# The multiple dimensions of spatial ecology in fisheries management

*How climate, economy, and connectivity shape Cod (Gadus morhua) dynamics in a changing North Sea.*

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# Acknowledgements

It is said that scientific work often results in more questions than answers.
When I look at what I have done in the past nine-and-a-half years, I have many questions. What have I done? Was it worth it? Why did it have to go this way?
In time, I have learned to accept things as they are. This does not mean passively accepting everything: I have also learned to fight for what I believe must be changed. And I have learned how to change things in life and in Science. My Scientific work can make the difference, by contributing -even if only marginally- to global knowledge about management of natural resources. That's not much, but not that little either. Almost ten years after starting, I now look with pride at this thesis, the result of my hard work.
This acquired awareness was not reached without pain. When I read that most PhD students face severe psychological strain during their work, I can reconnect. Nonetheless, here stands the written proof of my success.

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## List of papers

Paper 1:

Romagnoni G., Mackinson S., Hong J., Eikeset A.M. (2015). The Ecospace model applied to the North Sea: Evaluating spatial predictions with fish biomass and fishing effort data. *Ecological Modelling*, 300(0), 50–60

Paper 2:

Kvile* K.Ø., Romagnoni* G., Dagestad K-F., Langangen Ø., Kristiansen T. (2018). Sensitivity of modelled North Sea cod larvae transport to vertical behaviour, ocean model resolution and interannual variation in ocean dynamics. *ICES Journal of Marine Science* 75, 2413-2424.  *equal contribution

Paper 3:

Romagnoni G.*, Kvile K.Ø.*, Dagestad K-F., Kristiansen T., Eikeset A.M., Stenseth, N.C., Langangen Ø. (2020). Influence of larval transport and temperature on recruitment dynamics of North Sea cod (Gadus morhua) across spatial scales of observation. *Fisheries Oceanography* 29, 324-339. *equal contribution

Paper 4:

Romagnoni G., Diekert F.K., Lindroos M.A., Eikeset, A.M. A Bioeconomic optimal management of spatially structured populations is independent of management scale under climate change: North Sea cod (*Gadus morhua*) as case study. *Manuscript*.

# Summary

This thesis is centred on the interactions between climate and spatial dynamics regulating the abundance and distribution of marine fish. In particular, the thesis focus on Atlantic cod (*Gadus morhua*) in the North Sea, and its ecology and management under climate change by adopting a multidisciplinary approach, where the boundaries of oceanography, ecology, economics and fisheries management meet. I explored this interface, proposing some answers toward adaptive fisheries management.

North Sea cod has been among the main target species of commercial fisheries for centuries. Intense fishing pressure, in combination with environmental change, has resulted in a dramatic stock decline in the past decades. Management of the fisheries has allowed a gradual a recovery of North Sea cod stock since the mid 2000's. However, in the past few years (since 2017) the North Sea cod stock has showed once again signs of decline. In addition to fishing pressure, recent declines in the North Sea cod may be due to global climate change (in particular, increase in sea surface temperature and related changes in the zooplankton community) that has been causally linked to reduced recruitment and increased predation of juvenile cod. Such effects are uneven across the area, seemingly more pronounced in the South and less in the North. This heterogeneous spatial response may be attributed to geographical and environmental factors such as the latitudinal gradient of temperature, differences in topography (i.e. depth) or oceanographic characteristics (e.g. current and tidal patterns). At the same time the presence of multiple populations within the North Sea stock may promote niche differentiation in response to climate change. These populations with independent dynamics may potentially require different management strategies. Such spatial heterogeneity is acknowledged but the stock is currently managed as a homogeneous unit. However, appropriate management should account for the spatial distribution of populations, their connectivity, their response to climate, and the effects of predator-prey interaction at the correct spatial scale.

Throughout this thesis, I attempted to investigate how the interaction between spatial dynamics and the effects of climate impact cod ecology and population dynamics, and in turn how these emerging interactions may influence management. First, I explored spatial ecosystem dynamics (Paper 1), then the effects of larval behaviour on their distribution across spatial scales (Paper 2), and effects of inclusion of larval transport and of connectivity on estimates of recruitment (Paper 3). Finally, I explored through modelling the potential effects of including spatial population structure and climate change on the projected optimal management strategies (Paper 4).

In particular, in Paper 1, my co-authors and I developed a spatial version of an existing (non-spatial) ecosystem model, using the Ecopath with Ecosim framework (a widely applied ecosystem modelling tool) and its spatial component Ecospace. We explored quantitatively the capability of the model to correctly reproduce known spatial patterns of fish biomass and fishing effort. Our results show a satisfactory capability to reproduce spatial distribution for fish biomass, but not for fishing effort. Moreover our study explored the sensitivity of model performance to variations in Ecospace parameters, identifying the most influential, and discussing the importance of accounting for parameter uncertainty.

In Papers 2, 3 and 4 we addressed the issue of multiple populations and their spatial distribution. In Paper 2 we applied a coupled physical-biological model that simulates spatial distribution of particles representing cod eggs and larvae in the North Sea. We assessed the relative importance of three factors commonly considered highly relevant for modelling early life stages of marine organisms, namely spatio-temporal resolution of the model, explicit inclusion of larval vertical movement, and interannual variability. We found that the predicted spatial distribution of particles is moderately influenced by vertical movement and ocean

model resolution. However, spatial distribution differs substantially between years. This implies that interannual variation in ocean dynamics plays a critical role in determining the degree of retention in the study area. We additionally observed that the effect of vertical movement strongly depends on the spatiotemporal scale of the analyses.

In Paper 3 we applied a coupled physical-biological model to assess whether explicit inclusion of eggs and larvae transport processes outputs can improve the performance of stock-recruitment models. We thus paired a 44-year long time series of cod recruitment and spawning stock biomass data with larval transport anomaly, connectivity and sea surface temperature, both population-specific and at stock scale. We proposed a novel method to account for connectivity explicitly. This showed an effect of connectivity on recruitment, albeit small, and only at the population scale. Conversely, the traditional method detects a small effect of transport anomaly, and only at the stock scale. Moreover, we investigated the relationship between temperature and populations connectivity. We found a correlation between increasing temperature and larval drift from south to north, revealing potential effects of changing climate on population connectivity in the area.

Finally, in Paper 4 we developed a bioeconomic model, based on an age-specific population dynamic model, to assess whether management that accounts for population structure could provide higher long-term economic returns. We explored alternative management strategies for the North Sea cod metapopulation, where two sub-populations are managed either independently or as unique stock unit. We tested the hypothesis that the advantage of managing populations separately increases under rising temperature, given different population sensitivity to temperature. Our results showed that, in the context of optimal management, moving from non-spatial management to population specific management was not economically advantageous under any climate scenario, likely due to the similar response to temperature of our modelled populations. The economic impacts caused by increasing temperature or by adopting a suboptimal constant harvest rate (irrespective of population scale) were larger than managing at the incorrect spatial scale.

This thesis proposes that interactions between climate change, fish population structure and the spatial distribution of fish eggs and larvae influence the population dynamics and, therefore, the sustainability and profitability of the fishery. These interactions should be accounted for by management, despite the existing gaps in our understanding of the interrelationships between ecology, oceanography, economics and management.

## Table of Contents

Paper 1

Supplementary Information to Paper 1

Paper 2

Supplementary Information to Paper 2

Paper 3

Supplementary Information to Paper 3

Paper 4

Supplementary Information to Paper 4

# 1. Introduction

The marine environment is a multidimensional realm, concealing its true nature beneath a curtain of waves and foam. The capability of modern scientists to grasp its underlying complexity is only marginally better compared to our colleagues from a century ago. Through modern technology, we have considerably advanced our knowledge and understanding in the last decades, but so much is still lying ahead (or underneath) of us. This thesis investigates some aspects of spatial dynamics of fish ecology and the approaches we apply to understand it and to manage fisheries, in the context of a changing climate. This thesis touches upon different aspects of spatial ecology and other fields, from ecosystem dynamics and food-web theory, to fisheries management, to population and metapopulation dynamics, to oceanographic biology, and to bioeconomics.

This thesis focuses on North Sea cod stock (*Gadus morhua*) as a case study to investigate whether fisheries management may benefit from explicit considerations of the spatial relationships, and the dependencies between climate and stock components.

For the past 10 years, gradual recovery of North Sea cod from near-collapse to sustainable state has been the flagship of successful, science-based fisheries management from the European management system. Nonetheless, the latest assessment of this stock (2019) indicated a sharp stock decline in SSB in the last few years (ICES, 2019). This had consequences for the industry, such as the withdrawal of sustainability label from Marine Stewardship Council (MSC) in 2019, gained in 2017 (Marine Stewardship Council (MSC), 2017, 2019). The consequences were severe also for the scientific community, dismayed once again when facing the hard fact that managing nature is far more complex, and frustrating, than we would like. The credibility of the scientific process behind the assessment and scientific advice, however, is not impaired.

The present thesis promotes the message that aspects such as the influence of climate, spatial distribution of fishing fleets and population structure, and their interactions, should not be overlooked and could play a pivotal role for improving stock management, when fully understood and properly integrated. A spatially explicit management that can account for cod populations' dynamics in a warming North Sea ecosystem, and for a moving fishery, is needed now more than ever.

# 2. Study context

## 2.1 The North Sea

The North Sea is a semi-enclosed basin, physically divided into a southern shallow area and a northern deeper one. The Norwegian Deep and the continental slope constitute the natural borders of the basin in the North-East and North-West respectively (Figure 1), while the Dover Strait separates the basin from the English Channel at the South. Conventionally, the waters of the Norwegian Trench and Norwegian coast are included in the North Sea while the Skagerrak, Kattegat and English Channel are part of the so-called Greater North Sea Region, being oceanographically well connected but separate for management purpose (ICES, 2018).
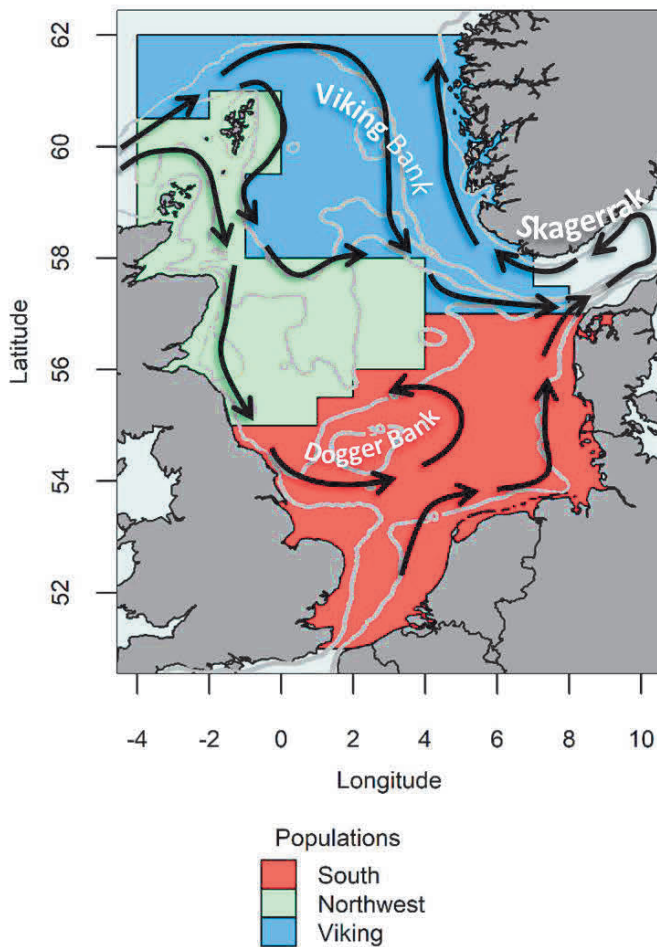
*Figure 1. Map of the study area with the population areas, main currents, and key topographic features. Source: the author.*

Ocean circulation is influenced by topography and inflow of North Atlantic water. The northern area, characterised by seasonal stratification in summer, is influenced by inflow of saline Atlantic water flowing along the western slope of the Norwegian Trench as well as from the channels between Orkneys and Shetland islands. This current transports into the region the copepod *Calanus finmarchicus*, an important food source for many species, including larval cod (Beaugrand *et al.*, 2003; Nicolas *et al.*, 2014). One branch of the current flows southward along the Scottish and English coast; another, larger branch flows along the Norwegian Trench and into Skagerrak. This follows a counter-clockwise trajectory along the Skagerrak coast, and after mixing with the less saline Norwegian coastal current, flows north-westward along the eastern slope of the Norwegian Trench and into the Norwegian Sea (Huserbråten *et al.*, 2018). The southern North Sea is dominated by continental freshwater runoff from the large rivers on mainland Europe, and by tidal patterns, which in combination with wind and wave turbulence and shallow topography result in permanent mixing. The intermediate saline current from the English Channel and the coastal, low saline Jutland Current flow along the continental coast and into the Skagerrak (Sundby *et al.*, 2017).

The North Sea area is characterised by temperate climate and by a mixed faunal assemblage, including Boreal (northern) and Lusitanic (southern) species. Species distribution is related to the changes in temperature observed in recent decades, with gradual expansion of southern species in warm periods, and contraction and deepening of northern, cold-related species (Barcelò *et al.*, 2016; Dulvy *et al.*, 2008; Petitgas *et al.*, 2012). The North Sea hosts areas with high natural value such as the Wadden sea, recognised as UNESCO world

heritage site for its specificities including biodiversity (Common Wadden Sea Secretariat, 2016) and an important seabird area (Reise *et al.*, 2010), and other valuable habitats, with over 80 000 km$^2$ protected as EU SAC within the Natura 2000 network (European Environment Agency, 2015; OSPAR, 2017). For example, the Dogger bank, the largest sand bank in the area, hosts important diversity including benthic communities and target and non-target fish species (Anonymous, 2016; Plumeridge and Roberts, 2017; STECF, 2019a), while seals and cetaceans occur around coastal and offshore areas (Russell *et al.*, 2017; Waggitt *et al.*, 2020).

Episodic productivity changes have been observed in the North Sea. These influence key components of the ecosystem, with phytoplankton, zooplankton, and demersal and pelagic fish all having exhibited cycles in variability. These cycles, sometimes linked to regime shifts (notably around 2000), are attributed to oscillations of the temperature cycle of the North Atlantic (the Atlantic Multidecadal Oscillation, AMO) (Alheit *et al.*, 2012; Goberville *et al.*, 2014; Stige *et al.*, 2006).

The North Sea has an important history of fishing (Barrett *et al.*, 2004a), the management of which has been complex due to the mixed nature of fisheries (Kempf *et al.*, 2016; Mackinson *et al.*, 2009; Ulrich *et al.*, 2016). The main fisheries can be divided in demersal and pelagic. Demersal fisheries target roundfish (in particular gadoids) and flatfish (especially sole and plaice), while pelagic fisheries target herring and mackerel for human consumption, and sandeel, sprat and Norway pout for fishmeal and other industrial use. Shrimp and Norway lobster also constitute important target species (ICES, 2018). Fisheries management is conducted in accordance with the EU Common Fisheries Policy (CFP), by coastal state agreements. Agreements cover area- species- and gear-specific limits in catches. The total allowable catches are established regularly on the basis of scientific advice from ICES and the Scientific Technical Economic Committee for Fisheries (STECF) of the European Union. Management has been partially successful: after years of systematic decline of most stocks, a moderate recovery was observed in recent years for several of the fish stocks after a large reduction in fishing effort and possibly also a reduction of bycatch (ICES, 2018, 2019).

Other activities such as shipping traffic, oil and gas extraction and wind farms, are increasingly causing conflicts with fishing activities (Klinger *et al.*, 2018). National efforts for the implementation of national Marine Spatial Planning regulations, under the directions of the European Union (EU) Marine Spatial Planning Directive (2014/89/EU), are attempting to address these conflicts (Lacroix and Pioch, 2011; Schupp *et al.*, 2019; Stelzenmüller *et al.*, 2016), and the North Sea is at the forefront of practical implementations of MSP and of multi-use of space at sea experiences (e.g. windfarm-fisheries and windfarm-aquaculture: Buck *et al.*, 2017; Stelzenmüller *et al.*, 2016).

### 2.2 Atlantic cod in the North Sea

Atlantic cod (*Gadus morhua;* Figure 2) is a widely distributed predatory teleost, occurring across both sides of the North Atlantic Ocean. It is a highly adaptable species, inhabiting bentho-pelagic areas from over 300 meters deep to coastal and inshore areas, displaying high plasticity and adaptability (Barth *et al.*, 2017; Malachowicz and Wenne, 2019; Wenne *et al.*, 2020). Individual populations have adapted to diverse lifestyles and behaviours: some display massive ocean-going spawning migrations (e.g. East Greenland cod: Bonanomi *et al.*, 2016; North-East Arctic cod: Langangen *et al.*, 2018), others favour localised sedentary lifestyle in inshore areas throughout their lifetime (e.g. Norwegian coastal cod and fjord populations: Knutsen *et al.*, 2018; Rogers and Stenseth, 2017; Roney *et al.*, 2018), with a range of migratory behaviours described (Robichaud and Rose, 2004).

*Figure 2. Atlantic cod captured during field work in Flødevigen, Arendal, Norway. The fish was captured with fyke nets, tagged and released shortly after. Cod can tolerate large stress and recover well from handling and even surgery for electronic tags implant. Photo: The author.*

Thanks to its characteristics, the large attained size and massive abundance, cod has been a target species since the Neolithic (Enghoff *et al.*, 2007; Hufthammer *et al.*, 2006) but only in the last millennium it became a key source of food (Geffen *et al.*, 2011; Rose *et al.*, 2019), permitting coastal societies to thrive (Barrett *et al.*, 1999; Sicking and Abreu-Ferreira, 2008). Thanks to its nutritional value and the unique suitability of its meat for drying and preserving, it fostered international trades across Europe and beyond (Barrett, 2018; Barrett *et al.*, 2004b, 2011; Wubs-Mrozewicz, 2008). Cod is thought to have been among the critical factors allowing colonization from European fishers and traders into the Americas (Kurlansky, 1999). For these reasons, Atlantic cod has an iconic value in cultures throughout Europe, including areas well beyond its actual occurrence range. While the global landings have declined through time with the depletion of most stocks (Figure 3), Atlantic cod remains among the top 10 landed species worldwide (FAO, 2020a, 2020b). Additionally, cod is one of the most studied species, in particular in the context of climate change (Ferreira *et al.*, 2017), and serves as the poster child for seminal studies of fish ecology that inspired generations of scientists (Beaugrand *et al.*, 2003; Beaugrand and Kirby, 2010; Brander, 2010; Cushing, 1990; Drinkwater, 2005; Durant *et al.*, 2007; Harden Jones, 1968; Hjort, 1914; Pörtner *et al.*, 2008, 2001; Stige *et al.*, 2006).
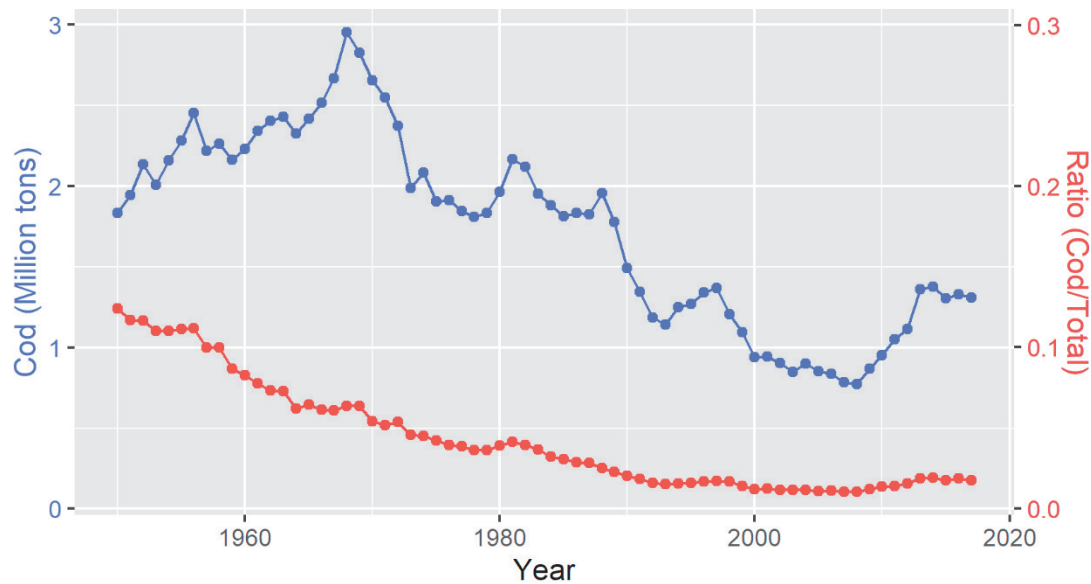
*Figure 3. Total landings of Atlantic cod (Gadus morhua, million tonnes in blue) and ratio between Cod landings and aggregated landings for all marine fish species globally (in red). Data from Fishstat database, FAO (2020b).*

The North Sea hosts one of the historically largest stocks in the Eastern side of the North Atlantic (cfr. for example supplementaty information in Sguotti *et al.*, 2019). North Sea cod is one of the main commercial species in the area. The stock has shown historical decline (Engelhard *et al.*, 2014) with the lowest point in abundance in the early 2000s, when the stock almost collapsed (Yletyinen *et al.*, 2018). Oscillations have been linked to climate fluctuations and overall changes in the ecosystem (Beaugrand *et al.*, 2003; Cushing, 1990; Edwards *et al.*, 2002; ICES, 2018). However, in the past decades the decline in biomass has been mostly linked to fisheries (Brander, 2018; Cook *et al.*, 1997; Froese and Quaas, 2012) or to a combination between negative climatic conditions for adults (Butzin and Pörtner, 2016; Engelhard *et al.*, 2014; Neuheimer and Grønkjær, 2012; Nunez-Riboni *et al.*, 2019), for larval stages (Beaugrand *et al.*, 2003, 2008; Nicolas *et al.*, 2014), and fisheries (Brander, 2005, 2010; Lilly *et al.*, 2013). A considerable improvement in selectivity, triggered by the recovery plan for cod (EC 1342/2008) and based on incentives linked to the fishing effort regime and to national measures, allowed a gradual recovery, compatible with rebuilding of the spawning stock (Brander, 2018; ICES, 2019). However, the recruitment may be still strongly subject to environmental variability and to the effect of climate change on temperature, on the plankton community and on the predation mortality in the first year of life at the planktonic and settlement stages of recruits (Akimova *et al.*, 2019; Hjermann *et al.*, 2013; Kempf *et al.*, 2010).

Although managed as a unitary stock (ICES, 2019), North Sea cod is considered to be composed of a mosaic of biologically resolved units (Figure 1), with limited overlap and varying degree of connectivity (André *et al.*, 2016; Heath *et al.*, 2014; ICES, 2015, 2020; Knutsen *et al.*, 2018; Neat *et al.*, 2014; Wright *et al.*, 2018). The units can be reduced to two main populations: the Viking bank and the South populations (Heath *et al.*, 2014; ICES, 2019; Wright *et al.*, 2018). The latter is often separated into a South proper (centred around the Dogger Bank) and a Northwest unit (González-Irusta and Wright, 2016; Holmes *et al.*, 2014; ICES, 2019). These two are genetically homogenous but show limited adult connectivity (so their relationship is as yet unclear (Heath *et al.*, 2014; ICES, 2020; Neat *et al.*, 2014). The Dogger Bank, the German Bight and Southern Bight are, or have been in the past, important nursery and spawning areas (Brander, 1994; Fox *et al.*, 2008; González-Irusta and Wright, 2016). The spatial variability and heterogeneity of North Sea cod has been shown by multiple means including population dynamics based on survey indices (Holmes *et al.*, 2008, 2014), otolith

microchemistry (Wright *et al.*, 2006a, 2018), genetics (Heath *et al.*, 2014; Nielsen *et al.*, 2009; Poulsen *et al.*, 2011), and behaviour with tagging studies revealing spatial segregation between areas (Neat *et al.*, 2014; Righton *et al.*, 2007; Wright *et al.*, 2006b). These differences correspond to differences in maturation and growth patterns (Neuheimer and Grønkjær, 2012; Wright *et al.*, 2011), depth distribution, possibly linked to thermal preferences (Neat *et al.*, 2014; Righton *et al.*, 2010) as well as varying influence of temperature, food and predation on early life stages and their effects on recruitment (Akimova *et al.*, 2016, 2019; Hjermann *et al.*, 2013; Holmes *et al.*, 2008; Nicolas *et al.*, 2014; Speirs *et al.*, 2010). These biological units are subject to uneven fishing mortality, present differing capability to sustain fishing pressure and to recover (Heath *et al.*, 2014; ICES, 2019), and potentially differing capability to withstand climate change (Barth *et al.*, 2017; Bonanomi *et al.*, 2015; Butzin and Pörtner, 2016; Nunez-Riboni *et al.*, 2019). Therefore, they may respond differently to harvesting. In this light, multiple authors have suggested that assessment should account for multiple populations, or for a metapopulation structure (e.g. González-Irusta and Wright, 2016; Heath *et al.*, 2014; Neat *et al.*, 2014; Wright *et al.*, 2018). However, up until now ICES WGNSSK provided advice at whole stock level. The capability to allocate catch and survey data to specific units, and uncertainty about the areas of overlap and mixing, prevented so far population-specific assessment (ICES, 2019), however explorations have been performed to further investigate population structure (ICES, 2015, 2019): trends in substock biomass have been monitored, and novel approaches combining assessment models with metapopulation theories have been tested (Jardim *et al.*, 2018). The current Benchmark Workshop on North Sea Stocks (WKNSEA 2021, ongoing at the time of writing this thesis) is evaluating the current data and assessment methodology in order to reach agreement on an assessment methodology to be used in future update assessments. To clarify the role of stock identification in North Sea cod, WKNSEA will make use of the results of the recent ICES Workshop On Stock Identification Of North Sea Cod (WKNSCodID), which reviewed information on the population structure of North Sea cod to recommend the most plausible scenario of population structure for stock assessment and fishery management advice. The workshop recommended that ICES stock assessments process should support advice for managing the Viking cod and Dogger cod populations as distinct units, in light of their genetic differences, and account for the phenotypic diversity in the Dogger population (ICES, 2020).

