, e.g., in tiger sharks (*Galeocerdo cuvier*) where only the larger sized sharks seemed to undertake long migrations while the smaller sized sharks would remain relatively resident (Lea et al. 2015). Interestingly, the opposite pattern has been observed in three-spined stickleback (*Gasterosteus aculeatus*) where the larger-sized individuals remained in a pond and the smaller individuals migrated to the sea (Kitamura et al. 2006). In the case of the three-spined stickleback, it is possible that smaller individuals could be pushed out through competition with larger individuals when resources are scarce (the competitive release hypothesis; Chapman et al. 2011), however, hypothesis testing is difficult when it comes to partial migration. As Chapman et al. (2012a) points out, multiple hypotheses may explain differences in body sizes between migratory and resident individuals, such as differences in physiological tolerances between individuals. Indeed, in the case of tiger sharks, a combination of several factors has been suggested to explain partial migration, e.g. biological (size, sex, thermal tolerances, etc.) and abiotic factors (e.g., hydrographic conditions; Lea et al. 2018). In addition, female fish may benefit from skipping spawning one year and thus increasing survival through avoiding spending extra energy on reproduction, leading to higher egg yield in later years (Rideout et al. 2005). However, despite difficulties in explaining what drives partial migration, partial migration is highly common in nature (Chapman et al. 2011, 2012a b) and is likely to help sustain populations.

2.2.3 Metapopulation structure as a concept

The metapopulation theory assumes the existence of several subpopulations with some degree of connectivity, and overall varies from the partial migration theory in that movement is considered on a higher scale rather than individual properties (**Figure 6**). In addition, reproductive isolation is assumed. In contrast to partial migration, this theory seems to have gained more support in the literature to explain cod behaviour (e.g., see Kent Smedbol & Wroblewski 2002, Wright et al. 2006, Hu & Wroblewski 2009), most likely due to the similarity with the stock concept.

A simple metapopulation model, as inspired by Levins' (1970) model, assumes one large metapopulation consisting of several smaller subpopulations (**Figure 6**). Each subpopulation is relatively isolated with local population dynamics and some small exchange between subpopulations. Importantly, local populations dynamics in each subpopulation are not influenced by immigration or emigration. While the overall metapopulation can be considered stable or static, it can be highly dynamic on the subpopulation level as subpopulation go extinct, recolonize new areas, or establish new subpopulations within the metapopulation (Smedbol & Wroblewski 2002). In this view, subpopulations can, depending on the degree of site fidelity, be considered to be comprised of relatively resident individuals while migratory individuals then move to neighbouring subpopulations. As for the partial migration concept, the causes are likely similar. For instance, it is

possible that individuals may decide to move to another subpopulation in case of intraspecific competition; indeed, this could potentially be the cause of recolonization as individuals from saturated subpopulations spill over and settle in other suitable habitats.

Previously the metapopulation concept has been applied to the Newfoundland and Labrador cod populations in an attempt to analyse the spatial structure of the populations (Smedbol & Wroblewski 2002). Smedbol & Wroblewski (2002) hypothesized that individual cod only breed in one area annually during the spawning season, meaning the subpopulations would correspond to a metapopulation. As such, fewer spawning grounds would be occupied as subpopulations die out; in support of this, they noted that some spawning grounds have had only minor activity due to previous overexploitation. A simple model further suggested that a low extinction rate, such as decreased fishing, would result in a higher proportion of occupied areas as colonization rates increase. Similarly, another study by Hu & Wroblewski (2009) considered the effect of protecting the Newfoundland and Labrador subpopulations through MPAs.

While the metapopulation concept generally does not focus on the causes of migration, it has demonstrated itself to be a highly useful way to describe movement within large populations. However, it should be noted that it can be difficult to apply fully, as populations may not completely conform to the original model as proposed by Levins (1970). As an example, the original model assumes that each subpopulation would have the same degree of isolation, but in reality, this is likely to differ as some subpopulations may be more isolated than others. Applying the concept thoroughly requires thoughtful consideration of potential processes to be incorporated into a model, as is outlined by Hastings & Harrison (1994). However, if done correctly, the metapopulation concept can present itself as a powerful tool to describe population dynamics.

2.2.4 The Atlantic cod – Partial migration or metapopulation structure?

It is clear that the two concepts are relatively similar, as they both seek to explain the effect of variations in migratory behaviour on overall population structure on two different scales (Le Bris et al. 2013). However, it can be difficult to determine which concept to apply, especially due to conflicting interpretations of the partial migration theory.

As an example, Le Bris et al. (2013) defines partial migration as the focus on the migration potential of individual cod within panmictic populations. In this view, reproduction isolation is then the main separator between the partial migration concept and the metapopulation concept. However, Shaw et al. (2011) suggests three types of partial migration where one indicates spawning grounds may be separate for resident and migratory individuals which voids the assumption of panmixia, as individuals cannot interbreed when different spawning grounds are used. In addition, while spawning grounds may be shared in some types of partial migration, this does not necessarily mean that residents and migratory cod interbreed, as has been noted in Icelandic cod (Grabowski et al. 2011).

As such, at times it can be difficult to assess whether a population is panmictic or reproductively isolated (e.g., see the opposing views of Beacham et al. 2002, Rose et al. 2011 in regards to

whether a metapopulation structure exists in Newfoundland and Labrador based on genetic isolation).

In addition, to further complicate things, the two concepts have previously even been combined in a study on European shags (*Gulosus aristotelis*) which denotes this bird species as forming 'partially migratory metapopulations' based on intra-individual variation in movement (Payo-Payo et al. 2022).

Based on this, while these two concepts are highly interesting, for the sake of this thesis it might be more useful to speak of 'alternative migratory behaviours' as coined by Le Bris et al. (2013), and instead focus on the differences in movement behaviour between ecotypes and life stages.

In light of this, the following sections will outline differences in movement patterns between and among juvenile and adult cod in an attempt to determine potential causes and to cover all aspects of horizontal cod movement, including the effect of the environment, before diving into analyses of movement.

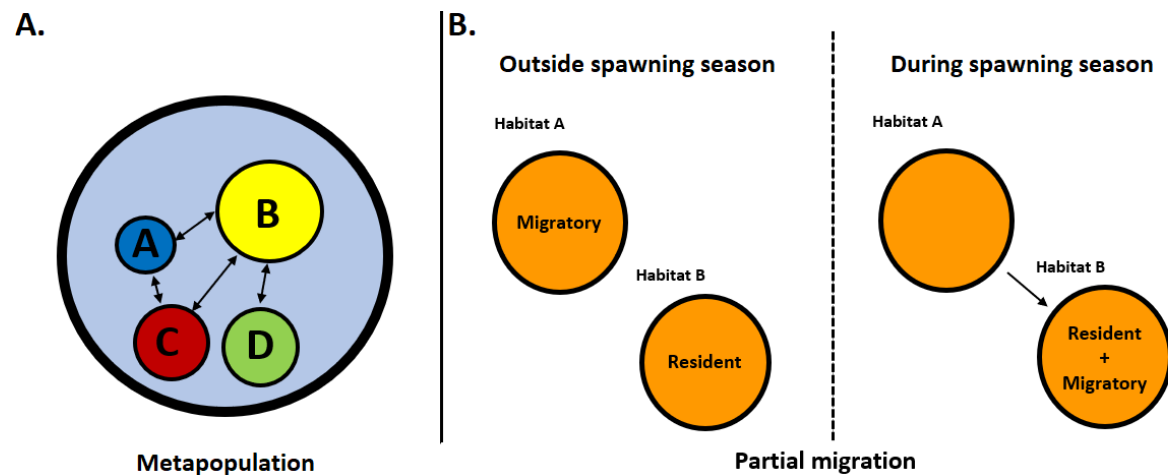


Figure 6. Metapopulation vs. partial migration. A. The metapopulation concept focuses on reproductively isolated subpopulations (A, B, C, D) within a larger metapopulation with some connectivity between the subpopulations.

B. The partial migration theory focuses on the migration properties of individuals (as an example, migratory and resident individuals may inhabit different habitats outside the spawning season and mix during the spawning season, e.g., in the habitat of the resident individuals). See Smedbol & Wroblewski (2002) and Shaw et al. (2011).

2.2.5 Differences in movement between juvenile and adult cod

Movement differs between adult and juvenile cod as migratory behaviour changes between life stages (see Robichaud & Rose 2004 and references therein). Juvenile cod are often coastal and prefer to stick to shallow waters (**Figure 7**; Linehan et al. 2001), which, for example, can be seen in the Kattegat-Skagerrak where nursery areas are located in shallow waters along the Swedish coast (Pihl & Ulmestrand 1993). As the cod mature, the adults move offshore to deeper areas, possibly to spawn (**Figure 7**; Pihl & Ulmestrand 1993). This difference in movement behaviour is likely important for the survival of Atlantic cod as cannibalism is highly widespread in this species (Folkvord 1997) and staying in shallow waters may protect the smaller cod from predation.

Linehan et al. (2002) attempted to determine if Heincke's Law (Heincke 1913), which states that fish size is proportional to occupied depth, could explain the preference of shallow waters by juvenile cod as larger predators would occupy deeper waters, possibly due to metabolic benefits. They found that predators were more common at greater depths, suggesting the juveniles' preference for shallow nearshore waters may be a behavioural response to predation pressure. Furthermore, habitat was found to be important as predation was lower in vegetated sites at shallow locations. Laboratory experiments have similarly shown a behavioural response to predators with higher utilization of safe habitats, such as cobble, eelgrass and kelp (Gotceitas et al. 1995, Laurel & Brown 2006). In addition, anti-predator behaviour, such as schooling, similarly increases when predation risk is high, such as during daytime in open habitats (Laurel et al. 2004, Anderson et al. 2007).

A study on coastal Newfoundland cod furthermore showed differences in habitat use between different ages and sizes of juvenile and sub-adult cod (Bradbury et al. 2008). Juveniles preferred to stay in locations with eelgrass, while larger 0-year-old and 1-2-year-old cod seemed to move into deeper waters and stayed in kelp beds near the eelgrass areas. In contrast, 2-3-year-old cod were less selective and could be found in more coarse environments with occasional macroalgae (Bradbury et al. 2008), most likely due to a lower risk of predation. Indeed, at age 2 and above cod are likely less exposed to predation, as can be seen in the western Baltic Sea where a model study showed that, on average between 1977-1994, 19% of the 0-year-olds and 9% of the 1-year-olds were consumed by adult cod per year in the western Baltic cod stock (Neuenfeldt & Köster 2000). Similarly, on average 25-38% of the 0-year-olds and 11-17% of the 1-year olds were consumed by adults in the eastern Baltic cod stock (Neuenfeldt & Köster 2000).

Overall, these results suggest a reduced dependence on dense habitats (e.g., eelgrass and kelp) as the cod grow and are likely to partially explain the switch from a generally more resident behaviour to a more migratory one in some cod populations, such as along the Swedish coast (Pihl & Ulmestrand 1993).

2.2.6 Differences within similar age classes

Movement differences between individuals of the same cohorts has previously been observed. While this can be small, as the example of different habitat and depth preferences by differently sized 0-year-old cod showed in the previous section (Bradbury et al. 2008), differences can also occur on a higher scale. In NEAC, females have been shown to frequently skip spawning migrations and remain on the feeding grounds, avoiding the cost of migrating and vitellogenesis (Skjæraasen et al. 2012). This proportion of resident females is sizeable, reaching approx. 24% of the female group (60-100 cm) and rivalling the amount of female spawners in 2008 (Skjæraasen et al. 2012). Another study on adult cod in the Gulf of St. Lawrence showed clear alternative migratory behaviours where resident individuals would forage in western Newfoundland waters during summer and autumn but would remain in shallow and near freezing coastal areas during winter and spring (Le Bris et al. 2012). In contrast, migratory individuals would stay in coastal shallow waters in Newfoundland for the summer but would remain in deep and warm waters during winter (Le Bris et al. 2012). During spring and fall, they would undertake migrations to their respective feeding and wintering grounds.

Similarly, it is also interesting to note the alternative migratory patterns of Pacific cod (*Gadus macrocephalus*) due to the similarities observed in the Atlantic cod. This species is found in the northern Pacific and has, like the Gulf of St. Lawrence cod, been found to exhibit alternative migratory behaviours. For example, a study using passive acoustic telemetry noted that fjord Pacific cod were generally resident but that some migratory cod would leave the fjords in summer and return the following winter (Lewandoski et al. 2018). A similar pattern has been observed near the Aleutian Islands (Bryan et al. 2021).

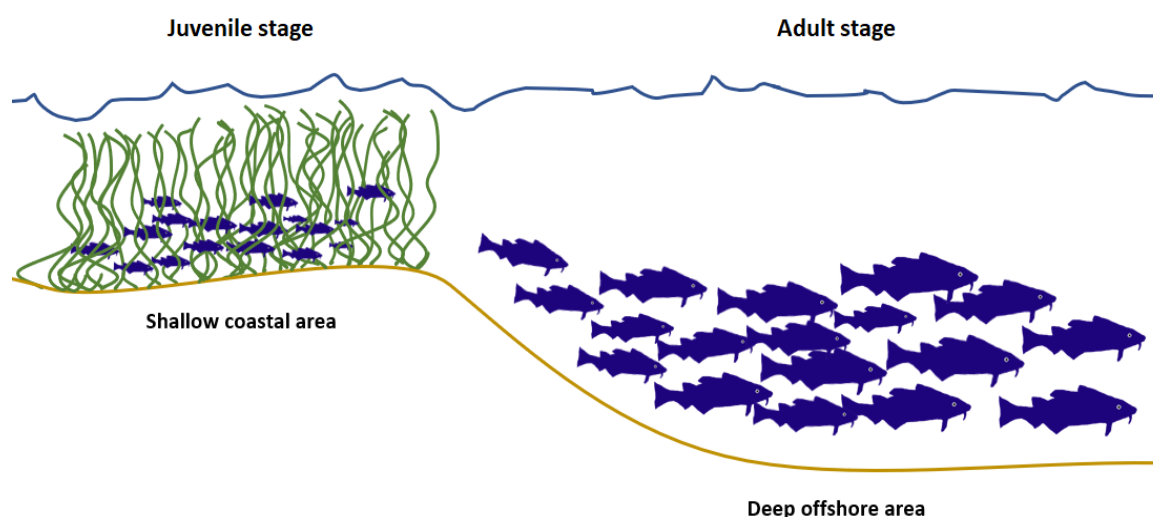


Figure 7. Differences in habitat preferences between juvenile and adult cod in areas such as along the Swedish coast. Juveniles tend to remain in shallower areas with dense habitats while adults move to more open and deeper areas.

2.3 The environmental aspect of migration

In contrast to the behaviour of juveniles, it is likely that the cause of alternative migratory strategies in adults is more related to the environment. Migration is a costly and risky process; if there were no benefit to fitness, there would be no reason to potentially travel hundreds of kilometres to separate wintering, spawning, or feeding grounds. However, the effect of the environment can be either relatively predictable, as occurs seasonally in some regions, or change slowly over decades as is caused by climate change, resulting in either spatial shifts or extinctions in local populations. In addition, the effect of the environment may be indirect, e.g., poor environmental conditions may affect growth and activity and potentially result in lower movement, or be more direct, e.g., cod abandon previously usable areas and modify their spatial distributions accordingly.

Before diving further into the environment's effect on movement, it is thus suitable to understand the overall effect of the environment on cod biology, as the environment is likely to be one of the underlying causes that may cause range contractions or expansions as conditions change, aside from acting as a cue that triggers migrations.

2.3.1 The environment's effect on cod biology

Temperature

Temperature is one of the most studied aspects of the environmental effect on cod and has a wide range of implications for cod biology, in particular growth rates and condition (Drinkwater 2005). The effect of temperature on growth rates is likely to differ between cod populations where cod growth in colder climates may be more limited by temperature (Krohn et al. 1997). Weight-at-age varies widely for North Atlantic cod stocks; as an example, the average weight of a 4-year-old cod is less than a kilogram in Labrador and over 7 kilograms in the Celtic Sea, and this variation can overall be explained by differences in mean bottom temperatures (Brander 1995), most likely due to Labrador generally being a subarctic climate in comparison to the warmer Celtic Sea. Laboratory observations have noted a decline in optimal growth temperature in relation to weight, as fish weighing 2 g prefer 17°C for growth compared to fish weighing 2000 g which prefer 7°C (Björnsson et al. 2001). A similar pattern has been noted for feed conversion as larger fish prefer lower temperatures for optimal feed conversion (Björnsson et al. 2001). In addition, increased growth in larvae has been found at high temperatures (Laurence 1978). Fish condition is similarly affected by temperature; however, it depends on the measure of condition. As such, gutted body condition was noted to be highest at higher temperatures but liver condition was greatest at lower temperatures in Newfoundland cod (Morgan et al. 2010).

The effect of temperature on reproduction is also considerable. As an example, in Newfoundland cod maturation is reliant on temperature where both high and low temperatures speed up the maturation process compared to medium temperatures; however, only temperatures in October-May have an effect on reproductive investment while fish condition is affected throughout the year by temperature (Morgan et al. 2010). However, this may depend on the population in question, as

laboratory studies on cod from Scottish waters have shown that low temperatures may arrest maturation in first-time spawning cod regardless of sex and result in a lower amount of mature fish (Yoneda & Wright 2005a b). These contrasting patterns may be due to the variability in climates and ambient temperatures in regions. Indeed, the effect of temperature on cod reproduction, such as spawning time, is affected by regional hydrography in even relatively close areas in Newfoundland (Hutchings & Myers 1994), and it is reasonable to assume that this pattern applies to cod populations in general.

In support of this, the effect of temperature on recruitment shows a similar dependence on regional hydrography. Planque & Frédou (1999) examined the effect of interannual fluctuations in temperature on recruitment in nine cod stocks and found that for individual stocks, no strong effect was found, but using a meta-analysis approach, clear effects of temperature were noted. As such, temperature was generally positively correlated with recruitment in stocks in cold water, but negative for stocks in warm water. However, for stocks in more temperate waters, no correlation was found. A similar pattern was found by Brander (2000) who overall looked at cold water stocks. In addition, ambient temperatures can affect the incubation period of eggs (time between fertilization to 50% hatching), as has been shown in Baltic cod where the incubation period decreased from approx. 28 days to 13 days as temperatures increased from 2°C to 7°C (Wieland et al. 1994).

Oxygen

Proper oxygen levels are vital for several aspects of the cod's life cycle. Oxygen consumption is independent of oxygen levels above the critical level at 3 ml⁻¹ but cod become asphyxiated and die at oxygen levels below 0.8 ml⁻¹ (Sundnes 1957, Jobling 1988). Respiratory volume, however, remains dependent on oxygen levels (Jobling 1988).

Food consumption has been shown to decrease at low oxygen levels in reared cod which in turn decreased growth; in addition, activity was also lower in hypoxic conditions (Chabot & Dutil 1999). In particular, oxygen saturation <65% has been found to significantly decrease growth and condition compared to cod reared at higher oxygen saturation levels (Chabot & Dutil 1999). Another study on reared cod similarly showed that oxygen saturation ≥100% was required to achieve maximum growth in juvenile Atlantic cod (Thorarensen et al. 2017). Additionally, while food consumption decreased, feed conversion was independent of oxygen levels (Thorarensen et al. 2017). Mild hypoxic levels has similarly been suggested to decrease food consumption in Balt Sea cod resulting in decreased growth and overall biomass (Brander 2020).

Comparatively, oxygen saturation is highly important for cod reproduction and recruitment. While oxygen levels do not seem to affect the incubation period, egg survivability is greatly dependent on oxygen levels and low levels can cease development completely regardless of development stage (Nissling 1994, Wieland et al. 1994). Similarly, initial larval survival might also be affected (Wieland et al. 1994).

Salinity

While the Atlantic cod is a marine fish, it can inhabit environments characterized by very different salinity levels. This can range from the highly saline Atlantic Ocean to the brackish eastern Baltic Sea. As such, different populations are likely to be adapted to different salinity levels. The costs, including changes to metabolism and particularly ion regulation, of remaining in environments with salinity levels that individuals are not adapted to appears to be high (Kijewska et al. 2016). A transplantation experiment where North Sea cod were placed in tanks mimicking Baltic Sea conditions (~ 9 ppt) and Baltic Sea cod in tanks mimicking North Sea conditions (33 ppt) showed high mortality (45% and 80%, respectively); however, this was only statistically significant for Baltic Sea cod (Larsen et al. 2012). In support of cod potentially being adapted to local salinity levels, the *Na/K-ATPase* α gene (a gene important for ion balance maintenance) was expressed more in North Sea cod compared to Baltic Sea cod in North Sea conditions (Larsen et al. 2012). This is further supported by a study on Baltic Sea cod subpopulations (Kijewska et al. 2016).

Growth can also be affected by salinity levels, where studies on Gulf of St. Lawrence cod showed highest growth at intermediate salinity levels (14 ppt; Lambert et al. 1994). In addition, increased growth was observed at lower salinities compared to seawater levels in spring due to a greater feed conversion efficiency (Lambert et al. 1994).

Successful cod spawning similarly depends on salinity levels, but these vary depending on the population. As an example, to achieve neutral egg buoyancy and activation of spermatozoa, salinity requirements of 20-22 and ≥ 15 -16 psu, respectively, are required for successful spawning in western Belt Sea cod in the Baltic (Nissling & Westin 1997). In contrast, salinity requirements of ~15 psu and ≥ 11 -12 psu are required for eastern Baltic cod (Nissling & Westin 1997).

Prey availability

While the abiotic factors of the environment have been studied intensely in regard to cod performance and distribution, studies have also noted the importance of prey. Indeed, this is only logical; to achieve somatic growth, it is necessary to have access to enough food in order to cover more than the maintenance functions. As such, it appears that food may at times be more important than the abiotic environmental conditions.

The Atlantic cod prefers different prey items throughout its life cycle, and this is mainly related to size. While early life stages often depend on copepods (see Sundby 2000 and references therein), the diet of juvenile cod primarily consists of small benthic organisms, while medium-sized cod prefer small forage fish, and the larger cod eat large fish, such as other cod (see Kulatska et al. 2019 and references therein). Notable important prey items include capelin (*Mallotus villosus*) in the northern regions such as Newfoundland and Labrador, and herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) for Baltic cod. In addition, invertebrate prey may be important in shallow areas (Funk et al. 2021).

In Labrador and Newfoundland, capelin abundances decreased sharply around the same time as the cod populations (DFO 2011) and have remained at low levels. In response, the cod shifted their diet to pandalid shrimp which are not as nutritionally sufficient as capelin due to a low content of

essential oils (Lawson et al. 1998, Krumsick & Rose 2012), and growth and condition have since remained low (Mullowney & Rose 2014). It is unlikely that the Newfoundland and Labrador cod will recover until capelin abundances increase; indeed, the importance of capelin cannot be overstated as even temperature was not noted to be as important in comparison (Mullowney & Rose 2014). In support of this, another study on Newfoundland cod noted that if food was abundant, growth generally increased even for cod in colder waters while it was possible growth decreased when food was limited (Mello & Rose 2005).

Reproductive investment can similarly be affected by food abundances as the excess energy from covering basic functions and growth can be allocated to reproduction; as an example, a study on first-time spawning male cod showed larger testes in cod with unlimited access to food compared to cod with limited access kept at the same temperature (Yoneda & Wright 2005a). In contrast, the fecundity of first-time spawning females does not appear to be affected by food availability and they may simply invest in reproduction first and foremost and allocate any remaining energy into somatic growth (Yoneda & Wright 2005b).

The synergy effects of multiple environmental factors

While the previous sections outlined several effects of individual environmental parameters, it is worth noting that these often act together in complex ways. This can be indirect, such as the temperature-recruitment response in cod likely being a result of copepod dynamics (Sundby 2000, Beaugrand et al. 2002, 2003), or direct, such as survivability of eggs exposed to low oxygen levels being higher at higher salinities in Baltic cod (Nissling 1994).

One notable synergy effect is the interaction of temperature and oxygen. As temperature increases, metabolic rates increase which in turn results in increased oxygen consumption. As such, preferred temperatures generally decrease when cod are exposed to hypoxia (Schurmann & Steffensen 1992). However, this depends on the haemoglobin type of the cod, as HbI-2 cod do not decrease their preferred temperature in hypoxia compared to HbI-1 cod (Petersen & Steffensen 2003).

Seasonal variations in physiological tolerance based on synergy effects of environmental factors have also been suggested. Magill & Sayer (2004) tested the combined effect of temperature and salinity in seasonally acclimated juvenile Atlantic cod. They found that summer-acclimated fish had a greater dilution of plasma ionic and osmotic concentrations when both temperature and salinity was low in comparison to winter-acclimated fish.

Overall, these examples clearly show that synergistic effects can complicate the interpretation of sole drivers as it is possible that perceived individual responses of a single factor may simply be due to a proxy effect, as has been suggested for copepods being the true driver of recruitment in Atlantic cod and not temperature (Sundby 2000). Furthermore, they illustrate the complexity of the physiological response of cod to environmental changes and can depend on the population or stock in question.

2.3.2 The environment's effect on cod movement

As shown by the multiple effects of biotic and abiotic factors, it appears to be imperative for cod to move towards optimal conditions in order to optimize several aspects of their life cycle. Indeed, laboratory experiments on Atlantic cod from Nova Scotia south-west of Newfoundland have shown thermoregulatory behaviour where cod most likely avoided changes in thermal conditions in order to avoid spending energy on reacclimation (Claireaux et al. 1995a). In addition, a supplementary study on Nova Scotia cod has shown a general preference of low salinities and low oxygen areas in a tower tank (Claireaux et al. 1995b). However, cod would still move into high salinity or low oxygen areas to briefly feed but return to their preferred conditions afterwards (Claireaux et al. 1995b). In addition, cod in temperate regions, such as Skagerrak, decrease their activity in winter in comparison to summer, highlighting the importance of environmental conditions for movement (Staveley et al. 2019).

As such, when considering the effect of the environment on cod movement, it is imperative to examine two aspects separately: the seasonal movements occurring annually and the long-term effects of climate change on global cod distributions.

2.3.3 Seasonality in movements

Seasonality has been noted to be an important aspect of the emergence of migration in cod populations. The main driver of seasonal movement has been suggested to be temperature (Drinkwater 2005, Le Bris et al. 2012). In the case of Gulf of St. Lawrence cod, cod have been found to adapt their movement behaviour in response to environmental cues, as wintering migrations are triggered by a decrease in temperature at mid-depth in some cod populations (Castonguay et al. 1999). By migrating to warmer wintering grounds, the cod can allocate more energy to somatic growth compared to more costly energy processes due to the cold (Lambert & Dutil 1997). In contrast, resident cod do not need to expend energy on migration and could potentially decrease activity to make up for the higher costs associated with being in cold areas. Furthermore, they do not expose themselves to predators (Le Bris et al. 2012). It is also possible that resident cod may in some cases not be able to pay the large costs associated with migrating and instead hope to survive by staying as dormant as possible (Speers-Roesch et al. 2018). Swimming activity in resident Gulf of St. Lawrence cod has been found to be much lower during winter and the cod could potentially produce plasma antifreeze glycoproteins to survive as has been observed in Trinity Bay cod (Goddard et al. 1994, Ruzzante et al. 1996, Le Bris et al. 2013).

Le Bris et al. (2013) further suggested that the persistence of these opposite behaviours in Newfoundland cod may be due to differences in condition based on differences between spawning peaks in spring and summer. This has been observed in other fish, as white perch (*Morone americana*) generally exhibit migratory behaviour and show slower growth if they are spawned earlier compared to white perch spawned later in the season (Kerr & Secor 2010). This is most likely due to larval growth conditions being better later in the season based on zooplankton densities

(Kerr & Secor 2010). This could potentially apply to the cod as well, as higher temperatures result in greater sized larvae (Pepin et al. 1997). However, while environmental conditions are clearly important for migrations and growth, whether or not it has an effect on the determination of ecotype in cod is still unknown. Additionally, it is interesting to note that low temperatures may cause some populations of Newfoundland cod to delay spawning in order to remain in warmer waters for a longer period of time (Hutchings & Myers 1994).

The clear changes in habitat preferences of cod due to seasonality has similarly been noted for western Baltic cod. Using the knowledge of local fishermen and gillnet trips, Funk et al. (2020) noted that fish distribution throughout the year was greatly reliant upon sea surface temperature (SST) and stratification. As such, shallow areas (<15 m) were preferred in general, except during low SSTs in late December-March when the cod preferred deep waters (>15 m); this pattern was similar for higher SSTs during July-August. Comparable temperature-dependent behaviour has been noted for NCC (Freitas et al. 2015).

Together, all the above examples indicate clear changes in responses to environmental parameters throughout the year. Indeed, as conditions slowly change, the cod can respond by either moving away to spawn or feed, or stay and acclimate to deal with changes in local conditions. However, while seasonal changes are often relatively predictable, in the sense that boreal winter usually comes with lower temperatures, climate change is a major threat to cod distribution as local conditions permanently change.

2.3.4 Climate change and the changes in environments over time

It is no secret that the future of the oceans is currently threatened by the long-term shifts in environmental conditions as caused by climate change. This particularly includes the 'deadly trio': warming, deoxygenation, and acidification which often, as noted previously, result in synergy effects (Bijma et al. 2013). In addition, freshening of the oceans is also likely to change ecosystems (Greene & Pershing 2007). The response to these changes may include redistribution, range shifts, and potentially changes in trophic levels. If a species cannot adjust or adapt to the changes, it risks going extinct in local areas which may not be colonized by other individuals of the species, resulting in a niche shift as other species colonize the area instead.

Warming

The warming of the oceans is continuing at an alarming rate. In the North Sea, the mean annual SST is expected to increase >1°C before 2040 (see Kell et al. (2005) and references therein), and the temperature of the bottom waters off the western coast of Newfoundland might increase by ~3°C by 2046-2065 (Stortini et al. 2017). In particular, it appears that a temperature increase of at least 2°C is to be expected by 2100 in all areas the cod stocks utilize, which might cause southern stocks such as the Celtic and Irish Sea stocks to disappear depending on the increase in bottom temperatures (Drinkwater 2005).

As outlined previously, this can have adverse effects on not only cod biology but also distribution. To satisfy their demands, the cod are likely to move north if possible; this might be disastrous for southern stocks but potentially benefit northern stocks, as the disappearance of sea ice would likely result in an increase in available habitat, as also surmised by Drinkwater (2005). Indeed, previous warm anomalies have been noted to result in higher recruitment in northern cod stocks (see Kristiansen et al. 2014 and references therein). In addition, increasing temperatures are likely responsible for a northwards shift in North Sea cod distribution (Engelhard et al. 2014). However, the previously mentioned synergy effects and complex interactions of several factors make it difficult to predict how the cod will respond. As an example, while higher temperatures can benefit cod inhabiting northern areas, larval survival may be reduced due to increased metabolic rates and if prey abundance decreases as a result of higher temperatures (Kristiansen et al. 2014).

Deoxygenation

The increase in dead zones (hypoxic areas) is a global problem (see Zhang et al. (2013) for examples of major dead zones). They mainly occur in coastal areas due to increased eutrophication caused by increased nutrient inputs. However, other factors include decreased solubility of oxygen as temperatures increase, and increased oxygen demand at higher temperatures (Bijma et al. 2013).

Dead zones are thus especially serious in semi-enclosed seas, such as the Gulf of St. Lawrence, the Baltic Sea, and the Kattegat due to limited exchange of water and the great extent of coastlines (Diaz & Rosenberg 2008, Stortini et al. 2017). The extent of dead zones in the eastern Baltic has increased greatly in just a hundred years (Carstensen et al. 2014) and the low oxygen conditions have resulted in historically important Baltic cod spawning grounds (Gdansk Deep and the Gotland Basin) being plagued by oxygen-dependent mortality (Hinrichsen et al. 2016), making them virtually unusable. This is also evident in the Kattegat and western Baltic Sea, and models have shown an increase in dead zones if temperatures continue to increase (Bendtsen & Hansen 2013), threatening the continued survival of the Baltic cod.

Acidification

While not covered in detail in this thesis, it is worth briefly mentioning the effect of acidification on cod. Acidification is a decrease in pH primarily due to an increase in uptake of CO₂ from the atmosphere which results in the oceans becoming more acidic. Acidification can have adverse effects on larval cod, in particular on organ development (Stiasny et al. 2019), increased size of otoliths (Maneja et al. 2013), and tissue condition (Frommel et al. 2011). Effects in other fish include impairment of larval homing ability (Munday et al. 2009).

Adult cod appear more resistant to acidification due to well-developed acid-base regulatory systems, meaning they can handle low pH conditions much more efficiently compared to early-life stages (see Frommel et al. 2010 and references therein). While fertilization success and thus spawning success might not be adversely affected either by acidification (Frommel et al. 2010), high sensitivity of early life stages are likely to severely affect recruitment and result in low abundances (Stiasny et al. 2016). However, this depends on the population and scenario in

question. As an example, acidification during thermal extremes can decrease hatching success in Baltic cod (Dahlke et al. 2016) but does not appear to significantly affect life stages at mid-level temperatures (Frommel et al. 2012, Dahlke et al. 2016).

Freshening

The northern Atlantic has experienced freshening since the middle of the last century (Curry & Mauritzen 2005). A notable example is the Great Salinity Anomaly which has been estimated to have inserted $\sim 10,000 \text{ km}^3$ freshwater from the Arctic into the sub-Arctic oceans between 1960-1970 (Dickson et al. 1988, Curry & Mauritzen 2005). As this is likely to continue due to increased glacial melting (e.g., see Pattyn et al. 2018), it is possible that cod may be affected as ecosystems change when salinity levels decrease, such as an increase in small copepods as has been observed in the Gulf of Maine and Georges Bank (Greene & Pershing 2007). As herring appear to have benefitted from this increase in copepods (Greene & Pershing 2007), it is possible that some cod may similarly benefit due to the importance of herring as a prey item in some cod populations. Similarly, early life stages may also benefit from an increase in copepod abundance. In addition, cod exhibiting higher growth rates at intermediate salinities compared to high salinities may benefit as well from increased freshening of the oceans, such as in the Gulf of St. Lawrence (Lambert et al. 1994).

What does climate change mean for the survival of the Atlantic cod?

It is difficult to predict if the Atlantic cod might survive the future changes in the climate. It depends on the overall adaptation potential of the species and how synergy effects will affect the cod. Looking at rising temperatures, it is possible that the southern populations will decline or completely disappear, and the overall distribution will shift northwards as has been observed previously around Greenland and Iceland (Jensen & Hansen 1931, Sæmundsson 1934, Hansen 1949, Vilhjálmsson 1997). However, ocean acidification will still be an issue in the northern regions and is likely to severely impact recruitment. In addition, depending on how the food web is affected, cod larvae mortality might increase if food availability is too low. As such, while adult cod are still affected by changes in environmental parameters, the future of the Atlantic cod appears mainly dependent on the sensitivity of early life stages. Thus, it is important for the cod to be able to move as northwards as possible and only time will show the extent of suitable habitat in the north.

2.4 Connectivity – Management complicated by movement behaviour

The differences in movement patterns, both current and projected, pose difficulties for management of fish stocks and populations, especially when this occurs between or outside management units. High degrees of movement between stock components can result in flawed stock assessments, e.g., wrongly estimated growth and mortality parameters, and this can result in a biased perception of stock status which may lead to over- or underexploitation (Huwer et al. 2016). As an example, in the Baltic Sea, the eastern Baltic cod stock briefly recovered after decades which resulted in a spill over of eastern Baltic cod into the western Baltic cod stock; as a consequence of this, the western Baltic cod stock appeared to be in a much better state despite the actual stock size of western Baltic cod being relatively low (**Figure 8**; Eero et al. 2014).

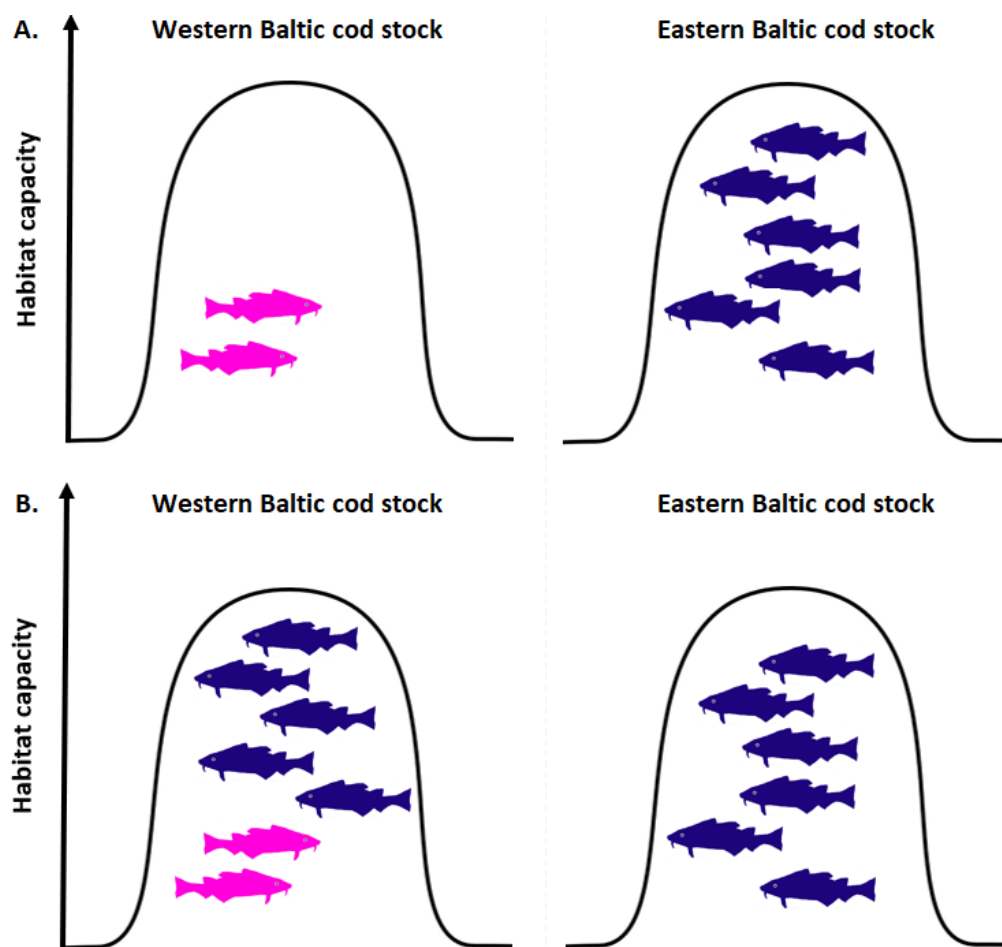


Figure 8. Potential consequences of movement between stocks. A. The recovery in the eastern Baltic cod stock leads to overcapacity while the western Baltic cod stock is not recovering. B. Spill over of eastern Baltic cod into the western Baltic cod stock results in the western Baltic cod stock appearing to be in a better condition than it is.

A similar issue is the effectiveness of MPAs in conserving and protecting subpopulations of a species, as the success of an MPA is dependent on the actual size of the area. In particular, it is important that the size of the MPA captures the relevant home range of a target species. Hence, MPA effectiveness is greatest for resident subpopulations but is likely to decrease for more migratory subpopulations (see Grüss et al. 2011 and references therein). As such, species such as Atlantic cod that can be of either a resident or migratory ecotype are difficult to manage. Some have attempted static closed MPAs (e.g., the Gilbert Bay cod; see Morris & Green 2014) while others have tried to solve this problem by having seasonal MPAs during the spawning season (e.g., see Johansen et al. 2018) with varying degrees of effectiveness.

However, the most optimal approach depends on the subpopulation or stock in question. Adaptive management has been recommended as a way to ensure success of stock and MPA management, as information is continuously generated to update management procedures and advances an understanding of the underlying system. However, it is not without its problems; management resources can be lacking and policy makers also consider other parameters when making policy choices and may ignore uncertainty (Walters 2007). Even stable annual stock assessments may suffer from these problems; as an example, poor monitoring data has been blamed for the sharp decrease in Newfoundland cod (Walters & Maguire 1996). In addition, scientists need to be willing to update their models with more complex interactions, such as diverse movement patterns across stock or stock components, and potentially admit and fix any model flaws (Walters 2007).

2.5 Analysing movement

Whether the issue concerns a stock or a population within an MPA, it is clear that quantifying the rates of movement outside of and between management units is important to evaluate either the status of a stock or the effectiveness of conservation. After all, the core issue in both situations is to ensure a healthy and sustainable abundance of fish that may persist into the future.

It is thus proper to turn our attention to the decades of tagging projects in the Baltic Sea and surrounding areas as an example on how movement has been analysed historically before we dive into more contemporary ways to handle tagging data.

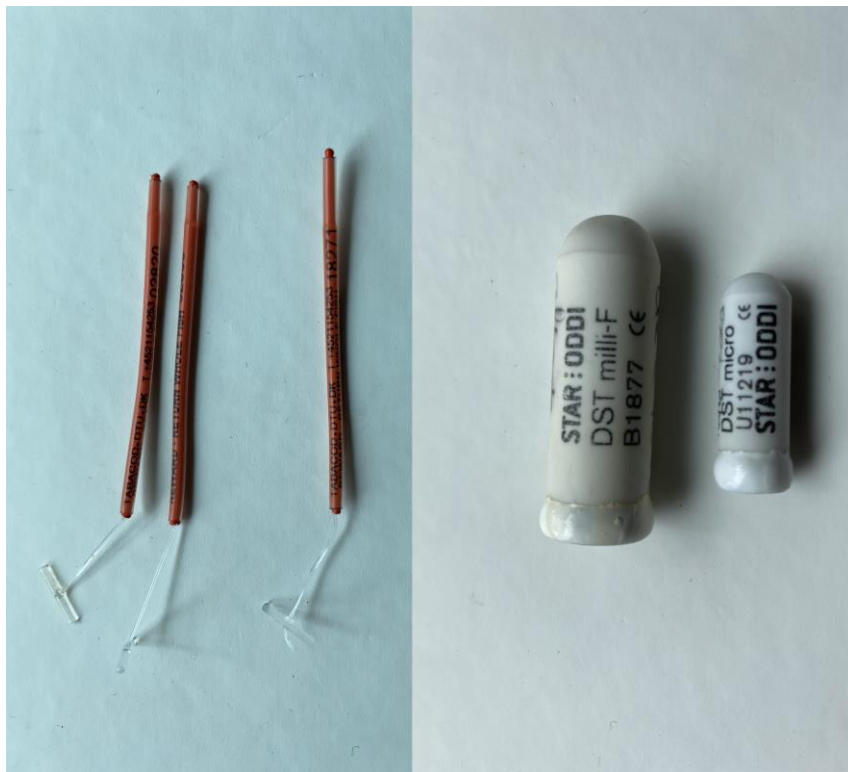


Figure 9. Types of tags. Left = conventional tags (T-bar). Right = electronic tags (DSTs). Photo credit: Karin Hüssy.

2.5.1 The historical Baltic tagging projects – Conventional tagging

Conventional tagging

Conventional tagging, or mark-recapture, has been the most used method to study fish movements historically. A fish is equipped with a tag (such as a T-bar tag, which is a colourful T-shaped plastic piece; **Figure 9-10**) and released into the sea. The tag usually has relevant information such as ID and contact details. Once caught, the fisher will notice the tag, contact the given project coordinator, and report the recapture position and other relevant details. In return, the fisher receives a finder's fee. The benefit of this methodology is that it is a relatively fast, low maintenance, and cost-effective tagging method, meaning lots of fish can be tagged within a short time frame. Thus, the number of tags retrieved seems to be positively related with the number of tagged fish as high amounts of tags are generally never recovered (e.g., see Björnsson et al. 2011), mainly due to either natural mortality, the tag falling off, or because the fisher fails to notice the tag. However, the main issue with this methodology is that no information between release and recapture is available; as such, a fish can be tagged on its feeding grounds, undertake complex migrations before returning to the feeding ground after a year, and be recaptured again. In this example, it would appear as if the fish had remained resident for a year, although migration did occur, which represents the possible bias and high uncertainty for these tags. It is thus the hope that if a lot of fish in the same area are tagged that general insights into their movement behaviour can be gained by looking at several recaptures.

The historical Baltic Sea tagging projects

The first tagging experiments on Baltic cod started in the 1950s and efforts increased from 1972 and onwards after the first ICES Working Group meeting on cod (Anonymous 1972, Bagge et al. 1994). In addition, occasional tagging of Kattegat-Skagerrak cod goes back to at least the early 1900s (see Poulsen 1931 and references therein).

In the 1950-60s, tagging experiments were carried out in the Skagerrak, mainly utilizing Lea hydrostatic tags placed in front of the first dorsal fin (Danielssen 1969). Returns were generally around 30% ($n = 367$ recaptured out of 1244 releases), and the cod were generally recaptured within 3 years of being tagged. These studies were not analysed in detail, but the recapture distribution was used to document movement into the North Sea.

Similarly, tagging experiments in the Kattegat and the western and eastern Baltic from the 1950s to the 1980s mainly documented release and recapture positions (Bagge 1969, 1973, Berner 1981, Bagge & Steffensen 1989, Pihl & Ulmestrand 1993). However, Bagge (1973) and Berner (1981) further analyzed the movement patterns in more detail by calculating dislocation parameters of release groups, mainly direction, velocity, and a mean square dispersion coefficient as described by Jones (1966). These can be compared to similar concepts, such as advection (directed movement) and diffusion (dispersal) which will be covered in more detail in Paper I.

In addition, several transplantation experiments were conducted in the 1960-1980s to study the migration behaviour of the cod; in particular, their homing ability (Otterlind 1965, 1985, Bagge 1983). Overall, they noted that the homing ability was relatively poor and that the transplanted cod showed

similar behaviour as cod from the native area which suggests different ecotypes. Similarly, they primarily relied upon recapture positions. In the 1990s, studies looking into contemporary cod movement seemed to slow down considerably.

In general, the historical tagging projects mainly relied upon recapture maps to study movement and connectivity. This is not surprising, as the scientists back then did not have sufficient computer power to do complicated calculations in a relatively short time. Despite not employing advanced methodology, however, these studies provided valuable insights into the movement behaviour of cod in the Baltic and Kattegat-Skagerrak and identified overall migration patterns (see Aro 1989, Bagge et al. 1994 and references therein).



Figure 10. Cod tagged with T-bar. Photo credit: Karin Hüsey.

2.5.2 Contemporary Baltic tagging studies – Electronic tagging

Electronic tagging

While contemporary tagging studies often still utilize conventional tags due to the benefits outlined earlier, the invention of the electronic tag, such as the data storage tag (DST; **Figure 9**), has given hitherto unknown insights into movements of fish on both a horizontal and vertical scale. One of the most common types of electronic tags is the DST (also known as an archival tag) which is a data logger equipped with various sensors which, depending on the model, can record temperature, conductivity (salinity), pressure (depth), tilt, heart rate, activity, and strength of magnetic field (compass). They need to be small and light weight in order to be as least invasive as possible, as abnormal behaviour is highly likely if the fish is bothered by the DST. They record data continuously at predetermined intervals, which will influence the battery life depending on how often data is recorded, and when the DST is recovered, the data can be extracted and analysed. DSTs are generally implemented by external attachment (e.g., to the dorsal fin) or surgically implementing the DST in the body cavity. Other electronic tag types include radio tags, acoustic transmitters, pop-up satellite archival tags (PSAT), and passive integrated transponder tags (PIT).

While each tag type offers its own advantages and disadvantages (e.g., a DST cannot be gastrically inserted or offer remote data logging in air or water, unlike a radio tag; however, a radio tag is not suited for use in oceans (Thorstad et al. 2014)), they are characterized by being relatively expensive compared to conventional tags. As such, studies appear to generally utilize around <100 DSTs and >100 conventional tags; as an example, a study on Icelandic cod tagged 2200 mature cod with conventional tags and 81 of those were also tagged with DSTs (Thorsteinsson 1995). In addition, electronic tags are more invasive than conventional tags. Examples of disadvantages from external electronic tags include potential disruption of normal swimming behaviour by interrupting the streamlined shape of the fish, increased predation risk and attacks from other fish, and tags are likely to be lost after 1 year (Thorstad et al. 2014). In addition, surgically implanted tags may be expelled, an additional external tag is required to catch the fisher's attention, and the wound needs to heal properly to avoid inflammation and infection (Thorstad et al. 2014). However, despite these difficulties, the higher resolution of a fish's journey offered by electronic tags is very attractive and has revealed how complex movements can be on both a daily and annual scale.