## 2.3 The influence of climate

Climate change is considered one of the most impacting threats to the marine environment (Boonstra *et al.*, 2015). While environmental variation has been studied for a longer time (e.g. Hjort, 1914), anthropogenic climate change has been broadly recognised only relatively recently (IPCC, 1990). Since then, the effect of climate change on marine environment has been the subject of intense research (Ferreira *et al.*, 2017; Grieneisen and Zhang, 2011; Pedersen *et al.*, 2016).

The increase in temperature seems to be the most commonly investigated effect of climate change in marine ecosystems (Ferreira *et al.*, 2017), possibly because of its crucial role in the functioning of biological systems at organismal level scaling up to ecosystems, affecting life-history strategies, productivity, and the geographic distribution of marine life (Beaugrand *et al.*, 2008; Cheung *et al.*, 2016; Perry *et al.*, 2005; Pinsky *et al.*, 2018). Sea surface temperature (SST) is often used as a proxy for experienced temperature; it is more easily measured compared to bottom temperature, and is generally considered an accurate proxy (but see Akimova *et al.*, 2016, for example).

In general, environmental factors influence marine organisms through direct and indirect pathways (Brander, 2010). Direct pathways include changes in physiological rates, in feeding success, and in behaviour. Indirect

effects may be due to changes in food, predators, parasites and diseases. Physiological rates and behaviour can be studied directly through experimental manipulation, while food-web effects are more complex to assess. Irrespectively, these changes affect the organisms in terms of growth, survival and reproductive output, highly relevant aspects for stock assessment of the commercial stocks. For example, trade-offs between somatic growth and metabolic costs due to temperature increase in cod and other fish species are well known (e.g. Brander, 2010; Holt and Jørgensen, 2015). Thermal tolerance influence metabolic activity and allocation of energy for reproduction and somatic growth (Pörtner *et al.*, 2008). These effects can scale up from individual to the whole population level (Butzin and Pörtner, 2016; Nunez-Riboni *et al.*, 2019). The effects are reflected on the patterns of maturation, survival and fitness (Holt and Jørgensen, 2014, 2015; Neuheimer and Grønkjær, 2012). When temperature exceeds the optimum, these changes affect fish distribution and local abundance (e.g. Dinesen *et al.*, 2019), as fish are assumed to move toward colder water, where available. Comparison between populations of Atlantic cod across its range showed that southernmost populations are closer to the thermal limits and will be negatively impacted by increasing temperature, while northernmost populations will benefit (Brander, 2010; Drinkwater, 2005). Notably, at local level seasonal patterns may matter more than average annual: the difference in SST increase between seasons may have diverging and counteracting effects (Rogers *et al.*, 2011). These effects can be confounded by other factors such as individual behaviour or ecological adaptations. For example, populations performing seasonal migration for reproduction will maintain historical spawning grounds also in the face of climate change. The southernmost spawning areas in the North Sea are still used by cod (Fox *et al.*, 2008; González-Irusta and Wright, 2016) despite the local thermal conditions are currently considered suboptimal, and are predicted to become unsuitable for reproduction (Butzin and Pörtner, 2016; Nunez-Riboni *et al.*, 2019). Individual behaviour can also appear counterintuitive: Neat and Righton (2007) observed that some cod individuals did not move to colder areas at reach, and rather suffered suboptimal warm temperature and increased vulnerability. The causes are not clear, highlighting the limited understanding even in one of the most studied fields. This shows that predictions of the effects of climate change on populations can be confounded by individual behaviour and may prove inaccurate.

Survey indices can show effectively the emergent changes in spatial distribution, resulting from combination of direct and indirect factors, the extent of which is difficult to disentangle, and to tell apart from the effects of fishing (Engelhard *et al.*, 2014; Heath *et al.*, 2014; Rindorf and Lewy, 2006).

Larval dispersal and population connectivity may be impacted by rising temperature as well: early life stages of marine organisms generally develop faster in a warmer water, reduce their pelagic time, and their dispersal distance. Their survival will depend on encountering enough food during the pelagic phase, given a higher metabolic demand; and in encountering favourable conditions at settlement. This may, in turn, affect the connectivity between subunits in the stock. The extent to which dispersal stage is affected by increasing temperature, is not well known in North Sea cod (but see Heath *et al.*, 2008), however some information can be drawn from other areas in the North Atlantic (Fuchs *et al.*, 2020), the Mediterranean Sea (Andrello *et al.*, 2015) or tropical coral reefs (Munday *et al.*, 2009).

Indirect effects of climate change include alterations of the trophic structure of the ecosystem across life stages: these include changes of prey and predators, as well as competitors, parasites and diseases. While the latter are little studied, the predator-prey relationships have received considerable attention, through analyses and modelling studies. The most important effects revolve around the food availability at the larval stage: thermal regimes alter the quantity and quality of food available, with consequences for growth, reproduction and mortality. Typical case is that of changes in calanoid community composition in the North Sea and in the North East Atlantic in general observed in the latest decades which has been indicated as the

main cause for the decline of cod recruitment in the North Sea (Beaugrand *et al.*, 2003; Beaugrand and Kirby, 2010; Nicolas *et al.*, 2014; Olsen *et al.*, 2011). Additional mechanisms include the match-mismatch between larval food and larvae hatching time (Asch *et al.*, 2019; Durant *et al.*, 2007) suggested for cod in the North Sea by Daewel *et al.*, (2011), and increased predation mortality from species that benefit from warming such as herring and grey gurnards (Akimova *et al.*, 2019; Hjermann *et al.*, 2013; Kempf *et al.*, 2013). For adults, an indirect effect may be the change in prey availability. Brander (2010) reports about the case of Icelandic cod, where temperature increase did not produce the expected increase in growth rate possibly due to the decline of their main prey, capelin *Mallotus villosus*.

The interaction between climate and other pressures, prominently fishing pressure, may lead to complex dynamics that need to be carefully considered. For example, heavily fished populations are more sensitive to environmental forcing due to the curtailed age structure (Ottersen *et al.*, 2006; Rouyer *et al.*, 2011), while their natural mortality may be influenced by fishing (Jørgensen and Holt, 2013). The interaction between climate change and fishing pressure can also influence the genetic diversity of populations: for example, loss of genetic diversity is associated to the collapse of West Greenland cod stock (Bonanomi *et al.*, 2015).

The spatial distribution of cod in the North Sea, instead, is suggested to be influenced by a combination of climate and fishing pressure: Blanchard *et al.* (2005) demonstrated that the range contraction of juvenile North Sea cod could be linked to reduced abundance as well as increased temperature, also noting that the distribution change may have increased cod vulnerability to fishing mortality. Rindorf and Lewy (2006) linked the northward shift in distribution to the effect of a series of warm, windy winters on cod larvae, and on the resultant distribution of settlers, further noting that this effect might be intensified by the curtailed age structure due to fishing pressure. Engelhard *et al.* (2014) found that the changing distribution of North Sea cod through the decades is linked to a combination of fishing and climate change, with a northward shift best explained by warming, and an eastward shift attributable instead to overexploitation of western fishing grounds.

Through effects on fish, climate change has profound consequences for the fisheries relying on them: the catch composition, fleet profitability and dynamics are also affected (Cheung *et al.*, 2013; Lam *et al.*, 2016), and the change in fish distribution can result in increasing conflicts for transboundary fish species (Diekert and Nieminen, 2015; Gullestad *et al.*, 2020; Pinsky *et al.*, 2018). This is already happening, for example, in the case of Atlantic Mackerel, which has expanded northward, causing a breakdown of the former agreements between countries sharing the stock (Elfarsdóttir, 2020; Østhagen *et al.*, 2020; Spijkers and Boonstra, 2017).

## 3. Methods and approaches applied

### 3.1 Ecosystem modelling

The interaction between species can be investigated through models of predator-prey dynamics, and in some cases whole ecosystems, including biotic and abiotic factors. When spatial considerations are critical for understanding the dynamics of the system, spatial food-web models have been applied (e.g. Kempf *et al.*, 2013; Lindegren *et al.*, 2014).

For the investigation of spatial dynamics of ecosystem interactions, we used the Ecopath with Ecosim (EwE) approach, and its spatial component Ecospace (Christensen and Walters, 2004). We used an existing non-spatial model parameterised for the North Sea (Mackinson and Daskalov, 2007) and developed the spatial component, Ecospace (Paper 1). We explored quantitatively the capability of the model to correctly reproduce known spatial patterns of fish biomass and fishing effort. Moreover our study explored the

sensitivity of model performance to parameters, identifying those with higher sensitivity, which seem to be the most important for model calibration.

The Ecopath with Ecosim approach is one of the most widely applied ecosystem modelling framework (Colléter *et al.*, 2015), with a long history of applications to marine ecosystem modelling and fisheries management questions (Heymans *et al.*, 2016). The model is built hierarchically: the base component is the Ecopath model, a static mass-balanced snapshot of a closed ecosystem, represented by functional groups connected through trophic interactions. Functional groups (species or groups of ecologically similar species) are represented as biomass "pools". Diet composition determines flows of energy and matters between functional groups. Ecopath is based on a system of linear equations which describe the average flow between groups and defined fishing fleets.

Ecosim, the time-dynamic module, uses the mass-balanced Ecopath model as a starting point to describe the temporal dynamics within the ecosystem, with annual or monthly time steps, through a system of differential equations. Ecosim is routinely parameterised through fitting to time series of biomass and catches of a subset of species or trophic groups. The model can include additional information to drive the dynamics (e.g. environmental variables, fishing mortality or fishing effort).

Ecospace is the spatial-temporal explicit module of EwE (Walters *et al.*, 1999, 2000). It is based on a two-dimensional "map", a grid of equally sized cells on which the biomass of functional groups is distributed and interacts with predators, prey and fishing fleets, according to a modified version of the Ecosim differential equations (Christensen and Walters, 2004). Ecospace was specifically developed to model the trophic dynamics of marine protected areas, assessing trade-offs between their relative size and effort redistribution, as well as effects of protection on non-target species, predators and preys (Walters *et al.*, 1999, 2000). Ecospace evolved considerably in the past decade: the implementation of externally derived habitat preference maps based on single species distribution models, effectively integrates a niche model in the spatial trophic model. This allows to measure cumulative impacts of multiple physical, oceanographic, and environmental factors (Christensen *et al.*, 2014; Püts *et al.*, 2020). Interoperability with GIS tools allows now to run spatio-temporal simulations (Coll *et al.*, 2016; Steenbeek *et al.*, 2013). These improvements allowed diversification of applications in fields such as development of renewable energy (Alexander *et al.*, 2016; Halouani *et al.*, 2020), Marine Spatial Planning (Romagnoni, 2019; Steenbeek *et al.*, 2020), and interactions between environmental-driven fish displacement and fisheries dynamics (Bauer *et al.*, 2018).

## 3.2 Drift model

The planktonic early life stage is considered, for broadcast spawning fish, a critical period, and one of the key phases for shaping a year class productivity (Cushing, 1990; Hjort, 1914), although evidence is growing that density dependence at settlement and juvenile phases have an important role too (Houde, 2008). Early life stages (eggs and larvae; hereafter ELS) can be studied through simulation models. In this context, coupled physical-biological models for early life stages of marine fish are increasingly applied (Huebert *et al.*, 2018; Peck and Hufnagl, 2012).

In Papers 2 and 3 we modelled the drift of cod planktonic eggs and larvae, using the open source particle tracking framework OpenDrift (Dagestad *et al.*, 2018, github.com/opendrift). To simulate transport with ocean currents and temperature-dependent development, we coupled offline a reanalysis of the regional ocean circulation model ROMS (Shchepetkin and McWilliams, 2005) configured for ocean regions including

the North Sea to a cod egg and larvae individual-based model (IBM), integrated as a module to OpenDrift. The IBM simulates development and transport of cod eggs and larvae based on earlier studies (Kristiansen *et al.*, 2009a, 2009b, 2014).

In Paper 2, we compared different reanalyses of the oceanographic model and formulations of the cod egg and larvae IBM, in order to assess the relative importance of spatiotemporal resolution of the oceanographic model, inclusion of vertical movement, and interannual variability in oceanographic conditions.

In Paper 3, we have combined >40 years of oceanographic model predictions to track the eggs and larval drift from and to putative population areas in order to assess the long-term changes to retention and connectivity. This information was then incorporated into stock-recruitment models in different ways, to account for effective spawning stock size when explicitly accounting for retention and connectivity.

Physical (hydrodynamic) models with Lagrangian particle-tracking subroutines, coupled IBMs can account for growth, behaviour and mortality of the simulated eggs and larvae of fish or other planktonic organisms (e.g. Fiksen *et al.*, 2007). Temperature-dependent growth allow to account for the differential increase in size based on the experienced temperature, while inclusion of vertical movement may allow to capture the important effects of diel vertical migrations. These features make biophysical modelling of early life stage IBMs very popular tools to investigate processes affecting distributions and productivity of marine fish species (Peck and Hufnagl, 2012) and to examine how environmental characteristics affect the distribution, growth and/or survival of marine organisms (Huebert *et al.*, 2018; Siddon *et al.*, 2013). Biophysical modelling of fish early life stages have been applied to study the spatial distribution of the spawning stages (Eriksen *et al.*, 2020; Muir *et al.*, 2020), connectivity between populations (Barbut *et al.*, 2019; Heath *et al.*, 2008; Ospina-alvarez *et al.*, 2020) and the effects of spatial mortality on fish ELS due to natural and anthropogenic factors (Fiksen *et al.*, 2007; Langangen *et al.*, 2014a, 2014b, 2017; Peck and Hufnagl, 2012; Stige *et al.*, 2018).

### 3.3 Bioeconomic model and optimisation

Fisheries management, in addition to biological considerations, needs to ensure the viability of the fishery in socioeconomic terms (Hilborn and Walters, 1992). Bioeconomics is a branch of resource economics that addresses the use of living resources, and it is widely applied to study fisheries management. Modelling such dynamics can be useful and important to gain understanding of the different impacts from the ecological, economic and social assumptions criteria for management policies for exploitation of the natural resources. In the marine realm, they are often applied for assessing the economic profitability of management scenarios aimed at obtaining maximum sustainable yield or to evaluate alternative measures and their impacts on the ecological, economics, and social goals (Nielsen *et al.*, 2017; STECF, 2019b).

In Paper 4, we compare two alternative management strategies in terms of their bioeconomic optimal long-term performance. We explore the management options of a spatially structured stock, comparing explicit population-specific management against an aggregated management where two populations are managed disregarding their individual dynamics. We build a bioeconomic model based on an age-structure population model for each of the two populations (described by Equation 1), and compare the optimized economic gain of population specific and undifferentiated management under three climate scenarios. The biological model described population dynamics through abundance ($N_{i,t,a}$) for each population *i*, age *a*, at time *t* as:

$$N_{i,t,a} = \left( N_{i,t-1,a-1} - \frac{H_{i,t-1,a-1}^m}{W_{t-1,a-1}} \right) e^{-M_{a-1}}$$

*Equation 1.*

The number of fish harvested are obtained dividing harvest $H$ (in weight) by mean weight at age $W_{t,a}$. Natural mortality at age $M_a$ accounts for natural loss. Average individual weight at age and proportion of mature fish at age $P_a$, are used to calculate $SSB_{i,t}$ that is used to calculate recruitment $R_t$ (entering the population as abundance at age 1) through a stock-recruitment function. Multiple stock-recruitment model formulations were explored, including different functional forms and with inclusion of temperature and/or zooplankton following Olsen *et al.* (2011). For consistency, we selected a model that performed satisfactorily for both population, rather than using different models for the two populations. The selected stock-recruitment model (Equation 2) was based on the Beverton-Holt function with temperature influencing recruitment through change of maximum recruitment level (asymptote height).

$$R_{i,t} = e^{(\alpha_i - \theta_i T_{i,t})} \frac{SSB_{i,t}}{\left(1 + \left(e^{\gamma_i} SSB_{i,t}\right)\right)} e^{\varepsilon_{i,t}}$$

*Equation 2*

The model calculated recruitment $R_{i,t}$ at each time step $t$ for each population $i$ as a function of $SSB_{i,t}$, scaled temperature $T_{i,t}$ and parameters $\alpha_i$, $\theta_i$, and $\gamma_i$. $e^{(\alpha_i - \theta_i T_{i,t})}$ was the maximum reproductive rate at temperature $T$, and positive temperature anomalies resulted in a negative effect on recruitment (lower asymptote height) and vice versa. Random noise $\varepsilon_{i,t}$ was introduced as lognormal error. Parameters were estimated from data for each population $i$.

The optimal harvest rate was obtained by maximising the net present value (NPV) over a long time horizon, for any of the two management scenarios $m$ to be compared. NPV (Equation 3) is the cumulative sum of the discounted annual profit:

$$NPV^m = \sum_{t=0}^{Z} \frac{1}{(1+\delta)^t} \Pi_t^m$$

*Equation 3*

where $\frac{1}{(1+\delta)^t}$ is the discount factor, $\delta$ is the interest rate, $\Pi_t^m$ is annual profit in year $t$, for management scenario $m$, and $Z$ is the time horizon. In this formulation, profit $\Pi_t^m$ is a function of harvest rate, and population-specific time paths of total biomass $B_{n,t}$ and $B_{s,t}$ for North and South populations respectively. The profit function for each management scenario $m$ was:

$$\Pi_t^m = p\left(H_{n,t}^m + H_{s,t}^m\right) - \kappa \left(\frac{H_{n,t}^m}{B_{n,t}} + \frac{H_{s,t}^m}{B_{s,t}}\right)$$

where $p$ is price per unit of biomass and $\kappa$ is a parameter for the cost functions (Equation 4 and Equation 5) Annual harvest of North and South populations $H_{n,t}^m$ and $H_{s,t}^m$ were functions of harvest rate (the control variable optimised) and total biomass $B_{n,t}$ and $B_{s,t}$. The harvest functions were:

$$H_{i,t}^{PSM} = h_i^* B_{i,t}$$

*Equation 4*

And

$$H_{i,t}^{UM} = h^* B_{i,t}$$

*Equation 5*

for each population *i*, at time *t*, for the Population Specific Management (PSM) and Undifferentiated Management (UM) scenarios.

The study explores climate change effects by specifying the diverse response of the two cod stocks to climate through a temperature-dependent, empirically derived stock-recruitment function. This study thus firstly focuses on the optimal management of population structure, and secondly on how the optimal strategy may change when heterogeneous climate sensitivity is included in the model and climate is forced with simulated predictions.

Several bioeconomic modelling frameworks and ad-hoc models exist and are currently applied in multiple contexts. For example, Nielsen *et al.* (2017) reviewed bioeconomic models applied in Europe, analysing the different capabilities to capture multispecies dynamics, spatial dynamics, and their levels of effectiveness and implementation in fisheries management. Bioeconomic models have been used to assess the effects of climate change on fisheries economic performance: for example, several studies propose approaches to include and mitigate the detrimental effects of climate change (e.g. Bastardie *et al.*, 2010; Miller *et al.*, 2013). Spatial bioeconomic models have been applied frequently in the study of spatially uneven distribution of resources or fishing effort with patchy environment (Sanchirico and Wilen, 1999, 2001). The spatial aspect acquires added relevance when stock distribution is influenced by the effect of climate change. This is key for example in the case of straddling stocks (Diekert and Nieminen, 2015), invasive species (Kaiser *et al.*, 2018), and spatial interaction between species. Voss *et al.* (2018) recently applied a spatially explicit bioeconomic model to investigate the role of recruitment strategies, i.e. connectivity, on the fisheries and, most important, on the traditional communities relying on them for subsistence and for cultural heritage. Although multiple studies of North Sea fisheries in bioeconomic terms exist (Bartelings *et al.*, 2015; Heymans *et al.*, 2011; Simons *et al.*, 2014; Ulrich *et al.*, 2011), the economic implications of predicted climate change on North Sea fisheries are relatively scarcely studied (Groeneveld *et al.*, 2018; Pinnegar *et al.*, 2016). In this sense, our study addresses an understudied research niche.

## 4. Results and Discussion

This thesis focuses on the interaction between spatial marine ecology, oceanography and management under climate change. The key hypothesis is that the interaction between spatial dynamics and climate influences population dynamics, with consequences for management and for the sustainability and profitability of the fishery. The overarching question of the thesis is thus: can we identify emerging interactions between spatial dynamics and climate change, and to what extent do these interactions influence fisheries management?

While the effects of environmental variation and climate change and those of spatial dynamics on North Sea cod have been investigated before, the interaction between climate change and spatial dynamics is relatively less studied, in particular under management and economic perspectives.

The overall answer provided by this thesis is that the effects of climate differ between subunits of the stock, and the spatial dynamics are influenced by climate through the connectivity between units and differential sensitivity to climate across the stock spatial distribution. Moreover we observed different effects depending on the scale of observation, i.e. at population vs. stock level, and across spatio-temporal resolution. These emergent interactions between climate and spatial dynamics are highly relevant for spatial ecology and for fisheries management. However, we did not observe a clear economic incentive in spatially explicit management, not even in light of differences in climate effect between populations. This result may be

bounded by the knowledge gaps and model limitations, revealing what relevant aspects remain to be explored and understood and opening new research perspectives.

The overarching research question was broken up into smaller parts, narrowing down on some aspects, albeit in a non-exhaustive way. We focused on four main aspects: three with an ecological focus and one with intertwined ecological, management and economic focus: 1) Spatial food-web dynamics, 2) scale of dynamics of drift models and their effect on connectivity, 3) metapopulation dynamics and interaction between larval transport, climate change and recruitment; and 4) bioeconomically optimal management strategy. These four aspects of interest correspond to the Papers composing this thesis.

### 4.1 Spatial food-web dynamics

The dynamics among species in a system, and between species and the abiotic factors, depend critically on the spatial distribution of these elements. Several ad-hoc spatial models have been applied to understand multispecies dynamics and their interaction in space (Akimova *et al.*, 2019; Hjermann *et al.*, 2013; Kempf *et al.*, 2013; Lindegren *et al.*, 2014).

Spatial multispecies models that can take into account the interaction between species and multiple pressures and impacts on the ecosystem, can be highly useful to capture complex spatial dynamics. These models may help to address questions where multi-species spatial dynamics play a key role for fisheries management perspectives. These models, however, face the challenging trade-off between complexity and accuracy. Spatial models can increase the number of parameters exponentially. Performance assessment of ecosystem models is critical, especially when their development is intended for applied purposes. Validation of spatio-temporal models with comparable data is an emerging field within ecological models (Rose *et al.*, 2009; Stow *et al.*, 2009; Vliet *et al.*, 2011), and only few marine ecosystem models have been critically evaluated with data in terms of their predictive capability (Lynam *et al.*, 2017; Püts *et al.*, 2020).

The research question developed in Paper 1 is: Can spatial ecosystem models capture known spatial dynamics effectively? Can we measure quantitatively the fit to data and the sensitivity of the model to parameter uncertainty?

In detail, the first chapter of the thesis assesses the spatial ecosystem dynamics and interactions between fleets and species. Based on an existing ecosystem model (Mackinson and Daskalov, 2007), a spatial version was developed. Model outputs were compared with spatio-temporal data to assess both model performance and sensitivity to parameters setting through an ad-hoc procedure for quantitative prediction to data evaluation. Results show that the model is sensitive to some parameters in particular, highlighting that information such as fish dispersal rate and the behaviour of fishing fleets, are key to understand how the system responds spatially. The model was capable or reproducing fish distribution patterns. Effort distribution, in turn, seems not to follow rational, medium-term profit-based solutions as assumed by the model. Instead, we propose that effort distribution in this system might be driven by processes acting at fine temporal scale and by decisions related to concerns other than immediate profit, perhaps driven by market dynamics and to the quota system and the multispecies nature of the fishery.

This Paper sets the baseline for the thesis, confirming the role of spatial information, such as fish dispersal and fisheries distribution as well as predator-prey overlap, in understanding the ecology of target fish species including cod. In general terms, moreover, the paper serve the spatial ecosystem modelling community, setting the baseline of critical assessment of spatial predictions of species and fleets distribution for rigorous application of fisheries models. In perspective, the application of this work could be highly useful for

management applications: well-tested models can be reliably applied to inform spatial management measures, such as fishing closures or effort restrictions in some areas (e.g. north versus south). Moreover, estimates of natural mortality for cod from a multispecies model is included into the currently applied stock assessment models. This, however, is not spatially resolved, while it is now clear that predation differ between areas. A robust Ecospace model could provide spatio-temporal mortality patterns, possibly resolved at sub-stock level for North Sea cod. Our work shows that model predictions of spatial distributions can reliably reproduce specie distribution. However spatial predictions require robust assessment, which, so far, is often lacking from spatial ecosystem modelling implementations. Recent studies started to focus on this aspect (e.g. Lynam *et al.*, 2017; Püts *et al.*, 2020), showing that our study identified an important gap, and provided a useful guideline for successive investigations in this field.

### 4.2 Sensitivity of larval transport models across spatial and temporal scales

The early life stages (ELS) play a key role in shaping the year class of most fish species, including Atlantic cod. Variability of direction and strength of currents may influence the transport of larvae into suitable areas for feeding and, thus, the success of a year class recruitment (e.g. Wilson and Laman, 2020). Moreover, the variability in transport might affect the potential connectivity between areas and sub-populations.

In Paper 2, we assess how vertical movement, ocean model resolution and interannual variation in ocean dynamics influence drift patterns and population connectivity. The research question posed was: What are the most important aspects that influence the spatial distribution of simulated eggs and larvae of cod in the North Sea? We studied how alternative setup for ELS transport models provide different results, quantifying the most influential aspects, across spatial and temporal scales of spatial distribution.

We focused on these three aspects in particular, because of their known importance in modelling ELS distribution (Bolle *et al.*, 2009; Lacroix *et al.*, 2013). However, the inclusion of vertical movement and of fine-scale model reanalysis has a major computational demand. Similarly, inclusion of multiple years is constrained by availability of oceanographic models that go back in time. Our focus was on identifying trade-offs between inclusion of higher accuracy (e.g. vertical movement, high resolution), and computational cost.

We found that the results are moderately influenced by vertical movement and ocean model resolution but differ substantially between years, confirming previous studies on the importance of interannual variation in ocean circulation for modelled fish larvae drift in the North Sea (Bolle *et al.*, 2009; Henriksen *et al.*, 2018; Lacroix *et al.*, 2013). Interannual variability in ocean transport may be related to wind patterns (Bolle *et al.*, 2009; Wilson and Laman, 2020), and to large scale oceanographic patterns such as the North Atlantic Oscillation (NAO) index, (Henriksen *et al.*, 2018; Huserbråten *et al.*, 2018; Jonsson *et al.*, 2016) which can influence regional to local current patterns and strength. While ocean model resolution is consistently more influential than vertical movement, the effect of vertical movement strongly depends on the spatiotemporal scale of the analyses. These results add up to the growing literature on sensitivity of drift models (Peck and Hufnagl, 2012), revealing that some model features often considered highly relevant, might ultimately be of minor importance for a specific research question and case study such as the North Sea, where the limited stratification might result in reduced role of vertical movement for drift patterns and overall ELS distribution. Sensitivity analysis should therefore be specific to the question and study area.

The importance of interannual variability is a critical result as it confirms the relevance of long-term analysis, enabled by long time series of ocean model reanalysis. This could not be possible with higher resolution models, which are only available for most recent years. These results find immediate application: we can

safely apply models with relatively coarse resolution but with longer time series, allowing to monitor long-term changes and use them for population dynamics, and effects of climate change. This study paves the way to Paper 3, by demonstrating that a computationally less intensive model, but with a longer time series, may perform similarly well than a more advanced model.

### 4.3 metapopulation dynamics and interaction between larval transport, climate change and recruitment

The interaction between ELS transport, environment, connectivity and recruitment dynamics is relatively well known for cod in the North Sea. However, the relevance of these dynamics for management is scarcely studied. In Paper 3, we ask the question: Can we include advection and connectivity into analysis of population dynamics that are useful for management? We focus on stock-recruitment models: these are commonly used in fisheries science to relate the amount of spawning stock in one year with the recruitment in the next year. These models are widely recognised to poorly capture the relationship but are nonetheless commonly used due to the intuitive mechanism relating stock size to production (Subbey *et al.*, 2014). In many cases, their performance has been improved when introducing environmental anomalies as a parameter (Akimova *et al.*, 2016; Hilborn and Walters, 1992), or when weighting the spawning stock by, among other variables, the age or sex structure in the spawning component (Marshall *et al.*, 2006).

Here, we applied the quantitative measures of larval retention and of connectivity between subpopulations to the stock-recruitment curves commonly used in stock assessment, in place of other, commonly used environmental variables such as SST. In addition, we propose a novel method for accounting for population connectivity in stock-recruitment models, weighting SSB by the effective larval contribution to a determinate population. Paper 3 shows that the importance of the retention anomaly, and of the connectivity between populations, differ across scales of observation. The effect of retention anomaly is small but not negligible, and comparable in magnitude to those of other commonly used variables such as SST. Moreover, the modelled connectivity between populations seems to present a correlation with SST, indicating a potential interaction between climate change and spatial population structure.

These results allow us to apply the stock-recruitment curves with ELS drift, and our newly developed method, to this and other stocks. More important, these results help to investigate hypotheses about connectivity and its interaction with climate through transport, and to explore their application for management (Hidalgo *et al.*, 2019; Wilson and Laman, 2020), opening up for novel research directions and positioning our study in the emerging field of operational fisheries oceanography (Hidalgo *et al.*, 2019).

### 4.4 Economically optimal management and the problem of spatial population structure

In fisheries management, stocks are geographically defined. However, the stock resolution is rarely based on biological metrics and is generally an artefact. This has resulted in several stocks being managed at the incorrect spatial scale, often due to a lack of knowledge or insufficient data at population specific scale (Kerr *et al.*, 2017). Mismanagement of population structure may lead to incorrect estimation of reference points for management, increasing the probability of collapse (Sterner, 2007). Such effects might go unnoticed until it is too late, as plausibly happened with the abrupt collapse of the cod fishery off Newfoundland and Labrador (Hutchings, 1996; Lilly, 2008). The results of such mismanagement might have led to disappearance of individual populations, with the erosion of the diversity in a stock (e.g. Bonanomi *et al.*, 2015). Population diversity is a richness, offering a buffer to perturbations through the so-called portfolio effect (Schindler *et al.*, 2010), and implying genetic diversity that might result in higher adaptation potential to climate change

(Bonanomi *et al.*, 2015; Hauser and Carvalho, 2008). Where information is sufficient for informed population-specific management, it is important to investigate whether separated management could improve the sustainability of the fishery, and ultimately its management system, both under an ecological and economic perspective. For example, by estimating reference points at the correct biological scale, population-specific management might limit the danger of serial populations depletion and of stock collapse with resulting economic loss for the fishing sector.

North Sea cod is a strong candidate for separation of management for the two known populations. In Paper 4, we ask the question: Can we propose spatial management by population as a management measure that outperforms the non-spatial one, using economic justification? Do we observe a change in the optimal management strategy (i.e. spatial vs non-spatial), in light of their different temperature sensitivities? The latter question in particular is important in light of the growing focus on adaptation to climate change (Woods *et al.*, n.d.). If the differential effect of climate between populations is large, we can propose spatial management as a climate change adaptation strategy. Our results however cannot point at a difference in optimal management strategy: from an economic perspective it is equally profitable to harvest two populations individually or as one, when either management strategy is optimised. This result does not change when climate influences the recruitment dynamics of the two stocks. These results might be bounded by the simplification of our model that adopts an optimal, time-invariant harvest rate and by the relative similarity in response to climate of the two modelled populations. The response to climate is based on empirical stock-recruitment relationships including the effects of temperature. However, this analysis did not consider explicitly larval drift, nor the effects of climate variability and its interaction with connectivity between populations. Paper 3 showed that, the connectivity between populations is also influenced by temperature. The results may therefore differ if the additional effect of climate on drift was included in the bioeconomic model. In a similar analysis, Voss *et al.* (2018) found that biological heterogeneity explain differences in spatial management, whereas overlooking the heterogeneity might provide homogeneous optimal management.

Our overall result, however, is in line with the existing literature on economic profitability of population-specific management: for example, Holland and Herrera (2010, 2012) showed that the benefit of managing populations at their biological spatial scale depends on biological, economic and technical factors including uncertainty in spatial aggregation as well as mixing and migration between populations, especially if asymmetric. They found that the risk of mismanagement might be such that aggregated management may be a safer solution in determinate cases. Lindegren *et al.* (2013) performed a similar analysis on Öresund cod population, highlighting the need for developing sub-stock-specific management recommendations to allow the maintenance of population structuring, also in light of the economic benefits for local small scale fisheries. Our results highlight the importance of carefully assessing economic benefits and practical feasibility of alternative management strategies in the context of spatially structured populations (Kerr *et al.*, 2016; Voss *et al.*, 2018).

Although these results cannot be generalised, our bioeconomic exploration of spatial management options for spatially structured populations under climate change is a novel, and widely applicable, research question. Moreover we show that the effects of increasing temperature and of adopting optimal (rather than sub-optimal) harvest rate, irrespective of population scale, have a larger economic impact than managing at the correct spatial scale.

## 5. Conclusion and significance

The importance of spatial processes in population dynamics and ecosystems has been highlighted since the early ages of fisheries science, however their application into management has proven difficult. Nevertheless, the technological advancements and the improved understanding of marine fisheries dynamics and spatial populations structure has allowed considerable advancements of this field in the recent decades.

There is momentum for including complexity in the management of fish stocks, accounting for spatial structure and for environmental effects: many recent studies focus on this subject (e.g. Hidalgo *et al.*, 2019; Voss *et al.*, 2018), calling for inclusion of larval connectivity (the operational oceanography concept), of population structure, and of spatial multispecies interaction.

This thesis contributes to the field by identifying processes that can influence population dynamics at local and regional scales, and proposing approaches to assess the relevance of climate and spatial scale, and their interactions, on population dynamics and on fisheries management. I explored whether interactions between spatial dynamics and climate can influence population dynamics, and whether such interactions in turn can affect optimal management strategies. I proposed the integration between bioeconomic, oceanographic and ecosystemic aspects to assess the spatial scale of fish ecology dynamics and of fisheries management.

These results open up for novel research questions: for example, one could wonder whether accounting for temperature-dependent connectivity or inclusion of connectivity in stock-recruitment dynamics (as proposed by Paper 3), would influence the optimal management strategy in the context of spatially explicit management. Another possible research line could be the integration of spatially explicit, population-specific natural mortality into stock assessment. Natural mortality is likely to differ between the two populations based on the predators in the area and of differing sensitivity to climate changes. These aspects, and how they vary in time through the food-web, could be captured by a spatial ecosystem model such as that presented in Paper 1. Along the line of ecosystem dynamics, one may wonder whether and how spatial management measures for one species would fit in a mixed fisheries context such as the North Sea demersal fisheries? And with the impending Brexit process, what would be the trans-national negotiations for international sharing of the quotas when considering or disregarding the population structure, especially when the outlook for the two populations' sensitivity to climate change differs? These and many other questions come to mind, showing that the research exposed here is bearer of innovation, stimulating novel thinking.

Spatially explicit management strategies that can account for a moving fishery in relation to population dynamics as well as the impact of global warming are needed now more than ever due to the potential for future climate change and continued fishing pressure. For North Sea cod, an ICES benchmark workshop (WKNSEA) is ongoing at the time of writing this thesis. Among the topics, the workshop aims to assess whether stock assessment at population level is feasible. This shows once again that this thesis is highly timely. Hopefully, the results here presented could be of relevance for this and other future applications, towards sustainable exploitation of North Sea cod (and other stocks) in the face of climate change and its interactions with fish ecology and spatial dynamics.

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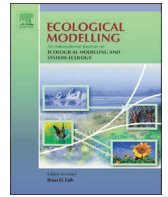
# Paper I

# The Ecospace model applied to the North Sea: Evaluating spatial predictions with fish biomass and fishing effort data

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## ABSTRACT

The Ecospace model has been developed from the Ecopath with Ecosim food web model to add a spatial dimension for investigating marine ecosystems. In this study, we evaluated the sensitivity of an Ecospace model developed for the North Sea ecosystem to some of its key parameters, and we examined this model's capability to reproduce trends in spatial time-series of fish biomass and fishing effort. We measured the fit between the spatiotemporal model predictions and the corresponding data of biomass for 12 species and effort for three fishing fleets. Our results suggest that the Ecospace model for the North Sea can predict quite successfully the species distribution, but not the distribution of fishing effort. We hypothesise that the reason might be that Ecospace assumes spatial effort distribution to be driven mainly by profit, while other factors might be more important in our system at the spatiotemporal scale explored. The model might thus fail to capture fisher's behaviour accurately for this system. Despite the limitations of our ad hoc approach for sensitivity analysis, these results hint that some problems exist in our model, which might extend to other Ecospace models and perhaps to the framework in general. This study highlights the importance of validating Ecospace models with data if their results are used for management advice. We suggest that, in order to make of Ecospace a more robust tool for management advice, some critical improvements are needed: the development of an algorithm for parameter optimisation through fitting the model predictions to data, and advancement of the effort distribution model.

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## 1. Introduction

Fisheries management is moving towards an Ecosystem Approach to Fisheries (EAF). EAF complements and integrates single-species management by accounting for trophic food web effects. Overlooking inter-specific interactions can result in unexpected deterioration of ecosystem structure and fish stocks (ICES, 2012b; Mackinson et al., 2009; Pikitch et al., 2004; Walters et al., 2005). Ecosystem models are promising tools for management advice, thanks to the appealing capability to include a wide range of processes across a wide range of scales, and to provide quantitative and easy-to-interpret results. Inclusion of these tools into management advice is getting increasingly advanced, most often in combination with other approaches (e.g., Dichmont et al., 2013; Fulton, 2011; Fulton et al., 2011). However, the model behaviour across different parameters values and prediction capability of the models should be accurately investigated in order to provide reliable tools for managers (e.g., Harwood and Stokes, 2003). In this study, we explored capabilities and limitations of a widely used model to provide a quantitative evaluation which could be useful for its future application for management advice.

The importance of spatial dimension in marine fisheries ecology is increasingly recognised (Ciannelli et al., 2008; Kempf et al., 2010, 2013). Marine organisms distribute spatially according to specific patterns, either statically (as a result of their habitat and environmental preferences) or actively moving (e.g., reproductive migration). Similarly, fishermen decide where to fish based on their knowledge about fish distribution and other factors. Neither fish nor fishers are thus homogenously or randomly distributed in space, an implicit assumption in non-spatial fisheries assessment and management. Spatial structure and processes can explain local dynamics with relevance at the whole basin level, while ignoring such structure and processes can undermine our understanding

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of the systems and our capability to manage them effectively (Hjermann et al., 2013; Kempf et al., 2010, 2013; Pelletier and Mahévas, 2005; Sanchirico, 2005).

By integrating spatial dynamics and food web interactions, spatially explicit ecosystem models can be useful to support an EAF. A number of modelling frameworks have undertaken this approach: Osmose (Shin and Cury, 2001), Atlantis (Fulton et al., 2011) and Ecopath with Ecosim (Christensen and Pauly, 1992; Walters et al., 1997) are among the most used tools (Fulton, 2011; Pelletier and Mahévas, 2005; Plagányi, 2007). These models are certainly not the panacea for the problem of fisheries management; however they can prove useful for selecting among policy choices. Ecopath with Ecosim (EwE) is an approach based on a mass-balanced food web model (Christensen and Pauly, 1992; Walters et al., 1997) and it includes the spatial component Ecospace (Walters et al., 1999). Ecospace was developed mainly for studying spatial management scenarios, in particular marine protected areas (MPAs), and their effect on ecosystem dynamics and fishing profitability (Beattie et al., 2002; Le Quesne et al., 2008; Metcalfe et al., in review). Rather than attempting to incorporate all possible processes that regulate spatial food-web dynamics (an arguably impossible task), Ecospace aims at reproducing general, but realistic, distribution patterns at a regional scale.

In order to make the Ecospace model a valuable and reliable tool, one needs to carefully evaluate the model performance in several ways. An important exercise is sensitivity analysis (Saltelli et al., 2008), which explores the variation in model fit across different values of the parameters. Formal parameter sensitivity analysis has already been performed for Ecopath (Essington, 2007) and Ecosim (Gaichas et al., 2012) but no analysis of the whole parameter dimension has to our knowledge been performed for Ecospace. Some studies explored model robustness to changes in parameters input of ±50% (e.g., Chen et al., 2009; Espinosa-Romero et al., 2011), focusing however on one parameter at a time, a procedure which does not allow to explore the whole parameter dimension (Saltelli and Annoni, 2010). In general, the large number of parameters is a major challenge in modelling, and especially for Ecospace, as it makes it difficult to explore the parameter dimension systematically. Furthermore, realistic estimates of parameter values can be difficult to quantify, due to the lack of detailed information at the species and fleet level for many of the parameters. Default or user-defined values for Ecospace parameters are thus often used, without any critical assessment of their robustness.

Another important practice is the evaluation of a model performance through comparison with data. In Ecospace, this analysis was performed in a few studies for species distribution (Daskalov et al., 2011; Mackinson et al., unpublished), however no study to our knowledge has compared predictions of spatial distribution of fishing effort to data. Given that the evaluation of MPA effects on fishery profitability is largely based on predicted fleet response, i.e., variation in effort distribution, fleet behaviour is a key feature in Ecospace. It is therefore fundamental to evaluate quantitatively the capability of the model to reproduce known spatial patterns of fleets' distribution.

Two complementary tools are then necessary for evaluating Ecospace: (i) sensitivity analysis to variation in parameters settings; and (ii) a systematic evaluation of model performance through comparison of model predictions to data. In this paper we use both these tools to firstly identify which parameters have the largest effect on the performance of the North Sea Ecospace model; and secondly quantify the North Sea Ecospace model capability of reproducing known trends and spatial distribution of fish species as well as fishing fleets. Our aim is to evaluate the realism and unmask what is needed in order to improve and set quality standards for this Ecospace model, but also the framework as such, in order to be an efficient tool for management advice.

## 2. Methods

### 2.1. Ecopath with Ecosim

Ecopath with Ecosim (EwE) is a food-web model based on the assumption of mass-balance. It was developed for modelling marine ecosystems and understanding the impact of fisheries and other pressures on the system (Christensen and Pauly, 1992; Walters et al., 1997, 1999). The model and its assumptions have been discussed widely in the literature (Christensen and Walters, 2004; Pauly et al., 2000; Plagányi and Butterworth, 2004). The model is built hierarchically: the base component is the Ecopath model, a static mass-balanced snapshot of a closed ecosystem, represented through a network of nodes (functional groups) and links (trophic interactions). Functional groups (which can be species, groups of ecologically similar species, ontogenetic classes, or detritus groups) are represented as biomass "pools". Diet composition determines flows of energy and matters between functional groups. Ecopath is based on a system of linear equations which describe the average flow between groups within an interval of time. The main equation is:

$$P_i = B_i \cdot M_i + Y_i + E_i + BA_i + P_i \cdot (1 - EE_i)$$

where, for each functional group $i$, $P_i$ is productivity, $B_i$ is biomass, $M_i$ is total mortality rate from predation, $Y_i$ is mortality rate from fishery, $E_i$ is net emigration rate (emigration-immigration), $BA_i$ is biomass accumulation rate, and $EE_i$ is ecotrophic efficiency (the proportion of production which is utilised in the system). The term $P_i \cdot (1 - EE_i)$ can be interpreted as the mortality from other causes than predation or fishery. The mortality from predation links predators and preys, through the equation:

$$B_i \cdot M_i = \sum_j B_j \cdot (Q/B)_j \cdot DC_{ji}$$

where the total predation mortality of group $i$ is given by the sum across all predators $j$ of the predator biomass $B_j$ times the consumption per unit of biomass of $j$ (i.e. the term $(Q/B)_j$) times the fraction of prey group $i$ in the diet of group $j$ (the term $DC_{ji}$). The second main equation of Ecopath states that consumption is equal to production plus respiration plus unassimilated food. Ecosim develops the Ecopath food web in a time-dynamic simulation through a system of differential equations, which calculates flow of biomass across functional groups through time. Information from the Ecopath module is combined with parameters and assumption about feeding relationships which are used to parameterise the differential equations. Ecosim is routinely parameterised through fitting to time series of biomass and catches. The basic Ecosim equation expresses the rate of variation in time of biomass $B$ for each group $i$ as:

$$\frac{dB_i}{dt} = g_i \cdot \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i$$

where $g_i$ is the net growth efficiency, $Q_{ji}$ is the consumption rate of group $i$ on group $j$, and $Q_{ij}$ is the consumption rate of group $j$ on group $i$. The first two terms represent the total consumption of group $i$ and the total predation suffered by group $i$ from all other groups, respectively. $I_i$ is the immigration rate, $M_i$ is the non-predation natural mortality rate, $F_i$ is the fishing mortality rate, and $e_i$ is the emigration rate. In Ecosim, consumption $Q_{ij}$ is calculated through the foraging arena theory (Walters et al., 1997), which splits the biomass pool of a prey species available to a predator into an available ("vulnerable") and an unavailable ("non-vulnerable") fraction, regulated by a parameter named "vulnerability". Ecosim is particularly sensitive to vulnerability, which is the parameter

estimated by fitting the model to time series data (Mackinson, 2014). For further details about the model framework we refer to Christensen and Walters (2004), Christensen et al. (2008) and Walters et al. (1997).

## 2.2. Ecospace

Ecospace is the spatial component of EwE (Walters, 2000; Walters et al., 2010, 1999). It is based on a two-dimensional "map", a grid of equally sized cells on which the biomass of functional groups is distributed. Species distribution is modelled through habitat assignment based on group-specific preference with respect to feeding and predation regimes, and dispersal rates. Temporal changes in biomass and consumption of species at the local scale are simulated with predator–prey relationships through a set of Ecosim differential equations for every cell in the map. Groups can move to adjacent cells through random-directional movements depending on swimming speed. Ecospace inherits parameters and data (e.g., time series of biomass, fishing effort, and environmental forcing functions) from the underlying Ecopath and Ecosim models. Additional parameters and inputs are required to regulate the initial allocation of biomass and fleet distributions, and their temporal and spatial dynamic developments (Christensen and Walters, 2004; Christensen et al., 2008; Martell et al., 2005; Walters et al., 1999). Details of the theory, parameterisation and robustness checks for habitat map and initialisation settings are provided in the Supplementary Appendix (A.1 and A.2).

The parameters in Ecospace that regulate spatial distribution of groups and species are: "Base Dispersal Rate", "Relative Dispersal in Bad Habitat", "Relative Vulnerability in Bad Habitat", and "Relative Feeding Rate in Bad Habitat" (Table 1). These can be fine-tuned at group level however they also have a default value. Base Dispersal rate, corresponding to swimming speed, is entered in Ecospace for each species in km/year. It can be set between 0 and infinite and has a default value of 300 km/year (Table 1). Recall that in Ecospace the performance of a species in non-favourable habitat is assumed to be worse than in favourable habitat. This is simulated through three parameters, which operate as weight factors. The Relative Dispersal in Bad Habitat parameter increases dispersal rate in non-favourable habitats to simulate greater active attempt to move elsewhere with better conditions. It can be set from 1 (which inactivates the mechanism) to 10 and at default is set at 2 (i.e., twice the speed in non-favourable habitat as in favourable habitat). Relative Vulnerability in Bad Habitat is a weight factor for the vulnerability parameter in Ecosim. It regulates the increased vulnerability to predation (or decreased sheltering capacity) in a less-than-optimal habitat. Its default value is 2 (twice more vulnerable in bad habitat), and it can be set between 1 and 100. Relative Feeding Rate in Bad Habitat governs how much a group will feed (and ultimately grow) in a bad habitat. It decreases the feeding rate (reducing the Ecopath value of $Q/B$, Consumption/Biomass ratio). This parameter can be set between 0 and 1, and its default value is 0.05 (Christensen et al., 2008).