The contemporary tagging projects

As mentioned previously, while several tagging studies in recent times also employ conventional tags, it is worth mentioning the studies that employ either both tag types or solely electronic data tags to showcase how movement can be analysed.

In general, the most common electronic tag type used in the Baltic Sea is the DST and, to the best of my knowledge, these were first used in the early 2000s in the Baltic Sea (Neuenfeldt et al. 2004). Due to exact geographic coordinates not being recorded by DSTs, it is necessary to utilize the information stored by the DST to infer the route taken by the fish. As such, Neuenfeldt et al. (2004) used geolocation to reconstruct migration routes for individual recaptured eastern Baltic cod

released near Bornholm ($n = 9$). They utilized environmental data recorded by the DST, such as pressure, temperature, and salinity and compared it to a hydrographical database of the Baltic Sea. To estimate the migration routes, they used a state-space-based method known as the extended Kalman filter (Harvey 1990) which utilized the entire route to estimate individual geolocations. From this, they managed to showcase that Baltic cod can move a lot between release and recapture; indeed, six of the nine cod were recaptured close to the point of release and if only conventional tagging had been used, it would have appeared as if they had not moved much. An updated study on this data was done in the late 2000s (Neuenfeldt et al. 2007).

The Kalman filter assumes that errors are normally distributed with a normal probability density function for the position; however, this is not applicable to situations where the position is near land or the hydrographical fields are complicated (Andersen et al. 2007). As such, Andersen et al. (2007) used the particle filter instead which is applicable for non-Gaussian problems. In essence, particles are simulated using a movement model and continuously analysed and evaluated through resampling, where particles with lower importance weights are replaced with particles with higher importance weights. Andersen et al. (2007) applied this method to the same data as Neuenfeldt et al. (2007) and showed how uncertainty can be dependent on time. However, it is not always necessary to use advanced geolocation methods depending on the avenue being explored. Nielsen et al. (2013) was mainly interested in sex-based activity differences in eastern Baltic cod and did not focus on precisely locating the cod; instead, they used the depth and salinity as recorded by the DSTs to study sex-based differences in timing and duration of spawning. Similarly, despite using both conventional and archival tags, Svedäng et al. (2010) did not use geolocation but only reported the release and recapture positions.

A recent large-scaled tagging project, TABACOD (Tagging Baltic Cod; Hüsey et al. 2020), looked at horizontal migrations in the eastern Baltic cod stock using DSTs recording time, temperature, and water pressure. In order to geolocate the cod, they used the R package “HMMocean” which is a geolocation tool that utilizes hidden Markov models (HMM; Braun et al. 2018). Hidden Markov models have been used extensively to analyse movement in fish (e.g., see Pedersen et al. 2008, Thygesen et al. 2009, Bacheler et al. 2019) and constitute a powerful tool to analyse animal tracks. In short, an HMM assumes a Markov process with unobservable states, meaning that the next state is only dependent on the current state, and the unobservable state is the true geographical location of the fish which can be inferred from the recorded information by the DST. As such, it is similar to the previously discussed methods where the most likely tracks are constructed. The project could thus conclude that the cod undertook extensive movements between two management areas (SD 24 and 25) although two ecotypes were observed; as such, the stationary type would generally remain near Bornholm while the migratory type would move between feeding and spawning grounds (Hüsey et al. 2020). This aspect of the project was further elaborated on by Haase et al. (2021).

2.5.3 Conventional or electronic tagging?

Overall, each tagging method offers its own benefits and disadvantages. In essence, it boils down to the research question asked and whether one prefers quality over quantity. It would appear at a glance, based on the amount of information offered and the demonstrated complexity in cod movements, that electronic tagging would be the preferred option as all information offered by conventional tags (release and recapture positions) is readily available for DSTs. Furthermore, geolocation tools are readily available to aid in analysis. However, the sheer cost of a large amount of DSTs is highly deterring and only large scale projects such as TABACOD are able to afford a high number of DSTs ($n = 1263$; Hüseyin et al. 2020). If a low number of DSTs are used, then the researcher runs a risk of only having a low sample size to analyse when tags are returned. This makes it difficult to judge if the fish are truly representative of the entire population, as movement might be abnormal for several reasons, such as the DST being improperly attached to the fish.

As is often the case, the preferred option would be to utilize the strengths of each tagging type. As an example, Righton et al. (2007) used a combination of both conventional and electronic tagging, and due to low tag returns ($n = 30$; 13% of releases) the information offered by the DSTs was limited. This was further confounded by unfortunate events, such as DSTs lost in the gutting process and data being unavailable for download upon return. Thus, in this study, the majority of information came from the conventional tag returns ($n = 2040$ following data screening) while the DSTs offered more details on a select few fish. If Righton et al. (2007) had mainly relied upon DSTs then it is doubtful that the results of the study would have been as informative.

3. Structure of the thesis

At this stage, it is finally proper to turn our attention to the thesis itself. Based on the information in the previous chapters, I sought to analyse the historical movement of cod in the Baltic Sea and the North Sea. To do this, I asked myself the following questions:

1. What has characterized the movement of cod in the Baltic Sea and North Sea through time? (**Paper I**)
2. Based on the information in Paper I, can the cod in the Sound be considered a separate management unit or is there considerable connectivity to the surrounding areas? (**Paper II**)
3. Can the historical movement patterns be linked to any changes in the environment at the time in the Baltic Sea? (**Paper III**)

To answer these questions, extensive historical tagging and hydrographical databases were required. The historical tagging database was assembled from digitalization of historical recapture sheets dating back to the 1950s from Danish tagging projects and supplemented with conventional tagging data from the United Kingdom and countries bordering the Baltic Sea. Details of this database are outlined in Paper I.

In addition, the hydrographical database used in the simulations was produced from the hydrodynamic model, BSIOM. Details of this database are outlined in Paper III.

A summary of the three papers used to answer the above questions are as follows:

Paper I deals with clarifying and documenting characteristics of historical movement in the Baltic Sea and North Sea by looking into directed movement and dispersion. In essence, this paper can be said to be a summary of the historical Danish tagging projects since the 1950s and shows general movement tendencies. The British tagging data was included to expand on the Danish tagging projects in the North Sea. (Title: *Examining fish movement in terms of advection and diffusion: a case study of northeastern Atlantic cod*)

Paper II focuses on the structure of the stock component in the Sound in order to study the connectivity to surrounding areas in more detail by way of transition matrices. In addition, contemporary growth patterns are examined to determine if the historical movement patterns might still be applicable. (Title: *Stock connectivity patterns and indications of sub-stock component structuring of cod in the Sound*)

Paper III attempts to determine the importance of the environment (oxygen, temperature, salinity) in regard to movement patterns by assuming that cod follow optimal environmental gradients. This is accomplished through simulations by using a simple random-walk model with taxis and mimicking

real life tagging projects to compare the simulated trajectories to the true recapture distributions.
(Title: *Simulating movement patterns in Baltic cod (Gadus morhua) in response to historical changes in environmental parameters*)

Chapter II

Paper I:

Examining fish movement in terms of advection or diffusion: a case study of northeastern Atlantic cod





Examining fish movement in terms of advection and diffusion: a case study of northeastern Atlantic cod

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ABSTRACT: Advection (directional movement) and diffusion (dispersed movement) were applied for the first time to describe movement patterns in Atlantic cod in the North Sea and Baltic Sea between 1955 and 2020. The advection–diffusion approach provided more detailed estimates of movement that corresponded to previously observed patterns using different analytical techniques. Spatial patterns were evident with greater movement distances in cod from the North Sea and eastern Baltic Sea compared to the western Baltic and Kattegat–Skagerrak. Furthermore, comparative case studies on different ecotypes in the western and eastern Baltic suggested that inshore cod were more resident compared to offshore cod. This preliminary study highlights the usefulness of the advection–diffusion method to describe movements in fish populations, and can be further expanded by incorporating information on environment and mortality and providing information to spatially explicit population models.

KEY WORDS: Atlantic cod · Movement · Advection–diffusion · Mark–recapture · Baltic Sea · North Sea

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1. INTRODUCTION

The Atlantic cod *Gadus morhua* is a commercially important fish species found across the Atlantic Ocean. It is one of the most heavily fished species, which has led to several populations collapsing. In the north-eastern Atlantic, the Atlantic cod can be found from the North Sea to the Baltic and Barents Seas. The

North Sea, located between Great Britain and the western coast of Europe, connects to the Baltic Sea through the straits Skagerrak and Kattegat. For management purposes, these adjacent seas are divided into units known as International Council for the Exploration of the Sea (ICES) subareas, divisions, and subdivisions (SDs; Fig. 1), and the populations are managed as the following stocks: the North Sea

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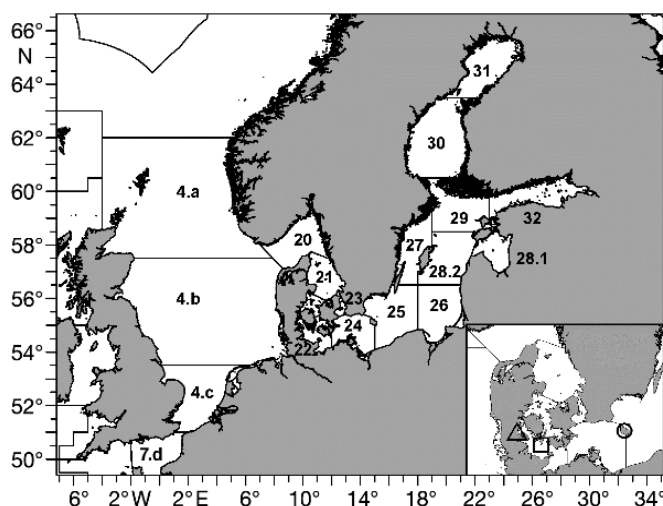


Fig. 1. Map of the North Sea and the Baltic Sea showing ICES areas. ICES areas are indicated by numbers: 4.a–c: The North Sea; 20: Skagerrak; 21: Kattegat; 22: Belt Sea; 23: The Sound/Øresund; 24: Arkona Sea; 25: Bornholm Sea; 26: southeastern Baltic Sea (SEBS); 27: The Western Gotland Basin; 28.1: Gulf of Riga; 28.2: Gotland Sea; 29: The Archipelago Sea; 30: Bothnian Sea; 31: Bothnian Bay; 32: Gulf of Finland. The relevant stocks are as follows: North Sea stock (ICES area 4.a–c, 7.d, 20), the Kattegat stock (21), the western Baltic stock (22–24), and the eastern Baltic stock (24–32). Inset shows noteworthy local locations. Δ : Aabenraa Fjord; \square : Bagenkop; \circ : Bornholm

stock (Divisions 4.a–c, 7.d, SD 20), the Kattegat stock (SD 21), the western Baltic stock (SD 22–24), and the eastern Baltic stock (SD 24–32). All ICES units are collectively referred to as ICES areas henceforth.

Declining cod stock sizes in the North Sea and Baltic Sea have been a great concern since the 1970s and 1980s, respectively. This is particularly evident in the North Sea, where the cod stock is currently at levels similar to after the collapse in the early 2000s (Huserbråten et al. 2018). In the southern North Sea, the cod is virtually absent due to historically high fishing pressure and continued low recruitment. In the nearby Kattegat, the stock was at a historically low spawning stock biomass (SSB) level in 2020, and ICES currently advises zero catch only (ICES 2021a). In the Baltic Sea, the western Baltic cod stock has experienced low recruitment since the mid-2000s (ICES 2021b). In addition, the eastern Baltic cod stock is in a poor state, partially due to high fishing pressure, low recruitment, and slow growth (Ecro et al. 2015, Orio et al. 2019).

Several factors may have affected the movement patterns in Atlantic cod stocks, such as changes in stock sizes due to density-dependent behaviour (Fretwell 1969), although cannibalism also plays a role (Neuenfeldt & Köster 2000). As stock sizes

increase, density-dependent behaviour may cause individuals to adjust their spatial distribution to avoid high-density patches, as has previously been observed in spawning eastern Baltic cod (Baranova 1995). In contrast, reduction in stock sizes has been linked to range contractions. This has previously been observed in capelin *Mallotus villosus* (Ingvaldsen & Gjøsæter 2013) and pike *Esox lucius* (Haugen et al. 2006). Furthermore, changes in the environment, such as an increase in hypoxic areas in the past decades in the Baltic Sea (Casini et al. 2016), could potentially have affected movement patterns as well, as cod move to more oxygen-rich areas. Additionally, movement may also be variable across stocks due to the presence of 2 distinct ecotypes of Atlantic cod – more resident inshore and more migratory offshore cod (e.g. see Lear & Green 1984, Robichaud & Rose 2004, Karlsen et al. 2013) – and both types can occur in the same area (e.g. Knutsen et al. 2018).

Movement patterns of cod in the North Sea and Baltic Sea have been studied using mark–recapture data (e.g. see Otterlind 1985, Aro 1989, Bagge & Stefensen 1989, Bagge & Thurow 1994, Wright et al. 2006a, Righton et al. 2007, Mion et al. 2022). The majority of these data, in addition to Danish mark–recapture data from the western Baltic Sea, the Sound, and Kattegat, have recently been compiled into a joint database for the Baltic Sea (Mion et al. 2020, 2021). Despite the limitations of mark–recapture data, as only the release and recapture locations are known, historical mark–recapture studies offer a good opportunity to study temporal movement patterns due to the quantity of data available, making it possible to discern general movement patterns and changes through time.

Numerous methods have been used to analyse mark–recapture data in the North Sea and Baltic Sea, including plotting recaptures (Otterlind 1985), employing kernel density distributions (Righton et al. 2007, Mion et al. 2022) and generalised additive models (GAMs; Espeland et al. 2008, Mion et al. 2022), as well as calculating metrics of movement (Righton et al. 2007). Occasionally, ancillary information such as that provided by otolith microchemistry (Wright et al. 2006b, Svedäng et al. 2010) or genetics (Heath et al. 2014, Hemmer-Hansen et al. 2020) has also been used in combination with tagging data to disentangle sub-population stock structuring (e.g. Zemeckis et al. 2014, ICES 2020). These methods often provide insight on movement behaviour and spatial distribution patterns, but do not provide mathematical links between individual-level movements and population-level patterns. A mathemati-

cal approach to assessing movement uses the concepts of advection (biased movement) and diffusion (dispersal). When applied to populations, they describe the average movement of a population within a selected time frame and coordinate system and to what extent average movement is directed or appears to be random. For instance, a high advection in one direction indicates the population has an overall tendency to move in this direction, while a high diffusion would indicate the population is characterized by random movement. Together, advection and diffusion can offer a dynamic approach to study movement in tagged fish in space and time and have previously been applied to skipjack tuna *Katsuwonus pelamis* (Sibert et al. 1999, Faugeras & Maury 2005). To the authors' knowledge, however, this approach has not been applied to Atlantic cod.

The main aim of this study was to gain preliminary insights into overall movement patterns in Atlantic cod in the North Sea and Baltic Sea based on mark–recapture data from 1955 to 2020 by applying the advection–diffusion approach and to test the applicability of this approach to reproduce movement patterns obtained by other methods, such as the kernel density distribution analyses performed by Mion et al. (2022), which also addressed seasonality in movements. Specifically, the objectives of this study were to compare spatial and temporal patterns in advection and diffusion of Atlantic cod between the North Sea, Kattegat–Skagerrak, western Baltic, and eastern Baltic. Additionally, we examined whether movement distances were higher in offshore ecotypes in comparison to inshore ecotypes in the eastern and western Baltic Sea.

2. MATERIALS AND METHODS

2.1. Data overview

Mark–recapture data from Danish tagging projects in the North Sea and Baltic Sea ($n = 7962$) were digitised and incorporated into a database containing mark–recapture data collected between 1955 and 2020 from several countries (Mion et al. 2020, 2021), including Denmark ($n = 325$), Sweden ($n = 4796$), Poland ($n = 1794$), Latvia ($n = 113$), Germany ($n = 910$), Finland ($n = 403$), and the United Kingdom ($n = 5361$). This also included the more recent tagging projects CODYSSEY (Cod spatial dynamics and vertical movements in European waters and implications for fishery management; Righton et al. 2009) and TABACOD (Tagging Baltic Cod; Hüsey et al. 2020)

($n = 21664$ in total). Archival tagging data from CODYSSEY and TABACOD were also included, but made up $<1\%$ of the overall data. The database included detailed information on release and recapture locations and dates, and biological information such as total length (mm) and weight (g). Recaptures were only considered if release and recapture locations and dates were known. Recaptures ≤ 15 d after release were excluded to allow for post-tagging recovery of neutral buoyancy (van der Kooij et al. 2007) and resumption of normal behaviour as cod live at depth. In total, 4295 recaptures were excluded resulting in a data set of 17369 recaptures for this study.

All Atlantic cod were tagged and released within the distribution areas of the North Sea stock (ICES areas 4.a, 4.b, 4.c, 20), the Kattegat stock (ICES area 21), the western Baltic stock (ICES areas 22–24), and the eastern Baltic stock (ICES areas 24–32, except 28.1 and 31) (see Fig. 1 for ICES areas and figure legend for important local area names), and the most common tag types were Lea, alcatheene, and t-bars. Information on total release numbers was not available due to a lack of available information within the historical part of the database.

All recaptures were grouped by release ICES areas. Skagerrak (ICES area 20) was grouped with Kattegat (ICES area 21) due to low recapture coverage in Skagerrak ($n = 4$) and all release locations being on the edge of Kattegat. Henceforth, cod tagged within this area will collectively be referred to as Kattegat–Skagerrak. Overall differences between ICES areas were first considered for all data collected within each ICES area, and the data were further grouped by recapture decades (<1960 , 1960–1970, 1971–1980, 1981–1999, 2000–2020) to determine temporal differences within and between ICES areas. Due to low recaptures in all areas in the 1990s ($n = 71$) and 2000s ($n = 256$), 1981–1999 and 2000–2020 were grouped to span 2 decades. Note that recaptures were unavailable for some years (1991–1993, 1997, 1998, 2008, 2009, 2012, 2014). For analyses of seasonal movements, we refer to Mion et al. (2022).

2.2. Analysis of movement

Assuming individuals move independently of each other, the direction-driven (anisotropic) movement from the release point was illustrated using advection (mean movement vector), $\hat{\alpha}$, and estimated for each release ICES area by (Nielsen 2004):

$$\hat{\alpha} = \left(\frac{\sum \Delta x}{\sum \Delta t}, \frac{\sum \Delta y}{\sum \Delta t} \right) \quad (1)$$

and assuming non-directional movement is the same in every direction (isotropic) from the release point, the isotropic diffusion coefficient, \hat{D} , was estimated by (Nielsen 2004):

$$\hat{D} = \frac{1}{4(n-1)} \left(\sum \left(\frac{\Delta x^2}{\Delta t} \right) - \frac{(\sum \Delta x)^2}{\sum \Delta t} + \sum \left(\frac{\Delta y^2}{\Delta t} \right) - \frac{(\sum \Delta y)^2}{\sum \Delta t} \right) \quad (2)$$

where Δx and Δy denote the difference between release and recapture coordinates (longitude and latitude) converted to a geodesic distance (km), Δt is the difference between release and recapture time, and n is the number of fish. To visualise the directed movements for each area, the advection was used to calculate a vector angle and distance, and the time frame was scaled to per half year by multiplying by 365/2 to see large-scale trends. The advection thus describes movement through mean changes in kilometres between release and recapture per half year for the large-scale study that included all ICES areas. Similarly, diffusion (the variance) describes mean changes in distance from the point of release over $\sqrt{\frac{1}{2} \text{ year}}$ for the large-scale study, and gives a relative indication of the degree of dispersal. To visualise the dispersal for each area, circles were used, and the radius was determined by the diffusion coefficient multiplied by 365/2.

To account for statistical uncertainty and assign a measure of accuracy to the observed patterns, each ICES area group was bootstrapped to create new data sets ($n = 10\,000$) by randomly sampling the original data set for the respective ICES area group and allowing duplicate data entries. These new data sets were used to calculate bootstrapped $\hat{\alpha}$ and \hat{D} values to use as confidence intervals to determine the stability of the $\hat{\alpha}$ and \hat{D} estimates from the raw data for each release ICES area group. Subsets per ICES area per decade with <30 recaptures were ignored for the bootstrap accuracy analyses due to low sample size.

2.3. Movement patterns in offshore and inshore ecotypes

In the western Baltic Sea, stock components in the Aabenraa Fjord and southern Belt Sea (SBS) were chosen to represent inshore and offshore ecotypes, respectively, based on the proximity to land (Fig. 1). Aabenraa Fjord is a short fjord located in the western part of the Baltic Sea and is constrained by land. In

comparison, the southern Belt Sea is one of the more offshore areas in the western Baltic. This group included all releases south of Bagenkop (see Fig. 1 for locations).

Stock components in the eastern Baltic (the Gulf of Finland and southeastern Baltic Sea (SEBS)) were similarly chosen to represent inshore and offshore ecotypes, respectively. The Gulf of Finland is a large inlet located in the easternmost Baltic Sea and is relatively constrained by land. This ecotype group included all releases in ICES area 32 (Fig. 1). In contrast, the southeastern Baltic Sea is an offshore area, and this group included all releases in ICES area 26 (Fig. 1).

The ecotype case studies were treated and analysed similarly to the large-scale case study (see previous section). To compare overall movement distances between ecotypes (offshore and inshore) in the eastern and western Baltic, distance travelled per month (km mo^{-1}) was assessed as a complementary analysis to the advection–diffusion methodology to illustrate pattern detection at even small time scales. Distance travelled per month was calculated as the geodesic distance between release and recapture location to account for the slight curvature of the Earth, which was then divided by days at liberty and multiplied by 30.

Distance per month between inshore and offshore ecotypes was compared using a pairwise bootstrap test on the median differences. The median was chosen as the test metric due to its robustness to outliers. For each group comparison (Aabenraa Fjord vs. SBS, Gulf of Finland vs. SEBS), the groups were combined into one data set that was used to construct 2 new data sets through sampling with replacement. The data sets would then represent the inshore and offshore group, respectively, and be of the same size as the original data sets. The median difference was calculated by subtracting the distance per month median for the inshore population from the offshore population. This was repeated 100000 times to compare to the true median difference between the ecotypes. If the ecotypes were statistically similar, the true median difference would be expected to fall within the bootstrapped distribution. However, if the ecotypes were different, the true median difference would be expected to fall outside the bootstrapped distribution.

Finally, a pairwise bootstrap test was performed to test for temporal differences within the areas based on recapture decade (Aabenraa Fjord = 1950s vs. 1960s; SBS = 1950s vs. 1960s; Gulf of Finland = 1970s vs. 1980s; SEBS = 1950 vs. 1960s vs. 1970s vs. 2010s). The median difference was calculated by subtracting

the distance per month median for the oldest decade from the youngest. The results of the tests were subsequently compared to recapture lengths and months to check for biases. Subsets per ecotype group per decade with <30 recaptures were ignored for the bootstrap analyses due to low sample size.

All analyses were done in R version 4.0.2 (R Core Team 2020). The packages *sp* (Pebesma & Bivand 2005), *rgeos* (Bivand & Rundel 2020), and *rgdal* (Bivand et al. 2020) were used to create the maps, and *beanplot* (Kampstra 2008) was used for the beanplots. The R script utilized for the analyses is available upon request.

3. RESULTS

3.1. Data overview

Cod were both released and recaptured in different months across the years (Table S1 in the Supplement at www.int-res.com/articles/suppl/m691p115_supp.pdf), indicating that both spawning and feeding seasonal movements were represented. However, release numbers were lower for June–September and recapture numbers were lower for August–December compared to the rest of the year (Table S1). In the case of recaptures, this is likely due to differences in

fishing pressure. The number of recaptures was variable among ICES areas (Fig. S1). Most areas were well represented across decades, although the northern North Sea (ICES area 4.a) and northern Baltic Sea (ICES areas 29, 30, and 32) were mainly represented by few recaptures across 1 or 2 decades. Most releases were recaptured within the same decade. Days at liberty were similarly variable for each release area (Fig. S2), with most cod being recaptured within the first 100 d after release.

In general, release and recapture lengths across the 4 stocks were similar, with a median total length around 400 and 450 mm, respectively (Fig. S3), with the largest sizes observed in the North Sea.

3.2. Analysis of movement

3.2.1. The North Sea (ICES areas 4.a–c)

The overall advection was low in the northern North Sea (ICES area 4.a) but increased towards the southern part of the North Sea (Fig. 2). The overall diffusion patterns in the North Sea were much stronger than in the adjacent ICES areas (Fig. 3) and comparable to those observed in the eastern Baltic. Across decades, the advection was strong and towards the north in the central and southern North Sea (ICES areas 4.b and 4.c, respectively), although the advection was relatively low in the central North

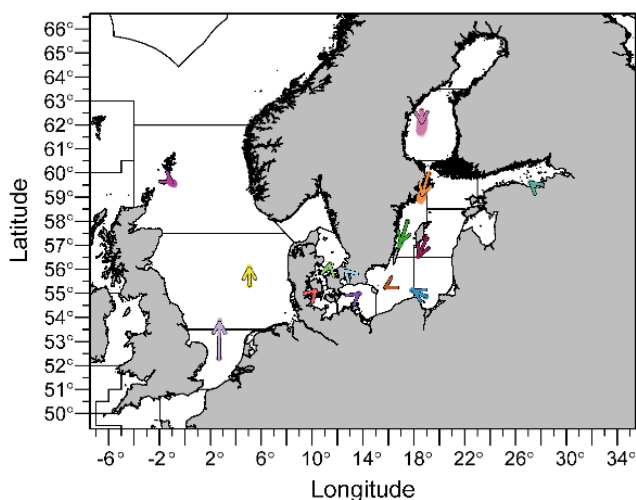


Fig. 2. Semi-annual advection patterns for each area for all years combined. Each arrow represents the advection in individual areas calculated from the raw data sets. The length of the arrow denotes the strength of the advection based on the difference between release and recapture positions. The start point of the arrow is the mean of the release coordinates. The small points at the end of the arrows denote the end points of 10000 advection arrows calculated for each area from bootstrapped data sets to show accuracy

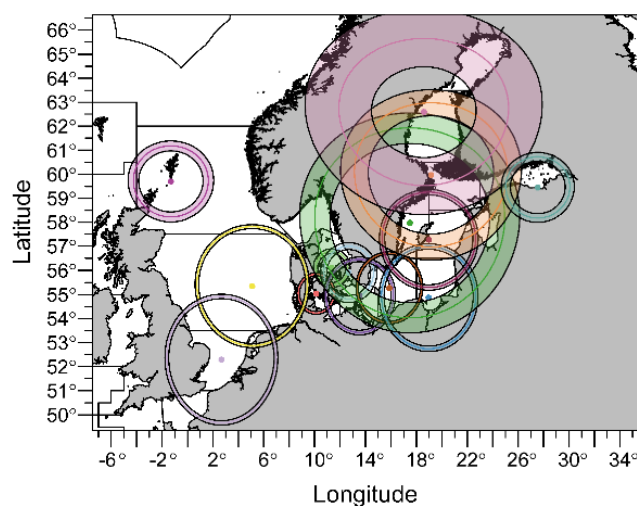


Fig. 3. Semi-annual diffusion patterns for each area for all years combined. The size of the circle indicates the relative strength and degree of diffusion in individual areas. The centre of the circle is the mean of the release coordinates. The middle line in each circle indicates the diffusion calculated from the raw data and the outer limits the 95% confidence intervals calculated from the bootstrapped datasets

Sea in 1971–1980 (Fig. 4a,c). Diffusion patterns were variable but generally high in both the central and southern North Sea (Fig. 4b,d). No decadal comparison was possible for the northern North Sea. The bootstrap accuracy analyses generally showed relatively stable estimates aside from the southern North Sea in the 2000s (Fig. 4c,d).

Overall, the patterns suggest high degrees of movement in a northerly direction in the central and southern North Sea, with some decadal variation. In contrast, the patterns suggest a relatively high degree of movement in the northern North Sea but with

no clear direction (see Tables S2 and S3 for the advection and diffusion values).

3.2.2. The Kattegat–Skagerrak (ICES areas 20–21)

Kattegat–Skagerrak exhibited very low overall advection towards the north (Fig. 2) and no strong historical changes in direction, although advection was slightly greater in 1971–1980 (Fig. 4e). While the overall diffusion was relatively low (Fig. 3), decadal variation could be observed, with greater diffusion in

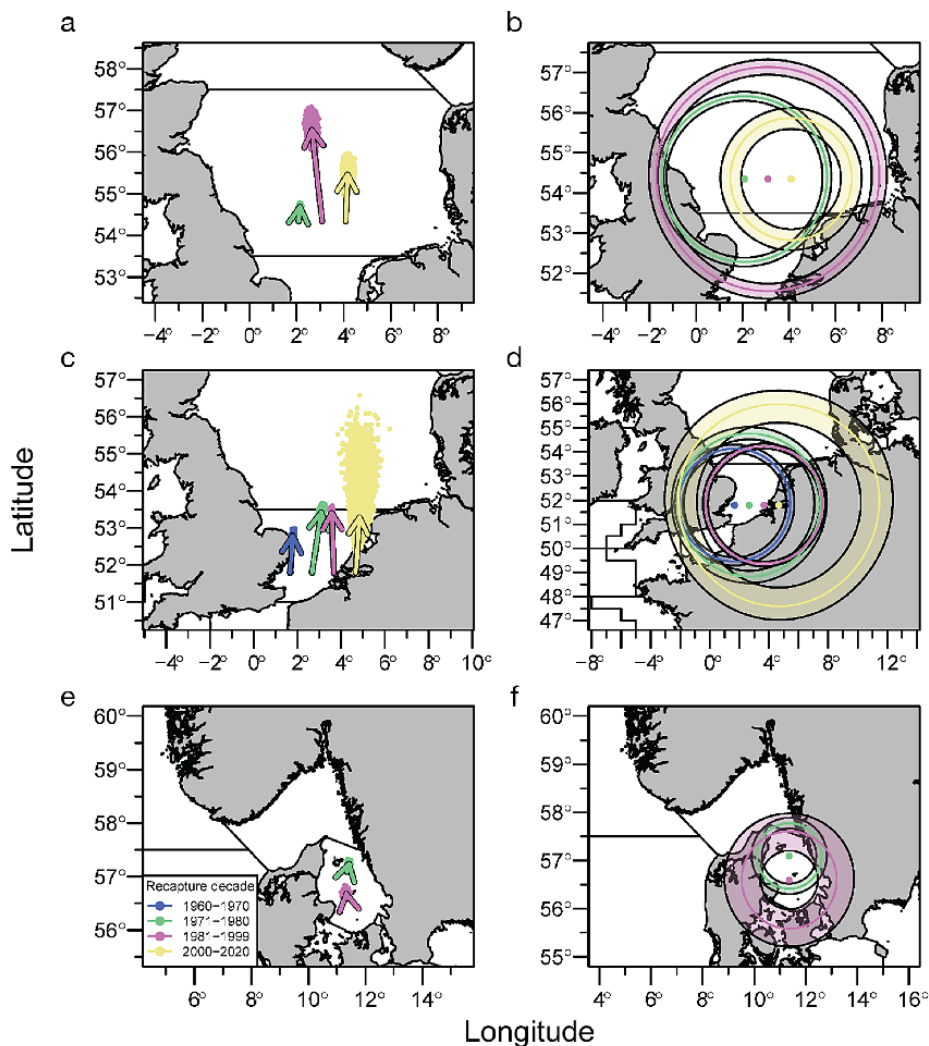


Fig. 4. Semi-annual advection and diffusion patterns across decades in the central and southern North Sea and Kattegat–Skagerrak. Advection and diffusion in (a,b) the central North Sea (ICES area 4.b), (c,d) the southern North Sea (ICES area 4.c), and (e,f) Kattegat–Skagerrak (ICES area 20+21). Each arrow and circle represent the advection and diffusion in individual areas calculated from the raw data sets, respectively. The start point of the arrow and centre of the circles do not represent release locations. The length of the arrow denotes the strength of the advection based on the difference between release and recapture positions and the size of the circles indicates the relative strength and degree of diffusion in individual areas. The small points denote the end points of 10 000 advection arrows calculated for each area from bootstrapped data sets to show accuracy. The middle line in each circle indicates the diffusion calculated from the raw data and the outer limits the 95 % confidence intervals calculated from the bootstrapped data sets

1981–1999 compared to 1971–1980 (Fig. 4f). Although the advection estimates were generally characterized by low uncertainty, the diffusion was characterized by wide confidence intervals (Fig. 4f). The observed patterns suggest a historical high degree of residency in the Kattegat–Skagerrak (see Tables S2 and S3 for the advection and diffusion values).

3.2.3. The Western Baltic Sea (ICES areas 22–24)

Advection and diffusion in the western Baltic were relatively low overall but with some decadal variation (Figs. 2, 3, 5). In the Belt Sea (ICES area 22), the direction of the advection was generally between north and east, and increased northeastern advection

and greater diffusion were observed in 1960–1970 (Fig. 5a,b). The Sound (ICES area 23) similarly exhibited low advection in earlier years, increasing slightly towards southern Kattegat in 1981–1999 (Fig. 5c). High degrees of variation in diffusion were observed among decadal groupings, with the highest observed in 1981–1999 and 1960–1970 (Fig. 5d). The Arkona Sea (ICES area 24) was characterized by low advection in opposing directions between 1960–1970 and 1971–1980, and a sharp increase in 2000–2020 towards Bornholm (Fig. 5e). The extent of diffusion did not change with time (Fig. 5f). The bootstrap accuracy analyses showed relatively low degrees of accuracy in the Sound and Arkona Basin (Fig. 5c–f), although the direction of the advection was relatively stable.

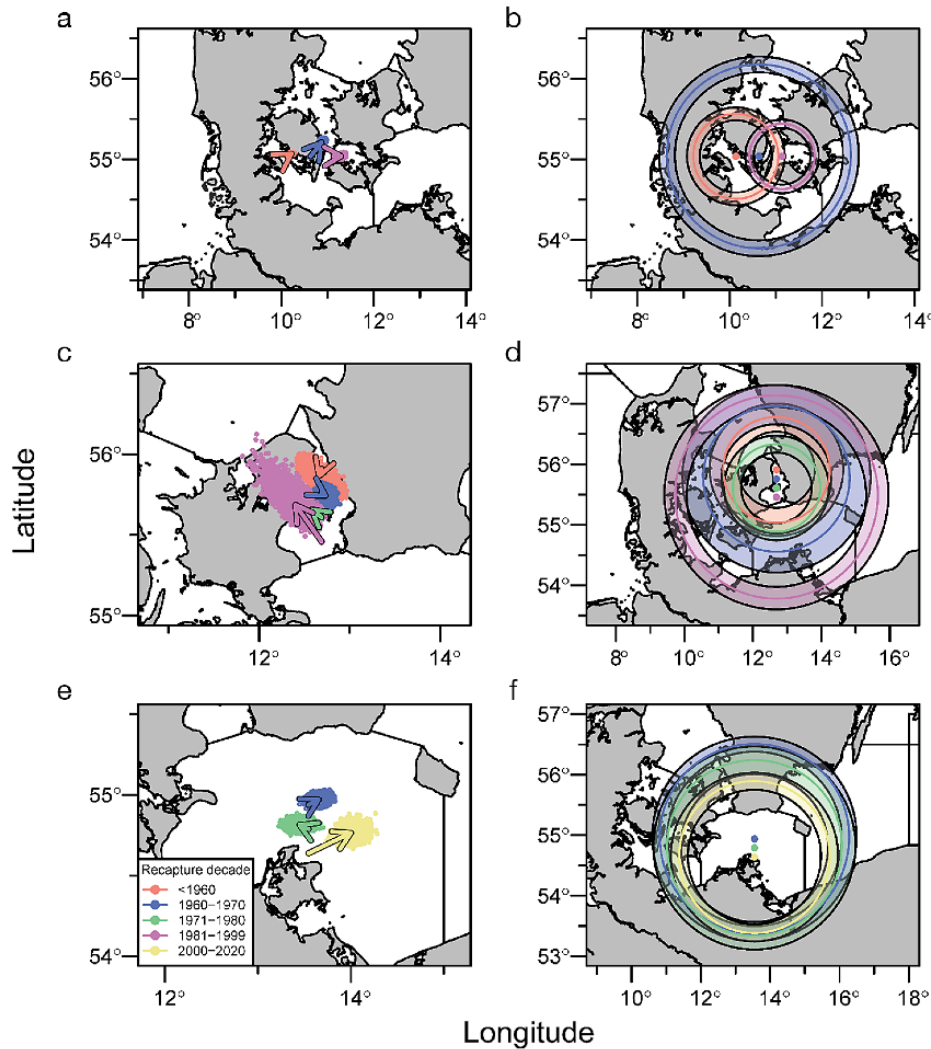


Fig. 5. Semi-annual advection and diffusion patterns across decades in the Belt Sea, the Sound, and the Arkona Sea. Advection and diffusion in (a,b) the Belt Sea (ICES area 22), (c,d) the Sound (ICES area 23), and (e,f) the Arkona Sea (ICES area 24). See Fig. 4 for definition of arrows, circles and points

Overall patterns in the western Baltic suggest a relatively low degree of movement, with a higher degree of movement towards the southern Kattegat since the 1970s (see Table S2 and S3 for the advection and diffusion values).

3.2.4. The Eastern Baltic Sea (ICES areas 25–32)

The eastern Baltic Sea generally exhibited high rates of advection and diffusion in the northern part compared to slightly lower rates in the Gulf of Finland (ICES area 32) and central Baltic (ICES areas 25–26; Figs. 2, 3, 6, 7). The Bornholm Sea (ICES area 25) was characterized by overall low advection in variable directions towards west and east over time (Fig. 6a).

Diffusion was relatively high but in the lower end for the eastern Baltic Sea, with a general decadal decrease in diffusion rates (Fig. 6b). In comparison, SEBS (ICES area 26) had strong overall advection west towards the Bornholm Sea and high diffusion, with highest rates observed before 1960 (Fig. 6c,d). The Western Gotland Basin (ICES area 27) exhibited very strong advection in a southerly direction towards the southern Baltic and similarly strong diffusion in 1960–1970 (Figs. 2, 3). However, due to low recaptures in other decades, a temporal comparison was not possible. The estimates were relatively accurate although the strength of the advection was slightly less certain, particularly in SEBS (Fig. 6c,d).

The Gotland Sea (ICES area 28.2) similarly showed strong advection towards the southern Baltic in

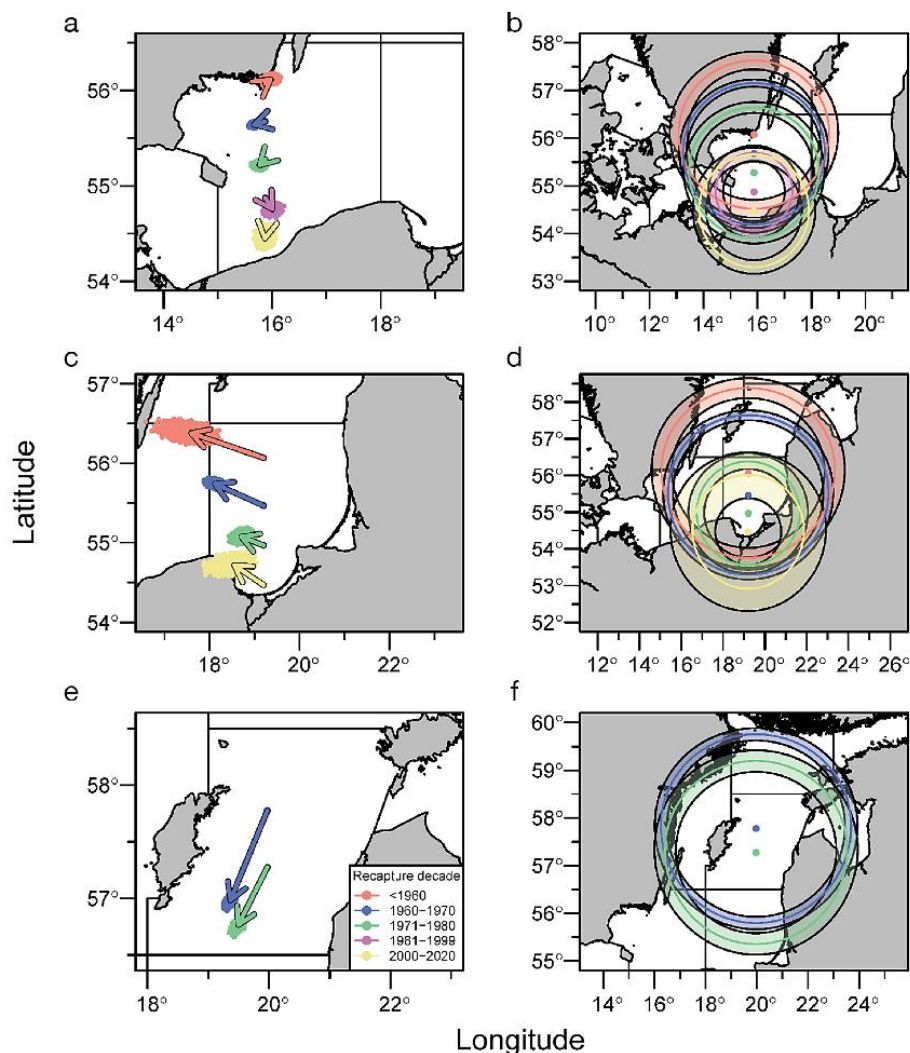


Fig. 6. Semi-annual advection and diffusion patterns across decades in the Bornholm Sea, southeastern Baltic Sea (SEBS), and the Gotland Sea. Advection and diffusion in (a,b) the Bornholm Sea (ICES area 25), (c,d) SEBS (ICES area 26), and (e,f) the Gotland Sea (ICES area 28.2). See Fig. 4 for definition of arrows, circles and points

1960–1970 and 1971–1980 (Fig. 6e). Diffusion was high across both decades but more similar to the patterns in the southern Baltic than the northern Baltic (Fig. 6f). Comparable patterns were observed in the Archipelago Sea (ICES area 29), with very strong advection towards the southern Baltic across all decades, although lower in 1960–1970 compared to before 1960 and 1981–1999 (Fig. 7a). A high degree of diffusion was observed, with the lowest observed in 1960–1970 (Fig. 7b). The Bothnian Sea (ICES area 30) also exhibited strong advection towards the southern Baltic in 1981–1999 (Fig. 2). Diffusion was very high, albeit with relatively wide 95% confidence intervals (Fig. 3), indicating a high degree of uncertainty. However, due to low recaptures in other decades, no temporal comparison was possible for this area either. The Gulf of Finland (ICES area 32) showed low advection towards the northwest, with slightly higher advection in 1971–1980 compared to 1981–1999 (Fig. 7c). Diffusion was greatly variable and was much higher in 1971–1980 compared to 1981–1999 (Fig. 7d). While the bootstrap accuracy analyses showed fairly stable estimates in the Gotland Sea and Gulf of Finland

(Figs. 6e,f, 7c,d), the Archipelago Sea was characterized by high uncertainty (Fig. 7a,b).

Overall patterns in the eastern Baltic Sea suggest high degrees of movement from the northern part towards the southern Baltic. The decadal patterns suggest generally higher degrees of movement before 1980s compared to more recent decades. In comparison, movement in the Gulf of Finland and east and south of Gotland appears to be lower but still higher or similar to the western Baltic Sea (see Tables S2 and S3 for the advection and diffusion values).

3.3. Movement patterns in inshore and offshore ecotypes

3.3.1. Western Baltic—Aabenraa Fjord vs. southern Belt Sea (SBS)

Ecotypes in Aabenraa Fjord (inshore) and SBS (offshore) exhibited different movement patterns, and both methodologies produced similar results with relatively accurate estimates (Figs. 8a,b, 9). While

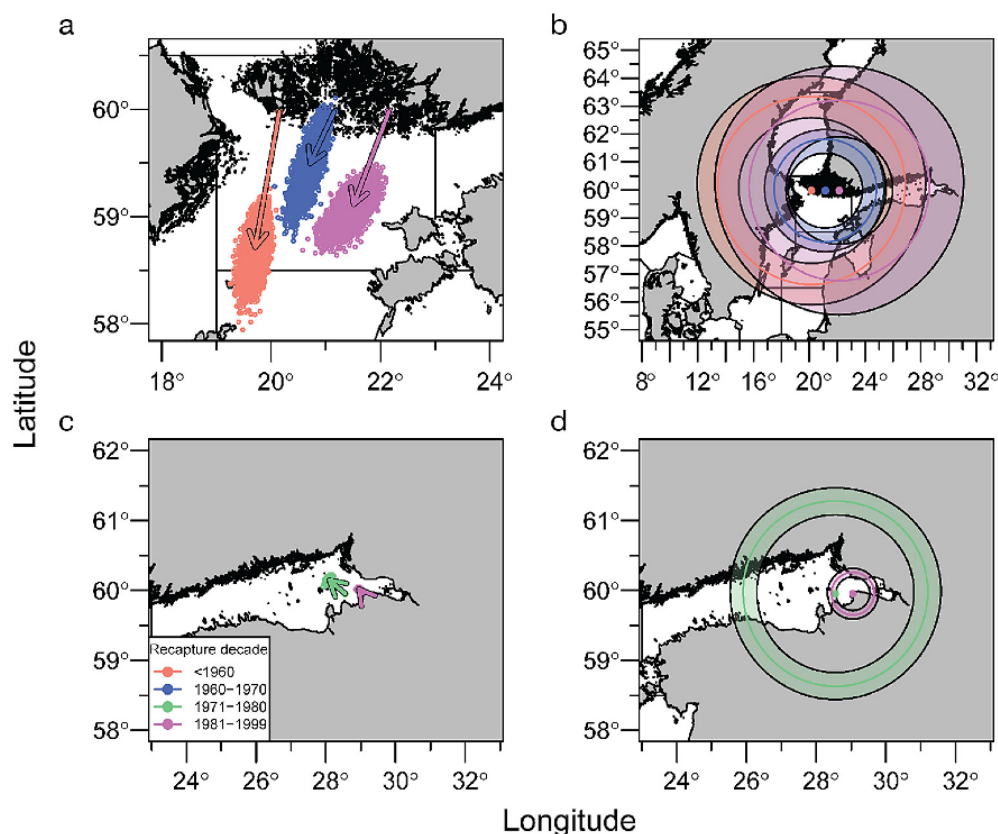


Fig. 7. Semi-annual advection and diffusion patterns across decades in the Archipelago Sea and the Gulf of Finland. (a,b) Advection and diffusion in the Archipelago Sea (ICES area 29), and (c,d) in the Gulf of Finland (ICES area 32). See Fig. 4 for definition of arrows, circles and points

most cod in both areas swam $<10 \text{ km mo}^{-1}$ (Fig. 9), movement distances $>10 \text{ km mo}^{-1}$ were more common in offshore cod in the SBS compared to inshore cod in Aabenraa Fjord, suggesting more resident behaviour in Aabenraa Fjord. The advection and diffusion (Table S4) and distance medians suggested similar patterns (0.67 and 7.32 km mo^{-1} for Aabenraa Fjord and SBS, respectively).

The bootstrap test on the median differences between Aabenraa Fjord and SBS supported this difference in behaviour, as the true difference between the medians ($6.65 \text{ km month}^{-1}$) was significantly higher than the bootstrapped distribution (Fig. S4a). Recapture lengths were similar between populations (Fig. S4c), but releases in Aabenraa Fjord were generally recaptured throughout the year compared to SBS, which was dominated by recaptures early in the year (Fig. S4e). Days at liberty were variable in both ecotypes, although the majority of recaptures occurred within 100 d of release, especially in the SBS (Fig. 9).

3.3.2 Eastern Baltic—Gulf of Finland vs. southeastern Baltic Sea (SEBS)

Similar patterns were observed in ecotypes in the Gulf of Finland (inshore) and SEBS (offshore; Figs. 8c,d, 9). Inshore cod in the Gulf of Finland generally swam $<20 \text{ km mo}^{-1}$, while a relatively small proportion of offshore cod in SEBS swam $>50 \text{ km mo}^{-1}$. The advection and diffusion, as well as the distance medians, similarly suggested more resident behaviour in cod in the Gulf of Finland (6.26 km mo^{-1}) compared to SEBS (17.79 km mo^{-1}) (Table S4, Fig. 8c,d).

As was also observed for the western Baltic ecotypes, the bootstrap test on the median differences between Gulf of Finland and SEBS further supported this distinction in behaviour as the true difference between the medians (11.53 km mo^{-1}) was significantly higher than the bootstrapped distribution (Fig. S4b). Overall recapture lengths were lower in SEBS compared to Gulf of Finland (Fig. S4d) and releases in SEBS were generally recaptured early on in the

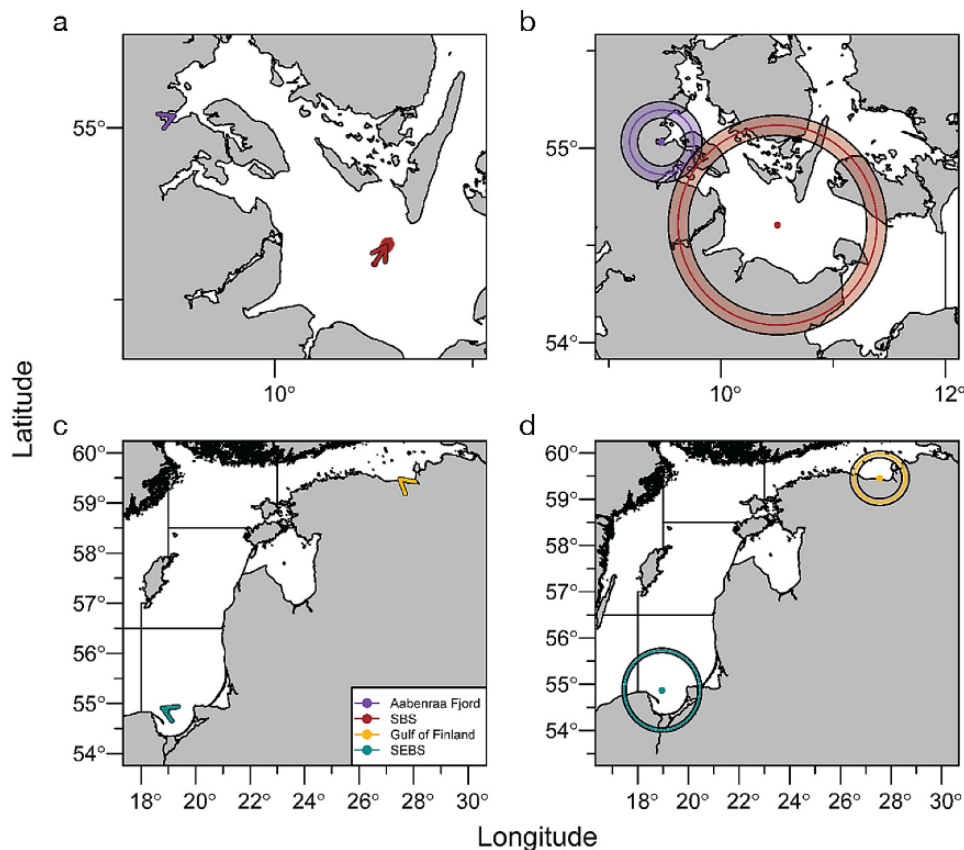


Fig. 8. Monthly advection and diffusion patterns in the western Baltic Sea and eastern Baltic Sea. (a) Advection patterns in the western Baltic Sea. (b) Diffusion patterns in the western Baltic Sea. (c) Advection patterns in the eastern Baltic Sea. (d) Diffusion patterns in the eastern Baltic Sea. See Fig. 4 for definition of arrows, circles and points. SBS: southern Belt Sea; SEBS: southeastern Baltic Sea

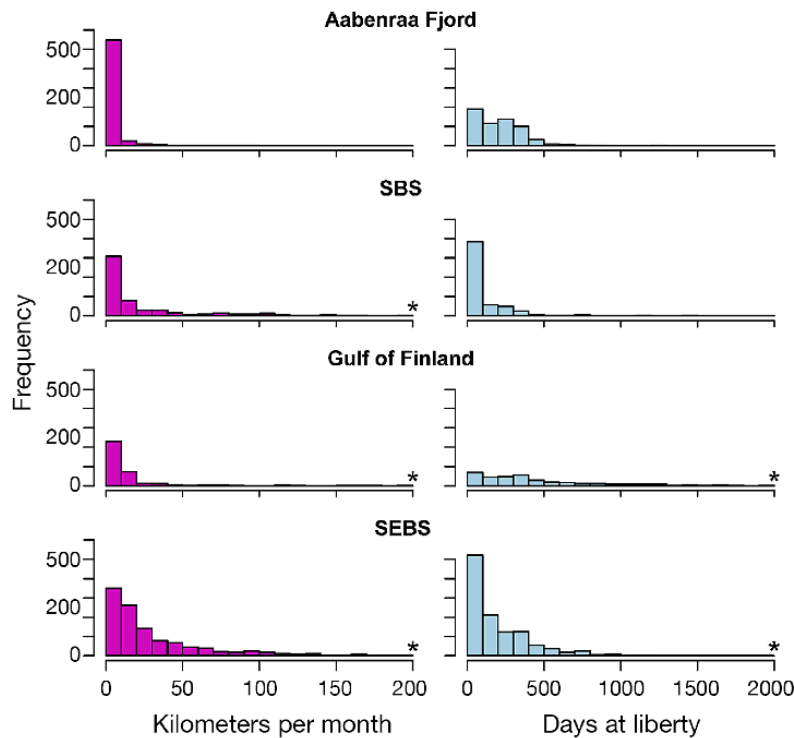


Fig. 9. Movement distances (km mo^{-1}) and days at liberty for recaptures released in Aabenraa Fjord, southern Belt Sea (SBS), Gulf of Finland, and south-eastern Baltic Sea (SEBS). Asterisks (*) indicate values above 3 km or 2000 d

year while releases in Gulf of Finland were recaptured throughout the year with peaks in spring and autumn (Fig. S4f). The majority of releases in SEBS were recaptured within 100 d of release while days at liberty were more evenly distributed in Gulf of Finland within the first 500 d (Fig. 9).

Overall, both case studies suggested a higher degree of resident behaviour in the inshore ecotypes in contrast to a more mobile behaviour in offshore ecotypes regardless of which stock they belonged to. Additionally, the offshore component in SBS resembled the inshore component in the Gulf of Finland (median = 7.32 and 6.26 km mo^{-1} , respectively), although Gulf of Finland cod were slightly more resident (Fig. 9).

3.3.3. Decadal variation in movement patterns within ecotypes

Clear variation in decadal movement patterns were observed within Aabenraa Fjord, SBS, and Gulf of Finland. The bootstrap test on the median differences showed that tagged cod in Aabenraa Fjord moved significantly farther in 1960–1970 compared

to <1960 (Fig. 10a), despite the recapture lengths and months being similar between the 2 time periods (median = 400 and 410 mm, and June and May in <1960 and 1960–1970, respectively). Similar patterns were observed in SBS (Fig. 10b), although the recapture lengths seemed to differ slightly more (median = 365 and 440 mm in <1960 and 1960–1970, respectively) with recaptures mainly occurring in early spring (median = March for both decades). In contrast, the true median difference for Gulf of Finland was negative and below the bootstrapped distribution, suggesting cod moved slightly less in 1981–1999 vs. 1970–1980 (Fig. 10c). Recapture lengths were slightly higher in 1981–1999 vs. 1970–1980 (median = 570 and 650 mm) and cod were recaptured slightly earlier in the year in 1981–1999 (median = July vs. May). No clear variation was observed across decades for SEBS, as the true median differences fell within the distribution of the bootstrapped decadal median differences across all decades.

Overall, these patterns show clear decadal variation in movement patterns across both ecotypes.

4. DISCUSSION

In the present study, we successfully applied the advection–diffusion methodology to study movement patterns in Atlantic cod in the North Sea and Baltic Sea for the first time. We surmised that the North Sea is most likely dominated by the more migratory offshore ecotype, and the combination of an expansive coastal area and offshore areas in the Baltic region suggested a mix of both the offshore and resident ecotypes. These patterns were evident from our data; however, in order to evaluate the usefulness of this method to analyse movement in cod, it is essential to compare our results to previous analyses of tagging data while also acknowledging the limitations of this methodology.

In the North Sea, tagging data have shown mixing between the southern and central North Sea, with limited mixing between these areas and the northern North Sea (e.g. see Bedford 1966, Righton et al. 2007). Indeed, cod in the northern North Sea appear

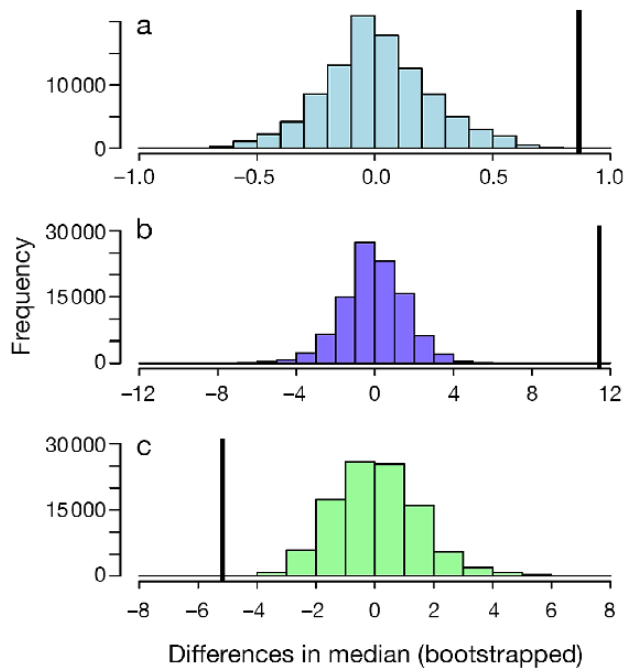


Fig. 10. Distributions of bootstrapped decadal median differences for swimming distances (km mo^{-1}) for recaptures released in Aabenraa Fjord, southern Belt Sea (SBS), and Gulf of Finland. (a) Aabenraa Fjord (<1960 vs. 1960–1970), (b) SBS (<1960 vs. 1960–1970), and (c) Gulf of Finland (1970–1980 vs. 1981–1999). Median differences were calculated from bootstrapped data sets ($n = 100\,000$). Thick black lines indicate true median values for respective populations. Due to a lack of differences across decades, southeastern Baltic Sea (SEBS) is not shown

to be relatively stationary (e.g. see Wright et al. 2006b, Nedreaas et al. 2008, Neat et al. 2014). In contrast, a recent study in the Baltic Sea by Mion et al. (2022) using kernel density distributions and GAMs showed greater movement distances in northern and central Baltic cod compared to cod in the southern Baltic (Mion et al. 2020, 2022). In addition, other studies have identified the migration routes between spawning and feeding areas in the Baltic Sea using tagging data (e.g. see Otterlind 1985, Aro 1989, Bagge & Steffensen 1989, Bagge & Thurow 1994). In general, these studies all agree that eastern Baltic cod migrate to the southern Baltic to spawn, whereas cod in the western part of the Baltic use spawning areas that cover most of the Belt Sea (Otterlind 1985, Hüsey 2011). Furthermore, Mion et al. (2022) showed seasonal patterns in movements with variations in home ranges during the spawning and feeding seasons and suggested a potential link to ecotype behaviour.

Our findings in the North Sea and the Baltic Sea aligned well with these earlier results, highlighting

the usefulness of this method. We expanded upon these results by presenting tools to separate movement into direction-driven and dispersed movement and assigning a measure of accuracy, providing more detailed analyses of movement. As an example, while northern North Sea cod have been shown to be relatively stationary, we showed that this movement was characterized by relatively high dispersal rather than being direction-driven. Similarly, combined with the kernel density distributions as presented in Mion et al. (2022), we further showed that movements in the eastern Baltic cod were characterized overall by both strong southerly advection and diffusion.

Inshore ecotypes in Aabenraa Fjord and Gulf of Finland had remarkably restricted movement patterns compared to offshore ecotypes in the southern Belt Sea and southeastern Baltic Sea, respectively. This aligns with earlier studies where inshore cod have been found to be relatively resident (Jakobsen 1987, Salvanes et al. 2004, Espeland et al. 2008) while offshore ecotypes appear to be more migratory (Robichaud and Rose 2004). For example, a study over 2 yr on Icelandic cod using data storage tags showed consistent behavioural patterns across inshore and offshore cod, with offshore cod migrating up to 4 times the depth of inshore cod to feed at thermal fronts (Thorsteinsson et al. 2012). Additionally, ecotypes can vary even within a single spawning ground (Thorsteinsson et al. 2012), as has been observed in Norwegian and Skagerrak cod (Godø & Michalsen 2000, Espeland et al. 2008). Our findings highlight the diversification of cod behaviour within even single stocks. Furthermore, the additional possibility of looking at shorter time scales and areas (as shown here in the ecotype case studies) could offer insights into movement within spawning and feeding seasons, respectively, although this requires a lot of data for bootstrapping to estimate accuracy. However, it should be noted that the movement behaviour of cod in Gulf of Finland may not have been properly captured, as the nearest spawning ground is further away than the local spawning grounds in the Belt Sea, possibly suggesting more migratory behaviour (Bleil et al. 2009).

The existence of different ecotypes within stock components at even small scales, as illustrated by the Aabenraa case study, poses challenges for the stocks in light of climate change. More resident cod in fjords and inlets (e.g. Aabenraa Fjord and Gulf of Finland) have largely disappeared over the years, and whether it is due to an inability to adapt to more migratory behaviour or failure of reproduction caused by changes in biotic and abiotic factors is currently

unknown. Cod are very sensitive to temperature changes and an increase of only 2.5°C in water temperature has been shown to cause an increase of 15–30% in metabolic rate (Claireaux et al. 1995). As Atlantic cod prefer to stay in colder, deeper water during the day and warmer, shallower water at night (Claireaux et al. 1995), it is possible that environmental changes in fjords have inferred a great metabolic cost to resident cod populations and affected reproduction. While low oxygen levels have a negative effect on egg survival in Baltic cod, lower oxygen levels are tolerated at low temperatures (Wieland et al. 1994), which has also been shown in Pacific cod, where eggs tolerate low levels of oxygen as long as temperatures are between 3 and 5°C (Alderdice & Forrester 1971). Warm conditions caused by a marine heatwave have been shown to persist for at least 4 yr in the deeper layers of a fjord (Jackson et al. 2018), and with the historical warming of the Baltic Sea (Siegel et al. 2006, Hinrichsen et al. 2007) and an increase in the extent of hypoxic coastal areas (Conley et al. 2011), it is likely that temperature and hypoxia have been factors in the disappearance of resident ecotypes. In comparison, stocks with highly migratory stock components are more likely to survive when conditions change, although range shifts will have local socio-economic consequences. Indeed, future studies into cod population dynamics should take behavioural ecotypes into consideration, possibly using genetics and otolith analyses.

The results presented here indicate clear differences in movement behaviour within ICES areas and across ecotypes. However, it should be noted that some of the observed variation may be attributed to other factors to a certain degree, especially across decades. The environment in the Baltic Sea and North Sea has greatly changed between 1955 and 2020; for example, there has been a historical rise in sea surface and bottom temperature (Carstensen et al. 2014) and an expansion in hypoxic and anoxic areas (Kabel et al. 2012, Casini et al. 2016), which could have influenced the movement patterns. Fishing effort was also not accounted for in the present study, and some of the observed movement patterns may not properly represent the true migratory behaviour of the population as fishing boats focus on areas with a higher abundance. This has been shown to be informative to the analysis of mark–recapture data (Solmundsson et al. 2005, Wright et al. 2006a), and, when coupled with differences in the reporting and return rates of tags (Taylor et al. 2011, Konrad et al. 2016), may influence our understanding of movement patterns. Additionally, the main fishing grounds

for Atlantic cod are not evenly distributed over the habitat range, and have likely changed over time (Engelhard et al. 2014). For instance, in the central North Sea, the observed patterns in the 1970s were likely affected by the strong presence of fisheries on the western coast of the Danish Jutland peninsula during this time period. Furthermore, the analyses suggested that a high proportion of cod did not move far, if at all, between release and recapture. This apparent lack of movement is most likely a combination of true movement behaviour and the nature of mark–recapture experiments missing information between release and recapture, particularly for individuals with long time intervals between release and recapture. The presence of seasonal movements in Atlantic cod will also influence the observed movement patterns, as will differences in body size and life stage (Righton et al. 2007, Griffiths et al. 2018, Mion et al. 2022).

5. CONCLUSIONS

The concepts of advection and diffusion have been demonstrated to be simple and useful tools for analysing dynamics of cod population movements. In conjunction with other methods, such as bootstrapping for accuracy analysis, movement can be described in greater detail by addressing both directional and dispersed movement at a predetermined time scale. Indeed, this approach can easily be applied to the majority of available tagging data sets for other studies to give a dynamic and in-depth description of movement patterns in fish at even finer time scales. We demonstrated this in the present study and our results agreed with previous analyses of tagging data, demonstrating the value of this simple method.

More advanced applications of the advection–diffusion approach may incorporate estimates of mortality or habitat indices to study how environmental conditions (e.g. temperature, salinity, and oxygen) affect movement patterns on a much finer spatiotemporal scale than the preliminary results shown in the present study. Applications of this linked methodology approach have been utilized greatly in population dynamics models such as the Spatial Ecosystem And Population Dynamics Model (SEAPODYM; Lehodey et al. 2008). In order to expand the methodology used in this study, efforts are currently ongoing to examine the link between changes in movement patterns through time and changes in environmental factors by incorporating hydrographic data. These

will provide useful information on how Atlantic cod will react to the changes in environmental conditions entrained by climate change.

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LITERATURE CITED

- ✦ Alderdice DF, Forrester CR (1971) Effects of salinity, temperature, and dissolved oxygen on early development of the Pacific Cod (*Gadus macrocephalus*). J Fish Res Board Can 28:883–902
- Aro E (1989) A review of fish migration patterns in the Baltic. Rap Proc-Verb Ré Cons Int Explor Mer 190:72–96
- Bagge O, Steffensen E (1989) Stock identification of demersal fish in the Baltic. Rap Proc-Verb Ré Cons Int Explor Mer 190:3–16
- Bagge O, Thurow F (1994) The Baltic cod stock, fluctuations and possible causes. In: ICES Mar Sci Symp 198:254–268
- Baranova T (1995) The structure of spawning cod stock in the eastern Baltic during 1972–1995. ICES CM 1995:1–6
- Bedford B (1966) English cod tagging experiments in the North Sea. ICES CM 1966/G:1–9
- Bivand R, Rundel C (2020) Rgeos: interface to Geometry Engine — Open Source ('GEOS'). R package version 0.5-3. <https://cran.r-project.org/package=rgeos>
- Bivand R, Keitt T, Rowlingson B (2020) Rgdal: bindings for the 'Geospatial' Data Abstraction Library. R package version 1.5-12. <https://cran.r-project.org/package=rgdal>
- ✦ Bleil M, Oeberst R, Urrutia P (2009) Seasonal maturity development of Baltic cod in different spawning areas: importance of the Arkona Sea for the summer spawning stock. J Appl Ichthyol 25:10–17
- ✦ Carstensen J, Andersen JH, Gustafsson BG, Conley DJ (2014) Deoxygenation of the Baltic Sea during the last century. Proc Natl Acad Sci USA 111:5628–5633
- ✦ Casini M, Käll F, Hansson M, Plüskens M and others (2016) Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. R Soc Open Sci 3:160416
- ✦ Claireaux G, Webber D, Kerr S, Boutilier R (1995) Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating temperature conditions. J Exp Biol 198:49–60
- ✦ Conley DJ, Carstensen J, Aigars J, Axe P and others (2011) Hypoxia is increasing in the coastal zone of the Baltic Sea. Environ Sci Technol 45:6777–6783
- ✦ Eero M, Hjelm J, Behrens J, Buchmann K and others (2015) Eastern Baltic cod in distress: biological changes and challenges for stock assessment. ICES J Mar Sci 72: 2180–2186
- ✦ Engelhard GH, Righton DA, Pinnegar JK (2014) Climate change and fishing: a century of shifting distribution in North Sea cod. Glob Change Biol 20:2473–2483
- ✦ Espeland SH, Olsen EM, Knutsen H, Gjosæter J, Danielssen D, Stenseth NC (2008) New perspectives on fish movement: kernel and GAM smoothers applied to a century of tagging data on coastal Atlantic cod. Mar Ecol Prog Ser 372:231–241
- ✦ Faugeras B, Maury O (2005) An advection-diffusion-reaction size-structured fish population dynamics model combined with a statistical parameter estimation procedure: Application to the Indian Ocean skipjack tuna fishery. Math Biosci Eng 2:719–741
- ✦ Fretwell SD (1969) On territorial behavior and other factors influencing habitat distribution in birds. III. Breeding success in a local population of field sparrows (*Spiza americana* Gmel). Acta Biotheor 19:45–52
- ✦ Godø OR, Michalsen K (2000) Migratory behaviour of north-east Arctic cod, studied by use of data storage tags. Fish Res 48:127–140
- ✦ Griffiths CA, Patterson TA, Blanchard JL, Righton DA, Wright SR, Pitchford JW, Blackwell PG (2018) Scaling marine fish movement behavior from individuals to populations. Ecol Evol 8:7031–7043
- ✦ Haugen TO, Winfield IJ, Vøllestad LA, Fletcher JM, James JB, Stenseth NC (2006) The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. Proc Biol Sci 273:2917–2924
- ✦ Heath MR, Culling MA, Crozier WW, Fox CJ and others (2014) Combination of genetics and spatial modelling highlights the sensitivity of cod (*Gadus morhua*) population diversity in the North Sea to distributions of fishing. ICES J Mar Sci 71:794–807
- Hemmer-Hansen J, Hüsey K, Vinther M, Albertsen C, Storru-Paulsen M, Eero M (2020) Sustainable management of Kattegat cod; better knowledge of stock components and migration. DTU Aqua Rep 357–2020. DTU Aqua, Lyngby
- Hinrichsen HH, Lehmann A, Petereit C, Schmidt J (2007) Correlation analyses of Baltic Sea winter water mass formation and its impact on secondary and tertiary production. Oceanologia 49:381–395
- ✦ Huserbråten MBO, Moland E, Albrechtsen J (2018) Cod at drift in the North Sea. Prog Oceanogr 167:116–124
- ✦ Hüsey K (2011) Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. ICES J Mar Sci 68: 1459–1471
- Hüsey K, Casini M, Haase S, Hilvarsson A and others (2020) Tagging Baltic cod—TABACOD: eastern Baltic cod: solving the ageing and stock assessment problems with combined state-of-the-art tagging methods. DTU Aqua Rep 368–2020. DTU Aqua, Lyngby
- ICES (2020) Workshop on stock identification of North Sea Cod (WKNScodID). ICES Sci Reports 2:82. ICES, Copenhagen
- ICES (2021a) Cod (*Gadus morhua*) in subdivision 21 (Kattegat). Rep ICES Advis Comm. ICES, Copenhagen
- ICES (2021b) Cod (*Gadus morhua*) in subdivisions 22–24, western Baltic stock (western Baltic Sea). Rep ICES Advis Comm. ICES, Copenhagen
- ✦ Ingvaldsen RB, Gjosæter H (2013) Responses in spatial distribution of Barents Sea capelin to changes in stock size, ocean temperature and ice cover. Mar Biol Res 9: 867–877
- ✦ Jackson JM, Johnson GC, Dosser IIV, Ross T (2018) Warming from recent marine heatwave lingers in deep British Columbia fjord. Geophys Res Lett 45:9757–9764

- ✦ Jakobsen T (1987) Coastal cod in northern Norway. *Fish Res* 5:223–234
- ✦ Kabel K, Moros M, Porsche C, Neumann T and others (2012) Impact of climate change on the Baltic Sea ecosystem over the past 1000 years. *Nat Clim Chang* 2: 871–874
- ✦ Kampstra P (2008) Beanplot: a boxplot alternative for visual comparison of distributions. *J Stat Softw* 28:1–9
- ✦ Karlsten BO, Klingan K, Emblem Å, Jørgensen TE and others (2013) Genomic divergence between the migratory and stationary ecotypes of Atlantic cod. *Mol Ecol* 22: 5098–5111
- ✦ Knutsen H, Jorde PE, Hutchings JA, Hemmer-Hansen J and others (2018) Stable coexistence of genetically divergent Atlantic cod ecotypes at multiple spatial scales. *Evol Appl* 11:1527–1539
- ✦ Konrad C, Bratley J, Cadigan NG (2016) Modelling temporal and spatial variability in tag reporting-rates for Newfoundland cod (*Gadus morhua*). *Environ Ecol Stat* 23: 387–403
- Lear WH, Green JM (1984) Migration of the ‘northern’ Atlantic cod and the mechanisms involved. In: McCleave JD (ed) *Mechanisms of migration in fishes*. Springer, Boston, MA, p 309–315
- ✦ Lehodey P, Senina I, Murtugudde R (2008) A spatial ecosystem and populations dynamics model (SEAPODYM)—modeling of tuna and tuna-like populations. *Prog Oceanogr* 78:304–318
- ✦ Mion M, Hilvarsson A, Hüsey K, Krumme U and others (2020) Historical growth of eastern Baltic cod (*Gadus morhua*): setting a baseline with international tagging data. *Fish Res* 223:105442
- ✦ Mion M, Haase S, Hemmer-Hansen J, Hilvarsson A and others (2021) Multidecadal changes in fish growth rates estimated from tagging data: a case study from the Eastern Baltic cod (*Gadus morhua*, Gadidae). *Fish Fish* 22: 413–427
- Mion M, Griffiths CA, Bartolino V, Haase S and others (2022) New perspectives on Eastern Baltic cod movement patterns from historical and contemporary tagging data. *Mar Ecol Prog Ser* 689:109–126
- ✦ Neat FC, Bendall V, Berx B, Wright PJ and others (2014) Movement of Atlantic cod around the British Isles: implications for finer scale stock management. *J Appl Ecol* 51: 1564–1574
- Nedreaas K, Aglen A, Gjøsæter J, Jorstad K, Knutsen H, Smedstad O, Svasand T, Agotnes P (2008) Management of cod in western Norway and on the Skagerrak coast-stock status and possible management measures. *Fisk og havet* 5:1–106
- ✦ Neuenfeldt S, Köster FW (2000) Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. *ICES J Mar Sci* 57:300–309
- Nielsen A (2004) Estimating fish movement. PhD thesis, Royal Veterinary and Agricultural University, Frederiksberg
- Orio A, Karpushevskaia A, Nielsen A, Sundelöf A and others (2019) Benchmark Workshop on Baltic Cod Stocks (WKBALTCOD2). *ICES Sci Rep* 1. ICES, Copenhagen
- ✦ Otterlind G (1985) Cod migration and transplantation experiments in the Baltic. *J Appl Ichthyology* 1:3–16
- Pebesma E, Bivand RS (2005) Classes and methods for spatial data in R. *R News* 5:9–13
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.r-project.org/>
- ✦ Righton D, Quayle VA, Hetherington S, Burt G (2007) Movements and distribution of cod (*Gadus morhua*) in the southern North Sea and English Channel: results from conventional and electronic tagging experiments. *J Mar Biol Assoc UK* 87:599–613
- Righton D, Metcalfe J, McCloghrie P, Hetherington S and others (2009) Cod spatial dynamics and vertical movements in European waters and implications for fishery management (CODYSSEY). <https://cordis.europa.eu/project/id/Q5RS-2002-00813/results>
- ✦ Robichaud D, Rose GA (2004) Migratory behaviour and range in Atlantic cod: inference from a century of tagging. *Fish Fish* 5:185–214
- ✦ Salvanes AGV, Skjæraasen JE, Nilsen T (2004) Sub-populations of coastal cod with different behaviour and life-history strategies. *Mar Ecol Prog Ser* 267:241–251
- ✦ Sibert JR, Hampton J, Fournier DA, Bills PJ (1999) An advection–diffusion–reaction model for the estimation of fish movement parameters from tagging data, with application to skipjack tuna (*Katsuwonus pelamis*). *Can J Fish Aquat Sci* 56:925–938
- Siegel H, Gerth M, Tschersich G (2006) Sea surface temperature development of the Baltic Sea in the period 1990–2004. *Oceanologia* 48(S):119–131
- ✦ Solmundsson J, Pálsson J, Karlsson H (2005) Fidelity of mature Icelandic plaice (*Pleuronectes platessa*) to spawning and feeding grounds. *ICES J Mar Sci* 62: 189–200
- ✦ Svedäng II, André C, Jonsson P, Elfman M, Limburg KE (2010) Migratory behaviour and otolith chemistry suggest fine-scale sub-population structure within a genetically homogenous Atlantic Cod population. *Environ Biol Fishes* 89:383–397
- ✦ Taylor RG, Whittington JA, Pine WE III, Pollock KH (2011) Effect of different reward levels on tag reporting rates and behavior of common snook anglers in southeast Florida. *N Am J Fish Manage* 26:645–651
- ✦ Thorsteinsson V, Pálsson ÓK, Tómasson GG, Jónsdóttir IG, Pampoulie C (2012) Consistency in the behaviour types of the Atlantic cod: repeatability, timing of migration and geo-location. *Mar Ecol Prog Ser* 462:251–260
- ✦ van der Kooij J, Righton D, Strand E, Michalsen K and others (2007) Life under pressure: insights from electronic data-storage tags into cod swimbladder function. *ICES J Mar Sci* 64:1293–1301
- Wieland K, Waller U, Schnack D (1994) Development of Baltic cod eggs at different levels of temperature and oxygen content. *Dana* 10:163–177
- ✦ Wright PJ, Galley E, Gibb IM, Neat FC (2006a) Fidelity of adult cod to spawning grounds in Scottish waters. *Fish Res* 77:148–158
- ✦ Wright PJ, Neat FC, Gibb FM, Gibb IM, Thordarson H (2006b) Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *J Fish Biol* 69: 181–199
- ✦ Zemeckis DR, Martins D, Kerr LA, Cadrin SX (2014) Stock identification of Atlantic cod (*Gadus morhua*) in US waters: an interdisciplinary approach. *ICES J Mar Sci* 71: 1490–1506

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Chapter III

Paper II:

Stock connectivity patterns and indications of sub-stock component structuring of cod in the Sound



Stock connectivity patterns and indications of sub-stock component structuring of cod in the Sound

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Abstract

Sustainable management of fish stocks requires knowledge of stock structure and connectivity between spawning and feeding habitats. Cod in the Sound are an example of a stock component with complex connectivity patterns. Currently cod in this area are managed as part of the western Baltic cod stock, while several studies suggest potential connectivity with the neighbouring stock in Kattegat. Here we assess the degree of connectivity of cod in the Sound with the neighbouring areas using historical tagging data from 1957-1987, and contemporary growth data from trawl surveys collected between 2007 and 2021. Furthermore, data from cod tagged outside of the Sound between 1960 – 2018 and recaptured in the Sound was used to examine immigration from outside areas. The connectivity between the Sound and Kattegat appeared to be considerable. Furthermore, cod tagged in the northern Sound were most likely to be recaptured in Kattegat while cod tagged in the southern part of the Sound were mainly recaptured in the Sound. Only 40 out of 16,789 tagged cod released outside of the Sound were eventually recaptured inside the Sound. Overall, these results highlight the need for further examination into the stock structure of cod in the western Baltic and adjacent areas.

1. Introduction

A fish stock is defined as a homogenous group of a fish species with similar biological features, such as growth, maturity, and mortality (Hilborn and Walters, 1992), and stock affiliation is based on spatio-temporal patterns in spawning. Stock identification is vital to effective fisheries management, hence stock structure and connectivity between adjacent areas should be documented to underpin efficient management (Begg and Waldman, 1999). In the Baltic Sea and adjacent waters, the Atlantic cod (*Gadus morhua*) is managed as three separate stocks divided by the subdivisions (SDs) used by the International Council for the Exploration of the Sea (ICES): The Kattegat stock (SD 21), the western Baltic stock (SD 22-24), and the eastern Baltic stock (SD 24-32). These divisions were defined based on the best available knowledge at the time of definitions, and subsequent studies have confirmed that the stock divisions, at least to some extent, are consistent with observed patterns of natal homing (Svedäng *et al.*, 2007).

One of these stocks, the western Baltic cod stock, is comprised of smaller units, known as stock components, from three different areas: the Belt Seas (SD 22), the Sound (SD 23), and the Arkona Basin (SD 24) (**Figure 1**). The Arkona Basin is known as a mixing ground between the eastern and western Baltic cod stocks (e.g., see Aro 1989, Hemmer-Hansen *et al.* 2019, Weist *et al.* 2019). This has previously caused issues for management, as the ratio between the two stocks in the Arkona Basin has changed over time due to a spill-over of cod from the eastern Baltic cod stock (Eero *et al.*, 2014), making it difficult to estimate the stock assessment parameters and reliable reference points. However, today this high degree of stock mixing is accounted for in stock assessment by the use of otolith shape analyses to separate the two stocks in this mixing zone (Orio *et al.*, 2019; Schade *et al.*, 2019; ICES, 2022).

Stock mixing has also been reported in the Kattegat stock where a North Sea component is transported in as juveniles or larvae and return to the North Sea upon reaching maturity around age 4 (Hemmer-Hansen *et al.*, 2020; Hüsey *et al.*, 2021). This annual removal of a large fraction of the cod in Kattegat caused an unrealistically high estimation of total mortality in the stock assessment. Furthermore, recruitment was artificially inflated due to the high influx of juveniles from the North Sea. These issues have recently been accounted for in stock assessments (ICES, 2021), but again illustrate the importance of studying stocks' connectivity between areas.

While cod in the Sound are formally considered as part of the western Baltic cod stock, connectivity between cod in the Sound and Kattegat has previously been reported (e.g., see Aro 1989, Bagge *et al.* 1994, Svedäng *et al.* 2010). However, the Kattegat cod stock has been depleted for more than a decade, while the same collapse has not been evident in the Sound, which at least until recently has appeared to be in a healthy state, displaying high productivity and a healthy population structure (Lindegren *et al.*, 2013; Svedäng and Hornborg, 2017). However, fishermen have reported a decrease in large-sized cod in the Sound in recent years (Olesen, unpubl.). The less exploited conditions in the Sound have been attributed to the combined effect of trawling being banned since 1932 (Anonymous, 1932) and the bell-shaped size selectivity of gill nets which is the preferable

type of commercial fishing gear used in the Sound resulting in less fishing pressure on older cod (Anonymous, 2007).

Connectivity between Kattegat and the Sound has been reported during the spawning season (Vitale *et al.*, 2008; Svedäng *et al.*, 2010), likely because the full extent of spawning grounds stretches from the central Sound into the southern Kattegat (Hüssy, 2011). The prevailing question is to what extent cod on the spawning grounds in southern Kattegat have moved in from the Sound or if cod from Kattegat display feeding migrations to the Sound; for example to feed during fall on herring to prepare for spawning (Aro, 1989; van Deurs *et al.*, 2016), which constitute a lipid rich diet (van Deurs *et al.*, 2016, 2022). Movements between Kattegat and the Sound could also be partially facilitated by seasonal differences in depth preferences due to changes in sea surface temperature and thermal stratification (Funk *et al.*, 2020). Baltic cod favour deeper waters during winter (>15 m; late December-March) and summer (July-August) and shallower water during the rest of the year (Funk *et al.*, 2020). This would suggest increased movement from the relative shallow central and southern Sound into the deeper northern Sound and southern Kattegat during winter and summer, or, alternatively, movement into deeper areas in the western Baltic Sea (i.e., the Arkona Basin). On the other hand, movement from the southern and central Baltic Sea into the Sound appears unlikely as cod move into or through the Belt Seas to enter Kattegat (Bagge, 1969; Berner, 1971a, 1971b, 1974). Depending on the proximity to either Kattegat or the Arkona Basin, it may thus be possible that cod in the northern and southern Sound have opposing movement patterns. It may even be possible that two separate populations exist in the Sound due to differences in timing of spawning in the northern and southern parts based on reports from fishermen (Olesen, unpubl.). Thus, to assess the degree of isolation of the Sound cod and to determine its stock identity, it is imperative to assess the degree of connectivity between the Sound and adjacent areas.

The overall aim of this study is to assess whether cod in the Sound are affiliated with the rest of the western Baltic cod, mix with the Kattegat stock, or constitute a local population of relatively resident cod. Furthermore, we consider a potential population divide in the Sound based on the prevailing geographic salinity gradient. We approach this by examining the extent and direction of historical movement patterns using conventional tagging data spanning four decades and assessing seasonal movements between the Sound and Kattegat. Additionally, we compare contemporary growth patterns across the western Baltic cod stock components and the Kattegat stock to provide support for the hypothesis that the historical population connectivity patterns observed from tagging data prevail to date. This analysis is based on the assumption that growth patterns of strongly connected populations will be similar, while differences in growth suggest geographically separated populations.

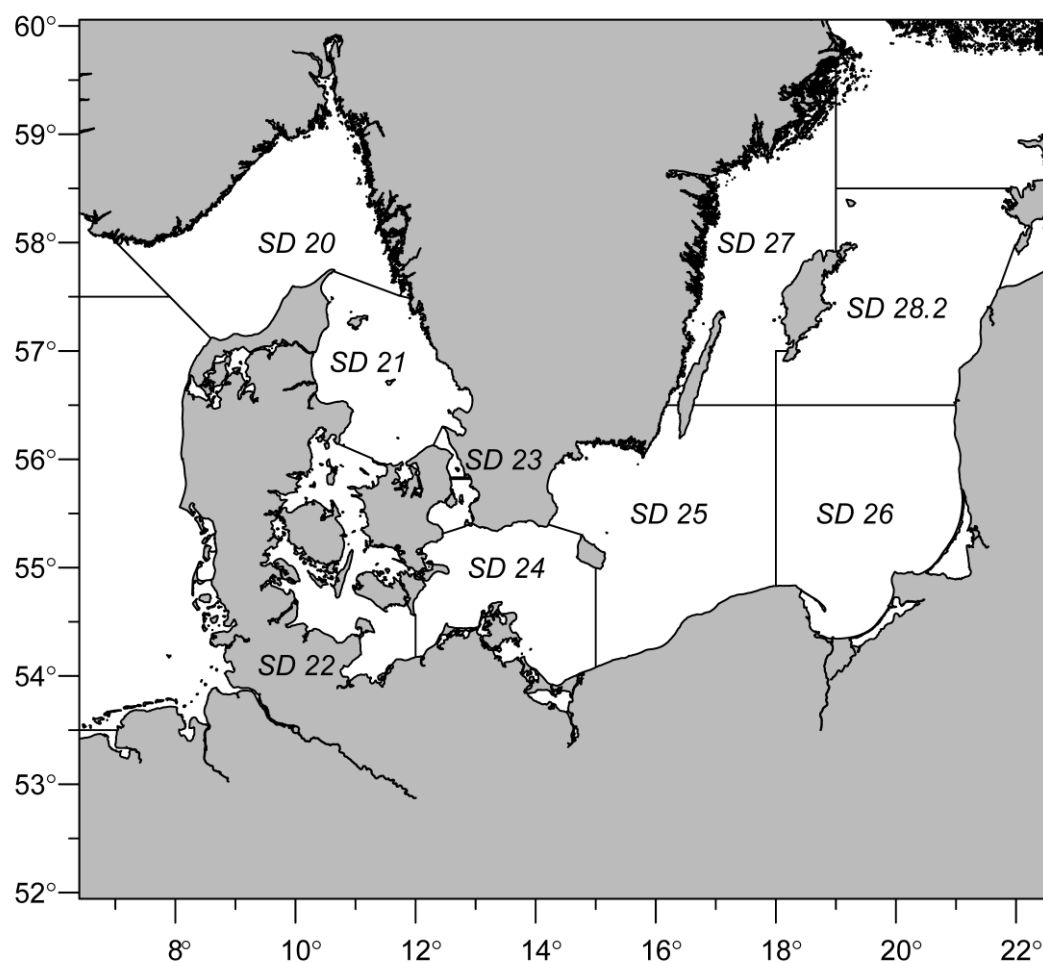


Figure 1. The Baltic Sea and relevant ICES subdivisions (SDs). SD 20: Skagerrak, SD 21: Kattegat, SD 22: The Belt Sea, SD 23: The Sound, SD 24: The Arkona Basin, SD 25: The Bornholm Sea, SD 26: the south-eastern Baltic Sea, SD 27: The Western Gotland Basin, SD 28.2: The Gotland Sea. Note the black horizontal line in SD 23 which indicates the geographical divide between the two areas based on the salinity division.

2. Methods

2.1 Tagging data

Releases in the Sound: Data for the Sound tagging projects were digitized from hand-written hard copy records of Danish and Swedish tagging projects and were combined with the Baltic cod tagging database (Mion *et al.*, 2020, n.d.; Lundgreen *et al.*, 2022). However, the full Baltic database was not utilized for this study but only releases in the Sound ($n = 797$). The database included spatial and temporal information of individual fish, such as release and recapture locations and time, days at liberty (DAL), and biological information such as total length (mm) and weight (g). No information on age was available, and information on depth intervals was only available for a small subset. Cod with $DAL < 15$ were excluded to allow resumption of normal behaviour following tagging (van der Kooij *et al.*, 2007), and recaptures with no information on release or recapture position or DAL were excluded. Cod with recapture positions on land were similarly removed. Following data screening, 215 recaptures were excluded from the analyses ($n = 582$; **Table 1**). Cod were released between 1957-1987 in the Sound and recaptured between 1957-1989. Tag types used were mainly Lea or t-bar tags (Mion *et al.*, 2020).

Releases outside the Sound: A subset of the Baltic cod tagging database (Mion *et al.*, 2020, n.d.; Lundgreen *et al.*, 2022) of cod released in other SDs but recaptured in the Sound ($n = 44$; $n = 40$ after data screening as above; **Table 1**) was used to evaluate the degree of immigration from other areas. This database included tagging data from Danish, Swedish, German, and Polish tagging projects (Mion *et al.*, 2020, n.d.; Lundgreen *et al.*, 2022). The same release and recapture information was available as in the Sound tagging database. Cod were released between 1960 - 2018 in Kattegat (SD 21), the Belt Sea (SD 22), the Arkona Basin (SD 24), the Bornholm Sea (SD 25), the south-eastern Baltic Sea (SD 26), and the Gotland Sea (SD 28.2), and recaptured between 1961 - 2020. Overall, the cod were released and recaptured in all quarters throughout the years. The tag types used were also primarily Lea or t-bar tags. See **Figure 1** and **figure text** for SD denotations and location names. Due to the small size of this subset, it was excluded from the transition matrix analyses.

Area	Q1	Q2	Q3	Q4
The Sound (Releases)	78	157	-	347
The Sound (Recaptures)	266	99	61	156
Outside The Sound (Releases)	21	2	4	13
Outside The Sound (Recaptures)	19	6	4	11

Table 1. Release and recapture quarters (Q) for cod released in the Sound between 1957 – 1987 and recaptured between 1957-1989 ($n = 582$), and cod released outside the Sound between 1960 – 2018 but recaptured within the Sound between 1961 – 2020 ($n = 40$).

Mortality: Release numbers were only available for a few of the tagging projects in the Baltic Sea database and do therefore not provide useful information on, e.g., survival for the analyses of this study. In order to consider the effect of mortality on the distribution of the historic recapture patterns, fishing mortality for the western Baltic cod stock and Kattegat were retrieved from stock assessment reports for comparison (Jørgensen *et al.*, 2011; ICES, 2014). No data on fishing mortality prior to 1970 was available. In addition, available relative fishing effort from the Danish fisheries per ICES rectangle was compiled from logbooks and used as a proxy for fisheries activity in the area combined with the fishing mortalities. This included cod-relevant trawl and gillnet effort between 1987-1990. While available data on gillnet landings were small in comparison to the trawl landings, gill-net landing effort was included due to the trawl ban in the Sound. No data on spatial effort was available prior to 1987 but it can be assumed that spatial effort has not changed drastically over time.

2.2 Estimating transition probabilities

To assess the connectivity of cod released in the Sound with the adjacent areas, a transition matrix was used. A transition matrix is a square matrix that describes the probability of transitioning between different states in a Markov chain. Thus, movement can be described by a Markov process where the probability of moving to a new state is only dependent on the current state, with states in our study representing neighbouring areas, such as the northern and southern Sound. In the case of cod moving between areas, a transition matrix then shows the probability of staying in an area or moving to neighbouring areas within one time step. When applied to the tagging data, the transition matrix shows the most probable area transition patterns based on all data and indicates overall connectivity. We applied this approach to two cases: 1) an overall transition matrix with the Sound divided into northern and southern areas connected to Kattegat and the southern Baltic, respectively, with no seasonal aspect, and 2) two seasonal transition matrices for only the Sound and Kattegat as it was not possible to include the southern Baltic due to a lack of seasonal data coverage. Both cases only utilised data for cod released in the Sound and thus we assume that area transitions are only representative of the Sound stock component for analysis purposes. In addition, it should be noted that recapture probability is dependent on spatio-temporal variations in fishing effort which was not accounted for. The potential implications of spatial variations in fishing effort are considered in the discussion.

As the transition matrix assumes that movement is possible between the areas within the chosen time step, it is necessary to choose a time step where area transitions are possible. Additionally, we chose a time step where it is unlikely for the cod to be able to skip areas in one time step, e.g., within the time step, an individual cod in the Sound is able to move to a neighbouring area, such as Kattegat, but not to an area further away, such as the Belt Sea. The definition of a suitable time step was based on observed swimming speeds in resident cod (Løkkeborg and Fernö, 1999). The smallest area, the southern Sound, is approx. 30 km long, and if cod are assumed to be active for around 10 hours per day with a mean swim speed of 20-30 cm s⁻¹ (Løkkeborg and Fernö, 1999;

Fernö *et al.*, 2011), it would take approx. 3-4 days for a cod to move from the northern part to the southern part of the Sound. As a lot of time is also spent foraging, the time step was set to one week for modelling purposes for both cases, as it is unlikely for the cod to be able to skip an area in one time step for a week.

To create a grid for the overall transition matrix, the relevant areas were divided into the following groups: Kattegat-Skagerrak (SD 20, 21), the northern Sound (SD 23N), the southern Sound (SD 23S), and the southern Baltic (SD 24-27). The Sound was divided horizontally at latitude 55.83 in order to coincide with the salinity gradient (Bendtsen *et al.*, 2007). We chose a salinity division as a topographic and hydrographic division that presents itself as a potential natural separator for a population in the deeper and more saline water in the north, and one in the shallower and fresher water in the south. Recaptures in SD 22 were ignored for the analyses of movement due to the focus on whether cod move north and south of the Sound, and due to low recaptures in SD 22 ($n = 4$). Additionally, this area does not seem to have a high connectivity to the Sound (Bagge, 1969; Berner, 1971a, 1971b, 1974). Note that Skagerrak was combined with Kattegat due to low recaptures ($n = 2$), and henceforth Kattegat-Skagerrak is referred to as Kattegat.

Maximum likelihood optimization was done to estimate the transition probabilities that would maximize the likelihood of observing the dataset. This means that different test values would be tried until the most likely values that would result in the observed dataset were found. To do this, a transition matrix, P_θ , was set up for each individual fish. Based on the test values, the probabilities of moving between areas for each individual fish were estimated by first calculating the probability of moving between the release and recapture area within the days at liberty, which were converted to weeks (t). This was done by raising the power of the transition matrix to the weeks at liberty (P_θ^t), where the transition matrix would then represent the possibilities of moving between each area at each individual time step. The transition matrix is then multiplied by itself for each individual time step and the final multiplication then represents the final transition probabilities between the areas based on t . This was done for each individual recapture.