Fleets distribution can be regulated through the parameters "Effective Power" and "Total Efficiency Multiplier" (Table 1). Fishing mortality per species per cell depends on the distribution of fishing effort. Initially, effort is distributed through assignation of fleets to habitats, and by closing cells to some or to all fleets to simulate MPAs. Then, a gravity model (Caddy, 1975; Walters et al., 1999) spreads yearly fishing effort values (inherited from Ecosim) across all cells open to fishing (i.e., cells which are not land, not MPAs and are set as suitable habitat to a certain fleet) proportionally to the "attractiveness" of each cell. At every time step, attractiveness $A_{n,k}$ to cell $n$ for fleet $k$, for all
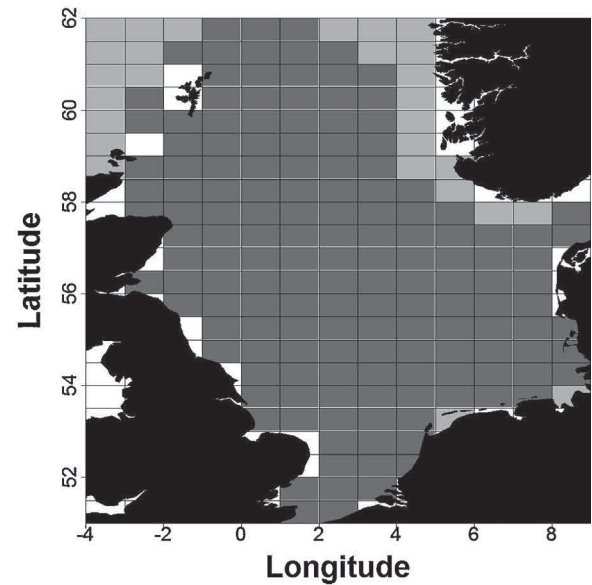


**Fig. 1.** Study area. The North Sea divided in the ICES statistical rectangles corresponding to Ecospace cells used in this study. The area included in the Ecospace model comprises cells shown in both dark and light grey. In dark grey are shown cells for which biomass data from the ICES survey were available. In light grey are shown cells included in the Ecospace model but for which biomass data was not available for comparison. White cells are not included in the Ecospace model.

$i$ species in $I$ (all species in the catch portfolio of fleet $k$) is:

$$A_{n,k} = \left( \frac{\sum_{i=1}^{I} p_{k,i} \cdot q_{k,i} \cdot B_{i,n}}{C_{n,k}} \right)^{1/\sigma}$$

where $p_{k,i}$ is the price for species $i$ for fleet $k$, $q_{k,i}$ is the catchability of species $i$ by fleet $k$, and $C_{n,k}$ is the cost for fleet $k$ of fishing in cell $n$. The argument in bracket corresponds to profit, and $\sigma$ measures variation among fishermen in the perception of profit from fishing in cell n. Profit depends thus on the abundance in the cell $n$ of target species of fleet $k$, and on fleet-specific and species-specific prices. Cost is based on a map of sailing costs, and on fixed costs (as assigned in Ecopath). The ratio $1/\sigma$ is called "$P$" and corresponds to the Effective Power, one of two parameters that can be changed to influence fleets effort distribution. $P$ is by default set equal to 1. Setting $P$ higher than 1 means a lower variation in the perception of profit among fishermen ($\sigma$). High $P$ results therefore in effort being concentrated in the most profitable cells (in these cells attractiveness grows, while in less profitable cells it decreases), whereas low $P$ results in smoother distribution of effort across the map. Maps of effort distribution are then converted to cell-specific fishing mortality per species at every time step. Finally, Total Efficiency Multiplier is a multiplier factor for effort, with a default value of 1.

## 2.3. Study area

The North Sea is a semi-enclosed basin, with temperate climate and mixed faunal assemblage, including boreal and Lusitanic species. The basin is divided in a southern shallow area and a northern deeper one. The Norwegian Deep and the continental slope constitute the natural borders of the basin in the North-East, and North-West respectively (Fig. 1). The North Sea has an important history of fishing, the management of which has been complex due to the mixed nature of fisheries and the large number of countries that fish in these waters. Other activities

**Table 1**
The parameters of Ecospace evaluated in this study and their characteristics: category (indicating parameters related to either species or fleets distribution), default value, unit of measure (dimensionless parameters are indicated by a dash), and the range of values explored in this study. For parameters Base Dispersal Rate, Effective Power and Total Efficiency Multiplier the upper limit of the range is not given in Ecospace. Range limits used in this study are displayed. Range limits can differ across sub-parameters within the same parameter.

| Parameter name | Category | Default value | Unit | Range explored in this study |
| --- | --- | --- | --- | --- |
| Base Dispersal Rate | Species | 300 | km/year | 0–2000[a]/2000[b]/300[c] |
| Relative Dispersal in Bad Habitat | Species | 2 | – | 0–100 |
| Relative Vulnerability in Bad Habitat | Species | 2 | – | 0–10 |
| Relative Feeding Rate in Bad Habitat | Species | 0.05 | – | 0–1 |
| Effective Power | Fleet | 1 | – | 0–30[d]/37[e]/150[f] |
| Total Efficiency Multiplier | Fleet | 1 | – | 0–1.3[d]/3[e]/1.5[f] |

[a] Pelagic species.
[b] Demersal species.
[c] Invertebrates.
[d] Otter trawl.
[e] Beam trawl.
[f] Pelagic trawl.

(e.g., shipping traffic, oil and gas extraction and wind farms) are increasingly causing conflicts with fishing activities (Gimpel et al., 2013). The main fisheries can be divided in demersal and pelagic. Demersal fisheries target roundfish (in particular gadoids) and flatfish (especially sole and plaice), while pelagic fisheries target herring and mackerel for human consumption, and sandeel and sprat for fishmeal and other industrial use. Shrimp and Norway lobster also constitute important target species (ICES, 2013). Fisheries management is based on bilateral agreement between European Union and Norway, with area-, species- and gear-specific limits in catches. The total allowable catches are established yearly on the basis of scientific advice from ICES and the Scientific Technical Economic Committee for Fisheries (STECF) of the European Union, a quota of which is assigned to each country and fleet. Management has been partially successful: after years of systematic decline of most stocks, a moderate recover was observed in recent years for several of the fish stocks after a large reduction in fishing effort and possibly also a reduction of bycatch (ICES, 2013). The food web structure and ecosystem functioning of the North Sea is just starting to be understood and the large number of species and their interactions make it a very complex system to manage (Mackinson et al., 2009).

### 2.4. Application of the Ecospace model for the North Sea ecosystem

The model used for this study is an Ecopath with Ecosim and Ecospace model based on Mackinson and Daskalov (2007) and its recent updates (Heymans et al., 2011; ICES, 2011, 2012b). Since the present study only focuses on Ecospace, the underlying Ecopath and Ecosim models were not explored and forcing functions, parameters and data for these components were unchanged from the model in ICES (2011). Details of the forcing functions used for the North Sea Ecosim model are provided by Mackinson (2014). The structure of the Ecospace model (i.e., the model building blocks, data and parameterisation) from Mackinson and Daskalov (2007) was also maintained, however some changes were brought in this study to the map, the habitat assignment and some initialisation parameters, and forcing functions were not included. The North Sea model is based on a "base year", 1991, and develops dynamically in time for 17 years until 2007. Ecospace models, once initialised, take a variable number of time steps to reach equilibrium. For this study, a burn-in period of 17 years (same length as the time series used) was included to allow the model to reach equilibrium. For the burn-in period all data were set equal to baseline (i.e., at the same level of 1991).

### 2.5. Data

We compared model predictions for biomass and fishing effort with corresponding spatially resolved data of biomass and fishing effort (hereafter, "observation"). Data of biomass for 12 selected species (namely: starry ray *Ambliraja radiata*, cod *Gadus morhua*, whiting *Merlangius merlangus*, haddock *Melanogrammus aeglefinus*, saithe *Pollachius virens*, norway pout *Trisopterus esmarkii*, gurnards *Eutrigla* sp., *Trigla* sp. and *Aspitrigla* sp., herring *Clupea harengus*, mackerel *Scomber scomber*, sandeel (family *Ammodytidae*), plaice *Pleuronectes platessa* and sole *Solea solea*) were obtained from the North Sea ICES International Bottom Trawl Survey (IBTS). Fishing effort data were obtained from STECF (2011). Six fleets (out of the 12 fleets present in the model) were included in the analysis: beam trawl, pelagic trawl, otter trawl, shrimp trawl, nephrops trawl, sandeel trawl. Since the partitioning between fleets in the spatial data from STECF was different from the Ecospace model, we lumped the last four fleets in the group named "Otter trawl".

Observations and predictions for both biomass and effort are comparable for spatial and temporal distribution: both sets are available on a yearly basis and at the same spatial scale, based on ICES statistical sub-rectangles (hereafter "cells") of 1 degree (Longitude) by 0.5 degree (Latitude). Due to changes in the data distribution across years, the spatial and temporal coverage is not uniform. For every year, only cells present in both observations and predictions were used, resulting in 154 cells for the base year and similar but varying number for other years. The unit of Ecospace biomass is $t/km^2$. In ICES IBTS data, the unit is in catch per unit effort, standardised to numbers/hour of trawling. This value was converted to kg/hour using species mean weight as conversion factor. The two datasets (predictions and observations) were made comparable using a constant (mean observed/mean predicted) as converting factor for each group. The two independent datasets have the same mean value after conversion. The same process was performed for fishing effort observations and predictions.

Ecospace uses price and cost data (which are species-and fleet-specific) and calculates fleet-specific maps of sailing cost based on distance from ports. Through a gravity model, Ecospace assigns effort in space based on these cost maps and fish biomass distribution (Walters et al., 1999; see also Section 2.2). Cost and price data in Ecospace are inherited from the underlying EwE model. The price and cost data used for this study are based on Heymans et al. (2011), in turn obtained from the SGECA 08-02 working group report (AER, 2008), reviewed by STECF. Other data required by Ecospace (fleets assignment to habitats and to ports, fixed costs, target species per fleet), were all based on information available in the previous EwE North Sea model (Heymans et al., 2011; ICES, 2011).

# 3. Theoretical background

## 3.1. Model parameters

The number of estimated parameters in the model is determined by (i) the number of functional groups that have parameters (either biomass, $P/B$, $Q/B$, or EE) estimated in solving the mass-balance equation in Ecopath, and (ii) the number of vulnerability and primary production anomalies in Ecosim. In the Ecospace component, parameters for distribution and dispersion are estimated outside the model and used as inputs. No parameters are directly estimated by Ecospace itself. Parameterisation of the North Sea model is described in detail in Mackinson and Daskalov (2007), Mackinson et al. (2009), Heymans et al. (2011), and ICES (2011). In this study, parameters for Ecopath and Ecosim were kept the same as in those publications, but Ecospace parameters were varied manually to evaluate their effect on the performance of the spatial predictions.

## 3.2. Measure of model fit

Spatially resolved observations and predictions for each of the 17 years of the simulation were compared through correlation coefficient. Data were found to be non-normally distributed for all 12 species groups (Shapiro–Wilks test for normality). Therefore, the Spearman's rank correlation coefficient (hereafter called "correlation") was chosen as measure of fit, as it is capable of dealing with non-normal data. Correlation provides a measure of how well high and low values are predicted by the model, i.e., the model capability of reproducing relative patterns. Positive values (close to 1) indicate a positive correlation of the model's prediction with the data, i.e., prediction of high values in the Ecospace grid cells where high values were observed, and prediction of low values where low values were observed. With negative correlation values (approaching $-1$) the model shows a negative correlation with the data (high values predicted where low values were observed and vice versa). Values close to 0 suggest a weak or unclear trend, i.e., the model is not assigning univocally high or low prediction to high or low data values. Correlation values between observations and predictions were calculated for each species and fleet for every year for which data were available: since biomass data are available from 1991 to 2005, and effort data from 2003 to 2007, the two time-series overlap only for three years. For our analysis, a value of overall fit for each model was calculated as follows: (i) for every year, the median across all 15 groups (including both species and fleets in the three years when both categories are present) was calculated; (ii) the 17 yearly values of median correlation were then averaged to obtain a mean value of model performance across the period of study. This value was used as total measure on the model fit. The diagram in Fig. 2 shows the framework for model initialisation, model run and the analysis of results.

## 3.3. Parameter sensitivity

The high number of parameters in Ecospace does not allow exploring all possible parameter combinations manually. However, no automated procedure is at present implemented in the Ecospace software. We therefore used an ad hoc method, with progressive exclusion of non-influential parameters and reduction of parameter space by aggregating groups into macro-groups of ecologically similar species. Following previous studies (e.g., Chen et al., 2009; Fouzai et al., 2012), the species were divided into three macro-groups: wide-range dispersing organisms (denominated "Pelagic"), medium-ranged ("Demersal") and small-ranged ("Invertebrates"). For fleets, aggregation in macro-group was necessary only for Otter trawl, as described in Section 2.5. Parameters explored were (see also Table 1): Base Dispersal Rate, Relative Dispersal in Bad Habitat,
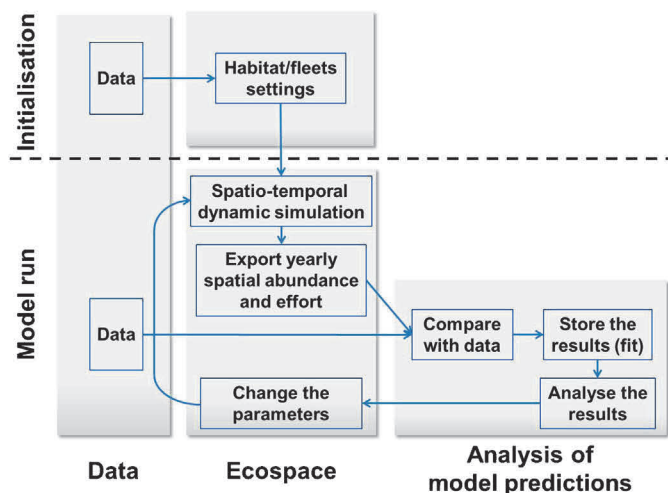


**Fig. 2.** Diagram of the framework for model initialisation, model run and analysis of model results. Setup of habitat and fleet distribution was based on data and maintained constant throughout the analyses. At every run, the Ecospace model produces output of spatial abundance and effort. These are externally compared to data, and the resulting values of model fit are then analysed. Model parameters are then changed after the analysis of previous results and the model is run again.

Relative Vulnerability in Bad Habitat, Relative Feeding Rate in Bad Habitat (related to species distribution), Effective Power and Total Efficiency Multiplier (related to effort distribution; see Sections 2.1 and 2.2). Each parameter was subset into "sub-parameters" corresponding to the macro-groups of species or fleets.

We then explored the behaviour of the model across the parameters' ranges. This process took two steps: firstly, each parameter was analysed individually. For each parameter, we identified the range of possible values assumed, explored the behaviour for each sub-parameter and the interaction across sub-parameters, and recorded the variation in fit from default value at each value. This allowed to quantify the effect of parameters on total fit and to identify non-influential parameters, which were excluded from further analyses. Every individual parameter exploration was an interaction across its three sub-parameters, resulting in a three-dimensional matrix for each of the six parameters.

Secondly, a set of models in which all influential parameters were changed simultaneously was examined to observe parameter changes and their reciprocal influences (i.e., interaction effect). For each parameter, the model was run alternatively with other parameters varying, and with other parameters at fixed default value. The difference between these was taken as the effect of the parameter on the total fit. To further reduce dimensionality, a sub-sample of parameter levels was used. Three levels were selected: high (with all sub-parameters at the highest value of their range), low (all sub-parameters at lowest value of their range) and intermediate (all sub-parameters set at the median or closest lower value). This method provided a distribution of fit (absolute and relative percentage change from the default value) for each parameter, corresponding to changes across the parameter's range. A flow chart (Fig. 3) describes the approach used to reduce the parameter dimension (see also supplementary appendix section A.3 for further details).

## 3.4. Model predictive capability

In order to understand the model's predictive capability, the results were separated into species and fleets because the methods used to predict these two categories differ substantially in Ecospace. A measure of fit for each of the two categories (species and fleets) was developed using the same method as for the total fit
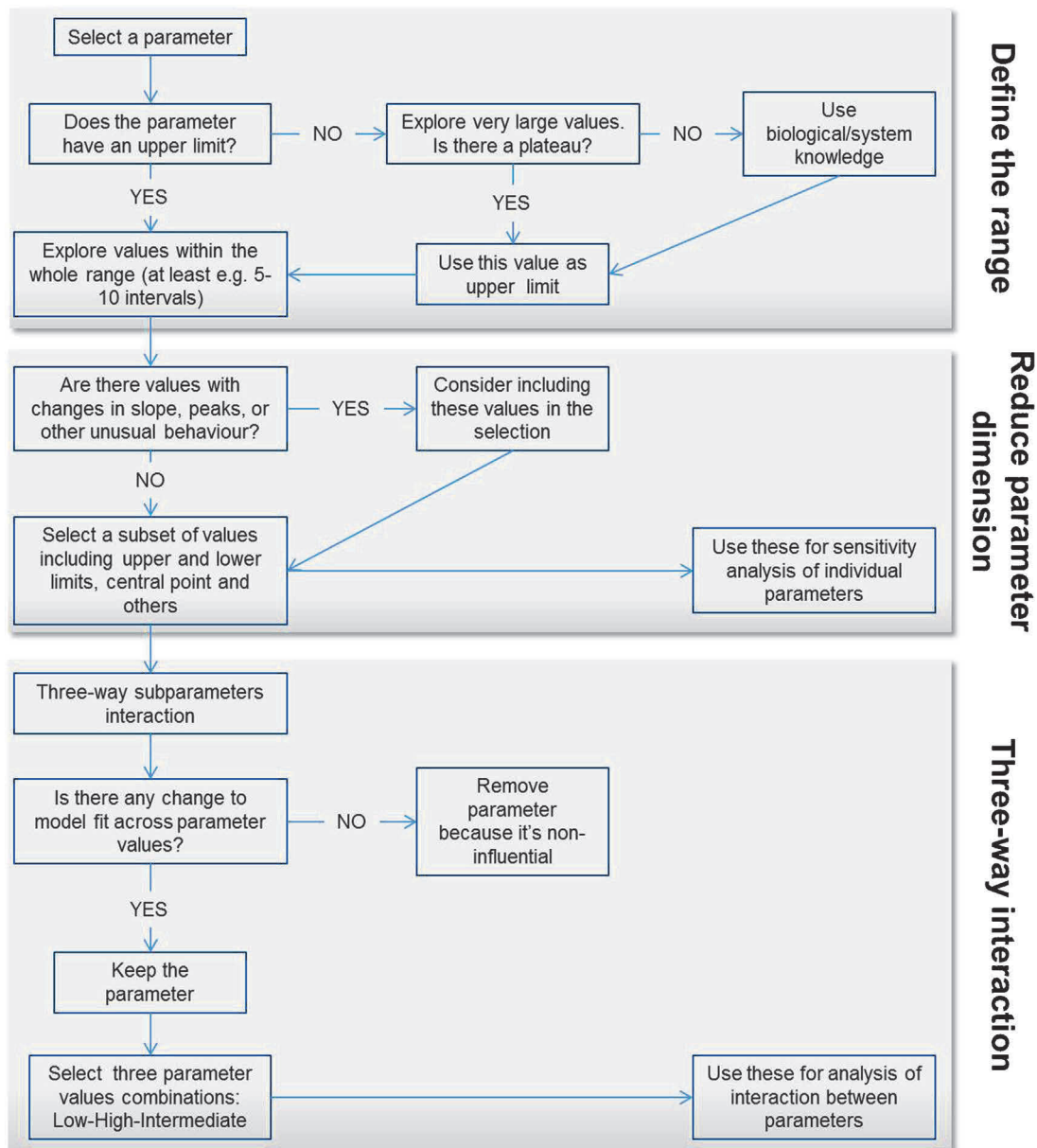
**Fig. 3.** Flow chart of the approach used to reduce the parameter dimension. The approach provided a selection of values for individual parameters' sensitivity analysis and a restricted number of parameter combinations, which were used for the analysis of interaction across all influential parameters.

(Section 3.2). Correlations for each category and for the total fit were calculated across a range of parameter values to investigate the magnitude and direction of effects of parameters on the model and if trends were consistent between categories and the total fit. Furthermore, group-specific correlations (for each species and fleet) were analysed to understand if trends observed for categories were driven by one or few groups, or if they were representative of trends observed across the groups, implying that the predictive capability was influenced by category-specific factors. All analyses were performed using R statistical package 2.15.0 (R Development Core Team, 2012).

## 4. Results

### 4.1. Model fit

The model at default values yielded a fit of 0.33 (Table 2). Calibration of the parameters across their range provided an improvement of up to 15% in fit between prediction and data compared to a model calibrated with parameters at the default values. This indicates that changes in parameters can modify the performance of the model, as expected. In comparison, a model with parameters set as in the Mackinson and Daskalov (2007) Ecospace model provided a fit of 0.27, a comparable (if slightly lower) fit to the model used in this study. Critically, in the exploration of one parameter at a time the highest fit were obtained with parameters set at the highest levels of the explored ranges (see supplementary Table A3), and the pattern was respected when using values higher than what is considered realistic. This is a problem because, if the model was to be parameterised through fit to data, it would lead to use unrealistic parameter values.