Finally, the negative log likelihood for each individual fish was calculated and summed to get the overall most likely transition probabilities for the entire dataset based on all recaptures:

$$L(\theta) = - \sum_i \log (P_\theta^{t_i})_{k,j}$$

where $P_\theta^{t_i}$ indicates a transition matrix for one fish raised to the power of the weekly time step t_i , k the index of the release area, and j the index of the recapture area in the transition matrix. The negative log likelihood was then optimized until the most likely test values were found to get the most likely probabilities for the observed movement patterns in the dataset and estimate the overall transition matrix.

For the seasonally resolved analyses, the transition matrices were constructed similarly as above, although the seasonal aspect required an additional time component. Peak spawning occurs between January-February and was chosen as the spawning season in this study as most spawning activity occurs during these months (Vitale *et al.*, 2005). Two transition matrices were compiled: a spawning season transition matrix (January-February) and a feeding season transition matrix (March-December). When calculating the probability of a cod moving between areas within the weeks at liberty, the month at each time step was registered. In the case of a cod being out during more than two seasons, the probabilities during the spawning season were used to estimate the spawning seasonal transition matrix while the probabilities during the feeding season were used to estimate the feeding seasonal transition matrix. As with the overall transition matrix, this was done for each individual recapture and summed to get the overall most probable area transitions within the two seasons.

Additionally, the geodesic distance between the release and recapture locations was calculated to determine the presence of cyclical patterns, as has been observed previously in North Sea cod (Righton *et al.*, 2007). Only Sound cod released during peak spawning were considered to determine whether they return following spawning migrations ($n = 73$).

2.3 Growth

Available data on individual length-at-age in the ICES Database of Trawl Surveys (DATRAS) from Baltic International Trawl Surveys (BITS) and North Sea International Bottom Trawl Surveys (NS-IBTS) was utilized for the growth analyses. This included data on length (cm), age, and sampling area. For the growth analyses, data from the Sound ($n = 2,052$), Kattegat ($n = 3,533$), the Belt Seas ($n = 6,352$), and the Arkona Basin ($n = 9,443$) was used following data screening which included removal of outliers based on unrealistic length and age combinations. Data from Q1 between 2007-2021 was selected to show contemporary patterns.

To test for growth differences between the four SDs, a global model assuming no differences in growth was first set up using the von Bertalanffy growth function:

$$L_t = L_{\infty}(1 - e^{(-K(t-t_0))})$$

where L_t is the length-at-age t , L_{∞} the asymptotic length, K the growth coefficient, t the age of the fish, and t_0 the theoretical size at age 0. This model used length-at-age data for all four SDs combined and estimated four parameters, including the standard deviation (L_{∞} , K , t_0 , σ) using maximum likelihood optimization.

Subsequently, another model was created that estimated SD-specific parameters:

$$L_t = L_{\infty_{SD}}(1 - e^{(-K_{SD}(t-t_{0_{SD}}))})$$

This resulted in 16 SD-specific parameters ($L_{\infty SD}$, K_{SD} , t_{0SD} , σ_{SD}), and the parameters were estimated similarly as above.

A likelihood ratio test was then used to compare the two models to test which model fit the data best by testing whether the ratio between the likelihoods was significantly different from zero. If growth were similar across SDs, the global model would describe the data better than the second model. Alternatively, if growth were different between the SDs, the second model would describe the data better than the global model.

Finally, to specifically address the connectivity between the Sound and the surrounding SDs (Kattegat, the Belt Seas, the Arkona Basin), the analyses were repeated with the Sound and each SD separately.

All analyses were done in R version 4.0.2 (R Core Team 2020). The package *beanplot* (Kampstra, 2008) was used to create the beanplot, and *sp* (Pebesma and Bivand 2005), *rgeos* (Bivand and Rundel 2020), and *rgdal* (Bivand et al. 2020) were used to create the maps.

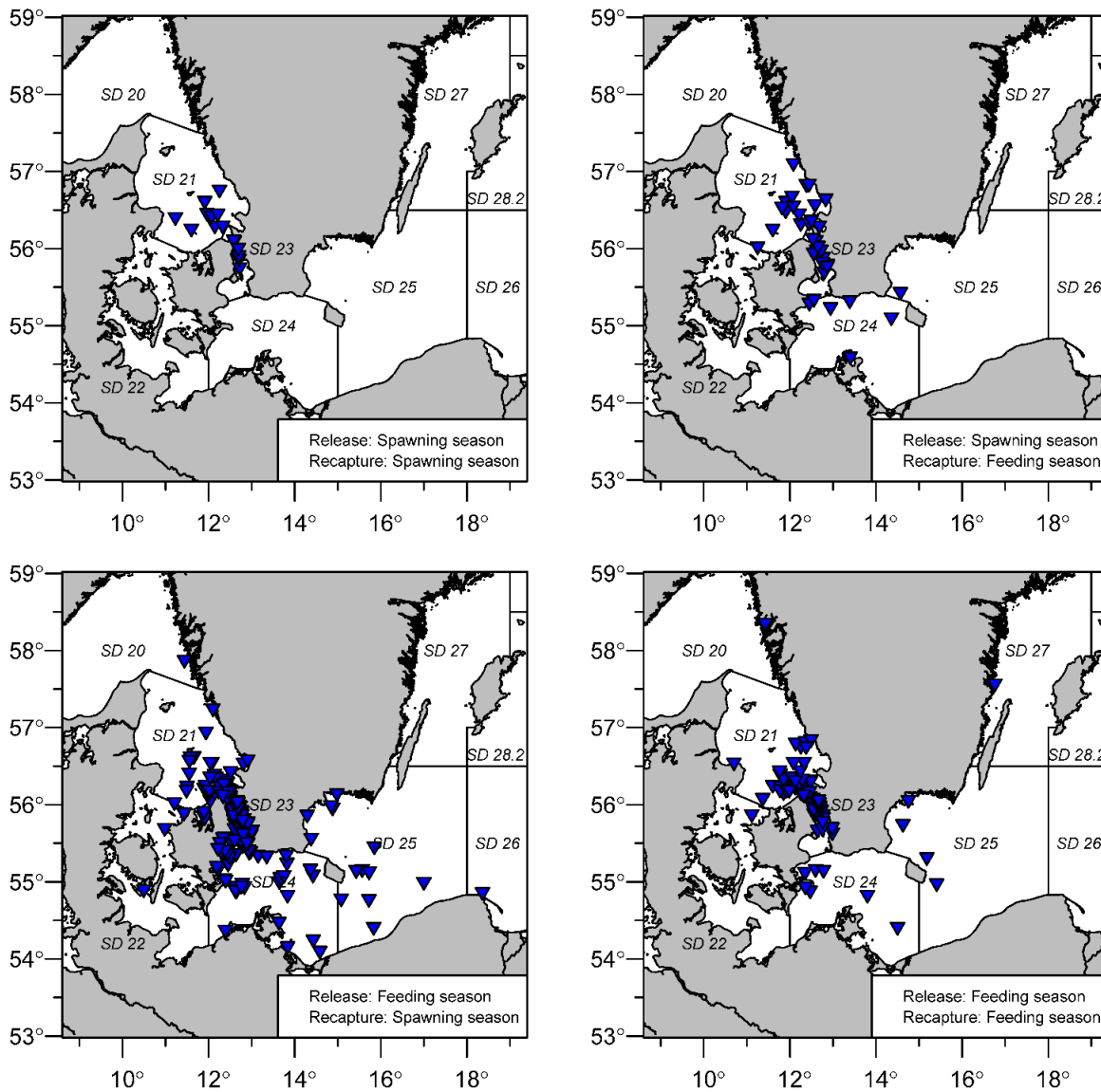


Figure 2. Map showing recapture positions for cod released in the Sound during peak spawning (January-February) and feeding seasons (March-December). Top left = released and recaptured within the spawning season ($n = 29$). Top right = released within the spawning season and recaptured within the feeding season ($n = 44$). Bottom left = released within the feeding season and recaptured within the spawning season ($n = 158$). Bottom right = released and recaptured within the feeding season ($n = 351$). Cod were recaptured in the following areas: SD 20: Skagerrak ($n = 2$), 21: Kattegat ($n = 162$), 22: the Belt Sea ($n = 4$), 23: the Sound ($n = 350$), 24: Arkona Sea ($n = 44$), 25: Bornholm Sea ($n = 18$), 26: the south-eastern Baltic Sea ($n = 1$), 27: the western Gotland Basin ($n = 1$).

3. Results

3.1 Tagging data

Releases in the Sound: Recaptured cod had been released throughout the year, with the majority released in Q4 ($n = 347$; **Table 1**). In contrast, cod were mainly recaptured in Q1 ($n = 266$), but recaptures occurred in all quarters (**Table 1**). 13% and 87% of recaptures were tagged during the peak spawning and feeding seasons, respectively ($n = 73$; $n = 509$). In comparison, 32% and 68% of recaptures were caught during the peak spawning and feeding seasons, respectively ($n = 187$; $n = 395$).

Recaptures were mainly from the Sound ($n = 350$) and Kattegat ($n = 162$) with occasional recaptures south of the Sound during both the spawning and feeding seasons ($n = 44$ in SD 24, $n = 18$ in SD 25, $n = 1$ in SD 26 and 27, respectively; **Figure 2**). Days at liberty ranged from 18 to 1,151 days, and most cod were recaptured within one year (median = 210 days).

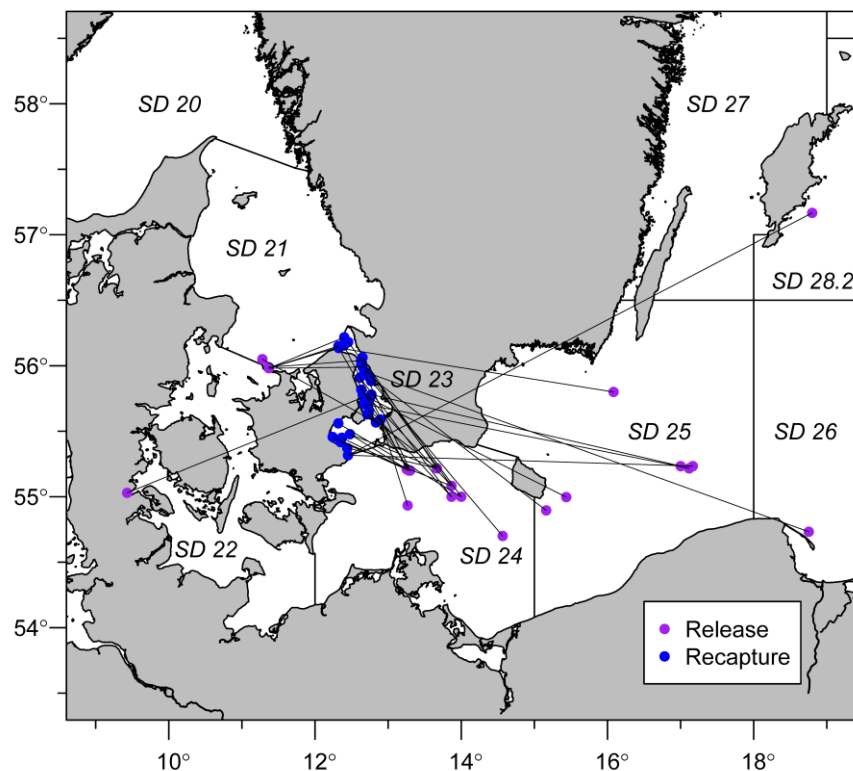


Figure 3. Recaptures in the Sound released in other areas. Recaptures originated from Kattegat ($n = 11$), the Belt Sea ($n = 1$), the Arkona Basin ($n = 20$), Bornholm Sea ($n = 6$), the south-eastern Baltic Sea ($n = 1$), and the Gotland Sea ($n = 1$).

Releases outside the Sound: Cod released outside the Sound and recaptured in the Sound consisted of only 0.24% of the full Baltic tagging database excluding the Sound releases ($n = 16,789$). These releases were from Kattegat ($n = 11$; 1.94% of 567 recaptures originating from

Kattegat), the Belt Sea ($n = 1$; 0.04% of 2,341 recaptures originating from the Belt Sea), the Arkona Basin ($n = 20$; 1.49% of 1,345 recaptures originating from the Arkona Basin), Bornholm Sea ($n = 6$; 0.19% of 3,174 recaptures originating from the Bornholm Sea), the south-eastern Baltic Sea ($n = 1$; 0.09% of 1,147 recaptures originating from the south-eastern Baltic Sea), and the Gotland Sea ($n = 1$; 0.09% of 1,132 recaptures originating from the Gotland Sea). This suggests the connectivity between the Sound and the Baltic is limited. Recaptures were generally medium sized when released, and recapture sizes ranged from 247 to 638 mm (median = 462.5 mm). Cod were recaptured evenly throughout the year with no apparent pattern (**Figure 3**). All cod released in Kattegat were released in January on the edge to the Belt Seas.

Fishing mortality. Fishing mortality (1970-1987) was very high for both stocks from age 2 and onwards (**Table S1**). While mortality seemed to decrease for age 2 over the years in the western Baltic cod stock, fishing mortality remained high in ages 3 and above. However, for the Kattegat stock, fishing mortality increased consistently over the years. Trawl effort was uneven but still high in most of Kattegat, while it was considerably lower in the Belt Seas and southern Baltic (**Figure 4**). In comparison, the gill net effort was highest in the southern Baltic but also considerable in all other areas aside from the Sound (**Figure 4**).

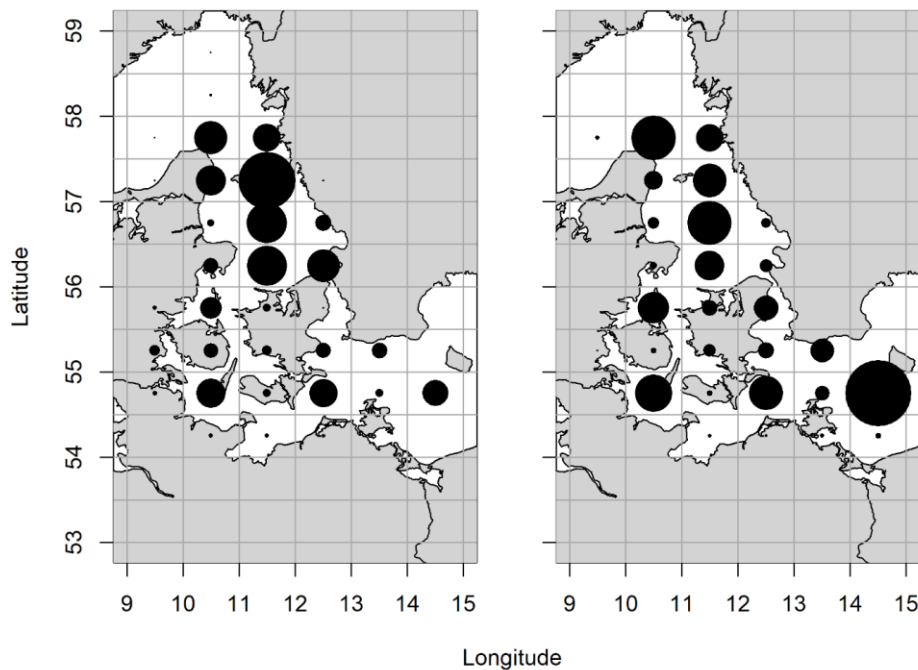


Figure 4. Relative Danish fisheries effort between 1987-1990 for cod-relevant trawl effort (left) and gill net effort (right).

Most cod were released in the northern part of the Sound (north: $n = 524$; south: $n = 54$). The recapture map showed that cod released south of the salinity divide were mainly recaptured in the northern Sound and slightly less in the Baltic while cod released north of the salinity division were mainly recaptured in the Sound and southern Kattegat (**Figure 5**). Days between release and

recapture ranged from 18 to 1,151 days for the northern population (median = 224.5 days), and 21 to 951 days for the southern population (median = 95 days).

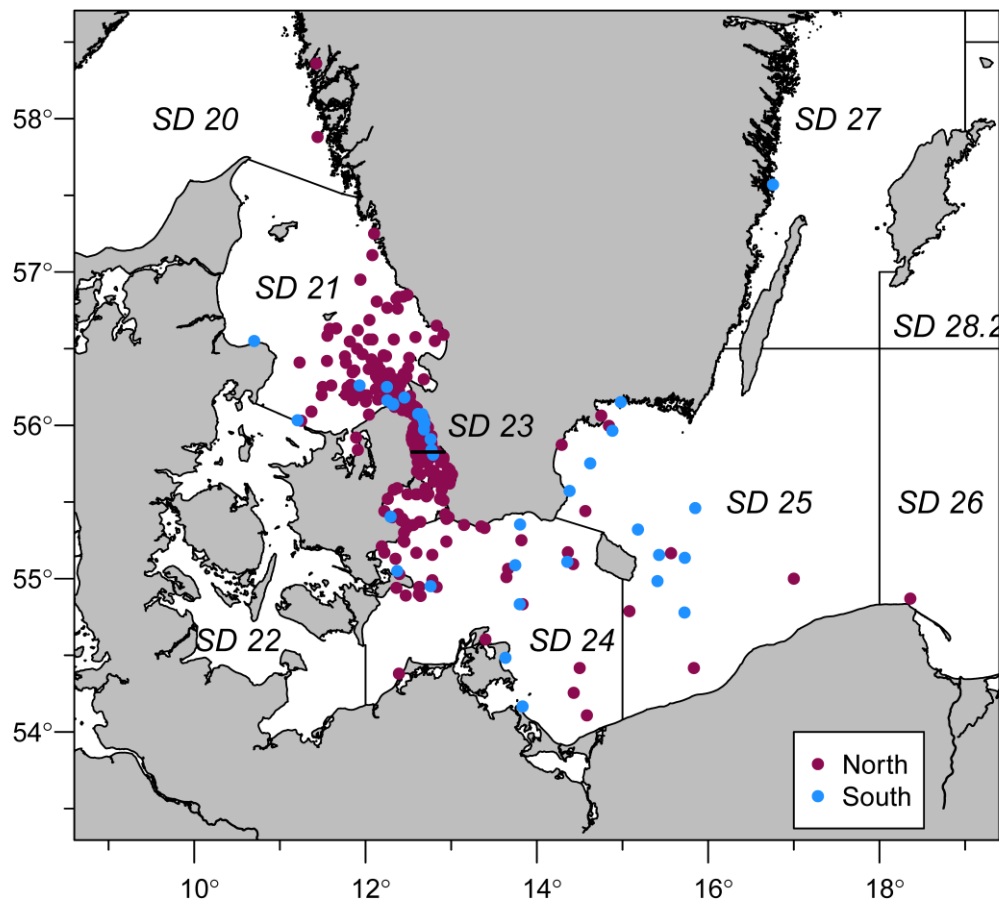


Figure 5. Recapture positions of cod tagged and released in the Sound, where the cod have been divided into a northern and a southern component depending on their release position. The black horizontal line indicates the geographical divide between the two areas. The division was based on topographic features in combination with the salinity gradient prevailing in the Sound (Bendtsen *et al.*, 2007).

The overall transition matrix suggested a divide into potential northern and southern stock components in the Sound (**Table 2**). Within a random week during the year, an individual cod tagged in the Sound but currently present in Kattegat was just as likely to stay as moving into the northern Sound (52% and 48%, respectively). However, a cod tagged in the Sound and currently present in the northern Sound was most likely to stay with some probability of movement towards Kattegat (66% and 29%, respectively). In comparison, it was very unlikely for the cod to move to the southern Sound (5%).

	Kattegat	Northern Sound	Southern Sound	Southern Baltic
Kattegat	0.52	0.48 (0.15, 0.83)		
Northern Sound	0.29 (0.11, 0.61)	0.66	0.05 (0.04, 0.15)	
Southern Sound		0.17 (0.09, 0.33)	0.75	0.08 (0.05, 0.18)
Southern Baltic			0.08 (0.04, 0.16)	0.92

Table 2. Overall transition matrix based on a salinity divide in the Sound showing the most likely area transitions. The table shows the probability of a cod tagged in the Sound moving from the current area (row) to a neighbouring area (column) within a random week during the year. Values in parentheses indicate confidence intervals for the estimated transition probabilities. Note that the diagonal values lack confidence intervals as they are not estimated but calculated by subtracting the estimated values from 1. The table is only based on releases in the Sound and gives an overall indication of connectivity.

An individual cod tagged in the Sound and currently present in the southern Sound was more likely to stay (75%), although with small probabilities of movement to the northern Sound or into the Baltic (17% and 8%, respectively). In contrast, a cod tagged in the Sound but currently present in the Baltic showed low probability for moving into the Sound (8%) and a high probability to stay in the Baltic (92%).

For the seasonally divided transition matrix, clear seasonal patterns were observed for Kattegat and the Sound (**Table 3**). In particular, the probability to leave the respective areas was similar for both areas, suggesting frequent movements between the two areas. Within a random week during the spawning season, a cod tagged in the Sound but currently present in Kattegat was most likely to stay in the Kattegat (75%), but still with a notable chance of moving into the Sound (25%). These patterns were similar for a cod tagged in and currently present in the Sound which would be more likely to stay (73%) than move to Kattegat (27%).

In comparison, within a random week during the feeding season, residency in each area was much more probable. While a cod tagged in the Sound but currently present in Kattegat would be more

likely to stay in the Kattegat (84%) than move to the Sound (16%) as in the spawning season, the probability to move to the Sound was lower. This was similar in the Sound where a cod originally tagged in the Sound was even more likely to stay than leave (96% vs. 4%) compared to the spawning season.

Spawning season	Kattegat	The Sound
Kattegat	0.75	0.25 (0.13, 0.41)
The Sound	0.27 (0.17, 0.40)	0.73
Feeding season		
Kattegat	0.84	0.16 (0.10, 0.25)
The Sound	0.04 (0.02, 0.07)	0.96

Table 3. Seasonal transition matrices between Kattegat and the Sound during peak spawning (January-February) and feeding season (March-December) showing the most likely area transitions. The table shows the probability of a cod tagged in the Sound moving from the current area (row) to a neighbouring area (column) within a random week during either the spawning or feeding season. Values in parentheses indicate confidence intervals for the estimated transition probabilities. The table is only based on releases in the Sound and gives an overall indication of connectivity.

Overall, these results suggest the existence of a population component in the northern Sound with frequent movements to and from Kattegat, predominantly in the spawning season. Additionally, there appears to be a relatively resident component in the southern Sound. Furthermore, cod in the Baltic appear to be relatively isolated from the Sound populations, with some connection to the southern Sound. The analyses of distances between release and recapture locations did not reveal any clear cyclical pattern related to spawning migrations (**Figure S1**).

3.3 Length distributions in cod in the Sound and growth across populations

The length distributions were similar between released cod from the tagging projects and cod collected in contemporary surveys (tagging: median = 44 cm, range = 18-110 cm; survey: median = 46 cm, range = 12-121 cm; **Figure S2**). This indicates that the population length distribution was well represented by the tagged individuals (**Figure S2**).

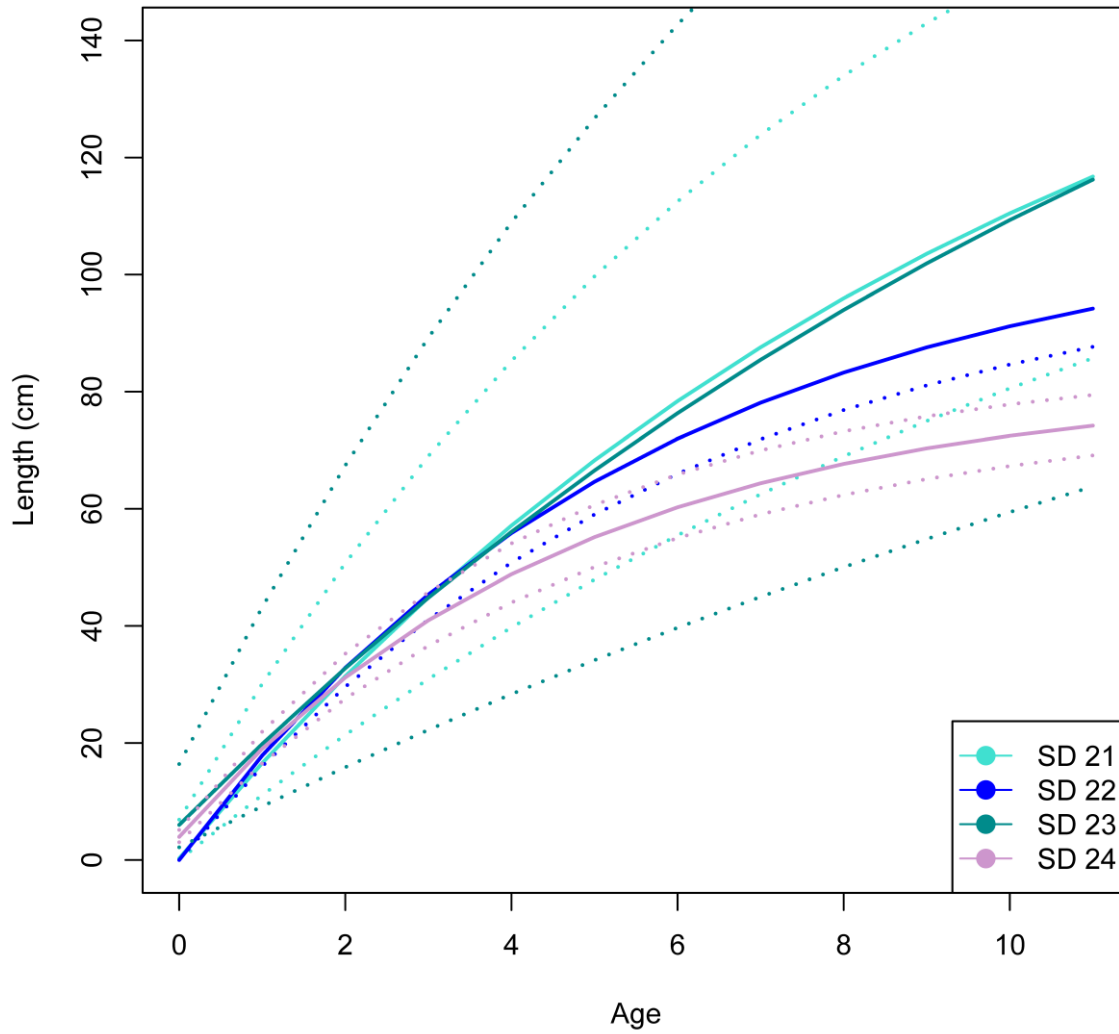


Figure 6. Von Bertalanffy growth curves for Kattegat and each SD in the western Baltic stock (SD 21, 22-24). The parameters for each growth curve were estimated from individual length-at-age data from Baltic International Trawl Surveys (BITS) and North Sea International Bottom Trawl Surveys (NS-IBTS) by using maximum likelihood estimation. Dotted lines show standard deviations. Note that the upper limit for SD 22 is not shown due to estimation issues. See Table 4 for parameter estimations and confidence intervals.

The von Bertalanffy growth curves showed higher growth rates in Kattegat and the Sound while the Belt Sea and Arkona Sea were characterized by lower sizes-at-age, although the estimates were generally characterized by high standard deviations (**Figure 6, S3-4**; see **Table 4** for the parameter estimations). Consequently, the likelihood ratio test also showed that the model with SD-specific parameters was significantly superior to the global model assuming non-SD-specific parameters (deviance = 2266, df = 12, p = 0), further supporting that growth is not equal across the four areas. Similarly, for the individual comparisons with the Sound, the likelihood ratio tests showed that there was a significant difference in growth between the Sound and the other SDs, indicating a certain degree of separation (Kattegat-Sound: deviance = 131, df = 4, p = 0; Belt Seas-Sound: deviance = 76, df = 4, p = ~0; Arkona Basin-Sound: deviance = 692, df = 4, p = 0).

Area	L_{∞} (cm)	K	t_0	σ
All data	119.85 (114.24, 125.74)	0.14 (0.13, 0.15)	0.18 (0.16, 0.20)	0.24 (0.24, 0.24)
Kattegat	179.53 (150.60, 214.02)	0.10 (0.08, 0.12)	0.02 (0, 0.28)	0.20 (0.19, 0.20)
Belt Seas	109.71 (104.30, 115.41)	0.18 (0.17, 0.19)	$1e^{-09}$ *	0.20 (0.20, 0.21)
The Sound	212.35 (155.20, 290.55)	0.07 (0.05, 0.10)	0.41 (0.30, 0.56)	0.19 (0.18, 0.20)
Arkona Basin	81.32 (77.31, 85.53)	0.22 (0.20, 0.23)	0.23 (0.20, 0.26)	0.27 (0.26, 0.27)

Table 4. Estimates of von Bertalanffy growth parameters for all data combined, and Kattegat, the Belt Sea, the Sound, and Arkona Basin. Values in parentheses indicate confidence intervals for the estimate. * = missing standard deviations due to poor estimate. See Figure S3-4 for growth curves.

4. Discussion

The main objective of this study was to assess whether cod in the Sound is indeed a stock component of the western Baltic cod stock, or alternatively, whether it can be considered an isolated stock component, or is connected to the Kattegat stock. Furthermore, we aimed to clarify the complex connectivity patterns within the Sound, including any seasonal movements between the Sound and Kattegat. To do this, we compiled historical tagging data which has been previously used in individual studies (e.g., see Berner 1967, 1981, Otterlind 1985, Aro 1989, Bagge & Thurow 1994). Overall, our results indicated a relatively high degree of movement between Kattegat and the Sound, whereas movement between the Sound and the Baltic appeared to be less pronounced. The seasonally divided transition matrix suggested that connectivity between Kattegat and the Sound was greatest during the spawning season, supporting the notion of a continuous stretch of spawning area transecting the border between the Sound and Kattegat. Furthermore, our results suggested some degree of disconnection between the southern and northern part of the Sound, as the exchange of cod across the salinity divide used to split the Sound into a northern and southern area was less than the exchange across the Kattegat-Sound border.

In earlier studies, the level of connectivity between the Sound and the remainder of the Baltic has not been clearly resolved. One study utilizing genetic analyses reported a clear genetic differentiation between cod in the Sound and the Arkona Basin (Nielsen *et al.*, 2003), but no differentiation between the Sound and the Belt Sea. However, differences between the Sound and the Belt Sea were found in another study (Moth-Poulsen, 1982). In comparison, our study suggests relatively low connectivity between the Sound and the remainder of the Baltic, and the same patterns emerge from previous tagging studies which generally relied on recapture maps and mapping trajectories (Berner, 1967, 1981; Otterlind, 1985; Aro, 1989; Bagge and Thurow, 1994; Svedäng *et al.*, 2010). Indeed, it is more likely that movement from the Baltic to Kattegat occurs through the Belt Seas instead of the Sound (Bagge, 1969; Berner, 1971a, 1971b, 1974), which may explain the low recaptures from the Belt Sea as shown by the historical tagging data. Some level of isolation between the Sound and the remainder of the western Baltic is also supported by differences in growth, as shown in the present study (data from 2017-2021) as well as in Svedäng & Hornborg (2017) where data from 1991-2016 was utilized. However, it should be emphasized that the Arkona Basin is a mixing area where the relatively slow growing eastern Baltic cod can be found, which complicates comparisons of growth in this area (McQueen *et al.*, 2020), and presumably results in an underestimation of growth.

The connectivity between Kattegat and the Sound is well documented in the literature and is greatly related to spawning migrations (e.g., see Aro 1989, Bagge *et al.* 1994, Svedäng *et al.* 2010). Similar patterns appear from our results where we used a more advanced analytical approach, and it is apparent that there is some mixing between cod in the Sound and cod in Kattegat. However, the spatial-temporal extent of this mixing appears to be largely confined to the northern part of the Sound and the south-eastern Kattegat, in particular during the spawning season. In contrast,

movement between the two areas appears slightly more limited during the feeding season which suggests separate feeding grounds. Similarly, we found differences in growth between the Kattegat and the Sound populations. This would suggest separate stocks, although the uncertainty was relatively high, most likely due to the combination of several age groups.

However, it is difficult to ascertain whether this means that the stocks are separate despite growth differences between the two areas. As growth in fish is influenced by fishing pressure (Wang *et al.*, 2021), the differences in fishing gear employed will select for different sizes and affect the overall size distributions due to the Rosa Lee phenomenon where faster growing individuals are caught earlier. It is common for larger-sized individuals to become rare in stocks subjected to high fishing pressure (Barnett *et al.*, 2017). This is the case for the Kattegat stock which has previously been subjected to an intensive mixed bottom trawl fishery (Eliassen, 2014) resulting in a truncated size distribution (Cardinale and Svedäng, 2004). While there is currently no targeted fishery in Kattegat, cod are still caught as bycatch and discarded at high rates, and the stock has yet to recover (ICES, 2020). In comparison, the most common fishing gear type in the Sound are gill nets which select for more average sizes compared to juveniles and large adults (Anonymous, 2007). Furthermore, recreational fisheries and other passive gear-types are also common in the Sound. This difference in size distributions caused by fishing gear variability makes it difficult to compare the two stocks using growth as viable metric.

Additionally, the overall lack of genetic differentiation between Kattegat and the Sound would suggest a singular stock. Several previous genetic analyses have relied on microsatellites (e.g., see Nielsen *et al.* 2003, Svedäng *et al.* 2010a) but it is possible that microsatellites may not be sensitive enough to detect differences. This is exemplified by single nucleotide polymorphism (SNPs) which have shown a clear genetic differentiation between adults from the North Sea, and the Kattegat/Sound grouped (Svedäng *et al.*, 2019). In contrast, no genetic differences have been found when using microsatellites (Nielsen *et al.*, 2003). Berg *et al.* (2015) categorized SNPs as either neutral or outlier, with neutral indicating loci not under selection and outlier indicating physically unlinked SNPs, and found no genetic differentiation between Kattegat and the Sound using the full and neutral datasets, while analyses of the outliers showed some genetic differentiation between the two stocks.

The spatially resolved movement patterns suggested a division of cod in the Sound into a northern and southern component based on a salinity and topographic divide. The salinity division revealed relatively well-defined geographic patterns in movements, where the north and south appeared to be separate components. Due to the importance of spawning migrations for stock structuring, these spatially distinct patterns within the Sound may be due to natal homing (Svedäng *et al.*, 2007). This may be due to the northern component potentially spawning in the northern part of the Sound and southern part of Kattegat, and the southern component in the central/southern part of the Sound which coincides with the location of known spawning grounds (Hüssy, 2011). Furthermore, it may be due to the seasonal depth preferences exhibited by the cod (Funk *et al.*, 2020). However, it is

possible that the salinity divide is not an adequate division. While the two Baltic cod stock are adapted to brackish water, it has been shown that both eastern and western Baltic cod are adapted to different salinity levels (Kijewska *et al.*, 2016) but these salinity differences are much greater than in the Sound (e.g., see Bendtsen *et al.* 2007). This may indicate that the salinity gradient in the Sound is not sharp enough to drive a potential population division and that the observed patterns merely coincide with the salinity divide. In addition, seasonal inflows are likely to change the strength and position of the salinity gradient, suggesting further study if the salinity divide is suitable. However, otolith microchemistry analyses have shown a similar structuring based on a slightly different division of the Sound where activity appears to be high in the northern Sound and southern Kattegat with a separate component in the central and southern Sound (Svedäng *et al.*, 2010), and it is possible that differences in topography instead of salinity may drive the observed differences in this study. We suggest further studies are undertaken to study potential sub-population structuring in the Sound utilizing genetic tools.

Overall, the combination of the results of the present study and previous studies utilizing analyses on otoliths (Svedäng *et al.*, 2010), tagging (Otterlind, 1985; Aro, 1989; Bagge and Thurow, 1994; Svedäng *et al.*, 2010), and genetics (Moth-Poulsen, 1982; Nielsen *et al.*, 2003; Berg *et al.*, 2015) suggests high complexity within the stock component structuring and connectivity in Sound cod. However, it should be noted that interpretation of the historic recapture-data and the resulting connectivity matrix is made difficult because of the lack of information about release numbers and spatial variation of fishing effort during this period, including the high fishing pressure. This is exemplified by high fishing effort in the south of Kattegat which may explain the high number of recaptures in this area, and thus it is likely that the true movement patterns were not captured as this study relied on recapture data. Additionally, the transition matrix approach relies greatly on the quality and quantity of the data available. As such, the transition matrix gives the most probable area transitions based on all the data, but it also assumes that all cod in the database are Sound cod which may not be the case. As stock affiliation depends on where the cod spawn, it is possible that Kattegat cod or southern Baltic cod have been included in the analyses. As an example, this could explain the high probability to remain in the southern Baltic as suggested by the transition matrix, and the lack of data for inclusion in a seasonal matrix. In addition, the transition matrix relies on recapture patterns, and so high fishing pressure and spatio-temporal variations in fishing effort will undoubtedly affect the results. It is thus unclear if Sound cod actually move further north and south of the Sound than the tagging results suggest but are likely to be caught due to the high risk of being caught near the edges of the Sound. In light of this, it is important to view the transition matrices as indications of overall movement tendencies which should be studied further using genetic tools.

5. Conclusion

Our results suggest the Sound stock component is to some degree connected with the Kattegat cod stock primarily during the spawning season, but is relatively isolated from the remaining western Baltic cod stock components. The analyses utilizing the historical data suggest high complexity in structure within the Sound cod stock component with a relatively resident southern component, and a northern component with frequent movements into Kattegat. These results may have implications for future stock assessments, and we suggest future studies focus on the connection between Kattegat, the Baltic, and the Sound using genetics in addition to tagging.

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7. Author contributions

K.H., M.M., S.H., M.C., and U.K. participated in the TABACOD project which produced the Baltic tagging database for the analyses. R.B.C.L. contributed to the tagging database and carried out the data analyses. A.N. assisted in the data analyses, and M.v.D. produced the figure showing the spatial effort. R.B.C.L. and K.H. drafted the manuscript. H.J.O. and M.v.D. assisted in conceptualizing the manuscript. All authors commented on the manuscript and gave final approval for publication.

8. References

- Anonymous. 1932. Kommissionen med Danmark angående fiskeriforhallandena i det till Sverige och Danmark gransande farvattnen.
- Anonymous. 2007. Report of the Baltic Fisheries Assessment Working Group.
- Aro, E. 1989. A review of fish migration patterns in the Baltic. *Rap. Proc.-Verb. Ré. Cons. Int. Explor. Mer*, 190: 72–96.
- Bagge, O. 1969. Preliminary results of the cod-tagging experiments in the Western Baltic 1969. ICES Document CM.
- Bagge, O., Thurow, F., Steffensen, E., and Bay, J. 1994. The Baltic cod. *Dana*.
- Bagge, O., and Thurow, F. 1994. The Baltic cod stock, fluctuations and possible causes. *In* ICES Marine Science Symposia, pp. 254–268. International Council for the Exploration of the Sea, Copenhagen.
- Barnett, L. A. K., Branch, T. A., Ranasinghe, R. A., and Essington, T. E. 2017. Old-Growth Fishes Become Scarce under Fishing. *Current Biology*, 27: 2843-2848.e2. Cell Press.
- Begg, G. A., and Waldman, J. R. 1999. An holistic approach to fish stock identification. *Fisheries Research*, 43: 35–44. Elsevier.
- Bendtsen, J., Söderkvist, J., Dahl, K., Hansen, J. L. S., Reker, J., and Andersson, Å. 2007. Model simulations of blue corridors in the Baltic Sea.
- Berg, P. R., Jentoft, S., Star, B., Ring, K. H., Knutsen, H., Lien, S., Jakobsen, K. S., *et al.* 2015. Adaptation to Low Salinity Promotes Genomic Divergence in Atlantic Cod (*Gadus morhua* L.). *Genome Biology and Evolution*, 7: 1644–1663. Oxford Academic.
- Berner, M. 1967. Results of cod taggings in the western and central Baltic in the period 1962–1965. ICES Document CM.
- Berner, M. 1971a. Ergebnisse der Dorschmarkierungen des Jahres 1968 in der Bornholm- und Arkonasee. *Fischerei-Forschung Wissenschaftliche Schriftenreihe*, 9: 15–20.
- Berner, M. 1971b. Ergebnisse der Dorschmarkierungen des Jahres 1969 in der Mecklenburger Bucht und der Arkonasee. *Fischerei-Forschung Wissenschaftliche Schriftenreihe*, 9: 21–27.
- Berner, M. 1974. Some results of cod tagging experiments of the GDR in the Baltic 1968-1971. ICES Document CM.
- Berner, M. 1981. Dislocation parameters of tagging experiments on cod in the Baltic (Sub-divisions 22–25) from 1959–1975. ICES Document CM.
- Cardinale, M., and Svedäng, H. 2004. Modelling recruitment and abundance of Atlantic cod, *Gadus morhua*, in the eastern Skagerrak-Kattegat (North Sea): Evidence of severe depletion due to a prolonged period of high fishing pressure. *Fisheries Research*.
- Eero, M., Hemmer-Hansen, J., and Hüßy, K. 2014. Implications of stock recovery for a neighbouring management unit: experience from the Baltic cod. *ICES Journal of Marine*

- Science, 71: 1458–1466. Oxford Academic.
- Eliassen, S. Q. 2014. Cod avoidance by area regulations in Kattegat – experiences for the implementation of a discard ban in the EU. *Marine Policy*, 45: 108–113. Pergamon.
- Fernö, A., Jørgensen, T., Løkkeborg, S., Fernö, A., and Winger, P. D. 2011. Variable swimming speeds in individual Atlantic cod (*Gadus morhua* L.) determined by high-resolution acoustic tracking. *Marine Biology Research*, 7: 310–313. Taylor & Francis Group .
- Funk, S., Krumme, U., Temming, A., and Möllmann, C. 2020. Gillnet fishers' knowledge reveals seasonality in depth and habitat use of cod (*Gadus morhua*) in the Western Baltic Sea. *ICES Journal of Marine Science*, 77: 1816–1829. Oxford Academic.
- Hemmer-Hansen, J., Hüsey, K., Baktoft, H., Huwer, B., Bekkevold, D., Haslob, H., Herrmann, J. P., *et al.* 2019. Genetic analyses reveal complex dynamics within a marine fish management area. *Evolutionary Applications*, 12: 830–844. Wiley-Blackwell.
- Hemmer-Hansen, J., Hüsey, K., Vinther, M., Albertsen, C., Storr-Paulsen, M., and Eero, M. 2020. Sustainable management of Kattegat cod; better know-ledge of stock components and migration. DTU Aqua Report, 357–2020.
- Hilborn, R., and Walters, C. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman & Hall, New York.
- Hüsey, K. 2011. Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. *ICES Journal of Marine Science*, 68: 1459–1471.
- Hüsey, K., Albertsen, C. M., Hemmer-Hansen, J., Vinther, M., Serre, S. H., Thomsen, T. B., and Eero, M. 2021. Where do you come from, where do you go: Early life stage drift and migrations of cod inferred from otolith microchemistry and genetic population assignment. *Canadian Journal of Fisheries and Aquatic Sciences*.
- ICES. 2014. Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 3–10 April 2014 ICES HQ.
- ICES. 2020. Cod (*Gadus morhua*) in Subdivision 21 (Kattegat). Report of the ICES Advisory Committee.
- ICES. 2021. Working Group for the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). ICES Scientific Reports.
- ICES. 2022. Baltic Fisheries Assessment Working Group (WGBFAS). ICES Scientific Reports, 4: 659.
- Jørgensen, O. A., Storr-Paulsen, M., Ringdahl, K., Lövgren, J., Gröhsler, T., Oberst, R., Schaber, M., *et al.* 2011. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). ICES.
- Kampstra, P. 2008. Beanplot: A boxplot alternative for visual comparison of distributions. *Journal of statistical software*, 28: 1–9.
- Kijewska, A., Kalamarz-Kubiak, H., Arciszewski, B., Guellard, T., Petereit, C., and Wenne, R. 2016. Adaptation to salinity in Atlantic cod from different regions of the Baltic Sea. *Journal of Experimental Marine Biology and Ecology*, 478: 62–67. Elsevier.

- Lindegren, M., Waldo, S., Nilsson, P. A., Svedäng, H., and Persson, A. 2013. Towards sustainable fisheries of the Öresund cod (*Gadus morhua*) through sub-stock-specific assessment and management recommendations. *ICES Journal of Marine Science*, 70: 1140–1150. Oxford Academic.
- Løkkeborg, S., and Fernö, A. 1999. Diel activity pattern and food search behaviour in cod, *Gadus morhua*. *Environmental Biology of Fishes* 1999 54:3, 54: 345–353. Springer.
- Lundgreen, R. B. C., Nielsen, A., Krüger-Johnsen, M., Righton, D., Mion, M., Radtke, K., Plikshs, M., *et al.* 2022. Examining fish movement in terms of advection or diffusion: a case study of northeastern Atlantic cod. *Marine Ecology Progress Series*, 691: 115–129.
- McQueen, K., Casini, M., Dolk, B., Haase, S., Hemmer-Hansen, J., Hilvarsson, A., Hüsey, K., *et al.* 2020. Regional and stock-specific differences in contemporary growth of Baltic cod revealed through tag-recapture data. *ICES Journal of Marine Science*, 77: 2078–2088.
- Mion, M., Hilvarsson, A., Hüsey, K., Krumme, U., Krüger-Johnsen, M., McQueen, K., Mohamed, E., *et al.* 2020. Historical growth of Eastern Baltic cod (*Gadus morhua*): setting a baseline with international tagging data. *Fisheries Research*, 223: 105442.
- Mion M, Griffiths C, Bartolino V, Haase S, Hilvarsson A, Hüsey K, Krüger-Johnsen M, Krumme U, Lundgreen R, Lövgren J, McQueen K, Plikshs M, Radtke K, Raitaniemi J, Casini M (2022) New perspectives on Eastern Baltic cod movement patterns from historical and contemporary tagging data. *Mar Ecol Prog Ser* 689:109–126.
- Moth-Poulsen, T. 1982. Genetic variation of cod from the Danish Sound: Interrelations of stocks from adjacent waters. *Danmarks Fiskeri-og Havundersøgelser*: 1–19.
- Nielsen, E. E., Hansen, M. M., Ruzzante, D. E., Meldrup, D., and Grønkjær, P. 2003. Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. *Molecular Ecology*.
- Orio, A., Karpushevskaya, A., Nielsen, A., Sundelöf, A., Berg, C. W., Albertsen, C. M., Stralka, C., *et al.* 2019. Benchmark Workshop on Baltic Cod Stocks (WKBALTCOD2). *ICES Scientific Report*, 1.
- Otterlind, G. 1985. Cod migration and transplantation experiments in the Baltic. *Journal of Applied Ichthyology*, 1: 3–16. John Wiley & Sons, Ltd.
- Righton, D., Quayle, V. A., Hetherington, S., and Burt, G. 2007. Movements and distribution of cod (*Gadus morhua*) in the southern North Sea and English Channel: Results from conventional and electronic tagging experiments. *Journal of the Marine Biological Association of the United Kingdom*, 87: 599–613. Cambridge University Press.
- Schade, F. M., Weist, P., and Krumme, U. 2019. Evaluation of four stock discrimination methods to assign individuals from mixed-stock fisheries using genetically validated baseline samples. *Marine Ecology Progress Series*, 627: 125–139. Inter-Research.
- Svedäng, H., Righton, D., and Jonsson, P. 2007. Migratory behaviour of Atlantic cod *Gadus morhua*: Natal homing is the prime stock-separating mechanism. *Marine Ecology Progress Series*.
- Svedäng, H., André, C., Jonsson, P., Elfman, M., and Limburg, K. E. 2010. Migratory behaviour and otolith chemistry suggest fine-scale sub-population structure within a genetically

- homogenous Atlantic Cod population. *Environmental Biology of Fishes*, 89: 383–397.
- Svedäng, H., and Hornborg, S. 2017. Historic changes in length distributions of three Baltic cod (*Gadus morhua*) stocks: Evidence of growth retardation. *Ecology and Evolution*, 7: 6089. Wiley-Blackwell.
- Svedäng, H., Barth, J. M. I., Svenson, A., Jonsson, P., Jentoft, S., Knutsen, H., and André, C. 2019. Local cod (*Gadus morhua*) revealed by egg surveys and population genetic analysis after longstanding depletion on the Swedish Skagerrak coast. *ICES Journal of Marine Science*, 76: 418–429.
- van der Kooij, J., Righton, D., Strand, E., Michalsen, K., Thorsteinsson, V., Svedäng, H., Neat, F. C., *et al.* 2007. Life under pressure: insights from electronic data-storage tags into cod swimbladder function. *ICES Journal of Marine Science*, 64: 1293–1301. Oxford Academic.
- van Deurs, M., Persson, A., Lindegren, M., Jacobsen, C., Neuenfeldt, S., Jørgensen, C., and Nilsson, P. A. 2016. Marine ecosystem connectivity mediated by migrant–resident interactions and the concomitant cross-system flux of lipids. *Ecology and Evolution*, 6: 4076–4087. John Wiley & Sons, Ltd.
- van Deurs, M., Persson, A., Nilsson, P. A., and Jørgensen, C. 2022. Fish resist temptation from junk food: state-dependent diet choice in reproductive Atlantic cod *Gadus morhua* facing seasonal fluxes of lipid-rich prey. *Oikos*. John Wiley & Sons, Ltd.
- Vitale, F., Cardinale, M., and Svedäng, H. 2005. Evaluation of the temporal development of the ovaries in *Gadus morhua* from the Sound and Kattegat, North Sea. *Journal of fish biology*, 67: 669–683.
- Vitale, F., Börjesson, P., Svedäng, H., and Casini, M. 2008. The spatial distribution of cod (*Gadus morhua* L.) spawning grounds in the Kattegat, eastern North Sea. *Fisheries Research*.
- Wang, K., Zhang, C., Sun, M., Xu, B., Ji, Y., Xue, Y., and Ren, Y. 2021. Fishing pressure and lifespan affect the estimation of growth parameters using ELEFAN. *Fisheries Research*, 238: 105903. Elsevier.
- Weist, P., Schade, F. M., Damerou, M., Barth, J. M. I., Dierking, J., André, C., Petereit, C., *et al.* 2019. Assessing SNP-markers to study population mixing and ecological adaptation in Baltic cod. *PLOS ONE*, 14: e0218127. Public Library of Science.

Chapter IV

Paper III:

*Simulating movement patterns in Baltic cod
(Gadus morhua) in response to historical changes
in environmental parameters*



Simulating movement patterns in Baltic cod (*Gadus morhua*) in response to historical changes in environmental parameters

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1. Abstract

Globally, Atlantic cod populations are threatened by climate change due to several factors, such as increasing hypoxia, temperatures, and freshening of salt water. It is thus important to understand how cod movement is affected by the changing environment to predict how they will respond to climate change. We developed a toy model (Simulating Baltic Cod; SimBaCod) to illustrate how Baltic cod might have moved in response to historical environmental parameters (oxygen, temperature, salinity) and comparing them to contemporary recapture distributions from conventional tagging data for qualitative validation of distribution patterns. We found that the movement patterns for cod in the Kattegat and Bornholm Sea could be relatively well reconstructed from an overall habitat index and oxygen index. In contrast, the model was unable to reconstruct the movement patterns in the Gotland Sea and Belt Sea which were characterized by more southern and resident behaviour, respectively, than predicted. This is likely due to strong spawning-related behaviour in the Gotland Sea, and the cod in the Belt Sea case study being a resident fjord ecotype. These initial results demonstrate the potential importance of the environment in shaping cod distributions, and we propose that a more advanced model is developed.

2. Introduction

The Baltic Sea has changed greatly in the past 100 years. Measurements of salinity, temperature, and dissolved oxygen levels have been taken annually since the late 1890s, offering a highly detailed overview of the changes in the conditions in the Baltic Sea (Fonselius & Valderrama 2003). Increasing freshwater flow has lowered mean salinity in the Baltic Sea since the 1980s (Winsor et al. 2001), and a rise in both surface and bottom temperatures has also been observed (Fonselius & Valderrama 2003, Stramska & Białogrodzka 2015). Furthermore, nutrient loads increased

between 1950-1980 but started declining afterwards although additional efforts are required to improve water quality (Nehring & Matthäus 1991, Gustafsson et al. 2012). In addition, the combination of higher temperatures and increased nutrient loads have caused an increase in the extent of hypoxic areas which have increased since the 1960s, particularly in the coastal zone (Diaz & Rosenberg 2008, Conley et al. 2011, Savchuk 2013, Carstensen et al. 2014). These changes have potentially had a great impact on the fauna (see Viitasalo & Bonsdorff 2022 and references therein), such as prolonged growing seasons in phytoplankton (Wasmund et al. 2019), shifts from mainly complex to more simple functional groups in the zooplankton (Jansson et al. 2020), and various effects on forage fish such as sprat (*Sprattus sprattus*) and herring (*Clupea harengus*; see Peltonen et al. 2012 and references therein).

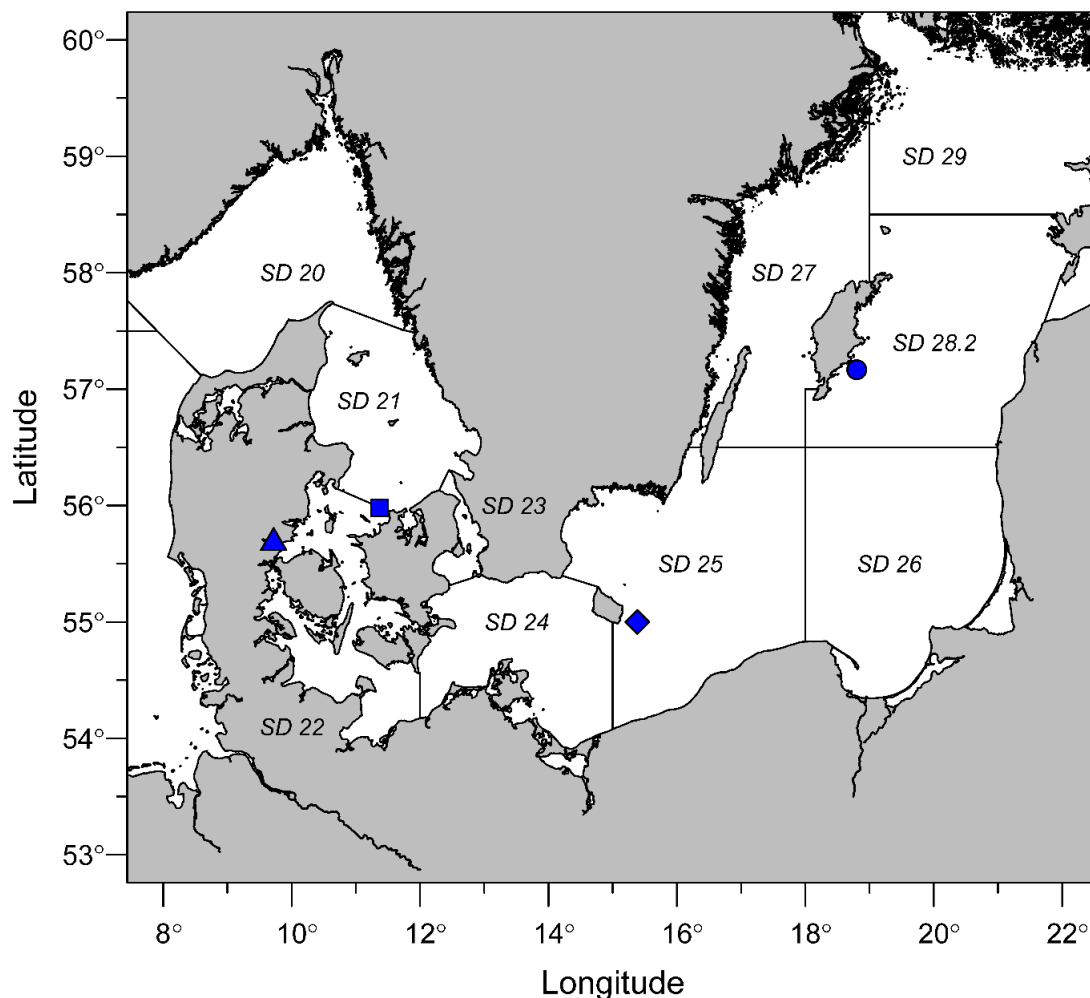


Figure 1. Map of the Baltic Sea showing ICES subdivisions and release positions for the four case studies. Relevant ICES subdivisions include SD 20 (Skagerrak), SD 21 (Kattegat), SD 22 (Belt Sea), SD 23 (the Sound), SD 24 (Arkona Sea), SD 25 (Bornholm Sea), SD 26 (south-eastern Baltic Sea), SD 27 (the Western Gotland Basin), and SD 28.2 (Gotland Sea). ● = case study 1. ■ = case study 2. ◆ = case study 3. ▲ = case study 4.

Another species greatly impacted by climate change is the Baltic cod (*Gadus morhua*) which historically was one of the commercially important species in the Baltic Sea. The Baltic cod is generally divided into the Kattegat stock (ICES subdivision (SD) 21), the western Baltic cod stock (SD 22-24), and the eastern Baltic cod stock (SD 24-32; see **Figure 1**). The Kattegat and western Baltic cod experience markedly different environments compared to the eastern Baltic cod, as the Baltic Sea is characterized by very different hydrological conditions (Bendtsen et al. 2007). This is mainly due to more saline water coming in from the North Sea which is continuously diluted by fresher water caused by river outflows and precipitation, creating a strong salinity gradient from west to east. The Baltic cod is in an overall poor shape, partially due to high fishing pressure for years (ICES 2021a b c), and the further stresses caused by changes in the environment has made recovery difficult (Eero et al. 2015). The decreasing oxygen content has lowered the extent of favourable areas for juveniles in the eastern Baltic (Hinrichsen et al. 2011), and the deep basins designated as important spawning grounds for the eastern Baltic cod are now suffering from hypoxic conditions (Carstensen et al. 2014, Hinrichsen et al. 2016). In addition, declining salinity, increasing warming, and acidification have been suggested to potentially cause collapses in the Baltic cod stocks even at low fishing pressure as these stressors affect the cod at different life stages (Lindgren et al. 2010, Voss et al. 2019).

It is likely that the changing conditions since the 1950s may have altered spatial distributions and movement patterns in Baltic cod, as Baltic cod stock components have been found to have different movement patterns through time (Lundgreen et al. 2022a). Cod, herring, and capelin (*Mallotus villosus*) residing in the waters around Greenland and Iceland moved north in response to the warming event in 1920-1940 (Rose 2005). As water temperatures decreased around Iceland in the 1960s, the cod stopped using the northern areas for spawning and returned to the previous spawning patterns (Drinkwater 2005). In addition, laboratory experiments have shown avoidance of suboptimal oxygen and salinity conditions (Claireaux et al. 1995) which suggests cod may be distributed according to optimal environmental conditions. As the Baltic Sea region has been projected to change greatly by 2100 (e.g., see Christensen et al. 2022, Meier et al. 2022), it is thus important to examine how cod may respond to changes in conditions and potentially predict future scenarios if the conditions continue to change.

One way is the utilization of toy models. Toy models are intentionally simple models with few details intended to examine specific mechanisms in isolated scenarios. Through simulations of cod where movement is governed by changes in the environment, a toy model can be used to examine the relationship between cod movements and changes in hydrography. By comparing the results of the simulations to real-life recapture patterns, it can be inferred if cod move in response to changes in habitat quality. This can then be used further to potentially develop more advanced models that can incorporate other potentially important factors, such as prey densities, food web dynamics, and human pressures. Examples of advanced models incorporating movement include the spatial ecosystem and population dynamics model (SEAPODYM; e.g., see Lehodey et al. 2008, Senina et

al. 2020), and the Individual-based Kinesis, Advection and Movement of Ocean ANimAls model (Ikamoana, Phillips et al. 2018).

The main aim of this study was to apply a toy model (Simulating Baltic Cod; SimBaCod) to study movement patterns in Baltic cod in response to changes in habitat quality between 1950-2020 based on temperature, oxygen, and salinity. Four case studies were chosen (Gotland Sea, Kattegat, Bornholm Sea, Belt Sea) to be recreated by the simulation model and were subsequently used to validate the assumptions of the model. We hypothesized that cod would, based on case-specific density dependent responses to environmental parameters, follow optimal gradients and avoid suboptimal conditions. Habitat preferences were determined by comparing recapture depths of cod from trawl surveys between 1991-2022 to experienced environmental conditions as suggested by the hydrodynamic model.

3. Methods

3.1 Case studies

Historical tagging data was compiled from a large Baltic cod tagging database and included Danish and Swedish tagging projects (Mion et al. 2020, Lundgreen et al. 2022a, Mion et al. 2022). The data used in this study included information on release and recapture time and location. In addition, recapture depth intervals were available but only for a few individual fish. Tagged cod recaptured ≤ 15 days at liberty (DAL) were removed as they were unlikely to have recovered from the tagging procedure (van der Kooij et al. 2007). Similarly, to ensure a good balance between number of recaptures and optimal simulation times, tagged cod with very high DALs were removed so the simulations would not run for exceedingly long times when only a few cod were caught within intervals of 100 days.

Four case studies were chosen to model the simulations on based on relatively high numbers of recaptures to ensure clear recapture patterns for comparison purposes with the simulations:

- **Case study 1** included releases on the 4th of December 1968 in SD 28.2 (Gotland Sea; $n = 196$; $n = 102$ after data screening). The tag type used was Lea, and the mean release length was 345 mm. The highest DAL was 425. The cod were released at the southern part of Gotland (**Figure 1-2**).
- **Case study 2** included releases on the 9th of January 1978 in SD 21 (Kattegat; $n = 193$; $n = 141$ after data screening). The tag type used was T-bars, and the mean release length was 420 mm. The highest DAL was 303. The cod were released near the edge between Kattegat and the Belt Sea as defined by the ICES SDs (**Figure 1-2**).
- **Case study 3** included releases on the 8th of May 1969 in SD 25 (Bornholm Sea; $n = 198$; $n = 120$ after data screening). Both Lea and T-bar tags were used, and the mean release length was 409 mm. The highest DAL was 302. The cod were released closed to the island of Bornholm (**Figure 1-2**).
- **Case study 4** included releases on the 3rd of November 1983 in SD 22 (Belt Sea; $n = 138$; $n = 83$ after data screening). The tag type used was red alkathene with monofil nylon, and the mean release length was 319 mm. The highest DAL was 301. The cod were released in Vejle Fjord (**Figure 1-2**).

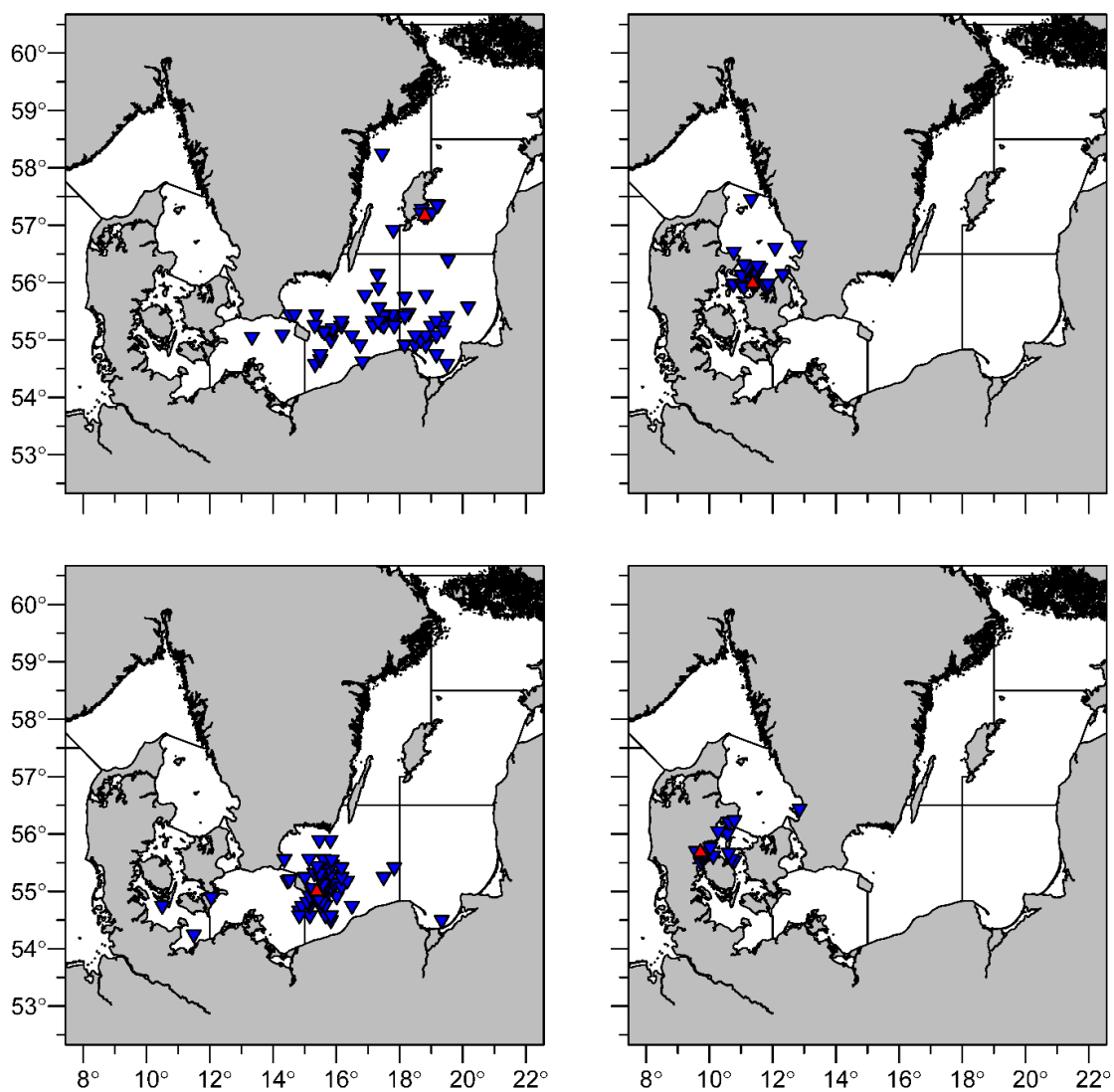


Figure 2. Historical recapture maps for each of the four case studies. Top left = Case study 1 (Gotland Sea). Top right = Case study 2 (Kattegat). Bottom left = Case study 3 (Bornholm Sea). Bottom right = Case study 4 (Belt Sea). ▲ = release position. ▼ = recapture position.

3.2 Hydrodynamic modelling

The hydrodynamic model used here is a coupled sea ice-ocean model of the entire Baltic Sea including Kattegat and Skagerrak (BSIOM, Lehmann et al. 2014). The performance and applicability of BSIOM has been demonstrated in a number of publications (e.g. Lennartz et al. 2014, Hinrichsen et al. 2016, 2017). The hydrodynamic model has a horizontal resolution of 2.5 km with 60 vertical levels of 3 m thickness down to 100 m depth. To the maximum model depth (250 m) the thickness of vertical levels increases to 6 m. The model domain includes the entire Baltic Sea including the Belt Sea, Kattegat as well as the Skagerrak. The hydrodynamic model is realistically forced using the ERA5 global re-analysis in the preliminary extension version back to 1950 (Bell et al. 2021), with a 3-hourly temporal and approximately 50 km spatial resolution, respectively. The forcing data were interpolated on the model grid. They include surface air pressure, precipitation, cloudiness, and air- and dew point temperatures at 2 m height from sea surface. Wind speed and wind direction at 10 m height from sea surface were calculated from geostrophic winds with respect to different degrees of roughness on the open sea and off the coast (Bumke et al. 1998). BSIOM forcing functions, such as wind stress, radiation and heat fluxes were calculated according to Rudolph (2006). Additionally, river runoff was prescribed from a monthly mean runoff data set (Kronsell & Andersson 2012). At the western boundary, a simplified North Sea basin is connected to the model domain to provide characteristic temperature and salinity profiles in case of inflow situations from the North Sea into the Skagerrak. Outflowing water leaving the model domain will be slowly relaxed at the surface to typical North Sea salinity conditions. The model is further forced by low frequency sea level variations in the North Sea/Skagerrak calculated from the BSI (Baltic Sea Index, Lehmann et al. 2002). Prognostic variables of the model are the baroclinic current field, the 3-D temperature, salinity and oxygen distributions, the 2-D surface elevations and the barotropic transport. Model data can be extracted as daily averages, which could be the basis for subsequent analyses.

The model was used to get monthly hydrographical data for the Baltic Sea between 1950 and 2020 divided by ICES statistical rectangles. The relevant data included temperature (°C), oxygen (ml l⁻¹), and salinity. The data was divided into even intervals starting from 1.5 m and increasing by 3 m until the bottom was reached.

3.3 Creating the case-specific hydrographical databases

As the tagged cod in the different case studies originate from areas with different hydrography and bathymetry, it is important to account for potential differences in habitat preferences and preferred depth. As an example, a cod used to a depth interval of approx. 10-20 m and a salinity of 34 (e.g., the western Baltic Sea) would not necessarily migrate to a depth > 100 m and a salinity of 10 (e.g., in the Gotland basin) if that opportunity should arise following movements to other areas.

To account for potential differences in habitat preferences between the case studies, a hydrographical database was thus constructed for each case study based on a case-specific

maximum preferred depth. This means that tagged cod within each case study are expected to exhibit a maximum depth preference and remain around this depth unless the rectangle is shallower, as it was unrealistic to fully account for vertical migration in the toy model. This means that as simulated cod move around in the simulation, they are compared to one value per variable per rectangle in the depth interval that they are known to prefer and not the entire water column. As such, simulated cod from each case study would not experience the same conditions as simulated cod from other case studies as they remain within different depth intervals. As an example, the eastern Baltic is characterized by a deeper bathymetry compared to the shallow western Baltic Sea, meaning cod released in the Gotland Sea would be expected to be distributed much deeper compared to cod in the Belt Sea.

Obtaining cod depth distributions: To obtain the depth range occupied by cod, trawl survey data from 1991-2020 from DATRAS (the Database of Trawl Surveys) was compiled for each case study and included information on individual capture depths to match to a subset of the hydrographical database for the same time period.

Based on the model assumption that the majority of cod remain within a preferred depth interval, the mean environmental values were calculated for a depth interval of approx. 10 m. The highest value in this interval corresponds to the maximum preferred depth which is a necessary cut-off due to the sheer amount of data and to ensure that, as an example, cod used to shallow water conditions remain around these conditions, and the middle depth value in the interval (D_m) is the closest value to the DATRAS mean capture depth. This was necessary due to the intervals in the hydrographical database never being identical to the DATRAS mean depths. As an example, if the DATRAS mean depth distribution was around 36.5 m, it would be matched to the nearest depth in the hydrographical database which would be 37.5 m.

Captured cod were then compared to the environmental conditions at D_m , e.g., for a D_m of 67.5 m, all captured cod caught within 60-69 m were matched to the environmental conditions at D_m . As such, only captured cod within the interval were considered for the comparisons by assuming that this represented the preferred habitat. Only this interval was considered as the simulated cod were assumed to remain within this interval throughout the simulation. In addition, if a rectangle was shallower than the maximum preferred depth for the case study, the maximum depth was used as the maximum preferred depth for the relevant rectangle.

The functional responses, meaning the density-dependent cod capture distributions at oxygen, temperature, and salinity levels around D_m , were then plotted for each case study to assess the optimal environmental conditions based on the assumption that cod remain around the preferred depth.

However, as cod were often caught at low oxygen values at greater depths, the maximum preferred depth was adjusted until distributions approaching optimal conditions were achieved (e.g., a peak around 4 oxygen ml l⁻¹ instead of 2 ml l⁻¹). This was done by checking the functional responses at D_m and gradually moving the interval upwards until optimal environmental conditions were achieved, and thus removing captured cod at greater depths from the functional responses to avoid movement towards suboptimal environmental conditions. See **table 1** for considerations when adjusting for optimal conditions.

Area	Temperature (°C)	Oxygen (ml l ⁻¹)	Salinity	Reference
Western Baltic*	Mean around 7°C, ~0-18°C range (Skagerrak/Kattegat)	Assumed to be similar to EB	Over 10-15 appears good based on salinity in the west	Kijewska et al. 2016 Righton et al. 2010
Eastern Baltic (spawning)	Below 5°C is avoided, 7-8°C preferred; 15°C sea surface temperature is suboptimal	Below 2.5 ml l ⁻¹ is avoided, preference is around 4.5 ml l ⁻¹ (but present around 1.25-5.75 ml l ⁻¹)	Below 10.7 is avoided, 11.3 to 17.2 is preferred	Schaber et al. 2009 Freitas et al. 2015
Eastern Baltic (non-spawning)	Assumed similar to Western Baltic	Assumed similar to during spawning	As salinity is approx. <11 in the east, this seems like a proper limit	

Table 1. Considerations when adjusting depth intervals for optimal environmental conditions. * = Note that spawning causes more narrow environmental preferences (see Righton et al. 2010).

3.4 Calculating habitat indices from habitat preferences

To judge the quality of a given habitat, case-specific habitat indices were calculated for each ICES rectangle based on the separate case-specific hydrographical databases. Assuming that cod aim for and thus cluster at optimal conditions, the functional responses for each environmental variable was converted to normalized habitat indices by dividing the densities by the highest density, thus normalizing the habitat index to 0-1. This effectively means that the better the habitat quality, the higher the score. Forsythe-Malcolm-Moler cubic spline interpolation was fitted to the data, and the spline interpolation function was then used to convert the hydrographical data for each rectangle to habitat index values. Habitat indices converted from environmental values outside the functional responses were manually checked and corrected if necessary. If habitat indices were negative or above 1 for a given ICES rectangle, they were manually corrected to 0 and 1, respectively. This approach was used to create three individual habitat indices for oxygen (HI_o), salinity (HI_s), and

temperature (HI_c), and the mean of the three environmental habitat indices was then used as the overall habitat index (HI_a) for each rectangle.

3.5 Model parametrization

To test the hypotheses of whether the cod follow optimal environmental gradients, it is necessary to create a movement model incorporating taxis and diffusion (D ; **Table 2**). Taxis is based on an orientation in response to a stimulus, such as a gradient, and is here used to ensure simulated cod follow positive gradients towards good habitats and avoid negative ones towards poor habitats. Similarly, diffusion is here used as random, or dispersing, movement and can be viewed as searching behaviour.

	<i>k</i>	<i>D</i>
Case study 1	Min = 300 (3.6 km d ¹) Mid = 1000 (12.1 km d ¹) Max = 1500 (18.2 km d ¹)	Min = 3.7 km d ¹ Mid = 12.4 km d ¹ Max = 18.6 km d ¹
Case study 2	Min = 350 (4.3 km d ¹) Mid = 1250 (15.2 km d ¹) Max = 1850 (22.5 km d ¹)	Min = 4.5 km d ¹ Mid = 15.1 km d ¹ Max = 22.7 km d ¹
Case study 3	Min = 350 (4.3 km d ¹) Mid = 1200 (14.6 km d ¹) Max = 1800 (21.8 km d ¹)	Min = 4.4 km d ¹ Mid = 14.7 km d ¹ Max = 22.1 km d ¹
Case study 4	Min = 300 (3.6 km d ¹) Mid = 950 (11.5 km d ¹) Max = 1400 (17 km d ¹)	Min = 3.4 km d ¹ Mid = 11.5 km d ¹ Max = 17.2 km d ¹

Table 2. Overview of levels of *k* and *D* for each case study. Speeds are based on the mean body lengths per case study (0.3 (min), 1 (mid), and 1.5 bl s¹ (max)) assuming the cod are active for approx. 10 hours (Løkkeborg & Fernö 1999). Each simulation was based on one index ($n = 4$), one level of *k* ($n = 3$), and one level of *D* ($n = 3$; $n = 144$ simulations in total). * = Total distance covered per day along longitude and latitude for $g_{lon} = 0.5$ and $g_{lat} = 0.5$. See text for details.

To simulate movement, a two-dimensional random walk model was used:

$$u_{t+1} = u_t + g_{lon} + \varepsilon$$

$$v_{t+1} = v_t + g_{lat} + \varepsilon$$

where u and v indicate positions as longitude and latitude, respectively, at time t in days, and g_{lon} and g_{lat} indicate the habitat gradient on the longitude and latitude axes, respectively, and represent taxis. ε indicates random noise and thus diffusion.

Habitat gradient: The habitat gradient was calculated using forward and backward differencing. In summary, this means the difference in habitat index, HI , between rectangles surrounding the current rectangle is calculated as a habitat gradient (**Figure 3**). As an example, if the rectangle above the current rectangle has a HI of 0.5 and the rectangle below has a HI of 0.3, the simulated cod would move upwards (**Figure 3**). If, however, the previously occupied rectangle has a HI of 0.9 and the rectangle above the currently occupied rectangle has a lower HI (e.g., 0.1), the simulated cod will be pushed back towards the previously occupied rectangle, ensuring the simulated cod will always move towards the most favourable conditions (**Figure 3**). Additionally, if diffusion is sufficiently high, simulated cod are ensured to not aggregate in nearby favourable cells. To account for land rectangles, these rectangles were not used in the habitat gradient calculations. This was similarly done for the domain edges, such as the North Sea. As such, if a simulated cod left for the North Sea, the simulated cod was considered to have left the simulation permanently.

Adjusting the speed of the simulated cod for each scenario: As it is difficult to assess which movement patterns produced the true observed recapture patterns in the case studies, several combinations of g_{lon} , g_{lat} , and D were tried. As these parameters decide how far a simulated cod moves in each time step (i.e., g_{lon} and g_{lat} determine the strength of the taxis and the higher the values, the further the simulated cod swim towards a positive gradient in a single time step; this is similar for D which can also weaken the taxis at sufficiently high levels and vice versa), they need to be set according to potential speeds of cod. Based on Fernö et al. (2011), three speeds were chosen based on realistic minimum and maximum swimming speeds (min = 0.3 bl s⁻¹, mid = 1 bl s⁻¹, max = 1.5 bl s⁻¹; **Table 2**) and assuming the cod were active for approx. 10 hours per day (Løkkeborg & Fernö 1999). The mean distance per day (km d⁻¹) was calculated based on the mean release length of the respective case studies. D was set to the mean distance covered per day at either a min, mid, or max level (**Table 2**). To adjust the taxis behaviour accordingly, g_{lon} and g_{lat} were multiplied by a constant k which was set to a value so at a habitat gradient of 0.5 (g_{lon}) and 0.5 (g_{lat}) across neighbouring rectangles on the longitudinal and latitudinal axis, respectively, the total distance covered would approximate the mean distance covered per day at either a min, mid, or max level (**Table 2**). This habitat gradient of 0.5 was chosen as it appeared to be realistic but not too common as a representation of a strong gradient; if it was set lower, the simulated cod

swimming speeds would increase overall and if it was set higher, the swimming speeds would slow down considerably overall due to the prevalence of lower gradients.

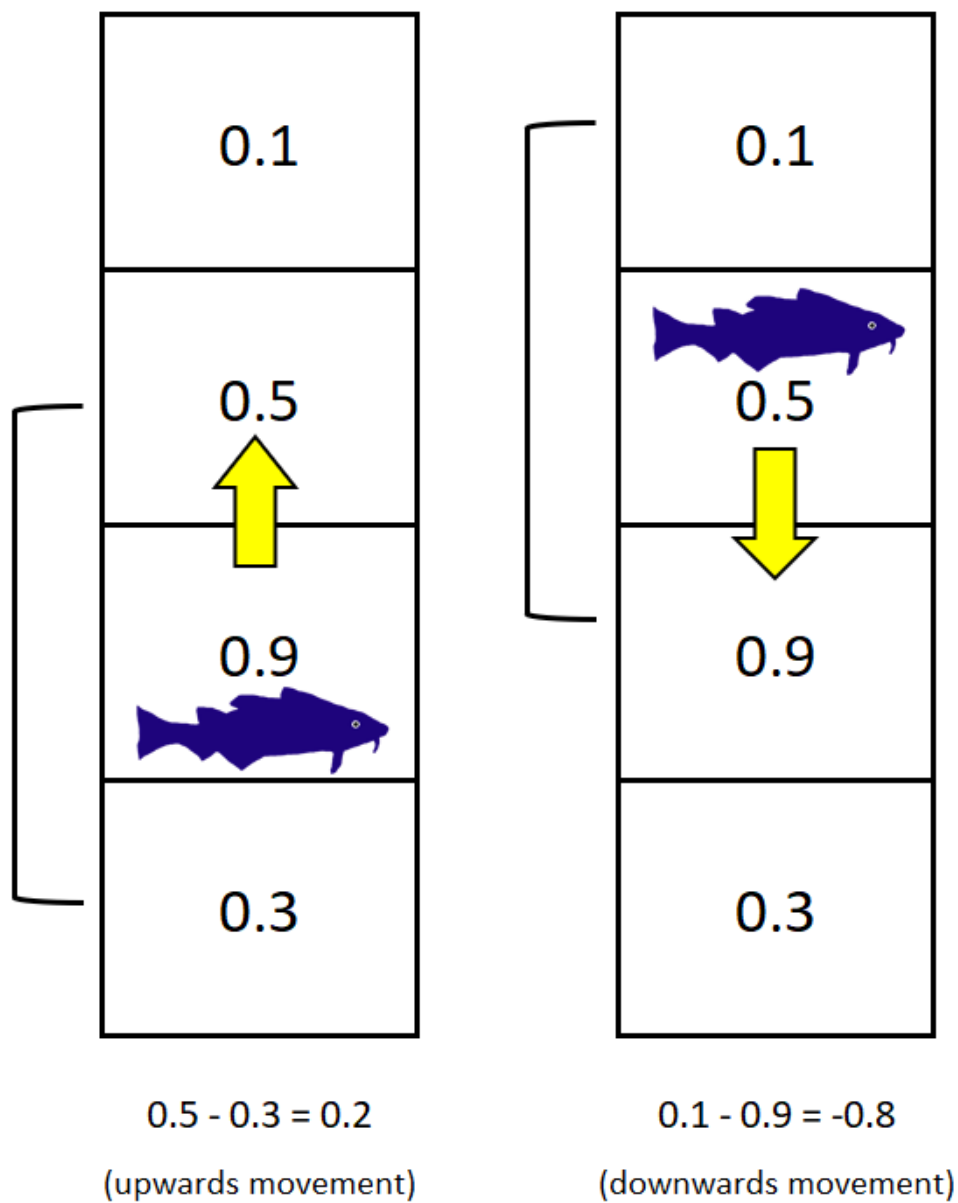


Figure 3. Example of how movement is implemented in the model in one dimension if no neighbouring cells are land-based or outside the domain. Only neighbouring boxes are compared; however, the cod will always move towards the most optimal habitat as illustrated by habitat indices.

Model scenarios tested: For each case study, the simulations ran for the entire duration, t , of the respective case studies based on the highest DAL, and simulated cod were released on the same day as the true tagging studies. The number of cod simulated was approximately 10 times the recapture numbers, as release numbers for the case studies were unknown ($n = 1000$ for case study 1; $n = 1400$ for case study 2; $n = 1200$ for case study 3; $n = 800$ for case study 4). For each simulation, taxis was based on one of the four habitat indices (HI_c , HI_s , HI_o , HI_a) to examine if some environmental variables were more likely to have produced the true recapture patterns.

For each of the four case studies, simulations were run for each habitat index and several combinations of k and D based on either a min, mid, or max level (**Table 2**; $n = 36$ simulations per case study; $n = 144$ simulations in total). For each time step, u , v , g_{lon} , and g_{lat} were converted to kilometers prior to moving the position, and following the move, the new position was converted back to longitude and latitude. To account for mortality, M was set to 0.2 and SD-specific F rates were collected from ICES reports (Jørgensen et al. 2011, Storr-Paulsen et al. 2014, ICES 2019, 2020). As the simulation ran on a daily basis, the total mortality, Z , was divided by 365 and converted to a percentage which would indicate the chance to die in each time step in the current area. If F was unavailable for an area in a particular year, Z was set to 0.001. This was only relevant for case study 1 and 3 as F rates for SD 21 and SD 22-24 only extended back to 1971 and 1970, respectively, compared to 1946 for SD 25-32. During each time step, following the move to a new position, a random number was generated between 0-1, and if the number was lower than Z , the simulated cod was considered caught, and the final position was recorded.

As individual simulated cod would occasionally be pushed unto land, which was represented by polygons, landmasking was implemented by checking if the new position would end up inside a polygon. This meant that if a simulated cod ended up inside a polygon in the current timestep, the current location would be replaced by the previous one. As cod can be coastal for a time, simulated cod seemingly getting stuck near land for a while was considered realistic in the simulation.

4. Results

As the simulation scenarios were numerous ($n = 144$), the overall results have been condensed into a few representative simulations for each case study per environmental parameter (see **Figure 4-7 and S1**). Overall, the trajectories and extent of movement were highly dependent on the combined levels of taxis and diffusion, and the four habitat indices generally resulted in different movement patterns as the simulated cod followed other gradients. A more thorough descriptions of the overall patterns can be found in the supplementary material.

4.1 Case 1 – Gotland Sea

The true recapture pattern was generally characterized by strong movement towards the southern Baltic (**Figure 2**). However, this pattern was not captured well in the simulations (see **Figure 4-7, S1** for representative examples of the simulations). Overall, the simulated cod remained in the central Baltic and did not show the same southern movement pattern as the true recapture patterns, indicating other stronger taxis-driven behaviour rather than optimal environmental parameters.

In addition, following adjustment according to **table 1**, the maximum preferred depth was set to 58.5 m, and the functional responses indicated an optimal temperature around 4-5 °C, optimal salinity between 5-10, and an oxygen peak around 5 ml l⁻¹ (**Figure 8**).

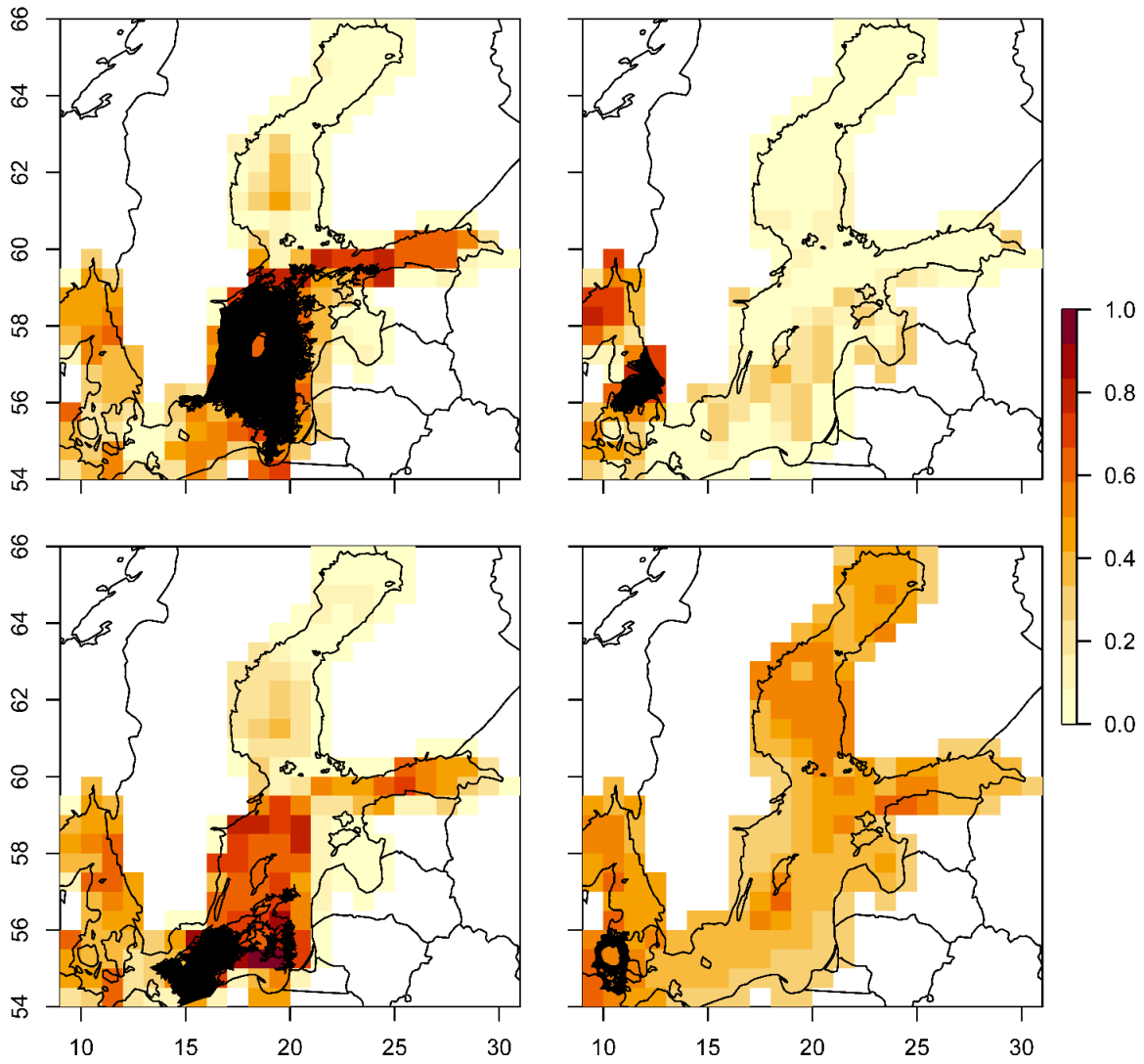


Figure 4. Examples of simulated trajectories for each of the four case studies for the overall habitat index (HI_a). Top left = Case study 1 ($k = \text{mid}$; $D = \text{max}$). Top right = Case study 2 ($k = \text{max}$; $D = \text{mid}$). Bottom left = Case study 3 ($k = \text{max}$; $D = \text{max}$). Bottom right = Case study 4 ($k = \text{max}$; $D = \text{min}$). k and D indicate coefficients used to adjust taxis and diffusion, respectively, and the higher, the stronger the effects and vice versa (**Table 2**). The coloured rectangles indicate the habitat index level for each rectangle on the final day of the simulation.

4.2 Case 2 – Kattegat

The true recapture pattern was characterized by cod generally remaining in the southern Kattegat, with occasional recaptures in the northern part (**Figure 2**). This pattern was generally captured well by the simulations, as the optimal conditions were generally highest in the release area (see **Figure 4-7, S1** for representative examples of the simulations). Overall, the simulated cod remained in the release area when the overall habitat or oxygen indices were used, aside from when diffusion was at least relatively high (mid) and taxis low (min) where movement into the Belt Sea also occurred. In contrast, strong northern movement into the Skagerrak was observed for the salinity index. For the temperature index, movement into the Belt Sea was observed except when taxis was high (max) and diffusion low (min). This suggests that movement is related to ambient oxygen levels, and the overall habitat index is likely mainly driven by the oxygen levels. Additionally, diffusion appears to be less important compared to taxis-driven behaviour.

In addition, following adjustment according to **table 1**, the maximum preferred depth was set to 43.5 m, and the functional responses indicated an optimal temperature around 7-8 °C, optimal salinity around 33-35, and an oxygen peak around 2 ml l⁻¹ (**Figure 8**). It was not possible to adjust for a higher oxygen peak due to generally poor oxygen conditions, and continuous adjustments reduced the amount of captured cod for comparison purposes considerably.

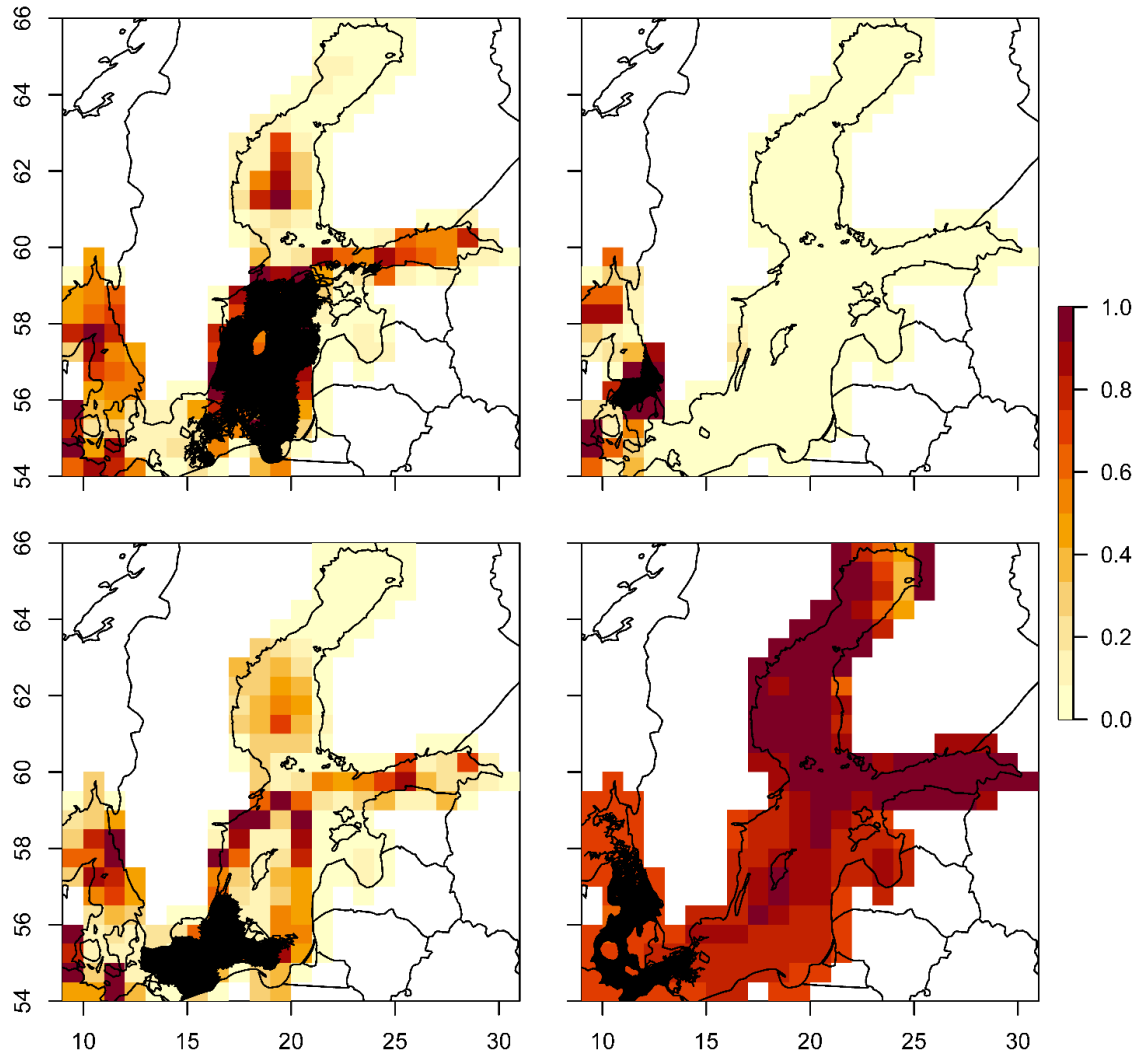


Figure 5. Examples of simulated trajectories for each of the four case studies for the oxygen habitat index (HI_o). Top left = Case study 1 ($k = \max$; $D = \max$). Top right = Case study 2 ($k = \max$; $D = \min$). Bottom left = Case study 3 ($k = \max$; $D = \max$). Bottom right = Case study 4 ($k = \text{mid}$; $D = \max$). k and D indicate coefficients used to adjust taxis and diffusion, respectively, and the higher, the stronger the effects and vice versa (**Table 2**). The coloured rectangles indicate the habitat index level for each rectangle on the final day of the simulation.