### 4.2. Sensitivity analysis

The model resulted to be sensitive to some, but not all of the parameters under investigation. Parameters Relative Dispersal in

**Table 2**

Spearman's rank correlation coefficient for each of the 12 fish species and three fleets, for each year from 1991 to 2007. Dashes are reported where no available data. Median across the 15 groups (or less) is reported in the far right column for each year. The mean across all median values, reported in bold character, is the value used for comparing across models in this study. The values reported in the table are from a model with all parameters set at the Ecospace default values. All reported correlation values in the table are statistically significant (P<0.05). Non-significant values are reported as 0.

| Year | Cod | Starry ray | Whiting | Haddock | Saithe | Norway pout | Gurnards | Herring | Mackerel | Sandeel | Plaice | Sole | Beam trawl | Otter trawl | Pelagic trawl | Median |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1991 | 0.271 | 0.505 | 0.375 | 0.815 | 0.654 | 0.773 | 0.472 | 0.42 | 0.321 | 0.446 | 0.775 | 0.72 | – | – | – | 0.489 |
| 1992 | 0.252 | 0.547 | 0 | 0.805 | 0.642 | 0.767 | 0.375 | 0.543 | 0.279 | 0.425 | 0.725 | 0.643 | – | – | – | 0.545 |
| 1993 | 0.215 | 0.469 | 0.217 | 0.86 | 0.62 | 0.781 | 0.307 | 0.562 | 0.353 | 0.456 | 0.74 | 0.501 | – | – | – | 0.485 |
| 1994 | 0.291 | 0.37 | 0.435 | 0.828 | 0.604 | 0.786 | 0.423 | 0.52 | 0.351 | 0.404 | 0.739 | 0.479 | – | – | – | 0.457 |
| 1995 | 0.233 | 0.388 | 0.4 | 0.83 | 0.642 | 0.779 | 0.382 | 0.366 | 0.233 | 0.396 | 0.74 | 0.563 | – | – | – | 0.398 |
| 1996 | 0.211 | 0.423 | 0 | 0.821 | 0.63 | 0.797 | 0.282 | 0.359 | 0 | 0.354 | 0.69 | 0.404 | – | – | – | 0.382 |
| 1997 | 0 | 0.488 | 0 | 0.803 | 0.695 | 0.728 | 0.265 | 0.508 | 0 | 0.428 | 0.767 | 0.524 | – | – | – | 0.498 |
| 1998 | 0.192 | 0.376 | 0 | 0.839 | 0.72 | 0.73 | 0.273 | 0.485 | 0 | 0.339 | 0.781 | 0.376 | – | – | – | 0.376 |
| 1999 | 0 | 0.403 | 0 | 0.816 | 0.76 | 0.764 | 0.204 | 0.315 | 0.161 | 0.33 | 0.789 | 0.465 | – | – | – | 0.367 |
| 2000 | 0 | 0.315 | 0 | 0.822 | 0.678 | 0.763 | 0.283 | 0.257 | 0 | 0.383 | 0.749 | 0.443 | – | – | – | 0.349 |
| 2001 | 0 | 0.384 | 0.453 | 0.841 | 0.667 | 0.717 | 0.375 | 0.279 | 0 | 0.447 | 0.752 | 0.273 | – | – | – | 0.416 |
| 2002 | 0 | 0.352 | 0.282 | 0.82 | 0.7 | 0.639 | 0.314 | 0.277 | 0 | 0.468 | 0.771 | 0.467 | – | – | – | 0.410 |
| 2003 | 0 | 0.39 | 0 | 0.842 | 0.666 | 0.623 | 0.28 | 0.199 | 0 | 0.6 | 0.795 | 0.356 | 0.83 | 0 | -0.17 | 0.356 |
| 2004 | 0 | 0.325 | 0 | 0.839 | 0.655 | 0.596 | 0.238 | 0.187 | 0 | 0.45 | 0.778 | 0.432 | -0.747 | -0.21 | -0.271 | 0.238 |
| 2005 | 0.17 | 0.351 | 0 | 0.898 | 0.663 | 0.661 | 0.322 | 0.229 | -0.174 | 0.377 | 0.752 | 0.378 | -0.72 | -0.166 | -0.225 | 0.322 |
| 2006 | – | – | – | – | – | – | – | – | – | – | – | – | -0.729 | -0.25 | -0.215 | -0.250 |
| 2007 | – | – | – | – | – | – | – | – | – | – | – | – | -0.744 | 0 | -0.171 | -0.171 |
| | | | | | | | | | | | | | | | | **0.333** |
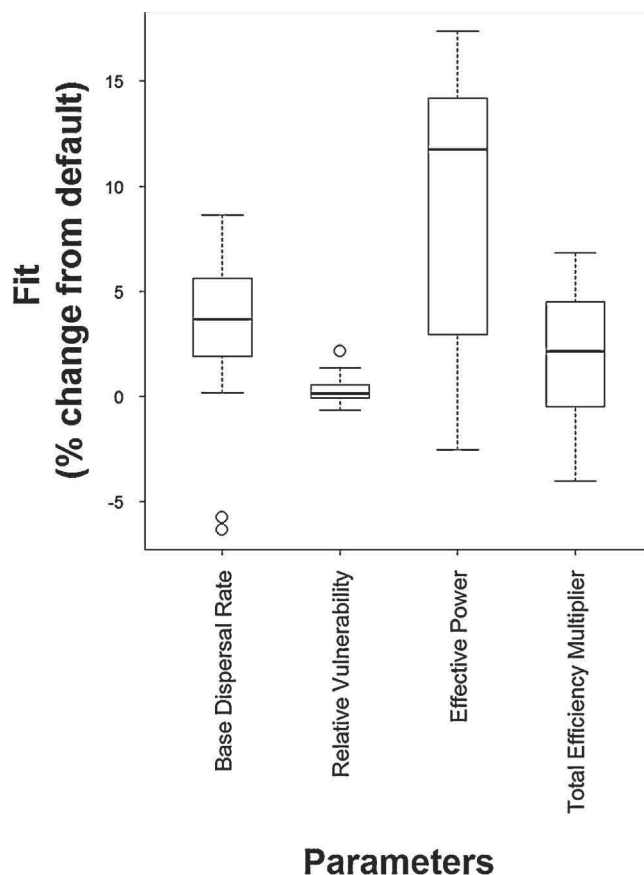


**Fig. 4.** Effect of parameters Base Dispersal Rate, Relative Vulnerability in Bad Habitat, Effective Power, Total Efficiency Multiplier on fit under interaction. Percentage change of fit is represented on the y axis.

Bad Habitat and Relative Feeding Rate in Bad Habitat caused no changes to model fit throughout their ranges both under individual parameter sensitivity and under interaction with other parameters. These two parameters were thus excluded from further analyses. The model was affected by all other parameters explored, and the model fit was generally improved by changing the parameters from the default values. Percentage change of fit from the default value (Fig. 4) was different in median value and in standard deviation for each of the parameters: Base Dispersal Rate had a median value of 3.7 (interquartile range 2.2–5.6); Relative Vulnerability had a median value of 0.12 (interquartile range −0.07 to 0.56); Effective Power had a median value of 11.7 (interquartile range 3.4–14.1); Total Efficiency Multiplier had a median value of 2.14 (interquartile range −0.45 to 4.15).

### 4.3. Model predictive capability

By splitting the model results into different categories, we could observe the differences in the model prediction capability for species and fleets distribution (Fig. 5). The predictions of fleets' distribution were consistently negatively correlated with data, with median values around -0.26 across all parameters and with small variability. Biomass predictions were much closer to the data, with correlation consistently above 0.4 across all parameters. The median across the 15 groups (12 species and three fleets), used throughout this study as a measure of fit, was slightly lower than species, as expected. Trends for individual parameters (with negative fit for fleets and positive for species) were confirmed also in an "interaction model" with all parameters changed simultaneously (Fig. 5). Looking at the differences between parameters,
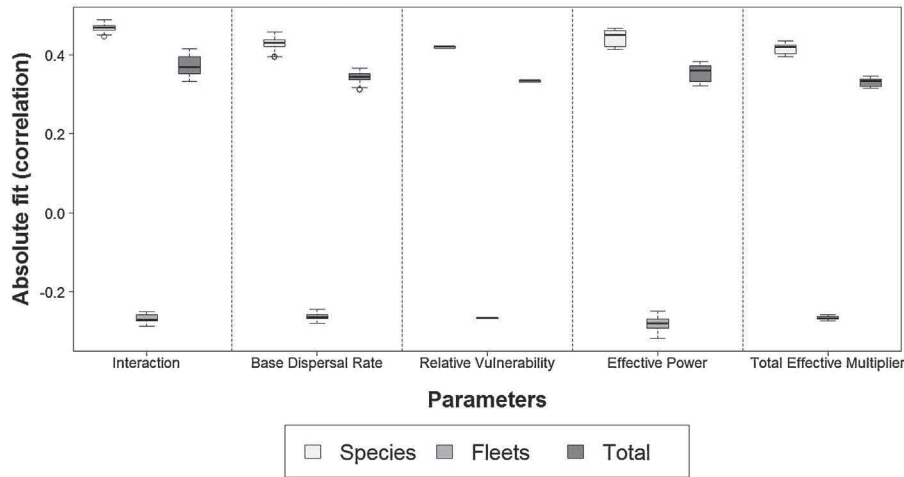
**Fig. 5.** Model fit for the full model ("interaction") and individual parameters Base Dispersal Rate, Relative Vulnerability in Bad Habitat, Effective Power, Total Efficiency Multiplier, divided by the categories species, fleets, and the total (combining species and fleets).

it is interesting to see that in general the median values were fairly stable but the interquartile ranges varied for different parameters. Largest variations around the median for fleets were observed with parameter Effective Power. For species, Effective Power had largest effect on the variation, followed by Total Efficiency Multiplier and Base Dispersal Rate. This suggests that the parameters might affect differently the two categories of the model, however the biological component (i.e., species) is affected also by the fleet-specific parameters (Effective Power and Total Efficiency Multiplier), but not so much the opposite. The model prediction, species-by-species and fleet-by-fleet, also confirmed the trend (Fig. 6). Most species showed a good fit: nine species out of 12 had correlation above 0.35, and 4 above 0.60, while only for Cod, Whiting and Mackerel the correlation was consistently low (below 0.2). Furthermore, Cod, Starry ray and Gurnard also showed larger variance around their median than all other groups. Fleets predictions were all negative or not significant. The total model fit, used to evaluate the model sensitivity, was closer to the values of species than to fleets.

## 5. Discussion

This study is, to the best of our knowledge, the first attempt to perform sensitivity analysis of Ecospace parameters using fit to data as a measure of model performance. Ecospace is a widely used tool for evaluating the outcomes of policy scenarios involving MPAs and other spatial management measures on both ecosystems and fisheries. There is a variety of uses for Ecospace: for instance, effects of aquaculture on the ecosystem (Piroddi et al., 2011), movement models (Martell et al., 2005), game theory (Beattie et al., 2002) and further progresses are made to add realism by inclusion of nutrient–phytoplankton–zooplankton models (e.g., Steenbeek et al., 2013; Walters et al., 2010) while moving towards an end-to-end modelling approach (e.g., Fulton, 2010; Rose et al., 2010; Travers et al., 2007). The original purpose and main application of Ecospace is however the evaluation of MPAs' effectiveness in light of ecosystem dynamics and of the effects of effort displacement (Walters, 2000; Walters et al., 1999). The use of Ecospace for management is now suggested within the framework of a shift towards ecosystem-based fisheries management in Europe (ICES, 2012b). For use within a theoretical and purely speculative approach, the model does not require to be validated with data. However, before its results and outcomes are included into management actions, a severe and rigorous evaluation process should take place, concerning the data quality, parameterisation and model capability to reproduce known trends. In this study we evaluated the model under two complementary aspects: we explored and quantified
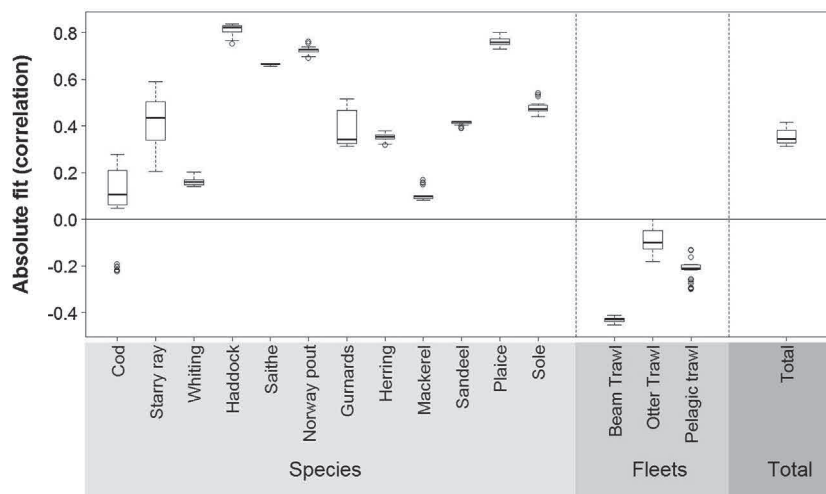


**Fig. 6.** Group-specific fits by species, fleets, and the total (combining species and fleets) across alternative parameter combinations for 3 alternative model settings, with all parameters set at the highest, lowest or median levels of the ranges, respectively.

first the sensitivity of the North Sea Ecospace model to parameter settings, and then the model's capability of predicting known distribution trends of species and fleets.

Our sensitivity analysis showed that some parameters are more influential on the model performance, while some others had no effect at all. The model seemed to be overall robust to variation in parameter settings as the largest change in fit showed an improvement of about 15% compared to the fit at default setting. The parameters to which the model was found to be most sensitive require further investigation: in particular, for the two fleets-related parameters (Effective Power and Total Efficiency Multiplier) there is little, if any, reference to sensitivity in the published models. These parameters affected the total fit the most, and further studies on the significance of these parameters and on realistic values should be undertaken in the future. Base Dispersal Rate also affected the model fit, and this value as well should be investigated in more detail. Few studies performed sensitivity analysis on this parameter (e.g., Chen et al., 2009; Espinosa-Romero et al., 2011; Martell et al., 2005). Reliable estimates for this parameter are scant, even for the best studied species. Base Dispersal Rate is based on random dispersal, which is scarcely studied: most of the fish movement studies focus on directional migration (such as spawning migration in flatfish, Hunter et al., 2004; Rjinsdorp and Pastoors, 1995), or on point estimates of tagged individuals across a period of days to months, but rarely through years (e.g., Righton et al., 2007). Furthermore, the variability in dispersal can be extremely large within a single species: some inshore populations of cod show a dispersal range <10 km (Knutsen et al., 2011), while others perform migrations of hundreds of km (Neuenfeldt et al., 2013). The attempt of defining an exact dispersal rate for every species is therefore intrinsically inappropriate, while it could be useful to explore a range of values. Several studies used simplifications such as lumping species into fast-moving, slow-moving and sedentary species, which was also adopted in this study, and of these, many used the arbitrary "300-30-3 rule" for assigning Base Dispersal Rate (e.g., Chen et al., 2009; Fouzai et al., 2012; Piroddi et al., 2011; Zeller and Reinert, 2004). This, in the lack of better estimates and coupled with adequate sensitivity analysis, could be a valid solution. Through the sensitivity analysis we also identified some problems of our Ecospace model. The best values for some of the parameters or sub-parameters were at the maximum of their ranges, suggesting that optimal values are outside of the range explored (see supplementary Table A3). This is of course a problem, especially in those cases when the parameter values providing the highest fit were unrealistic (e.g., for Base Dispersal Rate). These findings point at problems in either the model, the data (discussed further below), or the method used for sensitivity analysis. In this study we used a manually implemented ad hoc method for the sensitivity analysis, which did not cover the full parameter dimension. The analysis of parameter interactions was based on a subset of models with arbitrarily determined combinations of parameter values. The subset was selected so to be representative of the whole range of parameters, however it could have overlooked optimal combinations of parameters.

The model capability of predicting known spatial trends clearly differed between species and fleets: our North Sea Ecospace model did a relatively inaccurate job in predicting distribution of fleets. This result was consistent across ranges of parameters (the predictions for fleet distributions are negatively correlated with the data across all parameter ranges for every parameter tested) and within the groups: despite the fit for some species was worse than for others, for no species the fit was as low as for any fleet (Fig. 5). This result suggests that the fit of species distribution prediction to data (as done in Daskalov et al. (2011) and Mackinson et al. (unpublished)) provides a valuable and reliable evaluation for species distribution, but it does not provide a full picture of the whole ecosystem, since the human component (fisheries) is not explicitly included. Ecospace applications focus on spatial fisheries management, for example effects of MPAs on the ecosystem via spatial re-distribution of fleets (Walters, 2000). These applications assume that fleet behaviour is realistic, i.e., that the model is capable of reproducing choice criteria of fishers. In no Ecospace study so far, to the best of our knowledge, such prediction capability has been quantified with data. In our North Sea Ecospace model, the prediction capability for fleet effort was found to be relatively poor. While this might be due to the specificities of the study area, we cannot exclude that similar results could be observed in other models and areas. We therefore suggest that a quantitative assessment is routinely undertaken for parameterisation of Ecospace models, in particular for cases where the models' results are used for management advice.

Our hypothesis is that the reason for the low fit between effort predictions and data lies in the mismatch between the resolution of the spatial effort distribution model and the fishers' behaviour. The gravity model used in Ecospace to distribute fishing effort in space is rooted in decision-making theory: it assumes that fishermen's decisions on where to fish depend mainly on profitability. However, fishermen do not have perfect knowledge of the real profitability of fishing in an area beforehand. This is accounted for in Ecospace through attractiveness. The attractiveness of an area for fishermen is modelled as profit scaled by variation $\sigma$. This value represents the different decision criteria among fishers, and can be interpreted as a measure of different strategies adopted. Attractiveness is thus a measure of profitability scaled by the perception and knowledge of the system that fishermen in a fleet have. Effort allocation in Ecospace is therefore based on perceived profitability (Walters et al., 1999). However, in the real world the behaviour of fishermen might be strongly dependent on other factors: for example, other fisher's position might play a role (Poos et al., 2010; Poos and Rijnsdorp, 2007). A key factor for the North Sea might be the fact that the target species in any particular fishing trip is not necessarily the most profitable, but can depend on the available species-specific quotas, and by the daily oscillations in market price. In the model, the profitability is derived by aggregated profitability per all species in the area; however, fishers do in fact aim for one or few species at a time, and all the others are bycatch. Therefore, decisions on where to fish are based on considerations about the instantaneous profitability of one species. Lastly, effort data are aggregated across the year, while the fishers' decisions are taken on a daily or weekly basis, and this might not be captured well by the model.

There are a number of alternative explanations for the low fit observed between effort data and model prediction. Factors influencing the model results include for example data quality, objective function, initialisation parameters, grouping of species and fleets, and settings of the underlying Ecosim model. Biomass data, for example, could fail to reproduce adequately real species distribution, and IBTS data used here are known to have spatial dependence (Lewy and Kristensen, 2009). Given that the species prediction is relatively accurate, however, spatial dependence in biomass data was not considered problematic for this study. Effort data might also fail to adequately represent fleets distribution in space and time. We compared main distribution trends with data available at national level for few countries, and no major inconsistencies were found. Temporal trends were also explored by comparing effort time series (used in Ecosim) with aggregated STECF data. The two datasets were comparable only for four years, however two fleets out of three showed highly comparable trends. This suggests that the STECF data represent adequately fleets spatial distribution and temporal trends. The effects of the objective function, initialisation parameters, cost and price data and other settings were investigated through robustness checks (supplementary appendix section

A.4), and none of these affected the results. Alternative grouping of the Demersal trawl efforts, and alternative settings for vulnerability of Ecosim were also explored: under some combinations of values a small improvement in the fit of Demersal trawl fleet was observed. This suggests that Ecosim parameterisation and alternative fleet grouping might affect Ecospace spatial performance through species distribution. However, Beam trawl and Pelagic trawl consistently showed low fit across all parameters exploration. Overall, we cannot exclude completely that the low fit of effort predictions to data is due to effort data quality or to parameterisation and settings of the model. We however maintain that the results observed are due to limitations of the model for predictions of effort distribution.

For future applications of Ecospace, and especially when the results are used for management advice, we recommend that (i) validation with data is performed, using both biomass and effort data; this is in general good practice to ensure that the model works properly, and to quantify predictive capability. In addition it can reveal problems within the model, as in our case with the predictions of effort distributions. And (ii) we recommend that a thorough evaluation of sensitivity of the model to parameters setting is performed. In order to properly evaluate sensitivity, one needs to explore the whole parameter dimension (e.g., through Global Sensitivity Analysis; Morris et al., 2014; Saltelli et al., 2008, 1999). We used a manual, ad hoc approach to screen out parameters and reduce the number of parameter values to explore. This approach provided indications about the model behaviour and about its strength and weaknesses and was therefore a useful exercise but it is not suited to explore the whole parameter dimension. A thorough parameter exploration and a more rigorous sensitivity analysis could only be achieved through an optimisation algorithm, however no such tool is currently implemented in the Ecospace software. An algorithm could also be useful to parameterise the model through fit to data. This is already common practice in the Ecopath and Ecosim modules (Christensen and Walters, 2004), for which optimisation algorithms are implemented. Finally, we suggest that care must be taken when interpreting effort predictions, as our results suggest that not in all cases the model captures fleets' behaviour accurately. We suggest that further improvement in the effort model could be needed for Ecospace to become a robust tool for advice about fisheries dynamics across spatial management scenarios.

## 6. Conclusions

There is in general a need for management advice modelling tools that combine multispecies models, spatially explicit models, and socio-economic considerations (ICES, 2012a; Kempf et al., 2013; Thunberg et al., 2012). The ongoing progress of spatially explicit ecosystem models, among which Ecospace, coupled with improved understanding of mechanisms operating at the local scale (Hjermann et al., 2013; Kempf et al., 2013), could help improving spatial multispecies modelling and management.

This study is the first to quantify the fit between model predictions and data for Ecospace using both species and fleet distribution. Here we showed that comparison of model prediction to spatial distribution can be useful to evaluate the model performance, and that sensitivity analysis can help to understand the model behaviour. This approach could be part of a larger set of standard rules for calibration and evaluation of Ecospace models to be used for policy advice for the ecosystem-based management of marine resources.

This study finds its significance in the context of a larger effort to improve Ecospace through continuous development and testing (Walters et al., 2010), where the model is in continuous evolution and constantly changing to address new questions and challenges.

It has been suggested that Ecospace should not at present be considered as a management tool, and its primary goal should be scenario exploration and policy testing, for which the model is effective (Beattie et al., 2002; Dichmont et al., 2013; Martell et al., 2005; Walters, 2000; Walters et al., 2010, 1999), while caution should be used when interpreting results. We believe that, to develop this framework further, focus should be given to the development of an algorithm for parameter optimisation, and to the improvement of the model for fishing fleets' behaviour. Thanks to these improvements and to other recent developments (e.g., Christensen et al., 2014; Steenbeek et al., 2013; Walters et al., 2010) we are confident that the Ecospace model will become a more robust tool, suitable also for management advice.

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## Appendix A. Supplementary Information

Supplementary information associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2014.12.016.

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**Appendix A:**

**Additional information on Ecospace, a description of the model parameterization, assumptions and robustness checks.**

A.1. Background information on Ecospace model

A.1.1. Spatial model and habitat map

Ecosystems are not homogeneous in space, and to simulate this, the Ecospace map can be divided into a number of user-defined habitats. Each cell of the map is assigned to one and only one habitat, and every functional group and fleet can be assigned to one or more habitats by the user. The decision on habitat assignation is based on what is considered as "favourable" and "non-favourable" habitats. In Ecospace, non-favourable habitats can be imagined as portions of sea where a species has lower probability of surviving and reproducing successfully due to some characteristics of the area, for example bottom type. This can result in higher predation mortality and/or low feeding success for a species because it cannot hide or feed effectively. These factors are difficult to quantify through predator-prey relationship, and are thus represented through habitat setting. The classic example is that of a coral reef fish displaced in the open ocean. Although in absolute terms the potential predators could be more abundant on a coral reef, in the open ocean the coral fish can't hide as it would do on a reef, and will be therefore more vulnerable. For the coral reef fish, open ocean is a non-favourable habitat.

In previous versions of the model, both species and fleets were allocated to habitats with a presence-absence assignation. In the EwE software version 6.3 (used in this study), habitat assignment for fleets is still based on the presence-absence method, while the assignment of species to habitat has been improved (Christensen et al., 2014). For every habitat type, the user can set a continuous value between 0 and 1. This is valid for all cells belonging to the habitat. The

software then allocates to each cell of the habitat in question a proportion of the initial biomass corresponding to the given value. The Ecopath biomass of a group at the base year is then split between all cells of the habitats to which the group is assigned. Habitat assignment governs the initial spatial distribution of species in the model (initialisation). For effort, the fleet-specific Ecopath effort is spread in Ecospace based on the gravity model (see section 2.2 in the text), limiting to habitats to which the fleet has been assigned. In Ecospace, at every time step, an Ecosim model is run for every cell (and thus for the sub-food webs therein), while movement between adjacent cells is regulated by the parameters for species distribution. Thus, the results of Ecospace for each cell at each time step depend on trophic relationships and fishing (through an Ecosim run) and on movement across cells and the parameterisation of the Ecospace model.

A.1.2. Initialisation settings

Initialisation settings regulate the setting of the distribution of species at time step 0 and the type of model used for distribution of multi-stanza groups (i.e. groups divided in multiple age classes): either partial differential equations or an individual-based model. In EwE version 6.3, these settings include: Initialisation; Model Type; Capacity Calculation; Effort Calculation. These can be set through alternative choice. In particular, Initialisation can be set as either "Ecopath Base Biomass" or "Habitat-Adjusted Biomass". Initialisation determines how biomass for each group is assigned from Ecopath to Ecospace. Using "Ecopath Base Biomass", biomass assigned to each cell in favourable habitat is equal to the mean biomass value in Ecopath, and with lower value in the non-optimal habitat. Alternatively, the "Habitat-Adjusted Biomass" setting concentrates the whole biomass of a group to cells belonging to favourable habitat. If, for example, an organism is found in 10% of the ecosystem, and it has a mean Ecopath biomass of 10 t/km$^2$, it will be distributed in the favourable habitat with biomass of 100 t/km$^2$. Model Type can be set in three alternative possibilities, which regulate how multi-stanza groups are managed in Ecospace. In EwE version 6.3, three alternatives are possible: "EwE6 Multi-Stanza Model", "Individual-Based Model", and "Partial Differential Equation". Capacity Calculation can be set at two non-exclusive levels:

"Habitat" and "Capacity", and the option "Capacity and Habitat" is also allowed. This determines how the biomass is assigned, based on habitat assignment or on capacity (or both). Effort Calculation can be set as "Predict Effort" or "Ecopath Effort": the former calculates effort based on profit-based gravity model while the latter uses effort data directly from Ecopath (Christensen et al., 2008; Walters et al., 1999).