4.3 Case 3 – Bornholm Sea

The true recapture pattern was generally characterized by relatively stationary movement around the island of Bornholm albeit with occasional recaptures in the south-western and south-eastern Baltic Sea (**Figure 2**). This pattern was captured generally well by the simulations (see **Figure 4-7, S1** for representative examples of the simulations). Overall, the simulated cod remained in the southern Baltic with various degrees of movement east or west depending on the taxis and diffusion levels, and the most comparable pattern were produced by the habitat and oxygen indices. The least comparable

movement patterns were caused by salinity-driven movement which indicated stronger movement north-east. In particular, movement towards the east was generally more common, except for temperature-driven movement which indicated more western movement as well. This indicates that oxygen might be important for movement patterns. Furthermore, diffusion appears to be relatively low overall in this area, as the most comparable patterns indicated that the simulated cod remained near the island of Bornholm.

In addition, following adjustment according to **table 1**, the maximum preferred depth was set to 61.5 m, and the functional responses indicated an optimal temperature around 5-6 °C, optimal salinity between 10-11, and an oxygen peak around 4 ml l⁻¹ (**Figure 8**).

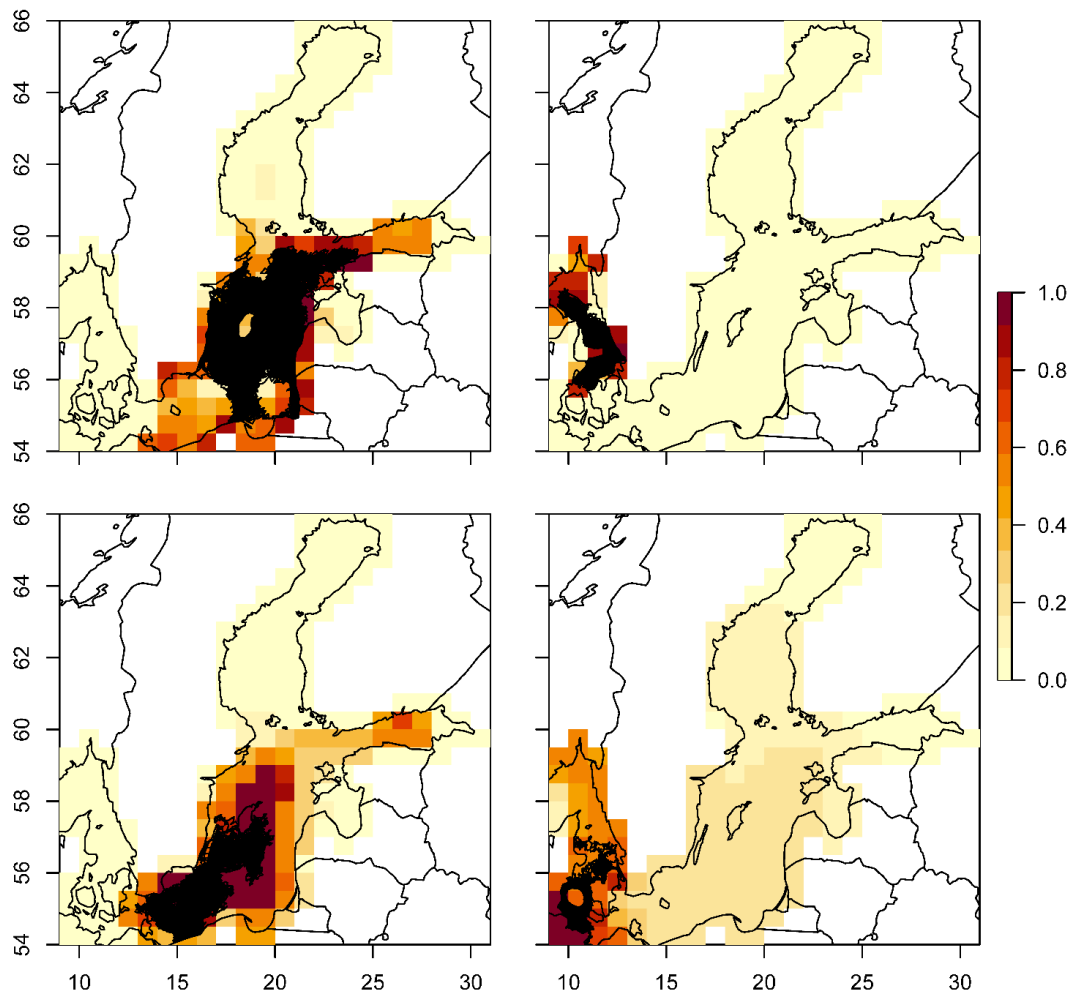


Figure 6. Examples of simulated trajectories for each of the four case studies for the salinity habitat index (HI_s). Top left = Case study 1 ($k = \text{mid}$; $D = \text{max}$). Top right = Case study 2 ($k = \text{mid}$; $D = \text{min}$). Bottom left = Case study 3 ($k = \text{mid}$; $D = \text{mid}$). Bottom right = Case study 4 ($k = \text{max}$; $D = \text{max}$). k and D indicate coefficients used to adjust taxis and diffusion, respectively, and the higher, the stronger the effects and vice versa (**Table 2**). The coloured rectangles indicate the habitat index level for each rectangle on the final day of the simulation.

4.4 Case 4 – Belt Sea

The true recapture pattern was generally characterized by relatively stationary movement around the release area in Vejle Fjord with some recaptures further east (**Figure 2**). However, this pattern was not captured well in the simulations (see **Figure 4-7, S1** for representative examples of the simulations). Overall, movement into the Belt Sea of the simulated cod was observed regardless of the environmental index used. In addition, movement into Kattegat was also common in the majority of the simulations, and when oxygen was the driver of movement, movement into the south-eastern Baltic occurred, except when diffusion was low (min). The most comparable pattern was observed when diffusion and taxis were both low (min) for temperature-driven behaviour, indicating movement is not only low but also not driven by environmental parameters.

In addition, following adjustment according to **table 1**, the maximum preferred depth was set to 19.5 m, and the functional responses indicated two peaks with optimal temperatures around 4°C and to a lesser extent 8°C, optimal salinity between 15-17, and an oxygen peak around 7-8 ml l⁻¹ (**Figure 8**).

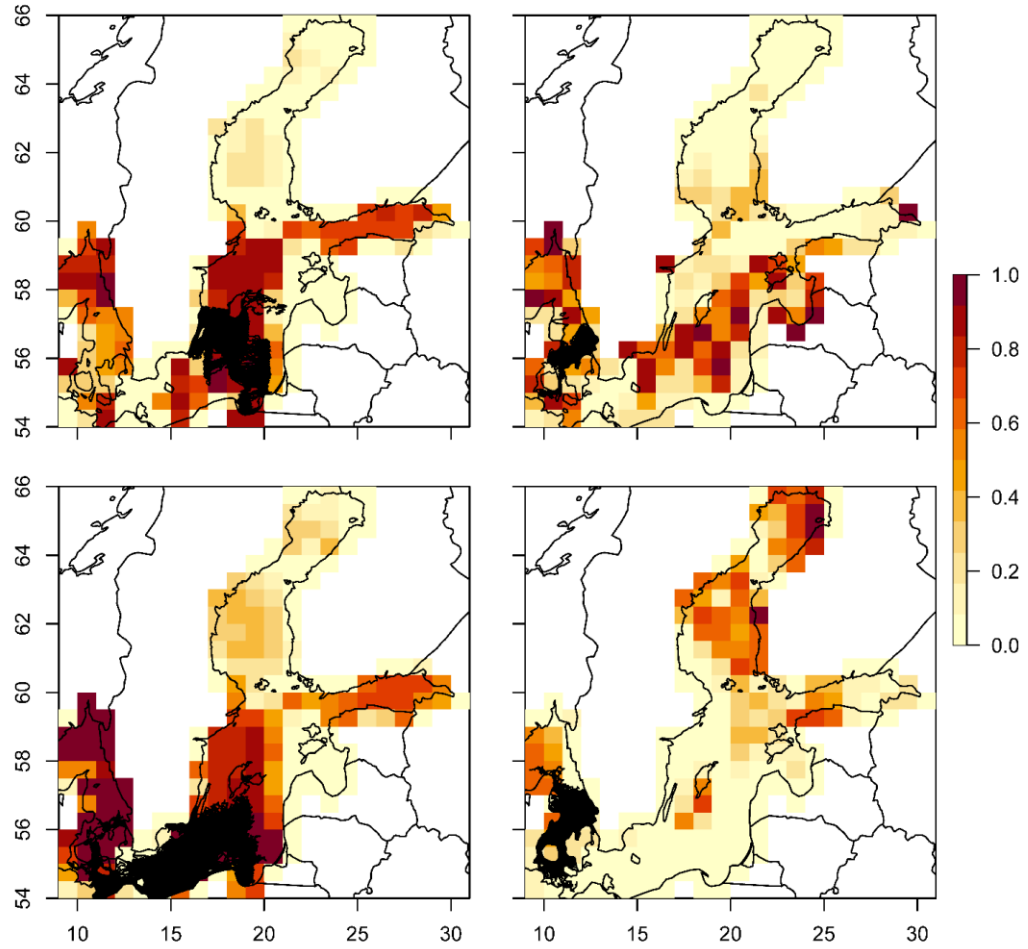


Figure 7. Examples of simulated trajectories for each of the four case studies for the temperature habitat index (HI_c). Top left = Case study 1 ($k = \text{max}$; $D = \text{min}$). Top right = Case study 2 ($k = \text{mid}$; $D = \text{min}$). Bottom left = Case study 3 ($k = \text{mid}$; $D = \text{max}$). Bottom right = Case study 4 ($k = \text{mid}$; $D = \text{mid}$). k and D indicate coefficients used to adjust taxis and diffusion, respectively, and the higher, the stronger the effects and vice versa (**Table 2**). The coloured rectangles indicate the habitat index level for each rectangle on the final day of the simulation.

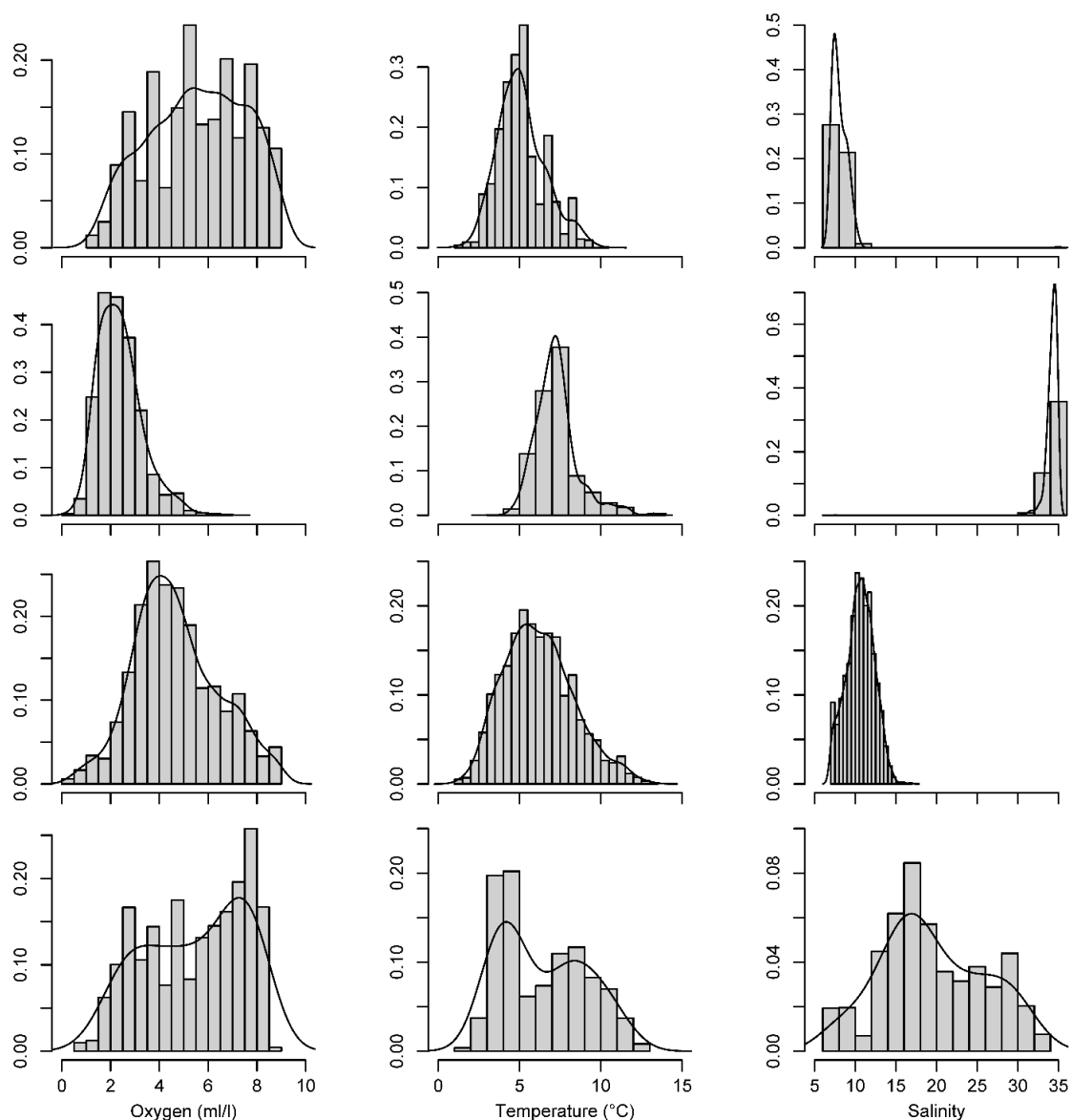


Figure 8. Functional responses for the four case studies shown as density plots. Each plot shows case-specific density dependent responses to environmental parameters based on DATRAS capture data. Note that adjustments according to **table 1** were performed to ensure cod would follow optimal gradients. First row = case study 1 (Gotland Sea). Second row = case study 2 (Kattegat). Third row = case study 3 (Bornholm Sea). Fourth row = case study 4 (Belt Sea). First column = oxygen (ml l^{-1}). Second column = temperature ($^{\circ}\text{C}$). Third column = salinity. Note different y-axes.

5. Discussion

As climate change has been projected to change cod distributions (e.g., see Drinkwater 2005 and references therein), it is imperative to understand the effect on historical Baltic cod distributions to gain insight into potential future spatial patterns. We used a simulation model to evaluate movement patterns in response to environmental parameters obtained from a hydrodynamic model, by comparing the modeled patterns with observed movements from historical tagging programs (Lundgreen et al., 2022a). We found that oxygen was generally a good predictor of movement in two of the case studies (Kattegat and the Bornholm Sea) while temperature and salinity were less important. This indicates that cod in these areas seek out better habitats based on oxygen but not temperature or salinity. In contrast, in the other two case studies (Gotland Sea and the Belt Sea), the recapture distributions could not be recreated, suggesting movement is dependent on other drivers than the environment and thus cod do not appear to move towards better habitats.

Case study 1 – The Gotland Sea: The movement patterns in the Gotland Sea were difficult to capture in the simulations. The simulations predicted more northerly movement in case study 1 in almost all cases, as the conditions were relatively optimal in most of the central Baltic. In the eastern Baltic, three historically important spawning grounds are located in the Gotland Basin, the Gdansk Basin, and the Bornholm Basin (Bleil et al. 2009). Looking at the true recapture patterns, it is likely that the continuous movement towards Bornholm is due to spawning migrations which was not captured in the model due to the complexity of cod spawning seasons (see Hüsey 2011 and references therein). This is similarly supported by distributions being greater in the south during the spawning season for cod originating in the Gotland Sea (Mion et al. 2022). In comparison, important western Baltic spawning grounds generally cover the distribution areas of the individual stocks (Hüsey 2011) which might help explain why the simulated movement was more similar for Kattegat cod. As such, our results suggest that strong spawning-related behaviour overrides any potential effect of the environment, meaning that migratory cod will consistently forego moving towards optimal habitats in light of moving towards spawning grounds. However, it is still possible that some routes towards the spawning grounds might be slightly modified based on gradients.

Case study 2 – Kattegat: Cod movements in Kattegat were generally well described by the simulations when diffusion was low and taxis high. For the trawl survey data, captured cod were primarily caught between 20-50 m, which were often characterized by oxygen levels declining to relatively low levels and this made it difficult to adjust for more optimal values. Based on this, the environmental conditions from the western Baltic to Skagerrak were the most optimal throughout the simulation which limited the simulated cods' need for movement. The simulated movement fit the real distributions relatively well, albeit with slightly more eastern movement, which fits the location of known spawning grounds (Hüsey 2011). When salinity or temperature was used as the habitat index, however, the patterns were highly dissimilar from the true patterns while the overall habitat index and the oxygen habitat index were the most accurate. It is interesting to note, however,

that Kattegat cod appear to seek out less favourable oxygen habitats than what would be expected, and it is possible that this is related to prey distributions as has been noted in Baltic cod previously (Neuenfeldt et al. 2009).

Case study 3 – The Bornholm Sea: The patterns in case study 3 were similar to those observed in case study 2, although optimal conditions were more widespread. The most similar movement patterns indicated cod seek out optimal habitats based on an oxygen gradient. Furthermore, spawning grounds are located right by the island of Bornholm, indicating a low need to move and might partially explain the low degree of movement (Hüssy 2011). This is similarly supported by the limited distributions of cod originating in the Bornholm Sea during the spawning and feeding seasons (Mion et al. 2022).

Case study 4 – The Belt Sea: The predicted movement patterns for the Belt Sea showed more southerly and occasional northerly movement compared to the stationary behaviour in the true case studies. The existence of ecotypes in cod, more specifically a migratory and resident type (e.g., see Neat et al. 2005, Lundgreen et al. 2022a), are likely to explain why the simulated cod did not fit the true migratory patterns. Coastal cod, such as cod in fjords, are generally relatively resident and do not move far from the fjords (e.g., see Nordeide & Salvanes 1988, Rogers et al. 2014), suggesting they do not follow environmental cues like more migratory cod. As such, if the cod had adhered to a more migratory type as suggested by the simulations, they would have ended up on spawning and potentially important feeding grounds of western Baltic cod (Hüssy 2011, Funk et al. 2021) which might have been expected for non-fjord western Baltic cod. As such, it appears that fjord cod are unlikely to seek out better habitats based on environmental cues.

The effect of the environment on cod: Low oxygen conditions infers stress such as increased respiratory volume and staying in hypoxic waters would require a higher cost in the form of increased metabolism (Saunders 1963). Since eutrophication peaked in the 1980s in the Baltic Sea (Gustafsson et al. 2012), Kattegat cod have avoided bottom waters at low oxygen levels (Pihl 1989) and similar patterns have been shown for Baltic cod in the Bornholm Basin (Tomkiewicz et al. 1998). As such, oxygen appears to be a good predictor for Baltic cod distribution which was suggested by our results in the Kattegat and Bornholm Sea, albeit the levels of optimal oxygen conditions differed between the two case studies. The lack of correlation with temperature is likely because of the relatively wide thermal niche in Baltic cod, as Baltic cod have been observed between 0-17°C in the Baltic Sea with a mean at 6.23 ± 2.21 (Righton et al. 2010), which is well within the range of the Baltic Sea (Fonselius & Valderrama 2003). Salinity was overall a poor indicator of movement but has still been noted to be a separator between the Baltic cod stocks (Kijewska et al. 2016).

Model considerations and potential improvements: While the model captured the movement patterns relatively well in half of the cases, it is important to keep in mind that the true observed patterns can be affected by factors that are not accounted for in the model. As the true recapture patterns are based on conventional tags, they are highly dependent on the temporal and spatial

distribution of fishing vessels (Salthaug & Aanes 2003) and may not represent true distributions as fishermen aim to maximize their catches. It is thus possible that some simulated movement patterns may be closer to the true movement patterns than suggested. As an example, cod related trawl and gill net effort can differ greatly between rectangles in the Baltic Sea (Lundgreen et al. 2022b).

Furthermore, as the model used is a toy model, the aim was to test relatively simple scenarios by guessing potential swimming speeds. This scope can further be expanded upon in a more advanced model, for instance by testing a greater range of speeds. Most obviously the inclusion of annual migrations would be beneficial, where, as an example, taxis based on spawning grounds could be included at the start of the spawning season. Based on our results, it appears that the ecotype of the cod is highly important, as resident cod in fjords (case study 4), relatively resident cod in the open ocean (case study 2-3), and highly migratory cod in the open ocean (case study 1) have highly different types of movement behaviour. Indeed, for highly migratory cod with long distances to the spawning grounds compared to relatively resident cod with short distances to the spawning grounds, it appears that a spawning-related behaviour will override any potential need to seek out better habitats. In addition, this can be combined with more narrow environmental preferences during the spawning season as has been observed in other cod (Rose 1993, Righton et al. 2010). Another aspect to consider is seasonality in preferences; as an example, western Baltic cod are known to favour different depths and habitats depending on the year (Funk et al. 2020) and in light of this, a more advanced inclusion of vertical depth movement would be beneficial. Indeed, the assumption that cod generally remain around a preferred maximum depth is likely an oversimplification, as DSTs on southern Baltic cod have shown high degrees of daily vertical migrations (Hüssy et al. 2020). As such, it might be more beneficial for cod to perform vertical and not horizontal migrations in certain cases to avoid poor environmental conditions.

It might also be beneficial to include age structuring in the model. Nursery grounds are generally located along the coast (Bagge et al. 1994) where juveniles remain until they mature and move to deeper waters, as is stated by Heincke's Law (Heincke 1913). It would have been interesting to see if, based on the assumptions of the model, juveniles would benefit more by leaving a nursery ground for another if conditions worsen. Additionally, it is likely that speeds would change as the cod grow, potentially producing other movement patterns.

Finally, to improve upon the model it would be valuable to include prey distributions if possible. Important prey items of Baltic cod include forage fish, such as herring or sprat, and invertebrate prey in shallow areas (Funk et al. 2021). While our simulations suggested oxygen was important for distributions, Baltic cod have been known to frequently visit and occupy hypoxic waters for short periods of time which is likely due to prey (Neuenfeldt et al. 2009), illustrating the importance of prey in regard to cod movement and may be used to further elaborate on the movement pattern in case study 2. However, the annual migrations of forage species might be complicated to include (see Aro 1989 and references therein) despite potentially explaining a lot of movement patterns.

6. Conclusion

The Baltic Sea is projected to change greatly within the next 80 years (Meier et al. 2022), posing high risk for the continued existence of the Baltic cod despite the decrease in fishing pressure. Our initial results based on a toy model suggest that oxygen may be important for Baltic cod distributions while salinity and temperature are less important. However, the ecotype of the cod is also likely to be important. We propose that a more advanced model, including more factors such as ecotypes and seasonality in movements, is developed to fully understand how Baltic cod have responded to changes in environmental parameters to infer if the cod can thrive in the Baltic in the future.

7. Acknowledgements

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8. Author contributions

H-H.H. provided the description of and ran the hydrodynamic model to get the data for the hydrographic database. M.M. provided the Swedish tagging data for the case studies. R.B.C.L. built the model and ran the simulations. A.N. provided feedback on and aided in improving the model. R.B.C.L. and K.H. drafted the manuscript.

9. References

- Aro E (1989) A review of fish migration patterns in the Baltic. *Rap Proc-Verb Ré Cons Int Explor Mer* 190:72–96.
- Bagge O, Thurow F, Steffensen E, Bay J (1994) The Baltic cod. *Dana*.
- Bell B, Hersbach H, Simmons A, Berrisford P, Dahlgren P, Horányi A, Muñoz-Sabater J, Nicolas J, Radu R, Schepers D, Soci C, Villaume S, Bidlot JR, Haimberger L, Woollen J, Buontempo C, Thépaut JN (2021) The ERA5 global reanalysis: Preliminary extension to 1950. *Q J R Meteorol Soc* 147:4186–4227.
- Bendtsen J, Söderkvist J, Dahl K, Hansen JL, Reker J (2007) Model Simulations of Blue Corridors in the Baltic Sea. *Balanc interim Rep* 9.
- Bleil M, Oeberst R, Urrutia P (2009) Seasonal maturity development of Baltic cod in different spawning areas: importance of the Arkona Sea for the summer spawning stock. *J Appl Ichthyol* 25:10–17.
- Bumke K, Uwe Karger, Lutz Hasse, Klauspeter Niekamp (1998) Evaporation over the Baltic Sea as an example of a semi-enclosed sea. *Contrib to Atmos Phys* 71:249–261.
- Carstensen J, Andersen JH, Gustafsson BG, Conley DJ (2014) Deoxygenation of the Baltic Sea during the last century. *Proc Natl Acad Sci* 111:5628–5633.
- Christensen OB, Kjellström E, Dieterich C, Gröger M, Meier HEM (2022) Atmospheric regional climate projections for the Baltic Sea region until 2100. *Earth Syst Dyn* 13:133–157.
- Claireaux G, Webber D, Kerr S, Boutilier R (1995) Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating temperature conditions. *J Exp Biol* 198:49–60.
- Conley DJ, Carstensen J, Aigars J, Axe P, Bonsdorff E, Eremina T, Haahti BM, Humborg C, Jonsson P, Kotta J, Lännegren C, Larsson U, Maximov A, Medina MR, Lysiak-Pastuszek E, Remeikaitė-Nikienė N, Walve J, Wilhelms S, Zillén L (2011) Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environ Sci Technol* 45:6777–6783.
- Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *Science* (80-) 321:926–929.
- Drinkwater KF (2005) The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES J Mar Sci* 62:1327–1337.
- Eero M, Hjelm J, Behrens J, Buchmann K, Cardinale M, Casini M, Gasyukov P, Holmgren N, Horbowy J, Hüseyin K, Kirkegaard E (2015) Eastern Baltic cod in distress: biological changes and challenges for stock assessment. *ICES J Mar Sci* 72:2180–2186.
- Fernö A, Jørgensen T, Løkkeborg S, Fernö A, Winger PD (2011) Variable swimming speeds in individual Atlantic cod (*Gadus morhua* L.) determined by high-resolution acoustic tracking. *Mar Biol Res* 7:310–313.
- Fonselius S, Valderrama J (2003) One hundred years of hydrographic measurements in the Baltic Sea. *J Sea Res* 49:229–241.

- Freitas C, Olsen EM, Moland E, Ciannelli L, Knutsen H (2015) Behavioral responses of Atlantic cod to sea temperature changes. *Ecol Evol* 5:2070–2083.
- Funk S, Krumme U, Temming A, Möllmann C (2020) Gillnet fishers' knowledge reveals seasonality in depth and habitat use of cod (*Gadus morhua*) in the Western Baltic Sea. *ICES J Mar Sci* 77:1816–1829.
- Funk S, Frelat R, Möllmann C, Temming A, Krumme U (2021) The forgotten feeding ground: patterns in seasonal and depth-specific food intake of adult cod *Gadus morhua* in the western Baltic Sea. *J Fish Biol* 98:707–722.
- Gustafsson BG, Schenk F, Blenckner T, Eilola K, Meier HEM, Müller-Karulis B, Neumann T, Ruoho-Airola T, Savchuk OP, Zorita E (2012) Reconstructing the development of baltic sea eutrophication 1850-2006. *Ambio* 41:534–548.
- Heincke F (1913) Untersuchungen über die Scholle-Generalbericht I. Schollenfischerei und Schonmassregeln. Vorläufige kurze Uebersicht über die wichtigsten Ergebnisse des Berichts. *Rapp Proc Verb Réun ICES* 16:1–70.
- Hinrichsen HH, Huwer B, Makarchouk A, Petereit C, Schaber M, Voss R (2011) Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (*Gadus morhua*). *ICES J Mar Sci* 68:2019–2028.
- Hinrichsen HH, Lehmann A, Petereit C, Nissling A, Ustups D, Bergström U, Hüsey K (2016) Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. *Prog Oceanogr* 143:13–25.
- Hinrichsen HH, von Dewitz B, Lehmann A, Bergström U, Hüsey K (2017) Spatio-temporal dynamics of cod nursery areas in the Baltic Sea. *Prog Oceanogr*.
- Hüsey K (2011) Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. *ICES J Mar Sci* 68:1459–1471.
- Hüsey K, Casini M, Haase S, Hilvarsson A, Horbowy J, Krüger-Johnsen, M. Krumme U, Limburg KE, McQueen K, Mion M, Olesen HJ (2020) Tagging Baltic Cod – TABACOD: Eastern Baltic cod: Solving the ageing and stock assessment problems with combined state-of-the-art tagging methods. *DTU Aqua Rep* 368–2020.
- ICES (2019) Cod (*Gadus morhua*) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). *ICES Advice Fish Oppor catch, effort Gt North Sea Ecoregion*.
- ICES (2020) Cod (*Gadus morhua*) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). *Rep ICES Advis Comm*.
- ICES (2021a) Cod (*Gadus morhua*) in Subdivision 21 (Kattegat). *Rep ICES Advis Comm*.
- ICES (2021b) Cod (*Gadus morhua*) in subdivisions 22–24, western Baltic stock (western Baltic Sea). *Rep ICES Advis Comm*.
- ICES (2021c) Cod (*Gadus morhua*) in subdivisions 24-32, eastern Baltic stock (eastern Baltic Sea). *Rep ICES Advis Comm*.

- Jansson A, Klais-Peets R, Grinienė E, Rubene G, Semenova A, Lewandowska A, Engström-Öst J (2020) Functional shifts in estuarine zooplankton in response to climate variability. *Ecol Evol* 10:11591–11606.
- Jørgensen OA, Storr-Paulsen M, Ringdahl K, Lövgren J, Gröhsler T, Oberst R, Schaber M, Bergenius J, Pönni J, Aho T, Holmgren N (2011) Report of the Baltic Fisheries Assessment Working Group (WGBFAS). ICES.
- Kijewska A, Kalamarz-Kubiak H, Arciszewski B, Guellard T, Petereit C, Wenne R (2016) Adaptation to salinity in Atlantic cod from different regions of the Baltic Sea. *J Exp Mar Bio Ecol* 478:62–67.
- van der Kooij J, Righton D, Strand E, Michalsen K, Thorsteinsson V, Svedäng H, Neat FC, Neuenfeldt S (2007) Life under pressure: insights from electronic data-storage tags into cod swimbladder function. *ICES J Mar Sci* 64:1293–1301.
- Kronsell J, Andersson P (2012) Total and regional Runoff to the Baltic Sea. HELCOM Baltic Sea Environment Fact Sheet.
- Lehmann A, Krauss W, Hinrichsen HH (2002) Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus, Ser A Dyn Meteorol Oceanogr* 54:299–316.
- Lehmann A, Hans-Harald Hinrichsen, Klaus Getzlaff, Kai Myrberg (2014) Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. *J Mar Syst* 134:20–28.
- Lehodey P, Senina I, Murtugudde R (2008) A spatial ecosystem and populations dynamics model (SEAPODYM) – Modeling of tuna and tuna-like populations. *Prog Oceanogr* 78:304–318.
- Lennartz ST, Lehmann A, Herrford J, Malien F, Hansen H-P, Biester H, Bange HW (2014) Long-term trends at the Boknis Eck time series station (Baltic Sea), 1957–2013: does climate change counteract the decline in eutrophication? *Biogeosciences* 11:6323–6339.
- Lindegren M, Möllmann C, Nielsen A, Brander K, MacKenzie BR, Stenseth NC (2010) Ecological forecasting under climate change: the case of Baltic cod. *Proc R Soc B Biol Sci* 277:2121–2130.
- Løkkeborg S, Fernö A (1999) Diel activity pattern and food search behaviour in cod, *Gadus morhua*. *Environ Biol Fishes* 1999 54:345–353.
- Lundgreen RBC, Nielsen A, Krüger-Johnsen M, Righton D, Mion M, Radtke K, Plikshs M, Leskelä AJ, Raitaniemi J, Griffiths CA, Casini M, Krumme U, Hüsey K (2022a) Examining fish movement in terms of advection or diffusion: a case study of northeastern Atlantic cod. *Mar Ecol Prog Ser* 691:115–129.
- Lundgreen RBC, Nielsen A, van Deurs M, Olesen HJ, Mion M, Haase S, Casini M, Krumme U, Hüsey K (2022b) Stock connectivity patterns and indications of sub-stock component structuring of cod in the Sound. Submitted.
- Meier HEM, Dieterich C, Gröger M, Dutheil C, Börgel F, Safonova K, Christensen OB, Kjellström E (2022) Oceanographic regional climate projections for the Baltic Sea until 2100. *Earth Syst Dyn* 13:159–199.
- Mion M, Hilvarsson A, Hüsey K, Krumme U, Krüger-Johnsen M, McQueen K, Mohamed E, Motyka

- R, Orio A, Plikshs M, Radtke K, Casini M (2020) Historical growth of Eastern Baltic cod (*Gadus morhua*): setting a baseline with international tagging data. *Fish Res* 223:105442.
- Mion M, Griffiths C, Bartolino V, Haase S, Hilvarsson A, Hüsey K, Krüger-Johnsen M, Krumme U, Lundgreen R, Lövgren J, McQueen K, Plikshs M, Radtke K, Raitaniemi J, Casini M (2022) New perspectives on Eastern Baltic cod movement patterns from historical and contemporary tagging data. *Mar Ecol Prog Ser* 689:109–126.
- Neat FC, Wright PJ, Zuur AF, Gibb IM, Gibb FM, Tulett D, Righton DA, Turner RJ (2005) Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). *Mar Biol* 2005 1483 148:643–654.
- Nehring D, Matthäus W (1991) Current Trends in Hydrographic and Chemical Parameters and Eutrophication in the Baltic Sea. *Int Rev der gesamten Hydrobiol und Hydrogr* 76:297–316.
- Neuenfeldt S, Andersen KH, Hinrichsen HH (2009) Some Atlantic cod *Gadus morhua* in the Baltic Sea visit hypoxic water briefly but often. *J Fish Biol* 75:290–294.
- Nordeide JT, Salvanes AG V (1988) The migration of coastal cod (*Gadus morhua* L.) tagged in a fjord of western Norway. *ICES C*.
- Peltonen H, Varjopuro R, Viitasalo M (2012) Climate Change Impacts on the Baltic Sea Fish Stocks and Fisheries - Review with a focus on Central Baltic herring, sprat and cod. *Coastline Reports* 35.
- Phillips JS, Gupta AS, Senina I, van Sebille E, Lange M, Lehodey P, Hampton J, Nicol S (2018) An individual-based model of skipjack tuna (*Katsuwonus pelamis*) movement in the tropical Pacific ocean. *Prog Oceanogr* 164:63–74.
- Pihl L (1989) Effects of oxygen depletion on demersal fish in coastal areas of the south-east Kattegat. In: *Proceedings of the 23rd European Marine Biology Symposium – Reproduction, Genetics and Distributions of Marine Organisms*. Ryland JS, Tyler P. (eds) Olsen and Olsen, Fredensborg, Denmark, p 431–439
- Righton DA, Andersen KH, Neat F, Thorsteinsson V, Steingrund P, Svedäng H, Michalsen K, Hinrichsen HH, Bendall V, Neuenfeldt S, Wright P, Jonsson P, Huse G, Van Der Kooij J, Mosegaard H, Hüsey K, Metcalfe J (2010) Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. *Mar Ecol Prog Ser* 420:1–13.
- Rogers LA, Olsen EM, Knutsen H, Stenseth NC (2014) Habitat effects on population connectivity in a coastal seascape. *Mar Ecol Prog Ser* 511:153–163.
- Rose GA (1993) Cod spawning on a migration highway in the north-west Atlantic. *Nature* 366:458–461.
- Rose GA (2005) On distributional responses of North Atlantic fish to climate change. *ICES J Mar Sci* 62:1360–1374.
- Rudolph C (2006) A model-measurements comparison of atmospheric forcing and surface fluxes of the Baltic Sea. *Christian-Albrechts-Universität*
- Salthaug A, Aanes S (2003) Catchability and the spatial distribution of fishing vessels. *Can J Fish Aquat Sci* 60.

- Saunders RL (1963) Respiration of the Atlantic Cod. J Fish Board Canada 20.
- Savchuk OP (2013) Large-scale dynamics of hypoxia in the baltic sea. In: *Handbook of Environmental Chemistry*. Springer Verlag, p 137–160
- Schaber M, Hinrichsen H, Neuenfeldt S, Voss R (2009) Hydroacoustic resolution of small-scale vertical distribution in Baltic cod *Gadus morhua*—habitat choice and limits during spawning. Mar Ecol Prog Ser 377:239–253.
- Senina I, Lehodey P, Sibert J, Hampton J (2020) Integrating tagging and fisheries data into a spatial population dynamics model to improve its predictive skills. Can J Fish Aquat Sci 77:576–593.
- Storr-Paulsen M, Anu A, Arula T, Boje J, Casini M, Degel H, Eero M, Gasyukov P, Gröhsler T, Hjelm J, Horbowy J (2014) Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 3-10 April 2014, ICES HQ, Copenhagen, Denmark.
- Stramska M, Białogrodzka J (2015) Spatial and temporal variability of sea surface temperature in the Baltic Sea based on 32-years (1982–2013) of satellite data. Oceanologia 57:223–235.
- Tomkiewicz J, Lehmann KM, John MA St. (1998) Oceanographic influences on the distribution of Baltic cod, *Gadus morhua*, during spawning in the Bornholm Basin of the Baltic Sea. Fish Oceanogr 7:48–62.
- Viitasalo M, Bonsdorff E (2022) Global climate change and the Baltic Sea ecosystem: direct and indirect effects on species, communities and ecosystem functioning. Earth Syst Dyn 13:711–747.
- Voss R, Petereit C, Schmidt JO, Lehmann A, Makarchouk A, Hinrichsen HH (2012) The spatial dimension of climate-driven temperature change in the Baltic Sea and its implication for cod and sprat early life stage survival. J Mar Syst 100–101:1–8.
- Voss R, Quaas MF, Stiasny MH, Hänsel M, Stecher Justiniano Pinto GA, Lehmann A, Reusch TBH, Schmidt JO (2019) Ecological-economic sustainability of the Baltic cod fisheries under ocean warming and acidification. J Environ Manage 238:110–118.
- Wasmund N, Nausch G, Gerth M, Busch S, Burmeister C, Hansen R, Sadkowiak B (2019) Extension of the growing season of phytoplankton in the western Baltic Sea in response to climate change. Mar Ecol Prog Ser 622:1–16.
- Winsor P, Rodhe J, Omstedt A (2001) Baltic Sea ocean climate: an analysis of 100 yr of hydrographic data with focus on the freshwater budget. Clim Res 18:5–15.

Chapter V

Synthesis and discussion



4. Synthesis of the thesis and general discussion

4.1 Summary of the thesis

Movement variability is widespread among fish populations and can differ greatly between species, life stage, and populations (e.g., see Maggs et al. 2019). This is particularly evident in Atlantic cod populations where alternative migratory strategies are prevalent, such as the more resident fjord cod and more migratory open ocean cod, where individuals of the other ecotype occasionally appear. While highly interesting phenomena, this poses issues for conservation and fisheries management and necessitates studies on movement patterns.

The Baltic cod is a highly studied species but our understanding of the movement patterns have, aside from recent large scale tagging projects, generally been limited to historical tagging studies (see Aro 1989, Bagge et al. 1994 and references therein) which sadly lacked the processing power of computers to do more advanced analyses. Combining the large databases from the historical and contemporary tagging projects, this thesis set out to improve our understanding of movement in Baltic and, to a lesser extent, North Sea cod by analysing both old and new data. The thesis provides new insights into the diverse movement behaviour of Baltic cod stocks and highlights the diversity of the different movement strategies.

The thesis has generally sought to clarify the ‘how’ and ‘why’ of movement by describing the historical movement patterns in greater detail (**Paper I-II**) and utilizing simulations based on environmentally based taxis (**Paper III**). By calculating movement-related parameters, such as those described by Jones (1966), it was shown that several stock components in both the Baltic and North Sea had different characteristic movement behaviour by way of direction-driven (advection) or dispersing (diffusion) behaviour (**Paper I**). This was done on a greater scale than in previous studies (Bagge 1973, Berner 1981) and Paper I thus essentially offers a summary of the historical tagging studies and includes contemporary data.

As by the submission of this thesis, the majority of all Baltic cod stock components are in a poor state, the Sound cod were used as a case study to study connectivity as it has historically been in a healthy state (Lindegren et al. 2013) and a National Park is currently being discussed in this area (**Paper II**). This component has been suggested to be relatively resident with some connection to the Kattegat (Svedäng et al. 2010), and the findings of this study support this. In addition, connectivity to the rest of the Baltic Sea was noted to be very low which has further implications for current stock management considerations, as the Sound is currently managed with cod in the Belt Sea and Arkona Sea. While it can be argued that historical patterns may not represent current times, the utilization of contemporary growth patterns and the recency of the study by Svedäng et al. (2010) suggests these patterns may persist into recent times. Another noteworthy finding was the potential sub-stock component structuring in the Sound, as also suggested by the findings of Svedäng et al. (2010), but this should be seen as more of an indication to be further elaborated on in a future project.

In contrast to Paper I-II, the aim of the final paper (**Paper III**) was to attempt to understand the underlying movement patterns in Baltic cod as suggested by the findings of Paper I-II, namely the temporal variations in overall movement behaviour. As the Baltic Sea has changed considerably during the time period in this study (Fonselius & Valderrama 2003) and previous studies have shown the importance of the environment in cod movement behaviour (e.g., Claireaux et al. 1995, Drinkwater 2005), it was deemed possible that movement could occur from suboptimal to optimal habitats. Simulations based on a simple random-walk model indicated that oxygen might be important for structuring Baltic cod movement, while temperature and salinity seemed less important. While it was not possible to mimic two of the four case studies, this is likely due to strong spawning behaviour and differences in ecotypes. The findings of this study suggest the need to develop a more advanced model to fully understand the complexity of cod behaviour.

4.2 Movement in eastern-Atlantic cod

4.2.1 The North Sea

In the North Sea, movement behaviour ranges from relatively resident behaviour in the central North Sea (ICES area 4.b) near Dogger Bank (Lefranc 1968) to more migratory behaviour in the southern North Sea (ICES area 4.c; Righton et al. 2007). However, in general movement appears to be characteristic of a migratory ecotype with either dispersing, or accurate or inaccurate homing (see Robichaud & Rose (2004) and references therein). In addition, general directions of movement appear to be stable through time although temporal variations in strengths of advection and diffusion occur (**Paper I**).

4.2.2 The northern North Sea (ICES area 4.a)

Cod in the northern North Sea (ICES area 4.a) appear to be relatively resident and have been suggested to maintain a metapopulation structure, preferring to remain within 100 km of spawning grounds both inside and outside the spawning season (Wright et al. 2006). Indeed, this area is characterized by relatively high diffusion with low advection, suggesting cod that move relatively far in comparison to other resident cod groups but remain within a home range (**Paper I**).

4.2.3 The central North Sea (ICES area 4.b)

In contrast, cod in the central North Sea appear to primarily exhibit some migratory behaviour, such as in the Clay Deep or Cleaver Bank (Bedford 1966). In general, dispersing and inaccurate homing appears to be common (see Robichaud & Rose (2004) and references therein). Indeed, advection appears relatively weak towards the north while diffusion is great in this area, although temporal variation can be high (**Paper I**).

4.2.4 The southern North Sea (ICES area 4.c)

The southern North Sea (ICES area 4.c) is dominated by the migratory ecotype where cod move north towards the central North Sea during the feeding season and remain at spawning grounds during the spawning season in coastal areas along the Netherlands and UK (Righton et al. 2007). This migratory behaviour is very prominent, as northerly advection is consistently high in this area with high levels of diffusion (**Paper I**), indicating high rates of movement in general.

4.2.5 The Kattegat-Skagerrak (SD 20-21)

Cod in the Kattegat (SD 21) have largely been noted to display alternative migratory strategies due to the mixture of migratory North Sea and more resident Kattegat cod (André et al. 2016, Hemmer-Hansen et al. 2020, Hüsey et al. 2021), and this appears to be a historically persistent pattern (**Paper I**). Similarly, cod located in the Skagerrak (SD 20) appear to display both ecotypes. The migratory ecotype moves into the North Sea during the spawning season (Danielssen 1969,

Svedäng et al. 2007), likely exhibiting homing behaviour (Svedäng et al. 2007), while the resident ecotype generally remains in the fjords (Kristensen et al. 2021).

4.2.6 The Baltic Sea

Movement patterns in the Baltic Sea can vary greatly between stock components. This is likely partially due to the unique features of the Baltic Sea; aside from the environmental aspects, the geography of the Baltic Sea offers a large combination of coastal and open sea areas, likely favoured by resident and migratory ecotypes, respectively. In addition, temporal variations in strengths of advection and diffusion appear to be common, although general directions appear to be stable outside the Arkona Sea (**Paper I**). These temporal variations may be caused by variations in environmental parameters, such as oxygen (**Paper III**).

Similarly to the North Sea cod, groups appearing to display either resident or migratory behaviour do not appear to switch between decades, e.g., a group with either high advection and diffusion will show either type in another decade and not switch to completely migratory or resident behaviour (**Paper I**). In summary, this means that despite temporal variations in patterns, a generally resident cod type, such as in the Belt Sea, might display high diffusion compared to other decades but this will not be comparable to a migratory cod type, e.g., the Gotland Sea, in the eastern Baltic Sea.

4.2.7 The western Baltic (SD 22-23)

In the western Baltic, the location of the spawning grounds is likely the main reason for movement being relatively stationary (Hüssy 2011), such as in the Sound cod (SD 23) which appear to either remain in or move to around the edges of the Sound (**Paper I-II**; Svedäng et al. 2010). In addition, homing has been suggested to be poorly developed (Bagge 1983).

Cod tagged in the south-western Baltic in Mecklenburg Bay (SD 22, 24) generally move west to spawn but do not favour any particular direction post-spawning (Berner 1981), most likely due to feeding grounds being spread out among coastal areas (Funk et al. 2021). This would explain the dominance of dispersing behaviour in the Belt Sea (SD 22; **Paper I**). Movement in the Belt Sea also appears to have a slight eastern tendency (**Paper I**), most likely due to the connection to the Arkona Sea.

4.2.8 The Arkona Sea (SD 24)

The Arkona Sea (SD 24) is a rather unique area, as both the western Baltic and eastern Baltic cod stocks are present in the region. As such, spawning and feeding migrations occur both towards the west in the Belt Sea and can extend all the way east to the southern Gotland Basin (Lamp & Tiews 1974, Berner 1981, Aro 2002). As a result, advection in this region can show opposite patterns depending on the dominant stock represented and dispersing behaviour appears to be high as the combined movement behaviour of two different stocks are captured (**Paper I**).

4.2.9 The eastern Baltic (SD 25-32)

In contrast to the western Baltic, the eastern Baltic is generally characterized by more migratory behaviour (**Paper I**; Mion et al. 2022) and the large degree of diffusion in this area during the feeding season has similarly been noted previously (Otterlind 1985, Aro 1989, 2002). Homing behaviour has been considered to be poorly developed, as temporal variations in cod migrations can occur to different spawning grounds (Bagge 1983, Otterlind 1985, Aro 2002). Spawning migrations have historically been rather extensive towards the major spawning grounds (Bornholm Basin (SD 25), Gdansk Deep (SD 26), Gotland Deep (SD 28.2); Bleil et al. 2009). As outlined by Aro (2002), spawning migrations occur in December-February from the southern feeding grounds in Gdansk Bay and Słupsk Furrow and the northernly feeding ground of Hanö Bay (Netzel 1968, 1974) to the Bornholm Basin. This area (SD 25) is generally characterized by low degrees of advection (**Paper I**), most likely because the feeding and spawning grounds are relatively close (Mion et al. 2022). In comparison, spawning migrations towards the Gdansk Deep occur from areas stretching from south of the Bornholm Basin to the southern Gotland Deep (Netzel 1974, Otterlind 1976, Aro 2002). Both advection and diffusion are particularly strong in this area (SD 26), indicating high rates of movement, in particular towards the west which is likely return migrations following spawning (**Paper I**). As Aro (2002) also points out, there are additional spawning migrations from other areas in the eastern Baltic and Gulf of Finland to the three major spawning grounds occurring in December-March (Otterlind 1976, Sjöblom et al. 1980, Aro & Sjöblom 1983), highlighting the complexity of eastern cod migrations. In the western Gotland Basin and the Gotland Sea (SD 27 and 28.2), advection is very strong towards the southern Baltic Sea, indicative of spawning migrations, while high diffusion further indicates a migratory ecotype with high rates of movement (**Paper I**). These patterns are similar for the Archipelago Sea (SD 29) and the Bothnian Sea (SD 30; **Paper I**). In the Gulf of Finland (SD 32), however, advection and diffusion appear to be relatively small despite the December-March migrations (**Paper I**), but this might be related to either a temporal variation, as diffusion and advection appear to be rather dependent on the decade, or the lack of data between release and recapture.

4.3 Perspectives

Movement in fish species can be complex, and the Atlantic cod is no exception. The prevalence of alternative migratory strategies, as illustrated thoroughly in this thesis (**Paper I**) and in the literature, complicates management and emphasizes the need to properly account for movement behaviours. This is especially important for stock assessments, as the addition of movement can approve models (e.g., see Goethel et al. 2011, Senina et al. 2020).

Movement behaviour in cod in both the North Sea and Baltic Sea appears to be relatively stable overall across years, suggesting inherent ecotype behaviour (**Paper I**). This behaviour appears to be so strong that a changing environment does not appear to modify it severely, although it is unknown if migration pathways are slightly modified based on changes in environmental cues (**Paper III**). However, more resident ecotypes, aside from the fjord ecotype, may be reliant on environmental cues for distributions, in particular oxygen (**Paper III**), which needs to be studied further using more advanced models, as this behaviour may also be overridden by prey patterns (Claireaux et al. 1995b, Neuenfeldt et al. 2009).

In the case of management, the importance of clarifying the variation in movement within stock components cannot be overstated. As an example, this appears to be the case around Gotland and Åland based on an overview of tagging studies where the cod appear to display both dispersing, and inaccurate and accurate homing behaviour (SD 27-28.2; see Robichaud & Rose (2004) and references therein). While this can be explained by several possibilities, such as variations in fishing distributions and tag return rates, it might also be due to this area being characterized by subpopulations with slightly different movement behaviour, and, depending on the dominant subpopulation being tagged, this might result in different overall behavioural patterns.

Indeed, the prevalence of alternative migratory behaviours within stock components may be relatively common, as is further exemplified in the Belt Sea by resident cod types from fjords and comparatively more migratory cod from open areas (**Paper I**). Furthermore, in the Sound case study as outlined in Paper II, it is possible that some sub structuring exists where northern Sound cod appear to have a greater connection to the southern Kattegat compared to more resident southern Sound cod; indeed, sub structuring has been suggested previously for cod in the Sound (Svedäng et al. 2010). While this needs to be confirmed in dedicated studies utilizing a range of tools, such as genetics, it is, combined with the ecotype aspect of Paper I, nevertheless still illustrative of the importance of clarifying the degree of movement variations within stock components. As such, while movement behaviour may appear relatively stable overall, which is promising for management, potential sub structuring may be hidden by overall patterns and management plans need to account for this in order to protect potential subpopulations.

In regards to environmentally-based movement, the apparent overall lack of adjustment to a changing environment suggests that as conditions are expected to continue to change at an alarming rate (Meier et al. 2022), the Baltic cod may not be able to survive if they fail to modify their

spatial distributions. Indeed, this is possibly one of the reasons why cod have overall disappeared from the Danish fjords, as they may have been unable to adapt to changing conditions.

This is further suggested by forecasting scenarios which have noted the sensitivity of Baltic cod during several stages of their life cycle to changes in the environment even at a low fishing pressure (Lindegren et al. 2010, Voss et al. 2019). As new species are making their way into the Baltic Sea these years, such as the Atlantic tuna (*Thunnus thynnus*), it is furthermore unknown how the ecosystem is going to change and only the future will tell how the cod may respond as the world changes.

4.4 Conclusions

The contribution of this thesis has deepened our understanding of the complexity of cod movements in the North Sea and Baltic Sea. In particular, this thesis has utilized several sources of data, such as large conventional tagging and hydrographical databases and data from surveys, to examine and clarify movement patterns in eastern Atlantic cod. In combination with simulations and several other analytical tools, new insights into historical movement patterns have been presented and can be used to inform management and future studies on cod movements. In particular, the existence and extent of ecotypes has been emphasized, including the importance of accounting for ecotype behaviour when analysing movement patterns.

While this thesis has relied greatly on conventional tagging data, which offers an overall lower resolution of movement in comparison to electronic tagging data, the quantity of data and opportunity to study historical movement patterns has nevertheless offered a unique view into cod movements in both the North Sea and the Baltic Sea through several decades. Going forward, it is clear that a combination of several methods, such as not only electronic and conventional tagging data but also genetic tools, will provide the most optimal framework to further examine not only movement patterns but also ecotype behaviour in cod.

5. References

- Andersen KH, Nielsen A, Thygesen UH, Hinrichsen HH, Neuenfeldt S (2007) Using the particle filter to geolocate Atlantic cod (*Gadus morhua*) in the Baltic Sea, with special emphasis on determining uncertainty. *Can J Fish Aquat Sci* 64.
- Anderson JL, Laurel BJ, Brown JA (2007) Diel changes in behaviour and habitat use by age-0 Atlantic cod (*Gadus morhua* L.) in the laboratory and field. *J Exp Mar Bio Ecol* 351:267–275.
- André C, Chr Stenseth N, Halvor Knutsen S, Erik Jorde P, Skogen MD, Thuróczy E, Chr N, Knutsen H, Thuróczy E (2004) Transport of North Sea cod larvae into the Skagerrak coastal. *Proc R Soc London Ser B Biol Sci* 271:1337–1344.
- André C, Svedäng H, Knutsen H, Dahle G, Jonsson P, Ring AK, Sköld M, Jorde PE (2016) Population structure in Atlantic cod in the eastern North Sea-Skagerrak-Kattegat: Early life stage dispersal and adult migration Ecology. *BMC Res Notes* 9:1–11.
- Anonymous (1972) Report of the Working Group for Assessment of Demersal Stocks in the Baltic. ICES C 1972/F:5.
- Anonymous (1988) Report of the Working Group on Assessment of Demersal Stocks in the Baltic. ICES C 20.
- Anonymous (1991) Report of the Working Group on Assessment of Demersal Stocks in the Baltic. ICES C 16.
- Anonymous (1993) Report of the Working Group on Assessment of Demersal Stocks in the Baltic. ICES C 16.
- Aro E, Sjöblom V (1983) Cod off the coast of Finland in 1974-82. ICES C 1983/J:25:17.
- Aro E (1989) A review of fish migration patterns in the Baltic. *Rap Proc-Verb Ré Cons Int Explor Mer* 190:72–96.
- Aro E (2002) Fish migration studies in the Baltic Sea - a historical review. *ICES Mar Sci Symp* 215:361–370.
- Bacheler NM, Michelot T, Cheshire RT, Shertzer KW (2019) Fine-scale movement patterns and behavioral states of gray triggerfish *Balistes caprisus* determined from acoustic telemetry and hidden Markov models. *Fish Res* 215:76–89.
- Bagge O (1969) Preliminary results of the cod-tagging experiments in the Western Baltic 1969. ICES Doc C.
- Bagge O (1973) A preliminary report on Danish cod tagging experiments in the North Sea 1971 and the Kattegat 1972. ICES C 7.
- Bagge O (1983) Migrations of transplanted cod. ICES C 16.
- Bagge O, Steffensen E (1989) Stock identification of demersal fish in the Baltic. *Rapp P-v Réunion*

Cons int Explor Mer 190:16.

Bagge O, Thurow F, Steffensen E, Bay J (1994) The Baltic cod. Dana.

Beacham TD, Bratney J, Miller KM, Le KD, Withler RE, Beacham TD, Miller KM, Le KD, Withler RE (2002) Multiple stock structure of Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador determined from genetic variation. ICES J Mar Sci 59:650–665.

Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. Science (80-) 296:1692–1694.

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–664.

Beaugrand G, Kirby RR (2010) Climate, plankton and cod. Glob Chang Biol 16:1268–1280.

Bedford B. (1966) English cod tagging experiments in the North Sea. Int Counc Explor Sea.

Bendtsen J, Söderkvist J, Dahl K, Hansen JL, Reker J (2007) Model Simulations of Blue Corridors in the Baltic Sea. Balanc interim Rep 9.

Bendtsen J, Hansen JLS (2013) Effects of global warming on hypoxia in the Baltic Sea-North Sea transition zone. Ecol Modell 264:17–26.

Berg PR, Star B, Pampoulie C, Sodeland M, Barth JMI, Knutsen H, Jakobsen KS, Jentoft S (2016) Three chromosomal rearrangements promote genomic divergence between migratory and stationary ecotypes of Atlantic cod. Sci Rep 6:1–12.

Berg PR, Star B, Pampoulie C, Bradbury IR, Bentzen P, Hutchings JA, Jentoft S, Jakobsen KS (2017) Trans-oceanic genomic divergence of Atlantic cod ecotypes is associated with large inversions. Heredity (Edinb) 119:418–428.

Bergstad OA, Jørgensen T, Knutsen JA, Berge JA (2008) Site fidelity of Atlantic cod *Gadus morhua* L. as deduced from telemetry and stable isotope studies. J Fish Biol 72:131–142.

Berner M (1981) Dislocation parameters of tagging experiments on cod in the Baltic (Sub-divisions 22–25) from 1959–1975. ICES Doc C.

Bijma J, Pörtner HO, Yesson C, Rogers AD (2013) Climate change and the oceans – What does the future hold? Mar Pollut Bull 74:495–505.

Björnsson B, Steinarsson A, Oddgeirsson M (2001) Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). ICES J Mar Sci 58:29–38.

Björnsson B, Karlsson H, Thorsteinsson V, Solmundsson J (2011) Should all fish in mark–recapture experiments be double-tagged? Lessons learned from tagging coastal cod (*Gadus morhua*). ICES J Mar Sci 68:603–610.

Bleil M, Oeberst R, Urrutia P (2009) Seasonal maturity development of Baltic cod in different spawning areas: importance of the Arkona Sea for the summer spawning stock. J Appl Ichthyol 25:10–17.

Bradbury IR, Laurel BJ, Robichaud D, Rose GA, Snelgrove PVR, Gregory RS, Cote D, Windle MJS (2008) Discrete spatial dynamics in a marine broadcast spawner: Re-evaluating scales of

- connectivity and habitat associations in Atlantic cod (*Gadus morhua* L.) in coastal Newfoundland. *Fish Res* 91:299–309.
- Brander K (2000) Effects of environmental variability on growth and recruitment in cod (*Gadus morhua*) using a comparative approach. *Oceanol Acta* 23:485–496.
- Brander K (2020) Reduced growth in Baltic Sea cod may be due to mild hypoxia. *ICES J Mar Sci* 77:2003–2005.
- Brander KM (1995) The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES J Mar Sci* 52:1–10.
- Braun CD, Galuardi B, Thorrold SR (2018) HMMoce: An R package for improved geolocation of archival-tagged fishes using a hidden Markov method. *Methods Ecol Evol* 9:1212–1220.
- Le Bris A, Fréchet A, Galbraith PS, Wroblewski JS (2012) Partial migration in the northern Gulf of St. Lawrence Atlantic cod population. *ICES C* 15.
- Le Bris A, Fréchet A, Galbraith PS, Wroblewski JS (2013) Evidence for alternative migratory behaviours in the northern Gulf of St Lawrence population of Atlantic cod (*Gadus morhua* L.). *ICES J Mar Sci* 70:793–804.
- Bryan DR, McDermott SF, Nielsen JK, Fraser D, Rand KM (2021) Seasonal migratory patterns of Pacific cod (*Gadus macrocephalus*) in the Aleutian Islands. *Anim Biotelemetry* 9:1–18.
- Carstensen J, Andersen JH, Gustafsson BG, Conley DJ (2014) Deoxygenation of the Baltic Sea during the last century. *Proc Natl Acad Sci* 111:5628–5633.
- Casini M, Hansson M, Orio A, Limburg K (2021) Changes in population depth distribution and oxygen stratification are involved in the current low condition of the eastern Baltic Sea cod (*Gadus morhua*). *Biogeosciences* 18:1321–1331.
- Castonguay M, Rollet C, Fréchet A, Gagnon P, Gilbert D, Brêthes JC (1999) Distribution changes of Atlantic cod (*Gadus morhua* L.) in the northern Gulf of St Lawrence in relation to an oceanic cooling. *ICES J Mar Sci* 56:333–344.
- Chabot D, Dutil J (1999) Reduced growth of Atlantic cod in non-lethal hypoxic conditions. *J Fish Biol* 55:472–491.
- Chapman BB, Brönmark C, Nilsson JÅ, Hansson LA (2011) The ecology and evolution of partial migration. *Oikos* 120:1764–1775.
- Chapman BB, Hulthén K, Brodersen J, Nilsson PA, Skov C, Hansson LA, Brönmark C (2012a) Partial migration in fishes: causes and consequences. *J Fish Biol* 81:456–478.
- Chapman BB, Skov C, Hulthén K, Brodersen J, Nilsson PA, Hansson LA, Brönmark C (2012b) Partial migration in fishes: definitions, methodologies and taxonomic distribution. *J Fish Biol* 81:479–499.
- Claireaux G, Webber D, Kerr S, Boutilier R (1995a) Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating temperature conditions. *J Exp Biol* 198:49–60.
- Claireaux G, Webber DM, Kerr SR, Boutilier RG (1995b) Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating salinity and oxygenation conditions.

- J Exp Biol 198:61–69.
- Curry R, Mauritzen C (2005) Dilution of the Northern North Atlantic Ocean in recent decades. *Science* (80-) 308:1772–1774.
- Cushing D (1984) The gadoid outburst in the North Sea. *ICES J Mar Sci* 41:159–166.
- Dahlke FT, Leo E, Mark FC, Pörtner HO, Bickmeyer U, Frickenhaus S, Storch D (2016) Effects of ocean acidification increase embryonic sensitivity to thermal extremes in Atlantic cod, *Gadus morhua*. *Glob Chang Biol* 23:1499–1510.
- Danielssen DS (1969) On the migrations of the cod in the Skagerak shown by tagging experiments in the period 1954–1965. *FiskDir Skr Ser HavUnders* 15:331–338.
- DFO (2011) Assessment of capelin in SA2 + Div. 3KL in 2010. *Can Sci Advis Secr Sci Advis Rep* 2010:16.
- Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *Science* (80-) 321:926–929.
- Dickson RR, Meincke J, Malmberg SA, Lee AJ (1988) The “great salinity anomaly” in the Northern North Atlantic 1968–1982. *Prog Oceanogr* 20:103–151.
- Drinkwater KF (2005) The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES J Mar Sci* 62:1327–1337.
- Eero M, Hemmer-Hansen J, Hüsey K (2014) Implications of stock recovery for a neighbouring management unit: experience from the Baltic cod. *ICES J Mar Sci* 71:1458–1466.
- Engelhard GH, Righton DA, Pinnegar JK (2014) Climate change and fishing: A century of shifting distribution in North Sea cod. *Glob Chang Biol* 20:2473–2483.
- Fevolden SE, Pogson GH (1997) Genetic divergence at the synaptophysin (Syp I) locus among Norwegian coastal and north-east Arctic populations of Atlantic cod. *J Fish Biol* 51:895–908.
- Folkvord A (1997) Ontogeny of cannibalism in larval and juvenile fishes with special emphasis on Atlantic cod. In: *Early Life History and Recruitment in Fish Populations*. Springer, Dordrecht, p 251–278
- Fonselius S, Valderrama J (2003) One hundred years of hydrographic measurements in the Baltic Sea. *J Sea Res* 49:229–241.
- Freitas C, Olsen EM, Moland E, Ciannelli L, Knutsen H (2015) Behavioral responses of Atlantic cod to sea temperature changes. *Ecol Evol* 5:2070–2083.
- Frommel AY, Stiebens V, Clemmesen C, Havenhand J (2010) Effect of ocean acidification on marine fish sperm (Baltic cod: *Gadus morhua*). *Biogeosciences* 7:3915–3919.
- Frommel AY, Maneja R, Lowe D, Malzahn AM, Geffen AJ, Folkvord A, Piatkowski U, Reusch TBH, Clemmesen C (2011) Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. *Nat Clim Chang* 2:42–46.
- Frommel AY, Schubert A, Piatkowski U, Clemmesen C (2012) Egg and early larval stages of Baltic cod, *Gadus morhua*, are robust to high levels of ocean acidification. *Mar Biol* 160:1825–1834.

- Funk S, Krumme U, Temming A, Möllmann C (2020) Gillnet fishers' knowledge reveals seasonality in depth and habitat use of cod (*Gadus morhua*) in the Western Baltic Sea. *ICES J Mar Sci* 77:1816–1829.
- Funk S, Frelat R, Möllmann C, Temming A, Krumme U (2021) The forgotten feeding ground: patterns in seasonal and depth-specific food intake of adult cod *Gadus morhua* in the western Baltic Sea. *J Fish Biol* 98:707–722.
- Goddard S V., Wroblewski JS, Taggart CT, Howse KA, Bailey WL, Kao MH, Fletcher GL (1994) Overwintering of adult northern Atlantic cod (*Gadus morhua*) in cold inshore waters as evidenced by plasma antifreeze glycoprotein levels. *Can J Fish Aquat Sci* 51:2834–2842.
- Godø O. (1984) Migration, mingling and homing of north-east Arctic cod from two separated spawning grounds. In: *Reproduction and Recruitment of Arctic Cod*. Godø OR, Tilseth S (eds) p 298–302
- Goethel DR, Quinn TJ, Cadrin SX (2011) Incorporating Spatial Structure in Stock Assessment: Movement Modeling in Marine Fish Population Dynamics. *Rev Fish Sci* 19:119–136.
- Gotceitas V, Fraser S, Brown JA (1995) Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. *Mar Biol* 1995 1233 123:421–430.
- Grabowski TB, Thorsteinsson V, McAdam BJ, Marteinsdóttir G (2011) Evidence of Segregated Spawning in a Single Marine Fish Stock: Sympatric Divergence of Ecotypes in Icelandic Cod? *PLoS One* 6.
- Green JM, Wroblewski JS (2000) Movement patterns of Atlantic cod in Gilbert Bay, Labrador: evidence for bay residency and spawning site fidelity. *J Mar Biol Assoc United Kingdom* 80:1077–1085.
- Greene CH, Pershing AJ (2007) Climate drives sea change. *Science* (80-) 315:1084–1085.
- Grüss A, Kaplan DM, Guénette S, Roberts CM, Botsford LW (2011) Consequences of adult and juvenile movement for marine protected areas. *Biol Conserv* 144:692–702.
- Haase S, Krumme U, Gräwe U, Braun CD, Temming A (2021) Validation approaches of a geolocation framework to reconstruct movements of demersal fish equipped with data storage tags in a stratified environment. *Fish Res* 237:105884.
- Hansen P. (1949) Studies on the biology of the cod in Greenland waters. *Rapp Procès-Verbaux des Réunions du Cons Perm Int pour l'Exploration la Mer* 123:1–83.
- Harvey A (1990) Forecasting, structural time series models and the Kalman Filter. Cambridge University Press.
- Hastings A, Harrison S (1994) Metapopulation Dynamics and Genetics. *Annu Rev Ecol Syst* 25:167–188.
- Heincke F (1913) Untersuchungen über die Scholle-Generalbericht I. Schollenfischerei und Schonmassregeln. Vorläufige kurze Uebersicht über die wichtigsten Ergebnisse des Berichts. *Rapp Proc Verb Réun ICES* 16:1–70.
- Hemmer-Hansen J, Hüsey K, Vinther M, Albertsen C, Storr-Paulsen M, Eero M (2020) Sustainable

- management of Kattegat cod; better know-ledge of stock components and migration. DTU Aqua Rep 357–2020.
- Hinrichsen HH, Lehmann A, Petereit C, Nissling A, Ustups D, Bergström U, Hüsey K (2016) Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. *Prog Oceanogr* 143:13–25.
- Hu L, Wroblewski J (2009) Conserving a subpopulation of the northern Atlantic cod metapopulation with a marine protected area. *Aquat Conserv Mar Freshw Ecosyst* 19:178.
- Hüsey K (2011) Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. *ICES J Mar Sci* 68:1459–1471.
- Hüsey K, Casini M, Haase S, Hilvarsson A, Horbowy J, Krüger-Johnsen, M. Krumme U, Limburg KE, McQueen K, Mion M, Olesen HJ (2020) Tagging Baltic Cod – TABACOD: Eastern Baltic cod: Solving the ageing and stock assessment problems with combined state-of-the-art tagging methods. DTU Aqua Rep 368–2020.
- Hüsey K, Albertsen CM, Hemmer-Hansen J, Vinther M, Serre SH, Thomsen TB, Eero M (2021) Where do you come from, where do you go: Early life stage drift and migrations of cod inferred from otolith microchemistry and genetic population assignment. *Can J Fish Aquat Sci*.
- Hutchings JA, Myers RA, Lilly GR (1993) Geographic Variation in the Spawning of Atlantic Cod, *Gadus morhua*, in the Northwest Atlantic. *Can J Fish Aquat Sci* 50:2457–2467.
- Hutchings JA, Myers RA (1994) Timing of cod reproduction - Interannual variability and the influence of temperature. *Mar Ecol Prog Ser* 108:21–32.
- Huwer B, Hinrichsen HH, Hüsey K, Eero M (2016) Connectivity of larval cod in the transition area between North Sea and Baltic Sea and potential implications for fisheries management. *ICES J Mar Sci* 73:1815–1824.
- ICES (2014) Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 3–10 April 2014 ICES HQ.
- ICES (2019) Cod (*Gadus morhua*) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). Rep ICES Advis Committee, 2019 ICES Advice 2019, cod2747d20 20:1–15.
- ICES (2020) Cod (*Gadus morhua*) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). Rep ICES Advis Comm.
- ICES (2022a) Cod (*Gadus morhua*) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). Rep ICES Advis Comm.
- ICES (2022b) Cod (*Gadus morhua*) in Subdivision 21 (Kattegat). Rep ICES Advis Comm.
- ICES (2022c) Cod (*Gadus morhua*) in subdivisions 22–24, western Baltic stock (western Baltic Sea). Rep ICES Advis Comm.
- ICES (2022d) Cod (*Gadus morhua*) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). Rep ICES Advis Comm.

- Jakobsson M, Stranne C, O'Regan M, Greenwood S, Gustafsson B, Humborg C, Weidner E (2019) Bathymetric properties of the Baltic Sea. *Ocean Sci* 15:905–924.
- Jensen AS, Hansen PM (1931) Investigations on the Greenland cod (*Gadus callarias* L.). *Rapp Procès-Verbaux des Réunions du Cons Perm Int pour l'Exploration la Mer* 72:1–41.
- Jobling M (1988) A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. *Aquaculture* 70:1–19.
- Johansen T, Westgaard JI, Seliussen BB, Nedreaas K, Dahle G, Glover KA, Kvalsund R, Aglen A (2018) “Real-time” genetic monitoring of a commercial fishery on the doorstep of an MPA reveals unique insights into the interaction between coastal and migratory forms of the Atlantic cod. *ICES J Mar Sci* 75:1093–1104.
- Jones R (1966) *Manual of Methods for fish stock assessment, part IV - Marking*. Rome.
- Jørgensen C, Dunlop ES, Opdal AF, Fiksen Ø (2008) The evolution of spawning migrations: State dependence and fishing-induced changes. *Ecology* 89:3436–3448.
- Jørgensen KEM, Neuheimer AB, Jorde PE, Knutsen H, Grønkjær P (2020) Settlement processes induce differences in daily growth rates between two co-existing ecotypes of juvenile cod *Gadus morhua*. *Mar Ecol Prog Ser* 650:175–189.
- Jørgensen OA, Storr-Paulsen M, Ringdahl K, Lövgren J, Gröhsler T, Oberst R, Schaber M, Bergenius J, Pönni J, Aho T, Holmgren N (2011) Report of the Baltic Fisheries Assessment Working Group (WGBFAS). ICES.
- Jørstad KE, Nævdal G (1989) Genetic variation and population structure of cod, *Gadus morhua* L., in some fjords in northern Norway. *J Fish Biol* 35:245–252.
- Karlsen BO, Klingan K, Emblem Å, Jørgensen TE, Jueterbock A, Furmanek T, Hoarau G, Johansen SD, Nordeide JT, Moum T. (2013) Genomic divergence between the migratory and stationary ecotypes of Atlantic cod. *Mol Ecol* 22:5098–5111.
- Kell LT, Pilling GM, O'Brien CM (2005) Implications of climate change for the management of North Sea cod (*Gadus morhua*). *ICES J Mar Sci* 62:1483–1491.
- Kerr LA, Secor DH (2010) Latent effects of early life history on partial migration for an estuarine-dependent fish. *Environ Biol Fishes* 2010 893 89:479–492.
- Kijewska A, Kalamarz-Kubiak H, Arciszewski B, Guellard T, Petereit C, Wenne R (2016) Adaptation to salinity in Atlantic cod from different regions of the Baltic Sea. *J Exp Mar Bio Ecol* 478:62–67.
- Kirubakaran TG, Grove H, Kent MP, Sandve SR, Baranski M, Nome T, De Rosa MC, Righino B, Johansen T, Otterå H, Sonesson A, Lien S, Andersen Ø (2016) Two adjacent inversions maintain genomic differentiation between migratory and stationary ecotypes of Atlantic cod. *Mol Ecol* 25:2130–2143.
- Kitamura T, Kume M, Takahashi H, Goto A (2006) Juvenile bimodal length distribution and sea-run migration of the lower modal group in the Pacific Ocean form of three-spined stickleback. *J Fish Biol* 69:1245–1250.
- Knutsen H, Jorde PE, André C, Stenseth NC (2003) Fine-scaled geographical population

- structuring in a highly mobile marine species: The Atlantic cod. *Mol Ecol* 12:385–394.
- Knutsen H, Jorde PE, Hutchings JA, Hemmer-Hansen J, Grønkjær P, Jørgensen KEM, André C, Sodeland M, Albretsen J, Olsen EM (2018) Stable coexistence of genetically divergent Atlantic cod ecotypes at multiple spatial scales. *Evol Appl* 11:1527–1539.
- Kristensen ML, Olsen EM, Moland E, Knutsen H, Grønkjær P, Koed A, Källo K, Aarestrup K (2021) Disparate movement behavior and feeding ecology in sympatric ecotypes of Atlantic cod. *Ecol Evol* 11:11477–11490.
- Kristiansen T, Stock C, Drinkwater KF, Curchitser EN (2014) Mechanistic insights into the effects of climate change on larval cod. *Glob Chang Biol* 20:1559–1584.
- Krohn M, Reidy S, Kerr S (1997) Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). *Can J Fish Aquat Sci* 54:113–121.
- Krumsick KJ, Rose GA (2012) Atlantic cod (*Gadus morhua*) feed during spawning off Newfoundland and Labrador. *ICES J Mar Sci* 69:1701–1709.
- Kulatska N, Neuenfeldt S, Beier U, Elvarsson BP, Wennhage H, Stefansson G, Bartolino V (2019) Understanding ontogenetic and temporal variability of Eastern Baltic cod diet using a multispecies model and stomach data. *Fish Res* 211:338–349.
- Lambert Y, Dutil JD, Munro J (1994) Effects of Intermediate and Low Salinity Conditions on Growth Rate and Food Conversion of Atlantic Cod (*Gadus morhua*). *Can J Fish Aquat Sci* 51.
- Lambert Y, Dutil J (1997) Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)? . *Can J Fish Aquat Sci* 54:104–112.
- Lamp F, Tiews K (1974) Progress report of comparative tagging experiments on the Baltic cod. *Rapp Procès- Verbaux des Réunions du Cons Int pour l'Ex ploration la Mer*:47–50.
- Larsen G, Hemmingsen W, MacKenzie K, Lysne D (1997) A population study of cod, *Gadus morhua* L., in northern Norway using otolith structure and parasite tags. *Fish Res* 32:13–20.
- Larsen PF, Nielsen EE, Meier K, Olsvik PA, Hansen MM, Loeschcke V (2012) Differences in salinity tolerance and gene expression between two populations of Atlantic cod (*Gadus morhua*) in response to salinity stress. *Biochem Genet* 50:454–466.
- Laurel BJ, Gregory RS, Brown JA, Hancock JK, Schneider DC (2004) Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. *Mar Ecol Prog Ser* 272:257–270.
- Laurel BJ, Brown JA (2006) Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. *J Exp Mar Bio Ecol* 329:34–46.
- Laurence GC (1978) Comparative growth, respiration and delayed feeding abilities of larval cod (*Gadus morhua*) and Haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. *Mar Biol* 1978 501 50:1–7.
- Lawson JW, Magalhães AM, Miller EH (1998) Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. *Mar Ecol Prog Ser* 164:13–20.

- Lea JSE, Wetherbee BM, Queiroz N, Burnie N, Aming C, Sousa LL, Mucientes GR, Humphries NE, Harvey GM, Sims DW, Shivji MS (2015) Repeated, long-distance migrations by a philopatric predator targeting highly contrasting ecosystems. *Sci Rep* 5:1–11.
- Lea JSE, Wetherbee BM, Sousa LL, Aming C, Burnie N, Humphries NE, Queiroz N, Harvey GM, Sims DW, Shivji MS (2018) Ontogenetic partial migration is associated with environmental drivers and influences fisheries interactions in a marine predator. *ICES J Mar Sci* 75:1383–1392.
- Lear WH, Green JM (1984) Migration of the “Northern” Atlantic Cod and the Mechanisms Involved. In: *Mechanisms of Migration in Fishes*. Springer, Boston, MA, p 309–315
- Lefranc G (1968) Results of cod tagging carried out in June 1966 in the Dogger Bank area. *Sci Fish* 170:1–11.
- Levins R (1970) Extinction. In: *Some Mathematical Problems in Biology*. Desternhaber M (ed) American Mathematical Society, Providence, p 77–107
- Lewandoski SA, Bishop MA, McKinzie MK (2018) Evaluating Pacific cod migratory behavior and site fidelity in a fjord environment using acoustic telemetry¹. *Can J Fish Aquat Sci* 75:2084–2095.
- Lindgren M, Möllmann C, Nielsen A, Brander K, MacKenzie BR, Stenseth NC (2010) Ecological forecasting under climate change: the case of Baltic cod. *Proc R Soc B Biol Sci* 277:2121–2130.
- Lindgren M, Waldo S, Nilsson PA, Svedäng H, Persson A (2013) Towards sustainable fisheries of the Öresund cod (*Gadus morhua*) through sub-stock-specific assessment and management recommendations. *ICES J Mar Sci* 70:1140–1150.
- Linehan JE, Gregory RS, Schneider DC (2001) Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. *J Exp Mar Bio Ecol* 263:25–44.
- Maggs JQ, Cowley PD, Porter SN, Childs AR (2019) Should I stay or should I go? Intra-population variability in movement behaviour of wide-ranging and resident coastal fishes. *Mar Ecol Prog Ser* 619:111–124.
- Magill SH, Sayer MDJ (2004) The effect of reduced temperature and salinity on the blood physiology of juvenile Atlantic cod. *J Fish Biol* 64:1193–1205.
- Maneja RH, Frommel AY, Geffen AJ, Folkvord A, Piatkowski U, Chang MY, Clemmesen C (2013) Effects of ocean acidification on the calcification of otoliths of larval Atlantic cod *Gadus morhua*. *Mar Ecol Prog Ser* 477:251–258.
- Meier HEM, Dieterich C, Gröger M, Dutheil C, Börgel F, Safonova K, Christensen OB, Kjellström E (2022) Oceanographic regional climate projections for the Baltic Sea until 2100. *Earth Syst Dyn* 13:159–199.
- Mello LGS, Rose GA (2005) Seasonal growth of Atlantic cod: effects of temperature, feeding and reproduction. *J Fish Biol* 67:149–170.
- Mion M, Griffiths C, Bartolino V, Haase S, Hilvarsson A, Hüsey K, Krüger-Johnsen M, Krumme U, Lundgreen R, Lövgren J, McQueen K, Plikshs M, Radtke K, Raitaniemi J, Casini M (2022) New perspectives on Eastern Baltic cod movement patterns from historical and contemporary

- tagging data. *Mar Ecol Prog Ser* 689:109–126.
- Morgan MJ, Rideout RM, Colbourne EB (2010) Impact of environmental temperature on Atlantic cod *Gadus morhua* energy allocation to growth, condition and reproduction. *Mar Ecol Prog Ser* 404:185–195.
- Morris CJ, Green JM (2002) Biological characteristics of a resident population of Atlantic cod (*Gadus morhua* L.) in southern Labrador. *ICES J Mar Sci* 59:666–678.
- Morris CJ, Green JM (2014) MPA regulations should incorporate adaptive management—The case of Gilbert Bay Labrador Atlantic cod (*Gadus morhua*). *Mar Policy* 49:20–28.
- Morris CJ, Green JM, Snelgrove PVR, Pennell CJ, Ollerhead LMN (2014) Temporal and spatial migration of Atlantic cod (*Gadus morhua*) inside and outside a marine protected area and evidence for the role of prior experience in homing. *Can J Fish Aquat Sci* 71:1704–1712.
- Mullowney DRJ, Rose GA (2014) Is recovery of northern cod limited by poor feeding? The capelin hypothesis revisited. *ICES J Mar Sci* 71:784–793.
- Munday PL, Dixon DL, Donelson JM, Jones GP, Pratchett MS, Devitsina G V., Døving KB (2009) Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proc Natl Acad Sci U S A* 106:1848–1852.
- Myksvoll MS, Sundby S, Ådlandsvik B, Vikebø FB (2011) Retention of coastal cod eggs in a fjord caused by interactions between egg buoyancy and circulation pattern. *Mar Coast Fish* 3:279–294.
- Myksvoll M, Jung K, Albretsen J, Sundby S (2014) Modelling dispersal of eggs and quantifying connectivity among Norwegian coastal cod subpopulations. *ICES J Mar Sci* 71:957–969.
- Netzel J (1968) Polish cod tagging experiments in the region of Slupsk Furrow in the years 1957/1963. *ICES C* 1968:13.
- Netzel J (1974) Polish cod tagging experiments in the Baltic in 1969 and 1970. *Rapp Procès-Verbaux des Réunions du Cons Int pour l'Exploration la Mer* 166:40–46.
- Neuenfeldt S, Köster FW (2000) Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. *ICES J Mar Sci* 57:300–309.
- Neuenfeldt S, Hinrichsen HH, Nielsen A (2004) A method to geolocate eastern Baltic cod by using Data Storage Tags (DSTs). *ICES C* L:06.
- Neuenfeldt S, Hinrichsen HH, Nielsen A, Andersen KH (2007) Reconstructing migrations of individual cod (*Gadus morhua* L.) in the Baltic Sea by using electronic data storage tags. *Fish Oceanogr* 16:526–535.
- Neuenfeldt S, Andersen KH, Hinrichsen HH (2009) Some Atlantic cod *Gadus morhua* in the Baltic Sea visit hypoxic water briefly but often. *J Fish Biol* 75:290–294.
- Nielsen B, Hüsey K, Neuenfeldt S, Tomkiewicz J, Behrens JW, Andersen KH (2013) Individual behaviour of Baltic cod *Gadus morhua* in relation to sex and reproductive state. *Aquat Biol* 18:197–207.
- Nissling A (1994) Survival of eggs and yolk-sac larvae of Baltic cod (*Gadus morhua* L.) at low

- oxygen levels in different salinities. ICES Mar Sci Symp 198:626.
- Nissling A, Westin L (1997) Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. *Mar Ecol Prog Ser* 152:261–271.
- Nordeide JT, Johansen SD, Jørgensen TE, Karlsen BO, Moum T (2011) Population connectivity among migratory and stationary cod *Gadus morhua* in the Northeast Atlantic—a review of 80 years of study. *Mar Ecol Prog Ser* 435:269–283.
- Núñez-Riboni I, Taylor MH, Kempf A, Püts M, Mathis M, Ojaveer H (2019) Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (*Gadus morhua*) under climate change. *ICES J Mar Sci* 76:2389–2403.
- Otterlind G (1965) Transportation experiments with cod in the Baltic-Belt Seas. ICES C 163.
- Otterlind G (1976) Fish stocks and fish migration in the Baltic. *Ambio Spec Rep* 4:89–101.
- Otterlind G (1985) Cod migration and transplantation experiments in the Baltic. *J Appl Ichthyol* 1:3–16.
- Pattyn F, Ritz C, Hanna E, Asay-Davis X, DeConto R, Durand G, Favier L, Fettweis X, Goelzer H, Golledge NR, Kuipers Munneke P, Lenaerts JTM, Nowicki S, Payne AJ, Robinson A, Seroussi H, Trusel LD, van den Broeke M (2018) The Greenland and Antarctic ice sheets under 1.5 °C global warming. *Nat Clim Chang* 8:1053–1061.
- Payo-Payo A, Acker P, Bocedi G, Travis JMJ, Burthe SJ, Harris MP, Wanless S, Newell M, Daunt F, Reid JM (2022) Modelling the responses of partially-migratory metapopulations to changing seasonal migration rates: from theory to data. *J Anim Ecol*.
- Pedersen MW, Righton D, Thygesen UH, Andersen KH, Madsen H (2008) Geolocation of North Sea cod (*Gadus morhua*) using hidden Markov models and behavioural switching. *Can J Fish Aquat Sci* 65:2367–2377.
- Pepin P, Orr DC, Anderson JT (1997) Time to hatch and larval size in relation to temperature and egg size in atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 54:2–10.
- Petersen MF, Steffensen JF (2003) Preferred temperature of juvenile Atlantic cod *Gadus morhua* with different haemoglobin genotypes at normoxia and moderate hypoxia. *J Exp Biol* 206:359–364.
- Pethon P (1985) Aschehougs store fiskeboks.
- Pihl L, Ulmestrand M (1993) Migration pattern of juvenile cod (*Gadus morhua*) on the Swedish west coast. *ICES J Mar Sci* 50:63–70.
- Planque B, Frédou T (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 56.
- Pope JG, Macer CT (1996) An evaluation of the stock structure of North Sea cod, haddock, and whiting since 1920, together with a consideration of the impacts of fisheries and predation effects on their biomass and recruitment. *ICES J Mar Sci* 53:1157–1169.
- Poulsen E (1931) Biological investigations upon the cod in Danish waters. C.A. Reitzels Forlag.

- Rideout RM, Rose GA, Burton MPM (2005) Skipped spawning in female iteroparous fishes. *Fish Fish* 6:50–72.
- Righton D, Quayle VA, Hetherington S, Burt G (2007) Movements and distribution of cod (*Gadus morhua*) in the southern North Sea and English Channel: Results from conventional and electronic tagging experiments. *J Mar Biol Assoc United Kingdom* 87:599–613.
- Rijnsdorp A, Peck M, Engelhard G, Möllman C, Pinnegar J (2009) Resolving the effect of climate change on fish populations. *ICES J Mar Sci* 66:1570–1583.
- Robichaud D, Rose GA (2004) Migratory behaviour and range in Atlantic cod: Inference from a century of tagging. *Fish Fish* 5:185–214.
- Rose GA (1993) Cod spawning on a migration highway in the north-west Atlantic. *Nature* 366:458–461.
- Rose GA, Nelson RJ, Mello LGS (2011) Isolation or metapopulation: Whence and whither the Smith Sound cod? *Can J Fish Aquat Sci* 68:152–169.
- Ruzzante DE, Taggart CT, Cook D, Goddard S (1996) Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: Microsatellite DNA variation and antifreeze level. *Can J Fish Aquat Sci* 53:634–645.
- Sæmundsson B (1934) Probable influence of changes in temperature on the marine fauna of Iceland. *Rapp Procès-Verbaux des Réunions du Cons Perm Int pour l'Exploration la Mer* 86:1–6.
- Schade FM, Weist P, Krumme U (2019) Evaluation of four stock discrimination methods to assign individuals from mixed-stock fisheries using genetically validated baseline samples. *Mar Ecol Prog Ser* 627:125–139.
- Schijns R, Froese R, Hutchings JA, Pauly D (2021) Five centuries of cod catches in Eastern Canada. *ICES J Mar Sci* 78:2675–2683.
- Schurmann H, Steffensen J (1992) Lethal oxygen levels at different temperatures and the preferred temperature during hypoxia of the Atlantic cod, *Gadus morhua* L. *J Fish Biol* 41:927–934.
- Senina I, Lehodey P, Sibert J, Hampton J (2020) Integrating tagging and fisheries data into a spatial population dynamics model to improve its predictive skills. *Can J Fish Aquat Sci* 77:576–593.
- Shaw AK, Levin SA, Shaw AK, Levin SA (2011) To breed or not to breed: a model of partial migration. *Oikos* 120:1871–1879.
- Sjöblom V, Aro E, Suuronen P (1980) Migrations, mortality and growth of cod in the northern Baltic Sea. *ICES C* 1980/J:8:15.
- Skjærraasen JE, Meager J, Karlsen Ø, Hutchings J, Fernö A (2011) Extreme spawning-site fidelity in Atlantic cod. *ICES J Mar Sci du Cons* 68.
- Skjærraasen JE, Nash RDM, Korsbrekke K, Fonn M, Nilsen T, Kennedy J, Nedreaas KH, Thorsen A, Witthames PR, Geffen AJ, Høie H, Kjesbu OS (2012) Frequent skipped spawning in the world's largest cod population. *Proc Natl Acad Sci U S A* 109:8995–8999.
- Skov C, Baktoft H, Brodersen J, Brönmark C, Chapman BB, Hansson LA, Anders Nilsson P (2011)

- Sizing up your enemy: individual predation vulnerability predicts migratory probability. *Proc R Soc B Biol Sci* 278:1414–1418.
- Smedbol RK, Wroblewski JS (2002) Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a groundfish population. *Fish Res* 55:161–174.
- Speers-Roesch B, Norin T, Driedzic WR (2018) The benefit of being still: energy savings during winter dormancy in fish come from inactivity and the cold, not from metabolic rate depression. *Proc R Soc B Biol Sci* 285.
- Staveley TAB, Jacoby DMP, Perry D, van der Meijs F, Lagenfelt I, Cremle M, Gullström M (2019) Sea surface temperature dictates movement and habitat connectivity of Atlantic cod in a coastal fjord system. *Ecol Evol* 9:9076–9086.
- Stiasny MH, Mittermayer FH, Sswat M, Voss R, Jutfelt F, Chierici M, Puvanendran V, Mortensen A, Reusch TBH, Clemmesen C (2016) Ocean Acidification Effects on Atlantic Cod Larval Survival and Recruitment to the Fished Population. *PLoS One* 11.
- Stiasny MH, Sswat M, Mittermayer FH, Falk-Petersen IB, Schnell NK, Puvanendran V, Mortensen A, Reusch TBH, Clemmesen C (2019) Divergent responses of Atlantic cod to ocean acidification and food limitation. *Glob Chang Biol* 25:839–849.
- Storr-Paulsen M, Anu A, Arula T, Boje J, Casini M, Degel H, Eero M, Gasyukov P, Gröhsler T, Hjelm J, Horbowy J (2014) Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 3-10 April 2014, ICES HQ, Copenhagen, Denmark.
- Stortini CH, Chabot D, Shackell NL (2017) Marine species in ambient low-oxygen regions subject to double jeopardy impacts of climate change. *Glob Chang Biol* 23:2284–2296.
- Sundby S (2000) Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia* 85:277–298.
- Sundby S, Nakken O (2008) Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES J Mar Sci* 65:953–962.
- Sundnes G (1957) On the Transport of Live Cod and Coalfish. *ICES J Mar Sci* 22:191–196.
- Svedäng H (2003) The inshore demersal fish community on the Swedish Skagerrak coast: Regulation by recruitment from offshore sources. *ICES J Mar Sci*.
- Svedäng H, Bardon G (2003) Spatial and temporal aspects of the decline in cod (*Gadus morhua* L.) abundance in the Kattegat and eastern Skagerrak. *ICES J Mar Sci* 60:32–37.
- Svedäng H, Righton D, Jonsson P (2007) Migratory behaviour of Atlantic cod *Gadus morhua*: Natal homing is the prime stock-separating mechanism. *Mar Ecol Prog Ser*.
- Svedäng H, André C, Jonsson P, Elfman M, Limburg KE (2010) Migratory behaviour and otolith chemistry suggest fine-scale sub-population structure within a genetically homogenous Atlantic Cod population. *Environ Biol Fishes* 89:383–397.
- Svedäng H, Barth JMI, Svenson A, Jonsson P, Jentoft S, Knutsen H, André C (2019) Local cod (*Gadus morhua*) revealed by egg surveys and population genetic analysis after longstanding depletion on the Swedish Skagerrak coast. *ICES J Mar Sci* 76:418–429.

- Templeman W, Fleming AM (1962) Cod Tagging in the Newfoundland Area During 1947 and 1948. *J Fish Board Canada* 19:445–487.
- Templeman W (1966) Marine resources of Newfoundland. *Bull Fish Res Bd Can* 154:170.
- Templeman W (1979) Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962–66. *ICNAF Res Bull* 14:5–50.
- Thompson H (1943) A biological and economic study of cod (*Gadus callarias*, L.) in the Newfoundland area, including Labrador. *Res Bull (Fisheries)-Dept Nat Resour eng*.
- Thorarensen H, Gústavsson A, Gunnarsson S, Árnason J, Steinarsson A, Björnsdóttir R, Imsland AKD (2017) The effect of oxygen saturation on the growth and feed conversion of juvenile Atlantic cod (*Gadus morhua* L.). *Aquaculture* 475:24–28.
- Thorstad EB, Rikardsen AH, Alp A, Okland F (2014) The Use of Electronic Tags in Fish Research – An Overview of Fish Telemetry Methods. *Turkish J Fish Aquat Sci* 13:881–896.
- Thorsteinsson V (1995) Tagging experiments using conventional tags and electronic data storage tags for the observations of migration, homing and habitat choice in the Icelandic spawning stock of cod. *ICES C B*:19.
- Thurrow F (1974) Changes in the population parameters of cod in the Baltic. *Rapp P-v Réun Cons int Explor Mer* 166:170–192.
- Thygesen UH, Pedersen MW, Madsen H (2009) Geolocating Fish Using Hidden Markov Models and Data Storage Tags. In: *Tagging and Tracking of Marine Animals with Electronic Devices. Reviews: Methods and Technologies in Fish Biology and Fisheries*. Nielsen JL, Arrizabalaga H, Fragoso N, Hobday A, Lutcavage M, Sibert J (eds) Springer, Dordrecht, p 277–293
- Turesson G (1922) The genotypical response of the plant species to the habitat. *Hereditas* 3:211–350.
- Vilhjálmsón H (1997) Climatic variations and some examples of their effects on the marine ecology of Icelandic and Greenland waters, in particular during the present century. *Rit Fiskid* 15.
- Voss R, Quaas MF, Stiasny MH, Hänsel M, Stecher Justiniano Pinto GA, Lehmann A, Reusch TBH, Schmidt JO (2019) Ecological-economic sustainability of the Baltic cod fisheries under ocean warming and acidification. *J Environ Manage* 238:110–118.
- Walters C, Maguire JJ (1996) Lessons for stock assessment from the northern cod collapse. *Rev Fish Biol Fish* 6:125–137.
- Walters C (2007) Is Adaptive Management Helping to Solve Fisheries Problems? *AMBIO A J Hum Environ* 36:304–307.
- Wieland K, Waller U, Schnack D (1994) Development of Baltic cod eggs at different levels of temperature and oxygen content. *Dana* 10:163–177.
- Wright PJ, Neat FC, Gibb FM, Gibb IM, Thordarson H (2006) Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *J Fish Biol* 69:181–199.
- Wroblewski JS, Bailey WL, Howse KA (1994) Observations of Adult Atlantic Cod (*Gadus morhua*) Overwintering in Nearshore Waters of Trinity Bay, Newfoundland. *Can J Fish Aquat Sci*

51:142–150.