A.2. Specifications of the North Sea Ecospace model used in this study: settings and parameterization

A.2.1. Habitat map used in this study

The habitat map for the present study was based on the Ecospace model from Mackinson and Daskalov (2007). The study area was divided into 5 habitats based on bathymetry and other characteristics (<22 meters depth, 22-51; 52-115; >115 and "Coast"). Some modifications were brought from the map to ensure continuity across habitats. See figure A.1.
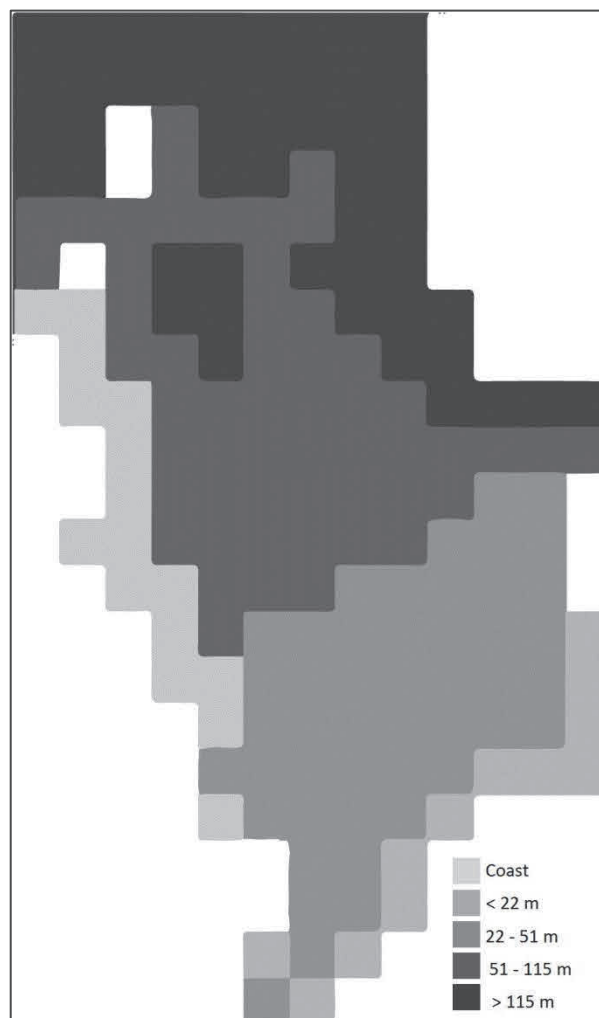


*Figure A.1. Ecospace Map and Habitats for the North Sea model used in this study. Cells in white represent land.*

A.2.2. Initialisation settings

Different combinations of initialisation settings were tested to explore how these settings affected model performance. All alternative combinations between "Initialisation", "Model Type" and "Capacity Calculation" were attempted, with other parameters (i.e. Ecospace species distribution and effort distribution parameters) at default level (table A.1). Effort Calculation was left at the default mode, "Predict Effort", because the alternative, "Use Ecopath Effort", provided no predictions of effort, and the outcomes were not directly comparable to the other parameters. This robustness test showed that habitat "Capacity Calculation" is the most impacting parameter, with Capacity and Habitat & Capacity providing lower fit (negative). Little changes occurred between "Initialisation" parameters, and between "Model Types", with changes of up to 2% of the initial value (relative fit shows percentage change from the default value). Individual-Based Model (IBM) and Partial Differential Equation (PDE) perform slightly better than Multi-Stanza Model (MSM) in general, but to a small extent.

For the final model, all Initialisation settings were maintained as default: Habitat-Adjusted Biomass setting for "Initialisation", EwE6 multi-stanza for "Model Type", Habitat only for "Capacity Calculations" and Predict Effort for "Effort Calculations". EwE6 Multi-Stanza model was chosen over the Individual Base Model, as it is more reliable for model building, as well as faster in computation (Walters et al., 2010), although Espinosa-Romero et al. (2011) found that Individual Based Model provided more conservative prediction for biomass production.

| Initialisation | Model type | Capacity calculation | Fit | Relative fit |
|---|---|---|---|---|
| EBB | MSM | H | 0.333 | 0.000 |
| EBB | MSM | C&H | -0.176 | -1.529 |
| EBB | MSM | C | -0.247 | -1.743 |
| EBB | IBM | H | 0.332 | -0.003 |
| EBB | IBM | C&H | -0.169 | -1.508 |
| EBB | IBM | C | -0.203 | -1.610 |
| EBB | PDE | H | 0.334 | 0.001 |
| EBB | PDE | C&H | -0.157 | -1.470 |
| EBB | PDE | C | -0.242 | -1.726 |
| HAB | MSM | H | 0.333 | -0.002 |
| HAB | MSM | C&H | -0.167 | -1.501 |
| HAB | MSM | C | -0.247 | -1.743 |
| HAB | IBM | H | 0.340 | 0.021 |
| HAB | IBM | C&H | -0.162 | -1.486 |
| HAB | IBM | C | -0.203 | -1.610 |
| HAB | PDE | H | 0.336 | 0.008 |
| HAB | PDE | C&H | -0.161 | -1.484 |
| HAB | PDE | C | -0.242 | -1.726 |

*Table A.1. Combination of initialisation settings and their performance. EBB: Ecopath Base Biomass; HAB: Habitat-Adjusted Biomass; MSM: Multi-Stanza Model; IBM: Individual Based Model; PDE: Partial Differential Equation; H: Habitat only; C&H: Capacity and Habitat; C: Capacity only. All other parameters are at default. Colour scale indicates the value of fit: light shades of grey indicate low fit, dark shades of grey indicate high fit.*

A.2.3. Habitat assignment

Following Mackinson and Daskalov (2007), groups were assigned to habitats on the basis of surveys of biomass distribution where available. ICES International Bottom Trawl Surveys (IBTS) and ICES Benthic Survey were used for most groups, in particular fish and macro-invertebrates.

The survey data are available at the same spatial resolution on which the Ecospace map cell grid was based, i.e. cells of 0.5 degrees in Latitude and 1 degree in Longitude, corresponding to ICES statistical rectangles. For all fish groups and most macro-invertebrate groups, biomass distribution data were used to calculate the relative density for each cell. For each group, biomass for each cell from IBTS survey was averaged between 1985 and 1995 to obtain an estimate of the long-term average for 1991, the base year of the model. For each habitat, average biomass was calculated (sum of biomass in cells/number of cells). Sum of all average biomasses was then calculated, and finally the relative density for each habitat was obtained as: average biomass for that habitat/sum of all average biomasses. For each species, the relative abundance in each habitat was thus obtained, summing across all habitats to unitary value. The relative biomass value for each habitat was then used in the Ecospace model.

For the groups Baleen whales, Toothed whales, Seals and Seabirds, habitat was assigned based on different sources. Species included in each of these groups were unchanged from the Mackinson and Daskalov (2007) model. Baleen whales (here only considering minke whales, *Balaenoptera acutorostrata*) are generally more abundant in the western North Sea (ICES, 2012). Abundance estimates available from SCANS (Small Cetacean Abundance in the North Sea survey, Hammond et al., 2002), Atlas of Cetaceans (Reid et al., 2003), and SCANS II final report (SCANS-II, 2008), all indicate higher abundance in the northern-central and western North Sea (roughly corresponding to habitats "52-115 m depth" and "Coastal", of the Ecospace map, figure A.1). Data from Reid et al. (2003) covered the 1979-1997 time-window, which was considered a reliable proxy for a long-term average close to the situation in 1991. SCANS II final report provides maps from 1994 and 2005, the former being used here as a proxy for 1991. Therefore, habitat for Baleen whales was decided to be "52-115 m" depth and "Coastal". Toothed whales considered in this model were harbour porpoise (*Phocoena phocoena*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*) and white-beaked dolphin (*Lagenorhynchus albirostris*). In SCANS II final report, the distribution of harbour porpoises in 1994 and 2005 is provided. The 1994 figure is used a basis for Ecospace habitat for Toothed whales. *Lagenorhynchus spp.* have much smaller biomass and distribution, so porpoises were used as proxy for the distribution of the whole Toothed

whales group. From this and other sources (Hammond et al., 2002; Reid et al., 2003), Toothed whales were set to habitats "22-51 m", "52-115 m" and "Coastal". The habitat for seals was mainly determined based on information contained in ICES (2012). Habitat for seals was thus set as "<21 m", "52-115 m", ">115 m" and "Coastal". Habitat for seabirds was based on species (or genus) maps for distribution from the online database Eurobis (http://bio.emodnet.eu/portal/index.php) from MarBEF (2004). All the 12 seabird species included in this group are widely distributed on the whole basin (except shag and great skua, only present on the west part of the North Sea). Based on this information, the Seabird group was assigned to all habitats in the Ecospace model.

Three groups of macro-invertebrates (Squids and cuttlefish, Large crabs, Nephrops) were present in both the IBTS and the Benthic Survey and the habitat estimation was applied for both survey data. Only for the Large crabs the results are similar, while there are some differences, probably due to sampling method, in the other groups among surveys. For the final model, habitat selection was based on data from the Benthic Survey.

A.3. Parameter exploration


A.3.1. Definition of sub-parameters

To reduce parameter dimension, we did not explore variations to parameters in all 68 trophic groups included in the model. We instead lumped the groups into macro-groups based on ecological similarities and according to the method used by, among others, Chen et al. (2009) and Fouzai et al. (2012). All groups were thus divided between fast-moving ("Pelagic"), slow-moving ("Demersal") and static organisms ("Invertebrates"). See table A.2 for classification of the groups to macro-groups. These macro-groups were then investigated separately and in combination and considered as "sub-parameters". For the fleets, we only investigated 6 out of 12 fleets included in the model because limitation in data availability did not allow us to investigate dynamics for all of the fleets. Fleets were grouped into three macro-groups: two of them corresponding to a single fleet (Beam and Pelagic trawl) while the Otter trawl included multiple fleets (Otter trawl proper, Shrimp trawl, Nephrops trawl and Sandeel trawl). The three macro-groups were used as sub-parameters for those parameters focusing on the fleet dynamics, namely Effective Power and Total Efficiency Multiplier.

| Group Name | Base Dispersal Rate | Macro-groups |
| --- | --- | --- |
| Baleen whales | 652.437 | Pelagic |
| Toothed whales | 974.725 | Pelagic |
| Seals | 275.124 | Pelagic |
| Seabirds | 275.124 | Pelagic |
| Juvenile sharks | 78.607 | Demersal |
| Spurdog | 275.124 | Demersal |
| Large piscivorous sharks | 275.124 | Pelagic |
| Small sharks | 78.607 | Demersal |
| Juvenile rays | 78.607 | Demersal |
| Starry ray + others | 157.214 | Demersal |
| Thornback & Spotted ray | 157.214 | Demersal |
| Skate + cuckoo ray | 157.214 | Demersal |

| | | |
|---|---|---|
| Juvenile Cod(0-2, 0-40cm) | 110.050 | Demersal |
| Cod (adult) | 196.517 | Pelagic |
| Juvenile Whiting (0-1, 0-20cm) | 110.050 | Demersal |
| Whiting (adult) | 157.214 | Pelagic |
| Juvenile Haddock (0-1, 0-20cm) | 110.050 | Demersal |
| Haddock (adult) | 157.214 | Pelagic |
| Juvenile Saithe (0-3, 0-40cm) | 110.050 | Demersal |
| Saithe (adult) | 196.517 | Pelagic |
| Hake | 196.517 | Demersal |
| Blue whiting | 157.214 | Pelagic |
| Norway pout | 500.000 | Pelagic |
| Other gadoids (large) | 157.214 | Demersal |
| Other gadoids (small) | 157.214 | Demersal |
| Monkfish | 157.214 | Demersal |
| Gurnards | 157.214 | Demersal |
| Herring (juvenile 0, 1) | 110.050 | Pelagic |
| Herring (adult) | 157.214 | Pelagic |
| Sprat | 78.607 | Pelagic |
| Mackerel | 235.820 | Pelagic |
| Horse mackerel | 1000.000 | Pelagic |
| Sandeels | 75.000 | Pelagic |
| Plaice | 75.000 | Demersal |
| Dab | 75.000 | Demersal |
| Long-rough dab | 78.607 | Demersal |
| Flounder | 78.607 | Demersal |
| Sole | 78.607 | Demersal |
| Lemon sole | 78.607 | Demersal |
| Witch | 78.607 | Demersal |
| Turbot and brill | 78.607 | Demersal |
| Megrim | 78.607 | Demersal |
| Halibut | 78.607 | Demersal |
| Dragonets | 78.607 | Demersal |
| Catfish (Wolf-fish) | 157.214 | Demersal |
| Large Demersal fish | 157.214 | Demersal |
| Small Demersal fish | 78.607 | Demersal |
| Miscellaneous filterfeeding pelagic fish | 141.492 | Pelagic |
| Squid & cuttlefish | 141.492 | Demersal |
| Fish larvae | 29.871 | Invertebrates |
| Carnivorous zooplankton | 29.871 | Invertebrates |
| Herbivorous & Omnivorous zooplankton | 29.871 | Invertebrates |
| Gelatinous zooplankton | 78.607 | Invertebrates |

| | | |
|---|---|---|
| Large crabs | 20.000 | Demersal |
| Nephrops | 5.000 | Demersal |
| Epifaunal macrobenthos (mobile grazers) | 30.000 | Demersal |
| Infaunal macrobenthos | 5.000 | Invertebrates |
| Shrimp | 29.871 | Demersal |
| Small mobile epifauna (swarming crustaceans) | 29.871 | Invertebrates |
| Small infauna (polychaetes) | 29.871 | Invertebrates |
| Sessile epifauna | 29.871 | Invertebrates |
| Meiofauna | 29.871 | Invertebrates |
| Benthic microflora | 29.871 | Invertebrates |
| Planktonic microflora | 29.871 | Invertebrates |
| Phytoplankton | 29.871 | Invertebrates |
| Detritus - DOM -water column | 29.871 | Invertebrates |
| Detritus - POM - sediment | 29.871 | Invertebrates |
| Discards | 10.000 | Invertebrates |

*Table A.2. Base Dispersal Rate values from Mackinson and Daskalov (2007) and assignation to macro-groups used in this study. The distinction in "Pelagic", "Demersal" and "Invertebrates" corresponds to wide-range, medium-range and small-range dispersing organisms, respectively.*

A.3.2. Upper range limits

For those parameters which do not have a specified upper range limit (namely, Base Dispersal Rate, Effective Power and Total Efficiency Multiplier), an upper limit was set for this study. Upper limit for Base Dispersal Rate was based on the highest value used by Mackinson and Daskalov (2007). The value of 1000 km/year was therefore considered as the upper limit of realistic dispersal value. However, since accurate information on dispersal are lacking, it was considered appropriate to include a "buffer" on the upper limit of realistic values. Larger values (up to and over 20000 km/year) were therefore explored. Threshold for inclusion in the final range was arbitrarily set to twice the reported maximum value of dispersal. Values of up to 2000 km/year (twice the "realistic" value) were therefore included in the range for Pelagic and Demersal. For Invertebrates, furthermore, preliminary analyses showed that values above 300 km/year provided negligible changes in fit, while values in the lower limit provided most of the change. For this reason, the upper limit for Invertebrates was set at 300. Upper range limits for Effective Power and Total

Efficiency Multiplier were based on exploratory analyses. For Effective Power, the range studied includes "realistic" values (roughly between 0.5 and 10, Carl Walters Pers. Comm.). Buffer values below and above the realistic values were explored. Values between 0 and 1 provided very little deviation from default fit and where therefore not included in the final range. Values above 10 provided large changes in fit and were included in the final exploration as buffer. Upper range limits were specific for each sub-parameter, and were selected as the highest values before the model collapsed. For Power Effort, these were 30, 150 and 37 for the sub-parameter Otter trawl, Pelagic trawl and Beam trawl respectively. For Total Efficiency Multiplier, these were 1.3, 3 and 1.5 for the sub-parameter Otter trawl, Pelagic trawl and Beam trawl respectively. See table 1 and table A.3.a-h.

A.3.3. Sub-parameters exploration

The exploration of sub-parameters took a number of steps:

i) Initially, each sub-parameter ("Pelagic", "Demersal", "Invertebrates" for species-related parameters and "Pelagic", "Otter" and "Beam" for fleet-related parameters) was explored individually throughout its range (for example, from 0 to 100 by steps of 10 for a parameter restrained between 0 and 100).

ii) Then, for each of the three sub-parameters a subset of values were selected, including the lowest value (0 or 1) and the highest (100 in this example), as well as intermediate values (50 in our example). Also, values at which the individual parameters exhibited peculiar behaviour (e.g., sudden changes of slope, threshold values above which the response curve flattened) were further investigated. The rationale for this was to reduce the number of parameter values to explore under interaction.

iii) The selected subsets of parameter values were explored in a three-way interaction for each of the three sub-parameter values, and for each of the six parameters studied. Matrices reporting the fit between data and model prediction for each combination for parameters Base Dispersal Rate,

Relative Vulnerability, Effective Power and Total Efficiency Multiplier are provided in table A.3 with both absolute fit (table A.3.a, c, e, g) and relative fit (table A.3.b, d, f, h). Relative fit is given as the percentage change that the model provides as compared with default values. For default values, the percentage change is of course equal 0. Models with percentage change >0 correspond to an improvement and vice versa. Changes of parameters Relative Dispersal in Bad Habitat and Relative Feeding Rate in Bad Habitat did not result in any change of fit of model. These parameters were therefore not further investigated and are not shown here.

A.3.4. Parameter interaction

For the exploration of parameter interactions, a sub-set of parameter values was selected so to represent the overall range of possible values assumed. For each parameter, three levels were selected: high (with all sub-parameters at the highest value of their range), low (all sub-parameters at lowest value of their range) and intermediate (all sub-parameters set at the median or closest lower value). For example, the three values selected for the parameter Total Efficiency Multiplier were:

low: Otter = 0.1, Pelagic = 0.1, Beam = 0.1;

intermediate: Otter = 1, Pelagic = 1, Beam = 1;

high: Otter = 1.3, Pelagic = 1.5, Beam = 3.

This method allowed exploring across all ranges of all sub-parameters. A combination of $3^4 = 64$ parameter combinations was finally used for the parameter interaction analysis.

a)

## Invertebrates 1

| Pelagic \ Demersal | 1 | 100 | 250 | 500 | 750 | 1000 | 1500 | 2000 |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.322 | 0.324 | 0.330 | 0.340 | 0.344 | 0.347 | 0.352 | 0.355 |
| 100 | 0.327 | 0.329 | 0.330 | 0.343 | 0.348 | 0.351 | 0.356 | 0.358 |
| 250 | 0.328 | 0.331 | 0.329 | 0.333 | 0.337 | 0.340 | 0.343 | 0.345 |
| 500 | 0.332 | 0.332 | 0.332 | 0.335 | 0.339 | 0.340 | 0.343 | 0.345 |
| 750 | 0.342 | 0.338 | 0.337 | 0.341 | 0.343 | 0.344 | 0.347 | 0.348 |
| 1000 | 0.351 | 0.347 | 0.343 | 0.347 | 0.347 | 0.347 | 0.349 | 0.350 |
| 1500 | 0.359 | 0.355 | 0.352 | 0.353 | 0.353 | 0.352 | 0.353 | 0.353 |
| 2000 | 0.366 | 0.361 | 0.359 | 0.359 | 0.358 | 0.357 | 0.356 | 0.357 |

## Invertebrates 10

| Pelagic \ Demersal | 1 | 100 | 250 | 500 | 750 | 1000 | 1500 | 2000 |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.312 | 0.324 | 0.330 | 0.340 | 0.345 | 0.348 | 0.353 | 0.355 |
| 100 | 0.328 | 0.330 | 0.331 | 0.344 | 0.349 | 0.352 | 0.356 | 0.349 |
| 250 | 0.329 | 0.331 | 0.329 | 0.333 | 0.337 | 0.340 | 0.343 | 0.346 |
| 500 | 0.332 | 0.333 | 0.332 | 0.335 | 0.339 | 0.340 | 0.343 | 0.345 |
| 750 | 0.341 | 0.338 | 0.337 | 0.341 | 0.344 | 0.344 | 0.347 | 0.348 |
| 1000 | 0.350 | 0.346 | 0.343 | 0.347 | 0.347 | 0.347 | 0.349 | 0.351 |
| 1500 | 0.359 | 0.355 | 0.352 | 0.353 | 0.353 | 0.352 | 0.353 | 0.354 |
| 2000 | 0.366 | 0.361 | 0.359 | 0.359 | 0.358 | 0.357 | 0.357 | 0.357 |

## Invertebrates 30

| Pelagic \ Demersal | 1 | 100 | 250 | 500 | 750 | 1000 | 1500 | 2000 |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.313 | 0.317 | 0.322 | 0.340 | 0.346 | 0.349 | 0.353 | 0.356 |
| 100 | 0.330 | 0.330 | 0.332 | 0.335 | 0.340 | 0.352 | 0.347 | 0.350 |
| 250 | 0.330 | 0.332 | 0.330 | 0.333 | 0.337 | 0.340 | 0.343 | 0.346 |
| 500 | 0.332 | 0.332 | 0.331 | 0.335 | 0.339 | 0.340 | 0.343 | 0.345 |
| 750 | 0.341 | 0.337 | 0.337 | 0.341 | 0.344 | 0.344 | 0.346 | 0.347 |
| 1000 | 0.349 | 0.345 | 0.343 | 0.347 | 0.347 | 0.347 | 0.349 | 0.350 |
| 1500 | 0.359 | 0.355 | 0.352 | 0.353 | 0.353 | 0.353 | 0.353 | 0.354 |
| 2000 | 0.366 | 0.361 | 0.360 | 0.359 | 0.358 | 0.357 | 0.357 | 0.357 |

## Invertebrates 100

| Pelagic \ Demersal | 1 | 100 | 250 | 500 | 750 | 1000 | 1500 | 2000 |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.318 | 0.320 | 0.325 | 0.331 | 0.336 | 0.339 | 0.344 | 0.347 |
| 100 | 0.333 | 0.333 | 0.334 | 0.336 | 0.340 | 0.343 | 0.348 | 0.351 |
| 250 | 0.332 | 0.332 | 0.331 | 0.334 | 0.338 | 0.341 | 0.344 | 0.347 |
| 500 | 0.331 | 0.330 | 0.331 | 0.335 | 0.338 | 0.341 | 0.343 | 0.345 |
| 750 | 0.338 | 0.335 | 0.336 | 0.341 | 0.343 | 0.344 | 0.346 | 0.347 |
| 1000 | 0.345 | 0.343 | 0.342 | 0.347 | 0.347 | 0.347 | 0.348 | 0.350 |
| 1500 | 0.357 | 0.353 | 0.353 | 0.354 | 0.353 | 0.353 | 0.353 | 0.354 |
| 2000 | 0.364 | 0.360 | 0.361 | 0.360 | 0.358 | 0.357 | 0.356 | 0.357 |

## Invertebrates 300

| Pelagic \ Demersal | 1 | 100 | 250 | 500 | 750 | 1000 | 1500 | 2000 |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.329 | 0.329 | 0.329 | 0.332 | 0.337 | 0.340 | 0.343 | 0.346 |
| 100 | 0.340 | 0.338 | 0.336 | 0.338 | 0.341 | 0.343 | 0.347 | 0.350 |
| 250 | 0.335 | 0.334 | 0.333 | 0.336 | 0.339 | 0.342 | 0.346 | 0.347 |
| 500 | 0.328 | 0.326 | 0.332 | 0.337 | 0.340 | 0.342 | 0.345 | 0.346 |
| 750 | 0.332 | 0.330 | 0.335 | 0.341 | 0.344 | 0.345 | 0.346 | 0.347 |
| 1000 | 0.339 | 0.338 | 0.342 | 0.347 | 0.348 | 0.347 | 0.348 | 0.349 |
| 1500 | 0.354 | 0.350 | 0.352 | 0.353 | 0.353 | 0.352 | 0.353 | 0.354 |
| 2000 | 0.361 | 0.359 | 0.360 | 0.359 | 0.358 | 0.357 | 0.356 | 0.356 |

b)

**Invertebrates 1**

| Pelagic \ Demersal | 1 | 100 | 250 | 500 | 750 | 1000 | 1500 | 2000 |
|---|---|---|---|---|---|---|---|---|
| 1 | -3.451 | -2.851 | -0.962 | 1.951 | 3.248 | 4.281 | 5.632 | 6.417 |
| 100 | -1.774 | -1.218 | -0.847 | 3.019 | 4.581 | 5.437 | 6.744 | 7.388 |
| 250 | -1.580 | -0.715 | -1.245 | 0.009 | 1.112 | 1.968 | 2.878 | 3.575 |
| 500 | -0.309 | -0.265 | -0.291 | 0.662 | 1.765 | 2.171 | 2.966 | 3.531 |
| 750 | 2.630 | 1.536 | 1.192 | 2.436 | 3.081 | 3.363 | 4.007 | 4.334 |
| 1000 | 5.270 | 4.016 | 3.081 | 4.202 | 4.202 | 4.219 | 4.714 | 5.120 |
| 1500 | 7.829 | 6.532 | 5.640 | 6.002 | 5.923 | 5.667 | 5.941 | 6.073 |
| 2000 | 9.921 | 8.315 | 7.715 | 7.653 | 7.503 | 7.000 | 6.938 | 7.070 |

**Invertebrates 10**

| Pelagic \ Demersal | 1 | 100 | 250 | 500 | 750 | 1000 | 1500 | 2000 |
|---|---|---|---|---|---|---|---|---|
| 1 | -6.435 | -2.754 | -0.909 | 2.039 | 3.425 | 4.422 | 5.808 | 6.558 |
| 100 | -1.439 | -1.059 | -0.715 | 3.089 | 4.590 | 5.499 | 6.806 | 4.846 |
| 250 | -1.412 | -0.538 | -1.209 | 0.009 | 1.174 | 1.968 | 2.983 | 3.690 |
| 500 | -0.291 | -0.212 | -0.335 | 0.574 | 1.668 | 2.171 | 2.913 | 3.557 |
| 750 | 2.480 | 1.474 | 1.130 | 2.410 | 3.134 | 3.337 | 3.990 | 4.343 |
| 1000 | 5.155 | 3.954 | 3.028 | 4.131 | 4.228 | 4.272 | 4.705 | 5.190 |
| 1500 | 7.794 | 6.444 | 5.729 | 6.082 | 5.949 | 5.782 | 5.932 | 6.108 |
| 2000 | 9.904 | 8.218 | 7.759 | 7.706 | 7.476 | 7.026 | 6.991 | 7.088 |

**Invertebrates 30**

| Pelagic \ Demersal | 1 | 100 | 250 | 500 | 750 | 1000 | 1500 | 2000 |
|---|---|---|---|---|---|---|---|---|
| 1 | -6.064 | -4.917 | -3.451 | 2.092 | 3.716 | 4.661 | 6.011 | 6.788 |
| 100 | -1.015 | -0.839 | -0.477 | 0.503 | 2.057 | 5.579 | 4.272 | 4.987 |
| 250 | -1.086 | -0.415 | -1.042 | 0.079 | 1.218 | 2.030 | 3.063 | 3.787 |
| 500 | -0.380 | -0.459 | -0.521 | 0.441 | 1.615 | 2.127 | 2.869 | 3.548 |
| 750 | 2.321 | 1.245 | 1.033 | 2.392 | 3.187 | 3.363 | 3.910 | 4.281 |
| 1000 | 4.811 | 3.584 | 3.028 | 4.122 | 4.219 | 4.246 | 4.608 | 5.146 |
| 1500 | 7.626 | 6.435 | 5.746 | 6.046 | 5.976 | 5.808 | 6.002 | 6.249 |
| 2000 | 9.789 | 8.271 | 7.918 | 7.803 | 7.529 | 7.106 | 7.070 | 7.114 |

**Invertebrates 100**

| Pelagic \ Demersal | 1 | 100 | 250 | 500 | 750 | 1000 | 1500 | 2000 |
|---|---|---|---|---|---|---|---|---|
| 1 | -4.625 | -3.866 | -2.392 | -0.600 | 0.971 | 1.774 | 3.310 | 4.131 |
| 100 | -0.124 | 0.053 | 0.132 | 0.830 | 2.110 | 2.975 | 4.290 | 5.208 |
| 250 | -0.397 | -0.247 | -0.671 | 0.238 | 1.403 | 2.313 | 3.266 | 4.122 |
| 500 | -0.644 | -0.927 | -0.680 | 0.415 | 1.571 | 2.216 | 2.878 | 3.601 |
| 750 | 1.562 | 0.494 | 0.874 | 2.277 | 2.957 | 3.222 | 3.725 | 4.210 |
| 1000 | 3.469 | 2.807 | 2.763 | 4.034 | 4.272 | 4.263 | 4.396 | 5.005 |
| 1500 | 7.088 | 5.914 | 5.790 | 6.108 | 6.020 | 5.826 | 5.905 | 6.179 |
| 2000 | 9.339 | 8.174 | 8.191 | 7.953 | 7.582 | 7.203 | 6.964 | 7.256 |

**Invertebrates 300**

| Pelagic \ Demersal | 1 | 100 | 250 | 500 | 750 | 1000 | 1500 | 2000 |
|---|---|---|---|---|---|---|---|---|
| 1 | -1.165 | -1.306 | -1.306 | -0.256 | 1.095 | 1.933 | 3.036 | 3.769 |
| 100 | 2.083 | 1.554 | 0.803 | 1.333 | 2.242 | 2.975 | 4.149 | 5.093 |
| 250 | 0.424 | 0.088 | -0.035 | 0.794 | 1.757 | 2.595 | 3.707 | 4.263 |
| 500 | -1.474 | -2.021 | -0.344 | 1.112 | 2.021 | 2.657 | 3.398 | 3.919 |
| 750 | -0.441 | -1.015 | 0.565 | 2.445 | 3.204 | 3.478 | 3.760 | 4.184 |
| 1000 | 1.880 | 1.580 | 2.710 | 4.166 | 4.387 | 4.237 | 4.369 | 4.758 |
| 1500 | 6.108 | 5.120 | 5.517 | 6.055 | 6.002 | 5.702 | 5.879 | 6.099 |
| 2000 | 8.306 | 7.741 | 8.165 | 7.882 | 7.432 | 7.044 | 6.823 | 6.982 |

c)

| | | Invertebrates 1 | | | | Invertebrates 10 | | | | Invertebrates 100 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Demersal | | | | Demersal | | | | Demersal | | |
| | | 1 | 10 | 100 | | 1 | 10 | 100 | | 1 | 10 | 100 |
| Pelagics | 1 | 0.331 | 0.336 | 0.336 | | 0.331 | 0.336 | 0.336 | | 0.331 | 0.336 | 0.336 |
| | 10 | 0.331 | 0.335 | 0.336 | | 0.331 | 0.335 | 0.336 | | 0.331 | 0.335 | 0.336 |
| | 100 | 0.331 | 0.335 | 0.335 | | 0.331 | 0.335 | 0.335 | | 0.331 | 0.335 | 0.335 |

d)

| | | Invertebrates 1 | | | | Invertebrates 10 | | | | Invertebrates 100 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Demersal | | | | Demersal | | | | Demersal | | |
| | | 1 | 10 | 100 | | 1 | 10 | 100 | | 1 | 10 | 100 |
| Pelagics | 1 | -0.521 | 0.697 | 0.768 | | -0.521 | 0.715 | 0.768 | | -0.521 | 0.697 | 0.768 |
| | 10 | -0.565 | 0.671 | 0.706 | | -0.574 | 0.680 | 0.724 | | -0.574 | 0.680 | 0.733 |
| | 100 | -0.618 | 0.583 | 0.662 | | -0.618 | 0.574 | 0.662 | | -0.609 | 0.574 | 0.662 |

e)

**Pelagic 1**

| Otter | Beam | | | | |
|---|---|---|---|---|---|
| | 1 | 5 | 10 | 20 | 37 |
| 1 | 0.333 | 0.334 | 0.334 | 0.334 | 0.334 |
| 2 | 0.334 | 0.336 | 0.335 | 0.335 | 0.335 |
| 5 | 0.358 | 0.358 | 0.358 | 0.358 | 0.358 |
| 10 | 0.371 | 0.371 | 0.371 | 0.371 | 0.371 |
| 20 | 0.378 | 0.378 | 0.378 | 0.378 | 0.378 |
| 30 | 0.384 | 0.384 | 0.384 | 0.384 | 0.384 |

**Pelagic 5**

| Otter | Beam | | | | |
|---|---|---|---|---|---|
| | 1 | 5 | 10 | 20 | 37 |
| 1 | 0.331 | 0.332 | 0.332 | 0.332 | 0.332 |
| 2 | 0.331 | 0.332 | 0.332 | 0.332 | 0.332 |
| 5 | 0.355 | 0.356 | 0.356 | 0.356 | 0.356 |
| 10 | 0.368 | 0.368 | 0.368 | 0.368 | 0.368 |
| 20 | 0.376 | 0.376 | 0.376 | 0.376 | 0.376 |
| 30 | 0.382 | 0.382 | 0.382 | 0.382 | 0.382 |

**Pelagic 10**

| Otter | Beam | | | | |
|---|---|---|---|---|---|
| | 1 | 5 | 10 | 20 | 37 |
| 1 | 0.330 | 0.331 | 0.331 | 0.331 | 0.331 |
| 2 | 0.330 | 0.331 | 0.331 | 0.331 | 0.331 |
| 5 | 0.354 | 0.355 | 0.355 | 0.355 | 0.355 |
| 10 | 0.367 | 0.367 | 0.367 | 0.367 | 0.367 |
| 20 | 0.375 | 0.375 | 0.375 | 0.375 | 0.375 |
| 30 | 0.381 | 0.381 | 0.381 | 0.381 | 0.381 |

**Pelagic 20**

| Otter | Beam | | | | |
|---|---|---|---|---|---|
| | 1 | 5 | 10 | 20 | 37 |
| 1 | 0.329 | 0.330 | 0.330 | 0.331 | 0.331 |
| 2 | 0.329 | 0.330 | 0.331 | 0.331 | 0.330 |
| 5 | 0.353 | 0.354 | 0.354 | 0.354 | 0.354 |
| 10 | 0.366 | 0.366 | 0.366 | 0.366 | 0.366 |
| 20 | 0.374 | 0.374 | 0.374 | 0.374 | 0.374 |
| 30 | 0.379 | 0.380 | 0.380 | 0.380 | 0.380 |

**Pelagic 100**

| Otter | Beam | | | | |
|---|---|---|---|---|---|
| | 1 | 5 | 10 | 20 | 37 |
| 1 | 0.327 | 0.328 | 0.327 | 0.328 | 0.328 |
| 2 | 0.328 | 0.328 | 0.330 | 0.330 | 0.330 |
| 5 | 0.351 | 0.352 | 0.352 | 0.352 | 0.353 |
| 10 | 0.365 | 0.363 | 0.364 | 0.364 | 0.363 |
| 20 | 0.371 | 0.371 | 0.371 | 0.372 | 0.371 |
| 30 | 0.373 | 0.373 | 0.373 | 0.373 | 0.373 |

**Pelagic 150**

| Otter | Beam | | | | |
|---|---|---|---|---|---|
| | 1 | 5 | 10 | 20 | 37 |
| 1 | 0.322 | 0.324 | 0.323 | 0.326 | 0.325 |
| 2 | 0.325 | 0.326 | 0.326 | 0.328 | 0.327 |
| 5 | 0.349 | 0.352 | 0.350 | 0.350 | 0.351 |
| 10 | 0.363 | 0.363 | 0.362 | 0.363 | 0.362 |
| 20 | 0.368 | 0.368 | 0.370 | 0.369 | 0.369 |
| 30 | 0.371 | 0.370 | 0.371 | 0.372 | 0.369 |

f)

| Pelagic 1 | Beam | | | | | Pelagic 5 | Beam | | | | | Pelagic 10 | Beam | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 5 | 10 | 20 | 37 | | 1 | 5 | 10 | 20 | 37 | | 1 | 5 | 10 | 20 | 37 |
| Otter 1 | 0.000 | 0.300 | 0.309 | 0.300 | 0.327 | | -0.697 | -0.371 | -0.335 | -0.318 | -0.318 | | -0.918 | -0.609 | -0.591 | -0.574 | -0.591 |
| Otter 2 | 0.106 | 0.856 | 0.521 | 0.521 | 0.530 | | -0.759 | -0.388 | -0.353 | -0.344 | -0.362 | | -1.006 | -0.680 | -0.618 | -0.609 | -0.636 |
| Otter 5 | 7.362 | 7.415 | 7.441 | 7.432 | 7.423 | | 6.497 | 6.726 | 6.779 | 6.788 | 6.797 | | 6.285 | 6.603 | 6.611 | 6.611 | 6.620 |
| Otter 10 | 11.210 | 11.263 | 11.316 | 11.307 | 11.272 | | 10.451 | 10.557 | 10.548 | 10.530 | 10.522 | | 10.195 | 10.248 | 10.266 | 10.266 | 10.248 |
| Otter 20 | 13.390 | 13.399 | 13.382 | 13.355 | 13.346 | | 12.790 | 12.887 | 12.878 | 12.878 | 12.870 | | 12.508 | 12.596 | 12.578 | 12.578 | 12.561 |
| Otter 30 | 15.129 | 15.129 | 15.147 | 15.120 | 15.120 | | 14.547 | 14.582 | 14.591 | 14.591 | 14.564 | | 14.211 | 14.300 | 14.317 | 14.300 | 14.282 |

| Pelagic 20 | Beam | | | | | Pelagic 100 | Beam | | | | | Pelagic 150 | Beam | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 5 | 10 | 20 | 37 | | 1 | 5 | 10 | 20 | 37 | | 1 | 5 | 10 | 20 | 37 |
| Otter 1 | -1.139 | -0.847 | -0.821 | -0.803 | -0.812 | | -1.915 | -1.518 | -1.730 | -1.562 | -1.659 | | -3.222 | -2.710 | -3.063 | -2.304 | -2.586 |
| Otter 2 | -1.192 | -0.874 | -0.794 | -0.803 | -0.821 | | -1.492 | -1.421 | -0.971 | -0.847 | -1.068 | | -2.463 | -2.251 | -2.074 | -1.598 | -1.730 |
| Otter 5 | 5.932 | 6.188 | 6.196 | 6.196 | 6.205 | | 5.455 | 5.605 | 5.755 | 5.773 | 5.835 | | 4.634 | 5.526 | 5.111 | 4.978 | 5.323 |
| Otter 10 | 9.789 | 9.824 | 9.833 | 9.833 | 9.824 | | 9.427 | 9.074 | 9.153 | 9.304 | 9.083 | | 8.986 | 9.021 | 8.571 | 8.827 | 8.597 |
| Otter 20 | 12.190 | 12.208 | 12.234 | 12.234 | 12.243 | | 11.254 | 11.369 | 11.360 | 11.572 | 11.237 | | 10.354 | 10.319 | 10.937 | 10.751 | 10.645 |
| Otter 30 | 13.770 | 13.902 | 13.938 | 13.920 | 13.902 | | 11.846 | 12.075 | 11.987 | 11.899 | 12.084 | | 11.298 | 11.087 | 11.193 | 11.607 | 10.875 |

g)

| | | Pelagic 0.1 | | | Pelagic 1 | | | Pelagic 1.5 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Beam | | | Beam | | | Beam | | |
| | | 0.1 | 1 | 3 | 0.1 | 1 | 3 | 0.1 | 1 | 3 |
| Otter | 0.1 | 0.322 | 0.321 | 0.321 | 0.318 | 0.317 | 0.316 | 0.317 | 0.316 | 0.315 |
| | 1 | 0.341 | 0.338 | 0.343 | 0.336 | 0.333 | 0.338 | 0.334 | 0.331 | 0.335 |
| | 1.3 | 0.345 | 0.342 | 0.347 | 0.338 | 0.334 | 0.339 | 0.336 | 0.332 | 0.336 |

h)

| | | Pelagic 0.1 | | | Pelagic 1 | | | Pelagic 1.5 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Beam | | | Beam | | | Beam | | |
| | | 0.1 | 1 | 3 | 0.1 | 1 | 3 | 0.1 | 1 | 3 |
| Otter | 0.1 | -3.487 | -3.725 | -3.698 | -4.678 | -4.890 | -5.075 | -4.731 | -5.049 | -5.429 |
| | 1 | 2.330 | 1.342 | 2.789 | 0.839 | 0.000 | 1.421 | 0.318 | -0.574 | 0.503 |
| | 1.3 | 3.487 | 2.507 | 4.087 | 1.456 | 0.344 | 1.765 | 0.768 | -0.291 | 0.962 |

*Table A.3. Absolute fit (a) and relative percentage change in fit (b) for Base Dispersal Rate; Absolute fit (c) and relative percentage change in fit (d) for Relative Vulnerability; Absolute fit (e) and relative percentage change in fit (f) for Effective Power; Absolute fit (g) and relative percentage change in fit (h) for Total Efficiency Multiplier. Colour scale indicates the value of fit: high improvements from default fit are represented in darker shades of grey, low improvement or decrease in fit are in lighter shades of grey. Note that colour scale differs across panels.*

## A.4. Limitations, assumptions and robustness checks

### A.4.1. Method limitations and assumptions

The results of this study are dependent on a number of factors which might affect the outcome, some of which are discussed below.

The method used to control model performance, Spearman's rank correlation between model prediction of biomass and effort for each cell and spatially resolved observations, allows evaluating areas with "good" and "bad" prediction capacity. The ranked correlation evaluates to what extent the rank of predictions follows the rank of data looking at cell-by-cell prediction and data values. Correlation is therefore capable of showing if the model is predicting high values in cells where data values are high, and vice versa; but it does not allow quantitative evaluation of the absolute values of residuals (as would, for example, Mean Sum of Square). Mean Sum of Square (MSS) was also calculated and the results were qualitatively similar to those of correlation. However, correlation has the advantage of being limited between -1 and +1, which makes it easy to interpret and compare across parameter values and potentially between different models. For this reason correlation was chosen as measure of fit for this study. The total measure of fit was calculated with an objective function which used the median of all correlations for each year, and then the mean of all yearly medians.  Medians were used due to the large dispersion of values across groups (with some species being around 0.8, some fleets down to -0.7). Between years, however, values were not so dispersed; therefore mean was chosen over median. An alternative objective function based on the median of medians overestimated the fit, providing higher total value than mean of medians. For these reasons, the objective function finally used to measure total fit was based on the mean of medians of Spearman's rank correlations across species and fleets.

The Ecospace model is strongly dependent on its underlying Ecopath with Ecosim model. For this study we did not modify the underlying Ecopath and Ecosim models. Therefore the results could differ for alternative parameterization of Ecosim. However, investigation over sensitivity to the

Ecosim vulnerability (see section A.4.2) showed moderate influence of Ecosim vulnerability setting on the Ecospace fit, with differences in spatial fit being influenced more by changes in Ecospace parameters than in Ecosim vulnerability. Only when vulnerability in Ecosim was set equal to 10 for all groups, the performance of Ecospace was affected visibly. This finding confirms once again that having a fully calibrated Ecosim model is fundamental in order to build a correct Ecospace model, however Ecospace parameters seemed to be more important for spatial distribution than Ecosim parameters.

Some of the Ecospace parameters related to initialisation, in particular the "Initialisation" and the "Model Type" for age-structured groups (Multistanza or Individual Base Model), were explored through combinations of these parameter settings, without performing a full sensitivity analysis, and we did not however observe major differences (see section A.2.2). The IBM model performed slightly better than the Multistanza model. The latter was however used because it is considered to be better for model building and fitting (Walters et al., 2010).

The model used in this study did not include Ecospace factors such as advection, primary productivity, and migration, which can be important for spatial distribution of fish species (e.g., Martell et al., 2005; Steenbeek et al., 2013). It is possible that inclusion of such data would provide better prediction for fish species, adding realism to the model.

Cost and price data are important for the effort allocation model, however they are also difficult to obtain. Robustness check with changes in prices and costs did not show any noticeable change in the model performance (see section A.4.2), and fleet distribution prediction did not improve.

Temporal and spatial resolution of the datasets might also be a reason for poor model predictions: effort data from STECF are resolved yearly, however they are a combination of a process that take place on a different scale, i.e. on a daily or weekly basis. Data could therefore not be reflective of the real effort distribution, a problematic extending also to the biomass data, which is known to be spatially dependent (Lewy and Kristensen, 2009). Effort spatial data and the aggregated effort data (used in the Ecosim model) were compared (aggregating the spatially resolved data). The two

datasets overlap for only four years. Demersal and Beam trawls resulted to have a high fit between spatial and aggregated time series. Pelagic trawl had a negative fit. Due to the few comparable years, the results were not significant, and these results should be interpreted cautiously.

Spatial coverage of effort data might also represent a problem: the STECF dataset of spatially resolved effort data cover most, but not all cells in the study area. It is possible that data availability for the first years of compilation of the dataset (used for the present study) was limited for some fleet-regions combinations. Other sources of effort data could be available through the Vessel Monitoring System (VMS). However these data are presently only available at national level and not for all fishing nations that operate in the study area.

Species groups and fleets groups were aggregated in order to reduce the dimensionality of the model. Species were grouped into sub-parameters (as explained in subsection A.3.1) based on their ecological characteristics. This grouping could affect the overall result of the model. We compared the results with model runs using alternative species grouping (using species dispersal setting at species level, as from Mackinson and Daskalov (2007). The model results were very similar, and in particular the fleet fit did not change noticeably when species were not grouped. This suggests that the lumping criteria for species used in this study did not affect the results. Fleets groups were also lumped into sub-parameters. Demersal Otter trawl sub-parameter was a macro-group including Otter trawl proper, and other trawler fleets: Shrimp trawler, Nephrops trawler, and Sandeel trawler. These were separate fleets in the Ecospace model but no separate data were available for the effort data from STECF. Since the four fleets were assumed to have similar behaviour, they were aggregated into one macro-group for the analysis. Parameters were therefore changed for the four fleets in Ecospace accordingly. The implication of this assumption might imply a slightly different response for the Otter trawl fleet, but would not touch upon the beam and pelagic fleet in any case, thus not affecting the overall result of the study. Robustness checks were run with alternative fleet assignation, which showed that results were similar with alternative settings, with only minor differences (A.4.2.6). Under  the combinations "Otter +

Shrimp", the fit for Demersal trawl improved slightly but noticeably. However, the fit of some species declined, bringing the overall model fit to lower levels than the default combination.

A.4.2. Robustness check

For some of the parameters we explored variation with alternative setting across a range of model parameters. We used 4 models representing the parameter ranges: Low, High (with all influential parameters at minima and maxima of their ranges, respectively), Default, and a "Conservative" model, with values arbitrarily set at an intermediate level. For each parameter tested, we selected a range of scenarios. This allowed to check whether the results obtained through the model are sensitive to any of the model assumptions, by observing whether the variation in model fit depend more on model settings (i.e. High, Low, Default or Conservative settings) or on the parameter scenarios. Parameters tested for robustness were Cost, Spatial cost, Prices, Ecosim vulnerability and a No fishing scenario. Cost and Prices are input of the Ecopath model, while Spatial cost was calculated by Ecospace based on the port distribution, retained for this model from the Mackinson and Daskalov (2007) model.

A.4.2.1 Cost

Costs are specified in Ecopath and divided into Fixed, Variable and Sailing costs (with Sailing cost being at 0 in the used model). The alternative scenarios explored changes in model fit with: all costs set at 0; Variable costs set at 0; Sailing costs being set at the values of Variable costs; costs being set without subsidies (following Heymans et al., 2011). All these scenarios were compared with the "normal" case, with all cost input at default. The expected differences across scenarios should be dependent on the changes that cost assignment should have on the gravity model for fleet effort assignment, and hence on the fleet fitness to data (and indirectly also affecting species distribution through fishing). See figure A.2 and table A.4.
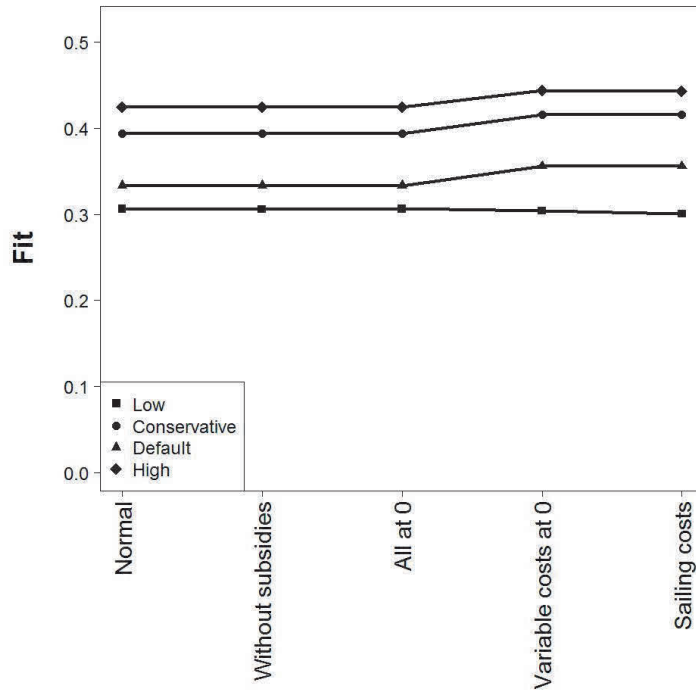
*Figure A.2. Robustness check for cost*

|  | Normal | Without subsidies | All at 0 | Variable costs at 0 | Sailing costs |
|---|---|---|---|---|---|
| Low | 0.305 | 0.305 | 0.306 | 0.303 | 0.300 |
| Conservative | 0.393 | 0.393 | 0.393 | 0.415 | 0.415 |
| Default | 0.333 | 0.333 | 0.333 | 0.355 | 0.355 |
| High | 0.424 | 0.424 | 0.424 | 0.443 | 0.442 |

*Table A.4. Robustness check for cost*

A.4.2.2. Spatial cost

Spatial cost scenarios investigated were based on alternative ports settings, since the spatial cost
layer were automatically generated by Ecospace on the basis of fleet-specific home port
designation and variable costs. We therefore tested an "all port" scenario where every fleet is
allowed in any port; a "no port" scenario" where no fleet has favoured ports; and a scenario where
all fleets have the same set of favoured port (we arbitrarily chose three cells on the Danish coast

as ports). These scenarios were compared with a "normal scenario with all ports set as default.