Yoneda M, Wright P (2005a) Effect of temperature and food availability on reproductive investment of first-time spawning male Atlantic cod, *Gadus morhua*. ICES J Mar Sci 62:1387–1393.

Yoneda M, Wright PJ (2005b) Effects of varying temperature and food availability on growth and reproduction in first-time spawning female Atlantic cod. J Fish Biol 67:1225–1241.

Zhang J, Cowie G, Naqvi SWA (2013) Hypoxia in the changing marine environment. Environ Res Lett 8:015025.

Appendix A

Supplementary material

(Examining fish movement in terms of advection or diffusion: a case study of northeastern Atlantic cod)



Table S1. Overview of releases and recaptures divided by month. Note that the differences in recapture numbers are likely due to seasonal variation in fishing pressure.

	January	February	March	April	May	June	July	August	September	October	November	December
Releases	2,478	2,594	3,652	974	1,388	590	96	312	423	995	2,242	1,625
Recaptures	1,357	1,752	2,056	2,248	2,358	1,838	1,186	950	862	963	908	891

	Overall	<1960	1960-1970	1971-1980	1981-1999	2000-2020
Kattegat-Skagerrak (SD 20-21)	(0.01, 0.07)	-	-	(0.02, 0.09)	(-0.01, 0.05)	-
Belt Sea (SD 22)	(0.05, 0.05)	(0.03, 0.02)	(0.08, 0.11)	-	(0.06, 0)	-
The Sound (SD 23)	(-0.02, 0.02)	(-0.01, -0.03)	(0.01, -0.01)	(-0.04, 0.03)	(-0.10, 0.14)	-
Arkona Sea (SD 24)	(0.04, 0.03)	-	(0.04, 0.02)	(-0.03, 0.02)	-	(0.16, 0.08)
Bornholm Sea (SD 25)	(-0.04, -0.02)	(0.03, 0.03)	(-0.07, -0.02)	(-0.04, -0.04)	(0.04, -0.07)	(0, -0.02)
South-eastern Baltic Sea (SD 26)	(-0.34, 0.15)	(-0.54, 0.19)	(-0.37, 0.17)	(-0.17, 0.07)	-	(-0.23, 0.15)
The Western Gotland Basin (SD 27)	(-0.17, -0.52)	-	(-0.17, -0.54)	-	-	-
Gotland Sea (SD 28.2)	(-0.19, -0.42)	-	(-0.20, -0.48)	(-0.16, -0.31)	-	-
The Archipelago Sea (SD 29)	(-0.16, -0.53)	(-0.14, -0.77)	(-0.14, -0.29)	-	(-0.20, -0.52)	-
The Bothnian Sea (SD 30)	(0.01, -0.30)	-	-	-	(0.04, -0.32)	-
Gulf of Finland (SD 32)	(-0.10, 0.09)	-	-	(-0.14, 0.12)	(-0.03, 0.04)	-
Northern North Sea (Div. 4.a)	(0.09, -0.06)	-	-	(0.10, -0.05)	-	-
Central North Sea (Div. 4.b)	(-0.01, 0.42)	-	-	(0.02, 0.21)	(-0.15, 1.33)	(0.03, 0.68)
Southern North Sea (Div. 4.c)	(0.02, 0.90)	-	(0.04, 0.61)	(0.15, 0.99)	(-0.04, 0.98)	(0.06, 0.91)

Table S2. Advection (mean movement vector) for each ICES area. Note that for visualisation, the advection was used to calculate vector angle and distance and was scaled to half a year on Figure 2, 4-7. For the results of the bootstrap accuracy analyses, see the small points at the end of each advection arrow on Figure 2, 4-7. Note that decadal values may differ from total due to exclusion of decadal subsets for individual analyses

	Overall	<1960	1960-1970	1971-1980	1981-1999	2000-2020
Kattegat-Skagerrak (SD 20-21)	4.17 (3.08, 5.48)	-	-	3.92 (2.79, 5.31)	8.65 (3.14, 16.15)	-
Belt Sea (SD 22)	5.47 (4.68, 6.31)	2.36 (1.69, 3.11)	11.01 (9.23, 12.99)	-	1.38 (1.04, 1.78)	-
The Sound (SD 23)	10.08 (7.72, 13.1)	6.45 (3.35, 10.14)	12.27 (6.82, 20.25)	4.40 (2.87, 6.31)	23.89 (18.62, 29.04)	-
Arkona Sea (SD 24)	19.55 (17.14, 22.15)	-	20.86 (17.65, 24.27)	17.90 (12.75, 23.88)	-	13.36 (10.45, 16.43)
Bornholm Sea (SD 25)	17.54 (16.19, 18.97)	20.47 (15.9, 25.64)	18.60 (16.79, 20.55)	15.86 (13.37, 18.7)	5.66 (3.62, 7.91)	11.82 (9.01, 14.89)
South-eastern Baltic Sea (SD 26)	38.25 (34.25, 42.42)	45.39 (35.19, 56.4)	40.03 (35.18, 45.15)	16.92 (12.32, 22.76)	-	20.30 (7.16, 40.04)
The Western Gotland Basin (SD 27)	132.01 (93.08, 177.05)	-	136.05 (94.8, 181.91)	-	-	-
Gotland Sea (SD 28.2)	33.33 (29.57, 37.22)	-	33.20 (29.04, 37.67)	31.29 (24.2, 38.83)	-	-
The Archipelago Sea (SD 29)	76.50 (51.32, 106.75)	95.69 (57.27, 141.47)	28.56 (14.87, 40.45)	-	88.07 (30.87, 166.9)	-
The Bothnian Sea (SD 30)	79.51 (30.23, 155.04)	-	-	-	87.27 (29.37, 180.74)	-
Gulf of Finland (SD 32)	13.92 (10.17, 18.03)	-	-	14.88 (10.77, 19.41)	0.79 (0.49, 1.13)	-
Northern North Sea (Div. 4.a)	18.64 (13.76, 24.28)	-	-	18.01 (13.04, 23.66)	-	-
Central North Sea (Div. 4.b)	51.78 (48.35, 55.32)	-	-	36.14 (32.36, 40.22)	66.06 (57.59, 75.06)	19.65 (13.24, 26.49)
Southern North Sea (Div. 4.c)	58.38 (54.41, 62.6)	-	46.35 (39.86, 53.17)	74.60 (62.84, 88.35)	50.63 (46.49, 55.14)	148.87 (99.29, 192.38)

Table S3. Diffusion (variance) for each ICES area. Note that for visualisation, the diffusion coefficient was used to calculate circle radius (kilometres) and was scaled to half a year on Figure 3-7. Parenthesis values indicate 2.5% and 97.5% confidence intervals, respectively. Note that decadal values may differ from total due to exclusion of decadal subsets for individual analyses.

	Advection	Diffusion
Aabenraa Fjord	(0.03, 0.01)	1.40 (0.78, 2.22)
Southern Belt Sea (SBS)	(0.13, 0.19)	13.57 (10.93, 16.32)
The Gulf of Finland	(-0.10, 0.09)	13.92 (10.17, 18.03)
South-eastern Baltic Sea (SEBS)	(-0.34, 0.15)	38.25 (34.25, 42.42)

Table S4. Advection (mean movement vector) and diffusion (variance) for the case studies. The values in the diffusion parenthesis indicate 2.5% and 97.5% confidence intervals for the diffusion, respectively. Note that for visualisation, the advection was used to calculate vector angle and distance, and the diffusion coefficient was used to calculate circle radius (kilometres); both were scaled to a month on Figure 8. For the results of the bootstrap accuracy analyses for advection, see the small points at the end of each advection arrow on Figure 8.

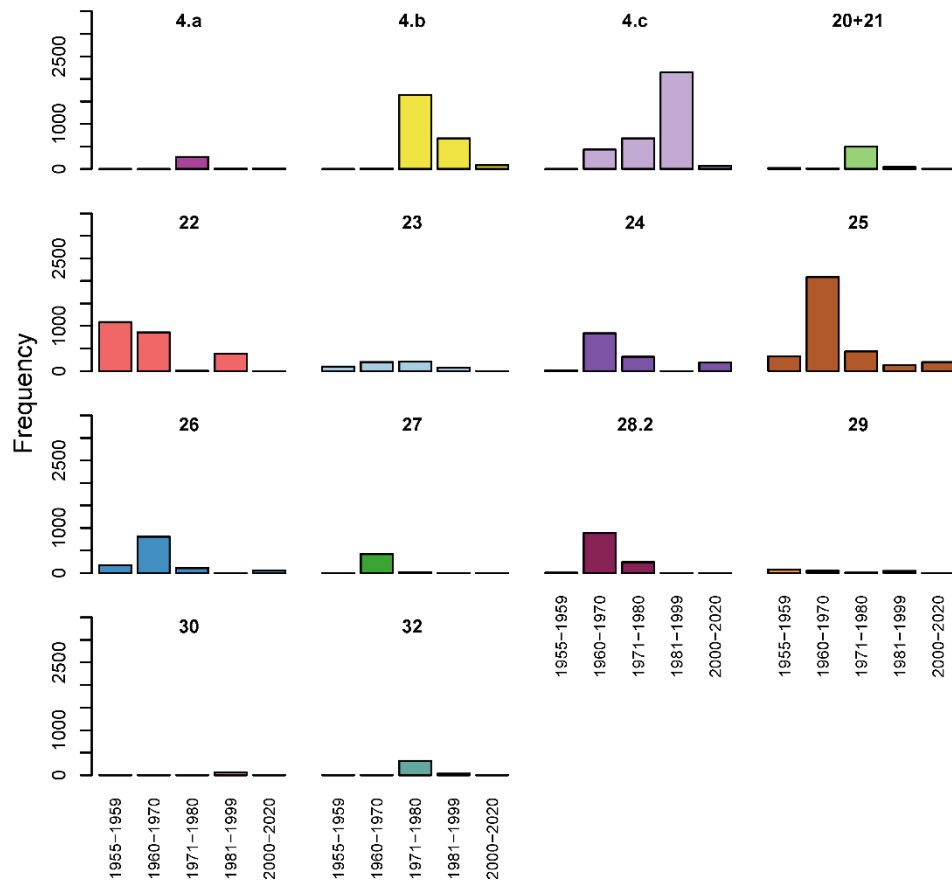


Figure S1. Overview of number of recaptures across decades per release area. Recaptures are grouped by release ICES area and recapture decade and were not necessarily recaptured in the same ICES area. Note that ICES area 20 and 21 have been combined.

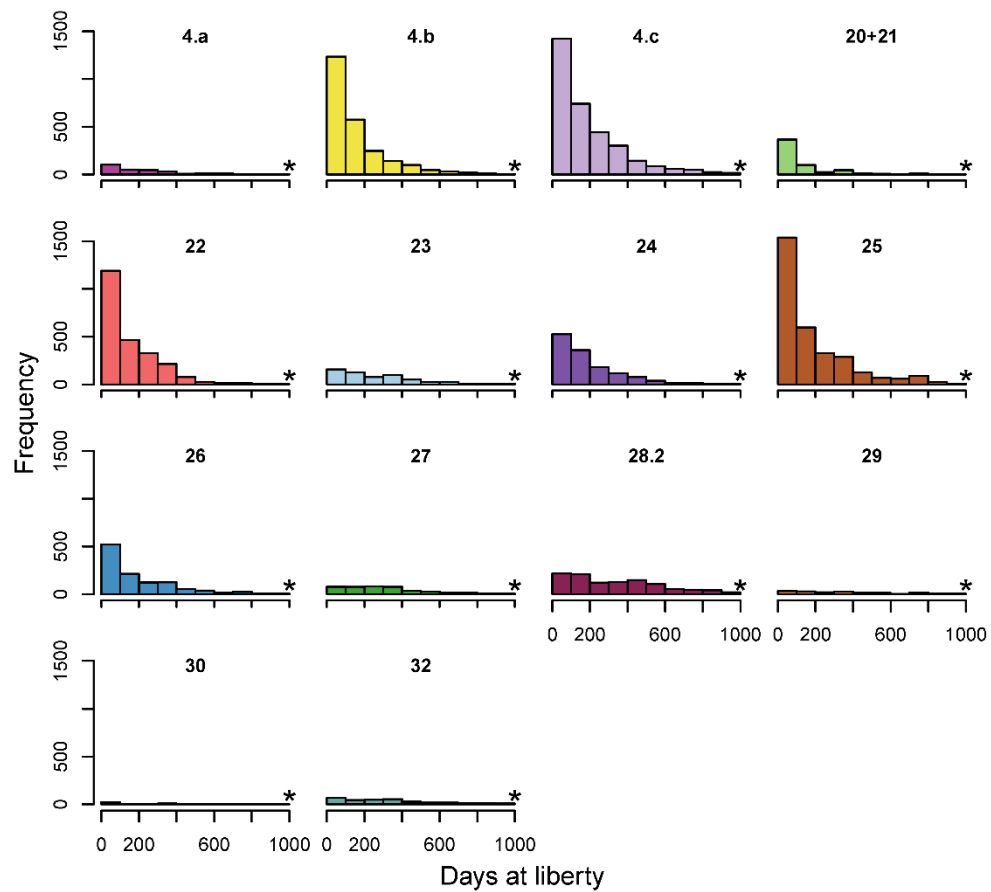


Figure S2. Days at liberty for recaptures per release area. Note that ICES area 20 and 21 have been combined. Asterisks (*) indicate values above 1,000.

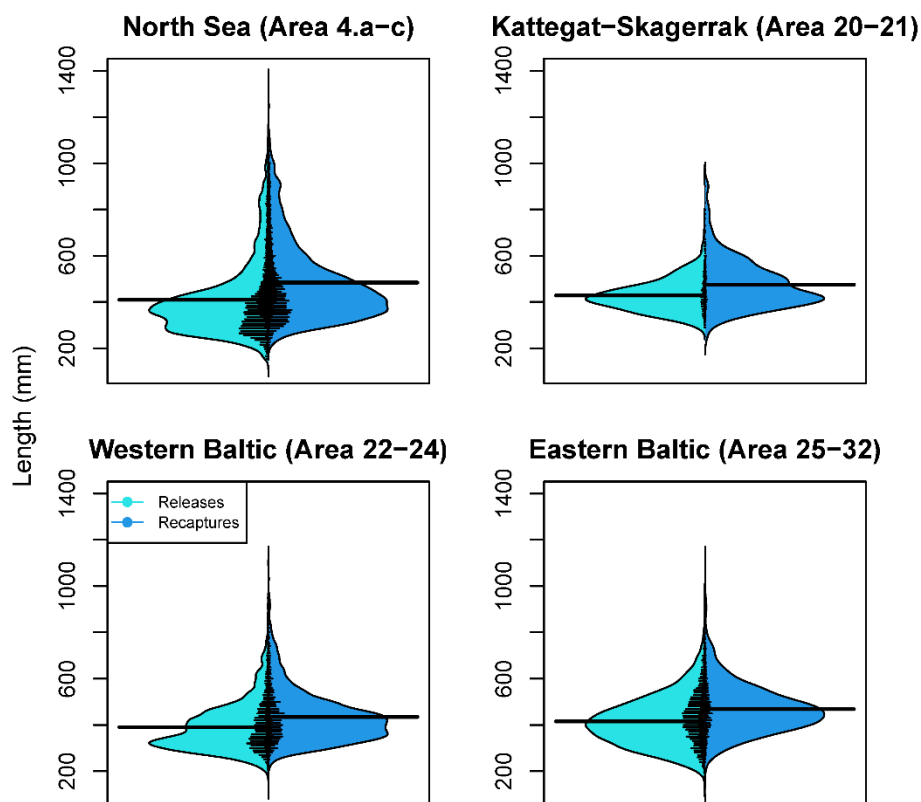


Fig. S3. Bean plots for release and recapture lengths across areas. Shaded areas depict density distributions, individual small lines indicate observations, and the vertical thick lines represent the medians.

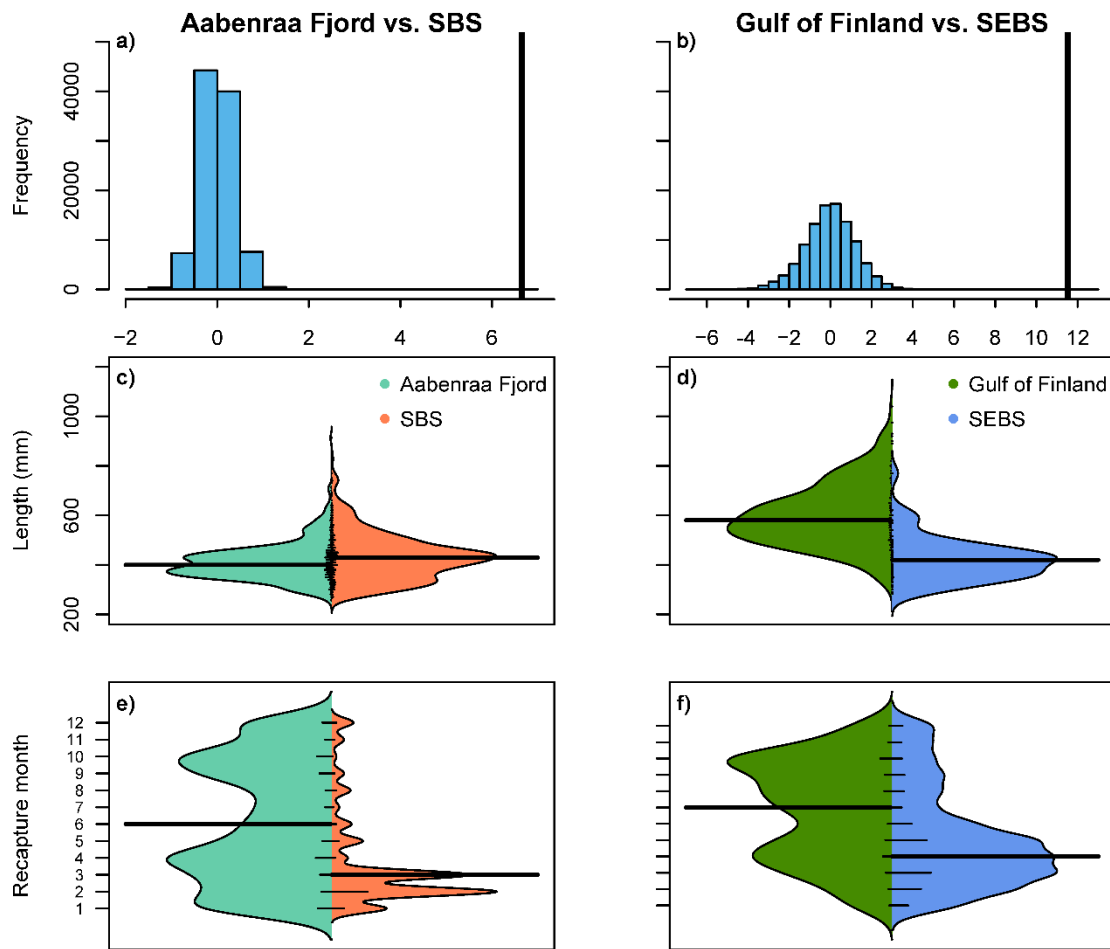


Figure S4. Distributions of bootstrapped median differences for swimming distances (km month⁻¹) between locations, and recapture lengths and months for recaptures released in Aabenraa Fjord, the southern Belt Sea (SBS), the Gulf of Finland, and the south-eastern Baltic Sea (SEBS). a-b) Comparisons of bootstrapped median differences ($n = 100,000$), c-d) bean plots of recapture lengths, and e-f) bean plots of recapture months. For each median difference comparison, new bootstrap datasets were created for each population to calculate the median differences. Bean plots of recapture months and lengths were not bootstrapped but included to show distributions. Thick black lines indicate true median values for respective populations. Shaded areas in bean plots depict density distributions and individual small lines indicate observations.

Appendix B

Supplementary material

(Stock connectivity patterns and indications of sub-stock component structuring of cod in the Sound)



Table S1. Fishing mortality for different age groups for the western Baltic cod stock and Kattegat stock during the tagging time series. Data has been compiled from WGBFAS reports (Jørgensen et al. 2011, ICES 2014).

			Western Baltic cod				Kattegat
Year	Age 1	Age 2	Age 3	Age 4	Age 5+	Age 3-5	Age 3-5
1970	0.39	1.08	1.17	0.97	0.76	0.97	-
1971	0.38	1.07	1.16	1.02	0.94	1.04	0.69
1972	0.35	1.01	1.18	1.09	1.11	1.13	0.71
1973	0.31	1	1.17	1.16	0.92	1.09	0.82
1974	0.28	1	1.24	1.29	1.06	1.20	0.86
1975	0.25	0.95	1.23	1.26	1.10	1.20	0.85
1976	0.23	1	1.34	1.23	1.19	1.25	0.89
1977	0.21	0.98	1.30	1.22	1.09	1.21	0.93
1978	0.20	0.88	1.16	1.04	0.76	0.99	0.88
1979	0.18	0.76	1.13	0.96	0.71	0.93	0.88
1980	0.19	0.70	1.19	1.01	0.82	1.01	0.92
1981	0.19	0.82	1.21	1.10	0.98	1.10	1.02
1982	0.22	0.85	1.13	0.91	0.92	0.99	1.11
1983	0.24	0.91	1.07	0.97	0.89	0.98	1.11
1984	0.24	0.87	1.08	1	0.95	1.01	1.15
1985	0.22	0.72	1.26	1.22	1.21	1.23	1.21
1986	0.21	0.65	1.27	1.40	1.40	1.36	1.24
1987	0.20	0.70	1.07	1.22	1.02	1.10	1.24

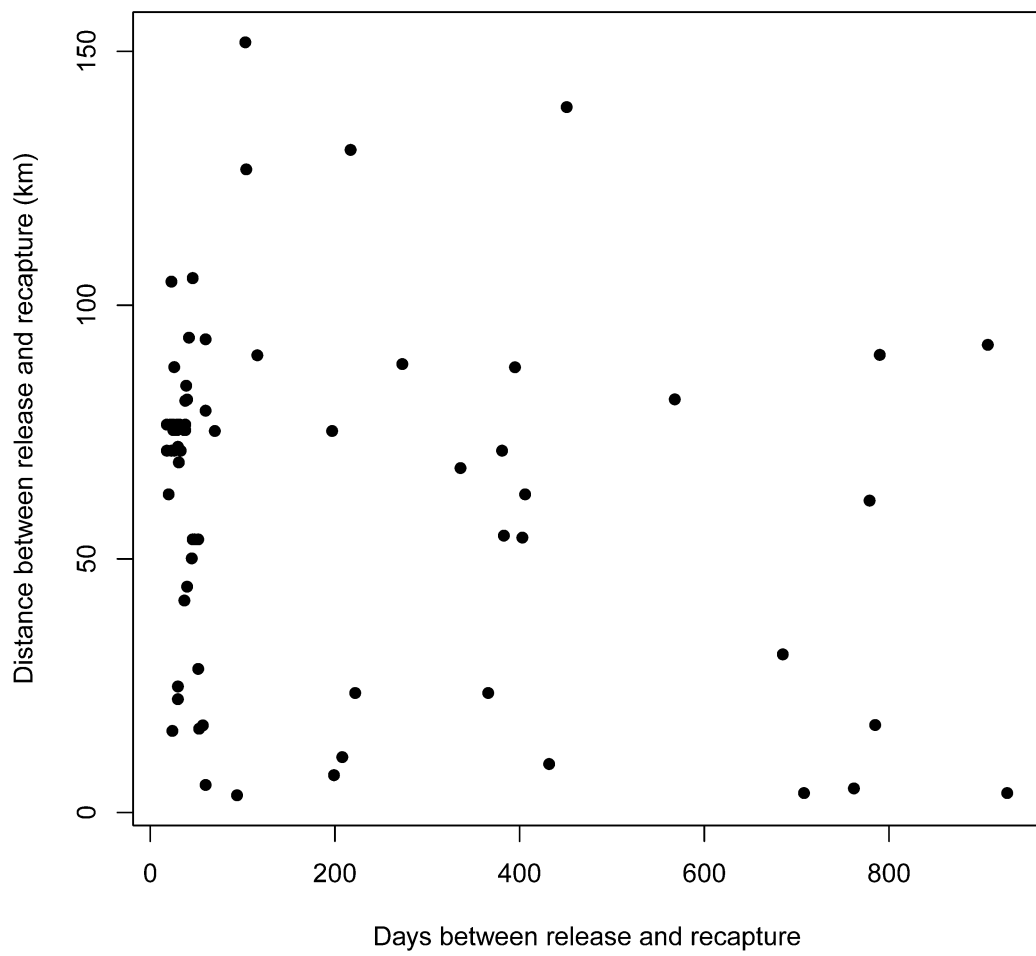


Figure S1. Distance between release and recapture locations for Sound cod released during peak spawning (January-February; n = 73).

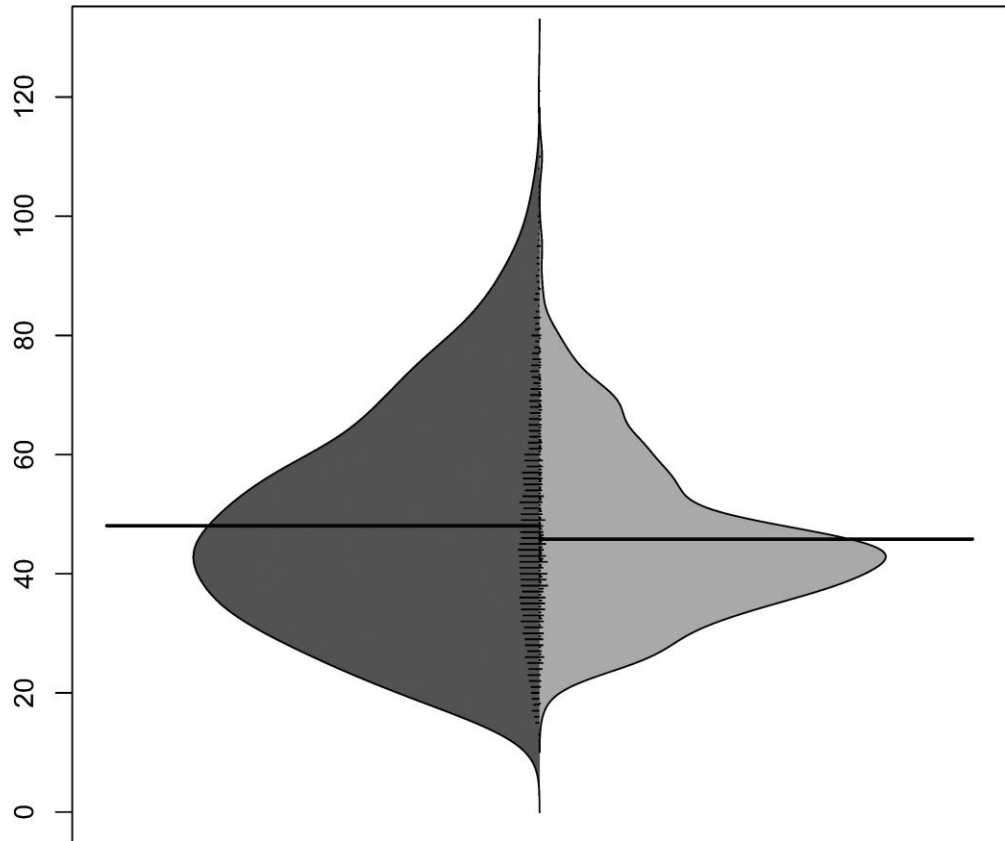


Figure S2. Bean plot showing length distributions for cod in the Sound. Left = length distributions (cm) from the Database of Trawl Surveys (DATRAS) and includes individual length-at-age data from Baltic International Trawl Surveys (BITS) and North Sea International Bottom Trawl Surveys (NS-IBTS) for Q1 between 2007-2021. Right = length distributions (cm) of releases from tagging projects. Shaded areas indicate density distributions, individual small lines show observations, and the vertical thick lines the medians.

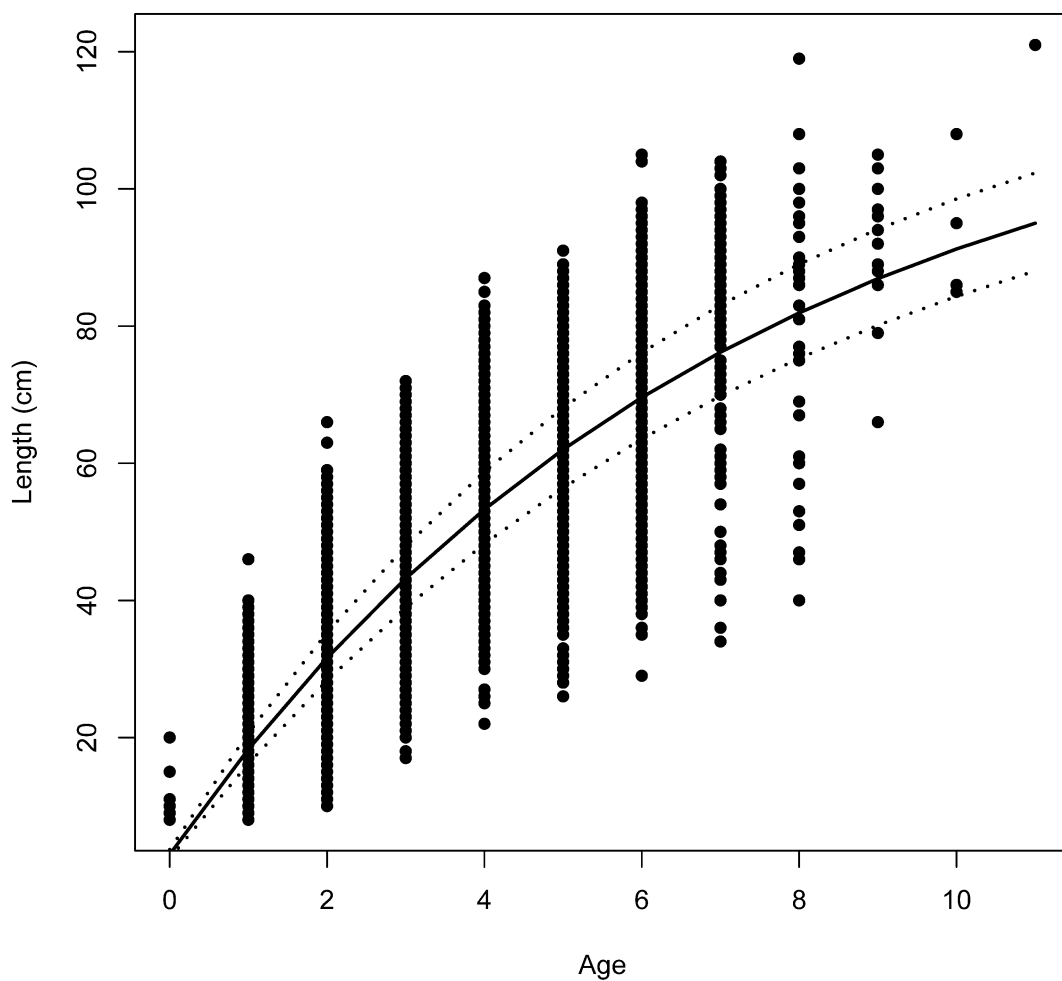


Figure S3. Von Bertalanffy growth curve for all the data, including Kattegat and each SD in the western Baltic stock (SD 21, 22-24). This model assumes that growth is equal in all SDs. The parameters for the growth curve were estimated from individual length-at-age data from Baltic International Trawl Surveys (BITS) and North Sea International Bottom Trawl Surveys (NS-IBTS) by using maximum likelihood estimation. Dotted lines show standard deviations. See Table 4 for parameter estimates.

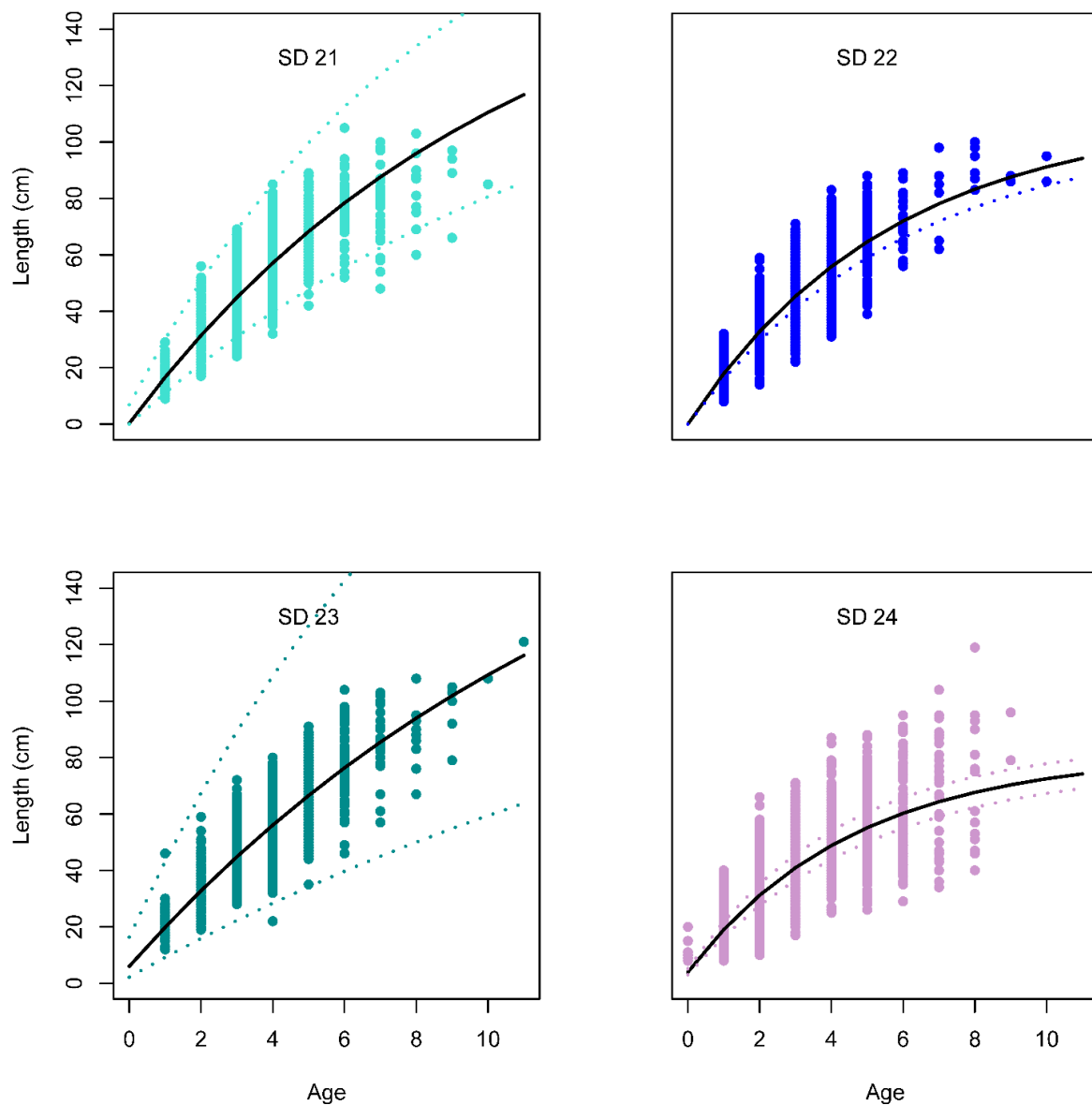


Figure S4. Von Bertalanffy growth curves for Kattegat and each SD in the western Baltic stock (SD 21, 22-24). This model assumed SD-specific parameters. The parameters for the growth curves were estimated from individual length-at-age data from Baltic International Trawl Surveys (BITS) and North Sea International Bottom Trawl Surveys (NS-IBTS) by using maximum likelihood estimation. Dotted lines show standard deviations. Note that the upper limit for SD 22 is not shown due to estimation issues. See Table 4 for parameter estimates.

Appendix C

Supplementary material

*(Simulating movement patterns in Baltic cod
(Gadus morhua) in response to historical changes
in environmental parameters)*



Methodology

Case 1 – Gotland Sea

HI_a : For the habitat index based on all three parameters, movement generally remained in the central Baltic (**Figure 4**). Overall, movement never extended all the way to the island of Bornholm due to conditions generally not being optimal in the southwestern Baltic, and movement north of Gotland was very common, as the central Baltic was overall the most optimal habitat. When diffusion was high, the cod would spread out more, and a few cod would move towards the Gulf of Finland which was indicated as a good overall habitat throughout the simulation. In general, higher HI_a were experienced when the taxis was strong and diffusion was low (**Figure S1**) but it was possible for a relatively high diffusion to push cod towards more favourable areas.

HI_o : When taxis was based on oxygen, the movement patterns were relatively similar to HI_a -based movement, as the cod generally remained in the central Baltic regardless of diffusion and taxis levels (**Figure 5**). However, movement towards Bornholm occurred in all simulations. In addition, the gradients were far sharper, and aside from the central Baltic, conditions were optimal in the Gulf of Finland and the northern Baltic throughout the simulation. Optimal conditions were also indicated in the western Baltic; however, the cod never moved past Bornholm.

HI_s : Salinity-based movement was relatively similar to HI_a -based movement; however, aside from the edges, the south-eastern Baltic was generally avoided and the cod never swam towards Bornholm regardless of taxis and diffusion levels (**Figure 6**). In addition, suitable habitat were present in the central Baltic, most of the southern Baltic, and the Gulf of Finland. Except when diffusion was set to low, movement towards the Gulf of Finland occurred in all simulations.

HI_c : In contrast to the HI_a -based movement, cod never moved to the Gulf of Finland but remained in the central or southern Baltic when following temperature gradients regardless of taxis and diffusion levels (**Figure 7**). Optimal conditions were present in the central and southern Baltic, and the Gulf of Finland. Occasionally, optimal conditions appeared in the western Baltic and Kattegat-Skagerrak; however, the cod never moved there.

Case 2 – Kattegat

HI_a : When taxis was based on all environmental parameters, the distribution patterns agreed relatively well with the true recapture patterns (**Figure 4**). Optimal conditions were generally the highest in Kattegat and Skagerrak, and only occasionally relatively optimal in the Belt Sea. Cod would generally remain in Kattegat except when diffusion was relatively high, where a few cod would occasionally move towards the Skagerrak, and if taxis was also low, movement into the

Sound and Belt Seas would occur. In general, higher HI_a were experienced when the taxis was strong and diffusion was low (**Figure S1**) but it was possible for a relatively high diffusion to push cod towards more favourable areas.

HI_o : The movement patterns based on the oxygen gradient were highly similar to the HI_a -based movement; however, no cod moved towards the Skagerrak (**Figure 5**). Similarly, optimal conditions were present primarily in the Kattegat and part of the Skagerrak and Belt Sea. When diffusion was relatively high and taxis low, movement would occur into the Belt Sea and Sound; otherwise, the cod would remain in Kattegat.

HI_s : Taxis based on salinity showed remarkably different movement patterns (**Figure 6**). Conditions were almost exclusively optimal in the Kattegat and Skagerrak, although conditions were occasionally relatively optimal in the northern Belt Sea and Sound. Regardless of the degree of taxis and diffusion, the cod would always move towards the Skagerrak. In addition, some movement into the northern Sound and northern Belt Sea occurred in the majority of simulations and was more pronounced when taxis was low and diffusion relatively high.

HI_t : When temperature was used for the taxis-based movements, movement deep into the Belt Sea occurred in all cases except when taxis was strong and diffusion low (**Figure 7**). In general, this pattern was stronger when diffusion was relatively high. Cod movement was also common in the central and southern Kattegat and extended into the northern Kattegat and Skagerrak mainly when diffusion was high. Optimal temperature conditions were present in both the western and eastern Baltic but very rarely extended into the northern Baltic Sea or Gulf of Finland.

Case 3 – Bornholm Sea

HI_a : Taxis based on all three environmental parameters showed cod would generally remain around the island of Bornholm (**Figure 4**). When diffusion was high, however, movement into the south-eastern Baltic Sea was relatively common and less common towards the south-western Baltic Sea. Optimal conditions were generally present in the central and southern Baltic Sea. In general, higher HI_a were experienced when the taxis was strong and diffusion was low (**Figure S1**) but it was possible for a relatively high diffusion to push cod towards more favourable areas.

HI_o : Movement patterns were relatively similar to HI_a -based movement when oxygen was used as the habitat index; however, cod movement towards the central and south-eastern Baltic was common in all simulations (**Figure 5**). Cod never moved far into the central Baltic, except in the case of a single cod when the taxis was relatively high and the diffusion was high, most likely because the central Baltic, aside from the edges, was characterized by poor habitat from $t = 207$

and onwards. In addition, some movement into the western Baltic occurred when taxis was low and diffusion was relatively high and above.

HI_s : When taxis was based on salinity, remarkably similar movement patterns were present across all simulations regardless of taxis and diffusion levels (**Figure 6**). Conditions were almost exclusively optimal from the southern Baltic through the central Baltic to the Gulf of Finland, and cod generally remained in the southern or central Baltic Sea. Almost no movement occurred into the south-eastern Baltic Sea.

HI_c : For temperature, optimal conditions were generally present in most of the Baltic Sea throughout most of the time series but were consistently highest in the western Baltic (**Figure 7**). When diffusion was low, cod generally remained in the release area with some movement towards the south-eastern Baltic; however, when diffusion was relatively high or above, movement towards the south-eastern and south-western Baltic was common, especially towards the east. When movement into the south-western Baltic occurred, cod would generally move through the Belt Sea and only rarely through the Sound.

Case 4 – Belt Sea

HI_a : When movement followed taxis based on all three environmental parameters, the cod had a general tendency to move towards and remain in the Belt Sea when diffusion was low (**Figure 4**). However, when diffusion was relatively high or above, movement into the Kattegat occurred aside from just the Belt Sea. While the environmental conditions were highest in the western Baltic, the conditions in the rest of the Baltic generally switched between relatively decent and poor throughout the simulations. In general, slightly higher HI_a were experienced when the taxis was strong and diffusion was low (**Figure S1**).

HI_o : For taxis based on oxygen, similar patterns to the HI_a -based movement were observed; however, movement was generally deeper into the Kattegat and south-eastern Baltic when diffusion was relatively high or above (**Figure 5**). When diffusion was low, movement patterns resembled the HI_a -based movement with low diffusion. Similar to HI_a , conditions were most optimal in the western and southern Baltic but progressed towards poorer conditions in all of the Baltic Sea except the western Baltic. However, this pattern switched and, at the end of the simulation, conditions were most optimal in the northern Baltic.

HI_s : Overall, the movement patterns related to salinity were relatively close to the HI_a -based movement patterns (**Figure 6**). Conditions were highest in the western Baltic and Kattegat-Skagerrak throughout the simulation while the rest of the Baltic Sea was characterized by poor

conditions. When diffusion was low, the cod moved to the Belt Seas and remained there; in contrast, movement into Kattegat would generally occur when diffusion was relatively high or above.

HI_c : Similar to HI_s , the movement patterns related to temperature were relatively close to the HI_a -based movement patterns (**Figure 7**). In all simulations, movement into Kattegat and the Belt Sea occurred at varying degrees. When diffusion was relatively high or above, occasional movement into Skagerrak would also occur. While conditions were generally most optimal from the Belt Sea to Skagerrak, the rest of the Baltic would generally switch between optimal and poor states throughout the simulation.

Figures

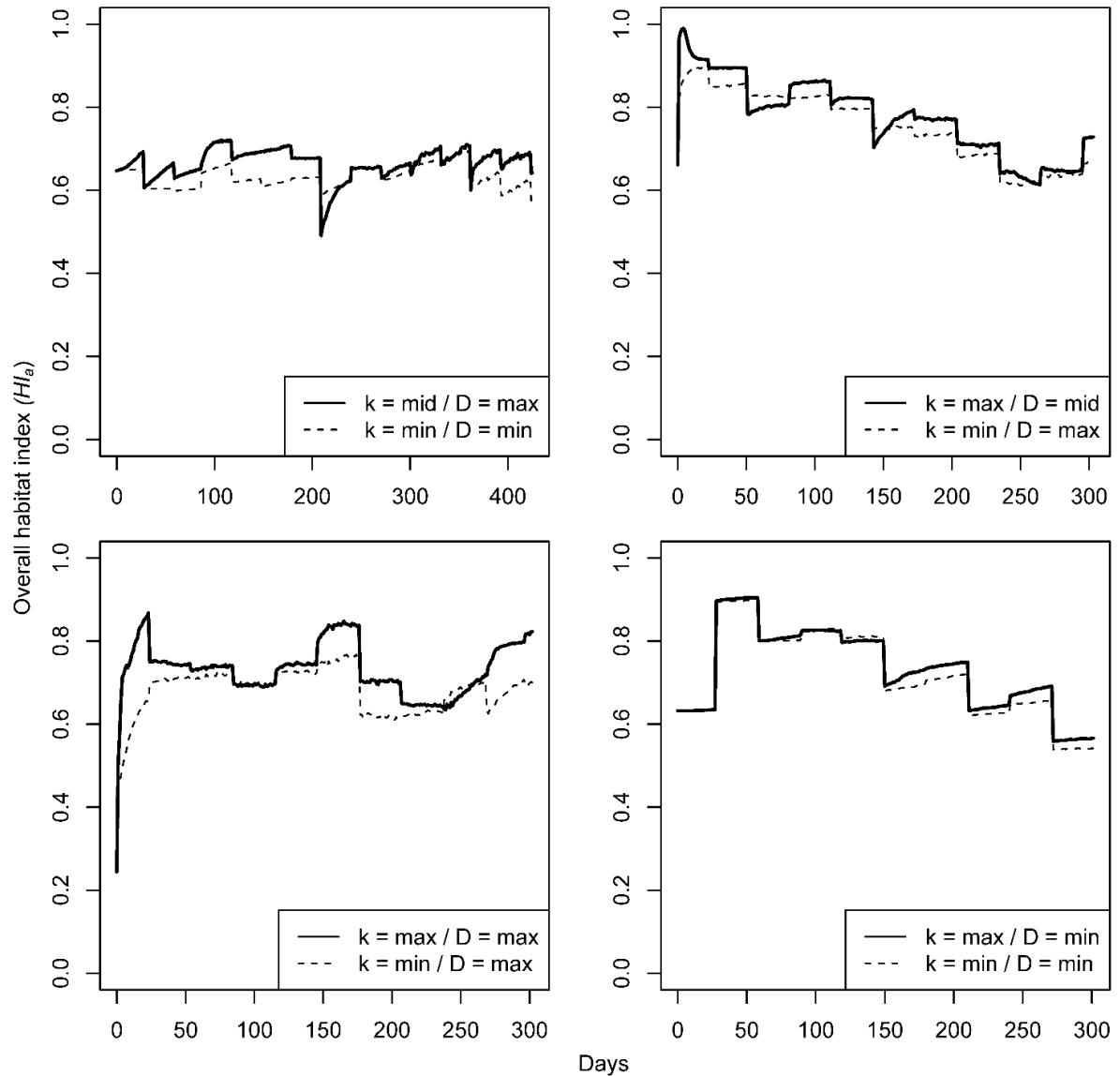


Figure S1. Examples of mean experienced habitat indices (HI_a) for strong and weak taxis driven movement throughout the simulation. Bold lines = strong taxis driven movement. Dotted lines = weak taxis driven movement. Top left = case study 1. Top right = case study 2. Bottom left = case study 3. Bottom right = case study 4. k and D indicate coefficients used to adjust taxis and diffusion, respectively, and the higher, the stronger the effects and vice versa (**Table 2**). Note the sharp increases or declines at the beginning of each month as hydrographical conditions change.

The Atlantic cod (*Gadus morhua*) is a species with complex movement patterns. Individuals can be either resident or migratory, and populations can harbour either or both types. This can cause issues for management as it is necessary to account for movement to avoid flawed stock assessments.

This PhD thesis focuses on documenting historical movement patterns in cod in the North Sea and Baltic Sea and understanding the link between the environment and movement. By utilizing large tagging and hydrographical databases and simulations, new insights into movement in these areas are gained which can be used in future management and conservation.

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