The expected differences across scenarios should depend on the role that spatial costs play in the

gravity model, and on how it affects the different fleet fitness to effort data and indirectly also

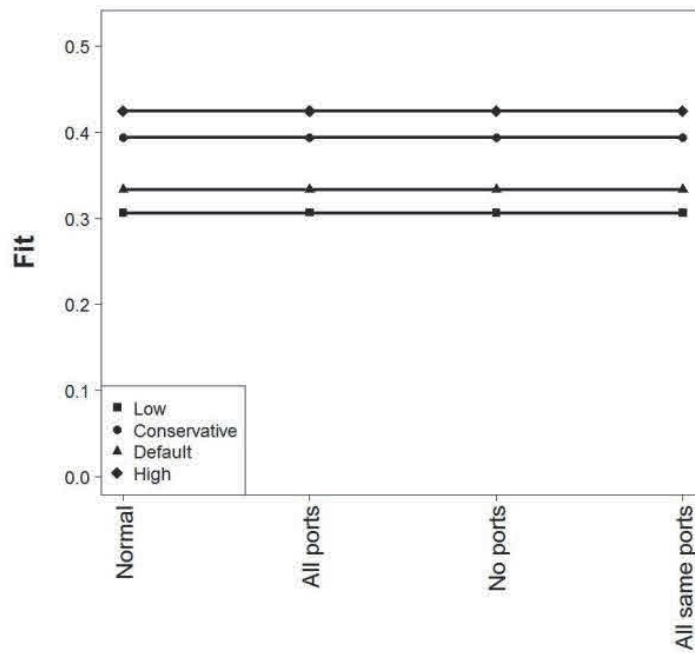species' fitness to biomass data. See figure A.3 and table A.5.



*Figure A.3. Robustness check for Spatial cost*

| | Normal | All ports | No ports | All same ports |
|---|---|---|---|---|
| Low | 0.305 | 0.306 | 0.305 | 0.305 |
| Conservative | 0.393 | 0.393 | 0.393 | 0.393 |
| Default | 0.333 | 0.333 | 0.333 | 0.333 |
| High | 0.424 | 0.424 | 0.424 | 0.424 |

Table A.5. Robustness check for Spatial cost

A.4.2.3. Price

Price scenarios investigated were aiming at identifying the sensitivity of the model to changes in the magnitude of price or in the species composition. The "price 10 times" scenario increased ten-fold all price data, and the "only target" scenarios set at 0 all prices for non-target species (i.e. only the 12 selected species). The rational for this was that many fleets target specifically species with low value (e.g. forage fish) but accidentally capture other species with higher price. Nonetheless, their fishing pattern is determined by the target species and not by the by-catch. Expected changes from these scenarios should depend on the changes in profitability expected by each fleet with an increase in price of their catches, and thus a change of the spatial effort patterns. See figure A.4 and table A.6.
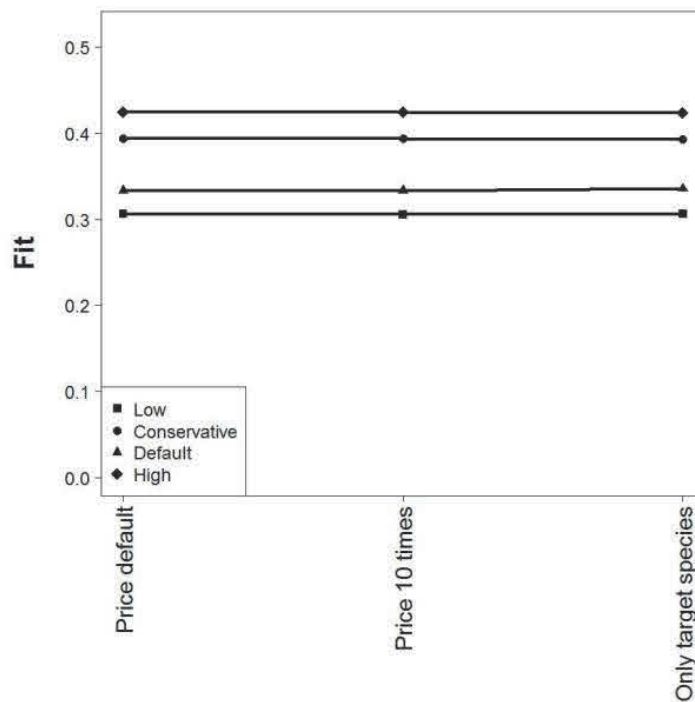


*Figure A.4. Robustness check for Price*

|               | Price default | Price 10 times | Only target spp. |
|---------------|---------------|----------------|------------------|
| Low           | 0.305         | 0.305          | 0.306            |
| Conservative  | 0.393         | 0.393          | 0.392            |
| Default       | 0.333         | 0.333          | 0.335            |
| High          | 0.424         | 0.424          | 0.423            |

*Table A.6. Robustness check for Price*

A.4.2.4. No Fishing

A "no fishing" scenario was investigated to explore whether the model fit changed when no fishing occurred. In Ecospace, fishing fleet can be allowed to fish in one or more habitats; for the "no fishing" scenario, all fleets were set as not allowed to fish in any of the habitats. This scenario was compared with a "default" scenario. For this scenario, furthermore, the biomass-specific fit was also investigated. The expected results were to see if the "no fishing" scenario would produce scarce fit. The fit on biomass only, instead was explored to test whether the lack of fishing would affect somehow the fish species distribution. See figure A.5 and A.6 and table A.7 and A.8.
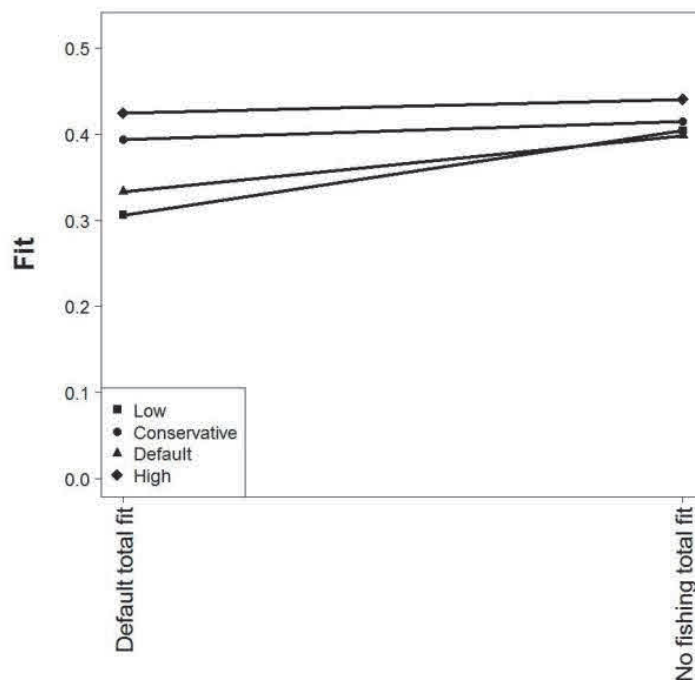


*Figure A.5. Robustness check for "no fishing" Total Fit*

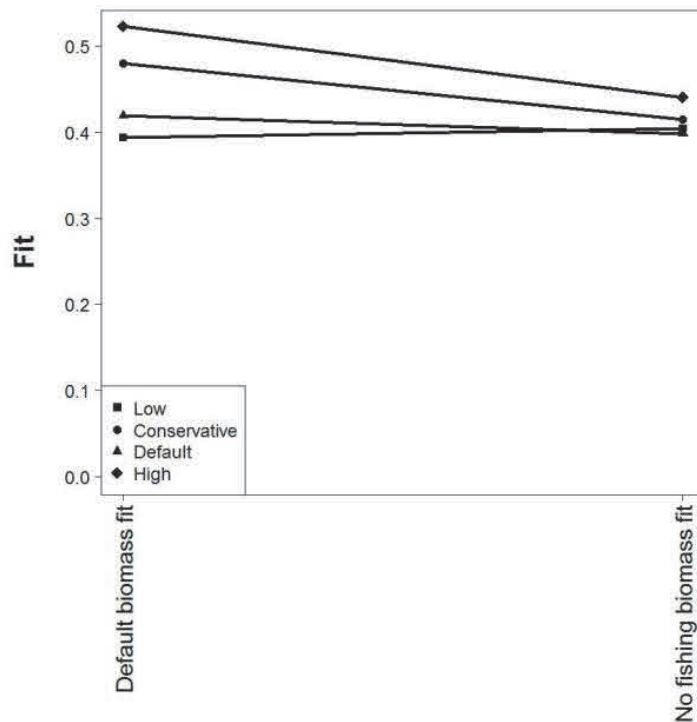|               | Default total  fit | No fishing total fit |
| ------------- | ------------------ | -------------------- |
| Low           | 0.305              | 0.403                |
| Conservative  | 0.393              | 0.414                |
| Default       | 0.333              | 0.398                |
| High          | 0.424              | 0.440                |

*Table A.7. Robustness check for "no fishing" Total Fit*



*Figure A.6. Robustness check for "no fishing" Biomass Fit*

|               | Default biomass fit | No fishing biomass fit |
| ------------- | ------------------- | ---------------------- |
| Low           | 0.393               | 0.403                  |
| Conservative  | 0.479               | 0.414                  |
| Default       | 0.419               | 0.398                  |
| High          | 0.522               | 0.440                  |

*Table A.8. Robustness check for "no fishing" Biomass Fit*

A.4.2.5. Ecosim vulnerability

The vulnerability in Ecosim was explored through 4 scenarios by setting it at default (i.e. with values from the model used in this study), all species at 1, all species at 2 and all species at 10. The changes in performance of the model were expected to explain if the Ecospace performance depends on the Ecosim parameters setup. Under the scenario V10 a slight improvement of the fit of Demersal trawl was observed. This suggests that the parameterisation of Ecosim vulnerability can have an effect on Ecospace spatial distribution of effort, through species distribution. See figure A.7 and table A.9.
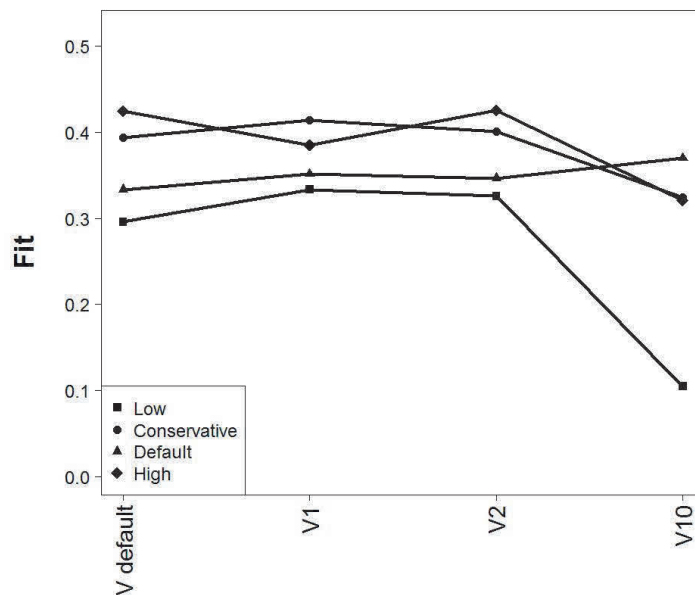


Figure A.7. Robustness check for Ecosim vulnerability setting

|              | V default | V1    | V2    | V10   |
|--------------|-----------|-------|-------|-------|
| Low          | 0.296     | 0.333 | 0.326 | 0.105 |
| Conservative | 0.394     | 0.413 | 0.400 | 0.324 |
| Default      | 0.333     | 0.351 | 0.346 | 0.370 |
| High         | 0.424     | 0.385 | 0.425 | 0.321 |

Table A.9. Robustness check for vulnerability

A.4.2.6. Setting of the macro-group Demersal trawl

Otter trawl macro-group assignation was explored by testing the default assignation (with Otter, Nephrops, Sandeel and Shrimp trawlers lumped together) against other assignations: Otter trawl alone, Otter and Nephrops trawls lumped, Otter and Sandeel trawls lumped, Otter and shrimp trawls lumped. See figure A.8 and table A.10.
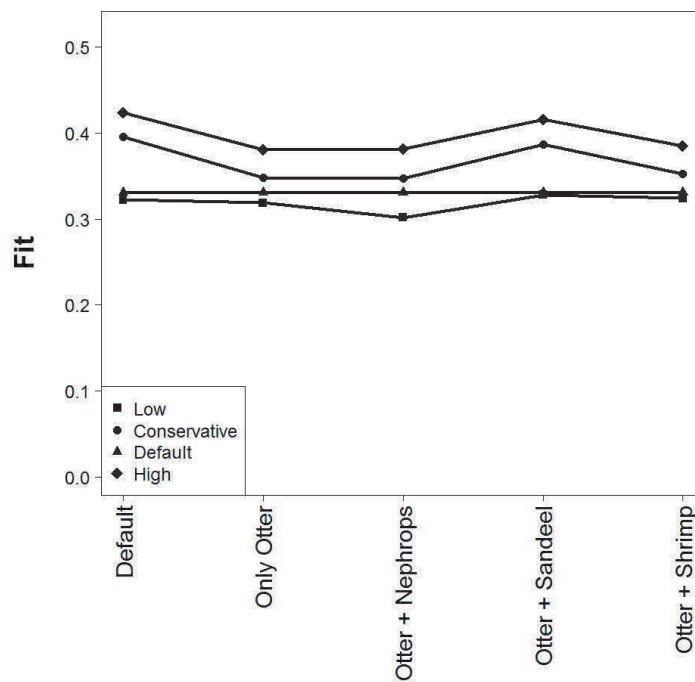


*Figure A.8. Robustness check for Demersal trawl Setting*

| | Default | Only Otter | Otter + Nephrops | Otter + Sandeel | Otter +Shrimp |
|---|---|---|---|---|---|
| Low | 0.322 | 0.319 | 0.302 | 0.328 | 0.324 |
| Conservative | 0.395 | 0.348 | 0.347 | 0.386 | 0.353 |
| Default | 0.331 | 0.331 | 0.331 | 0.331 | 0.331 |
| High | 0.423 | 0.380 | 0.381 | 0.415 | 0.385 |

*Table A.10. Robustness check of Demersal trawl Setting*

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# Paper II

# Paper III

ORIGINAL ARTICLE

# Influence of larval transport and temperature on recruitment dynamics of North Sea cod (*Gadus morhua*) across spatial scales of observation

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## Abstract

The survival of fish eggs and larvae, and therefore recruitment success, can be critically affected by transport in ocean currents. Combining a model of early-life stage dispersal with statistical stock–recruitment models, we investigated the role of larval transport for recruitment variability across spatial scales for the population complex of North Sea cod (*Gadus morhua*). By using a coupled physical–biological model, we estimated the egg and larval transport over a 44-year period. The oceanographic component of the model, capable of capturing the interannual variability of temperature and ocean current patterns, was coupled to the biological component, an individual-based model (IBM) that simulated the cod eggs and larvae development and mortality. This study proposes a novel method to account for larval transport and success in stock–recruitment models: weighting the spawning stock biomass by retention rate and, in the case of multiple populations, their connectivity. Our method provides an estimate of the stock biomass contributing to recruitment and the effect of larval transport on recruitment variability. Our results indicate an effect, albeit small, in some populations at the local level. Including transport anomaly as an environmental covariate in traditional stock–recruitment models in turn captures recruitment variability at larger scales. Our study aims to quantify the role of larval transport for recruitment across spatial scales, and disentangle the roles of temperature and larval transport on effective connectivity between populations, thus informing about the potential impacts of climate change on the cod population structure in the North Sea.

**KEYWORDS**

Atlantic cod, biophysical model, larval transport, North Sea, populations, stock–recruitment, temperature

Romagnoni and Kvile contributed equally to the article.

# 1 | INTRODUCTION

Recruitment of fish stocks depends largely on survival during the first year and in particular during the pelagic early-life stages (ELS) in broadcast spawning teleost fish (Houde, 2008;Leggett & Deblois, 1994). A number of factors affect the ELS survival, including temperature, food availability and predation (Folkvord, 2005;Peck & Hufnagl, 2012). In addition to these factors, the interannual variability in recruitment can be influenced by advective transport of eggs and larvae from spawning to nursery areas (Bailey, 1981;Henriksen et al., 2018). Recent physical–biological modelling studies have related larval transport and success to recruitment using various approaches (Peck & Hufnagl, 2012), including comparisons between modelled larval survival and observed recruitment (Daewel, Schrum, & Gupta, 2015) and between modelled and observed juvenile distributions (Huwer, Hinrichsen, Hussy, & Eero, 2016). One alternative approach to assess the effect of larval transport on recruitment is the application of stock–recruitment models. Historically, parametric stock–recruitment models have been used to link variation in stock size with recruitment success. While the predictive capability of these models remains limited (Subbey, Devine, Schaarschmidt, & Nash, 2014), inclusion of environmental variables such as temperature (Akimova, Núñez-Riboni, Kempf, & Taylor, 2016;Planque, Fox, Saunders, & Rockett, 2003), the North Atlantic Oscillation index (NAO) (Brander & Mohn, 2004), surface wind speed (Hare, Brooks, Palmer, & Churchill, 2015), zooplankton prey availability (Olsen et al., 2011) and interactions between these factors (Duplisea & Robert, 2008;Olsen et al., 2011) can help to identify key biological mechanisms driving the interannual variability in stock–recruitment. We hypothesise that accounting for transport variability in stock–recruitment models can help to explain parts of the observed recruitment variability. In fact, it has been suggested that ELS transport could be one of the drivers behind the unclear relationship between spawning stock size and recruitment (Huwer et al., 2016). While some studies have included proxies of larval transport in stock–recruitment relationships (Baumann et al., 2006; Zimmermann, Claireaux, & Enberg, 2019), few have included direct estimates of larval transport (but see Hidalgo et al., 2019).

Moreover, transport can influence connectivity among populations (e.g. through interannual variability in oceanographic current patterns, Huwer et al., 2016;Kvile, Romagnoni, Dagestad, Langangen, & Kristiansen, 2018) and recruitment dynamics across large geographic scales (Cadrin, Goethel, Morse, Fay, & Kerr, 2019;Henriksen et al., 2018;Hinrichsen, Von Dewitz, & Dierking, 2018) and thereby population management (Fogarty & Botsford, 2007;Hidalgo et al., 2019;Ramesh, Rising, & Oremus, 2019). Critically, the spatial scale of observation can affect the stock–recruitment relationship, providing contrasting results across scales (Chang, Chen, Halteman, & Wilson, 2016). The importance of environmental drivers for recruitment can also differ across subunits within a stock (Brosset et al., 2018). We therefore expect the importance of larval transport variability for recruitment to differ across spatial scales (i.e. basin vs. sub-basin) and between individual populations. In this study, we explore alternative approaches to explicitly include larval transport

in stock–recruitment functions, and quantitatively assess the effect of transport on recruitment across spatial scales. We use annual estimates of larval retention and population connectivity, obtained through a coupled physical–biological model of larval drift, focusing on North Sea cod (*Gadus morhua*) as a case study.

We initially include retention anomaly as an environmental covariate in traditional parametric stock–recruitment model formulations and compare its effect to alternative covariates, namely sea surface temperature (SST) and the North Atlantic Oscillation index (NAO). In addition, we propose a novel approach for inclusion of the effect of larval transport in stock–recruitment models by weighting spawning stock biomass (SSB) according to yearly retention and advection rates, providing a measure of "effective biomass." Two alternative approaches are proposed to account for effective biomass: including only retention in the spawning area of origin (retention-only SSB, *rSSB*), and including retention and inflow of larvae from other areas (net drift SSB, *ndSSB*), effectively accounting for connectivity. Additionally, we quantify temporal patterns in population connectivity and their relationship with SST and NAO.

# 2 | MATERIALS AND METHODS

## 2.1 | Ocean circulation in the North Sea

Ocean circulation in the semi-enclosed North Sea basin is influenced by topography and inflow of North Atlantic water, separating the basin into a shallow southern and a deeper northern area. The northern area is influenced by inflow of saline Atlantic water flowing along the western slope of the Norwegian Trench. This current transports the planktonic copepod, *Calanus finmarchicus*, an important food source for larval cod (Nicolas, Rochette, Llope, & Licandro, 2014) and other species, into the region. The current flows along the Norwegian Trench and into Skagerrak, where it enters the "Skagerrak loop." It follows a counterclockwise trajectory along the Skagerrak coast, and after mixing with the less saline Norwegian coastal current, flows north-westward along the eastern slope of the Norwegian Trench and into the Norwegian Sea (Huserbråten, Moland, & Albretsen, 2018). The southern North Sea is dominated by continental freshwater run-off and tidal patterns, which in combination with wind and wave turbulence and shallow topography result in permanent mixing. The intermediate saline current from the English Channel and the coastal, low saline Jutland Current flow along the continental coast and into the Skagerrak, entering the "Skagerrak loop" (Sundby, Kristiansen, Nash, & Johannessen, 2017).

## 2.2 | Cod populations in the North Sea

Although managed as one stock (ICES, 2018c), North Sea cod comprises a number of spatially segregated units, with limited overlap and varying degree of connectivity (Heath et al., 2014;Neat et al., 2014). The main units are the Viking and the South populations.

The latter is often separated into a South proper (centred around the Dogger Bank) and a Northwest unit; these two subpopulations are genetically homogenous but show contrasting demographic trends and limited adult connectivity, so their relationship is as yet unclear (Neat et al., 2014). In this study, we considered alternative scenarios with three populations (Viking, South and Northwest), two populations (Viking and South including Northwest) and a single population (aggregating Viking, South and Northwest), the latter roughly corresponding to the current management unit. The populations' spatial extent (Figure 1) was based on ICES (2015). We calculated larval connectivity between the populations and assessed drift into the Skagerrak (which is excluded from our populations) and the Norwegian Sea, Scottish sea and English Channel (hereafter called "outside"; Figure 1). Particles leaving the study area (i.e. entering the "outside" area) were considered lost.

## 2.3 | Early-Life Stage (ELS) dispersal model

To quantify larval retention and connectivity between populations, we used a coupled physical–biological model



**FIGURE 1** Study area showing distribution of populations (following ICES, 2015) and other potential sink areas for simulated cod larvae in our study. Nursery areas are overlaid to the population of appartenance

(hereafter, ELS dispersal model) for the time period 1971–2014 and included the model output in statistical stock–recruitment models for the same years. The individual-based model (IBM) simulates development and transport of cod eggs and larvae based on earlier studies of larval cod (Kristiansen, Lough, Werner, Broughton, & Buckley, 2009;Kristiansen, Stock, Drinkwater, & Curchitser, 2014;Kristiansen, Vikebø, Sundby, Huse, & Fiksen, 2009). The IBM is integrated as a module in the open source Lagrangian particle tracking framework OpenDrift (github. com/opendrift; Dagestad, Röhrs, Breivik, & Ådlandsvik, 2018;Kvile et al., 2018), and the code for the cod eggs and larvae module is available on github.com/trondkr/KINO-ROMS/tree/master/Romagnoni-2019-OpenDrift. To simulate transport with ocean currents and temperature-dependent development, the IBM was coupled offline to a reanalysis of the regional ocean circulation model ROMS (Shchepetkin & McWilliams, 2005) configured for ocean regions covering the Nordic Seas (including the North Sea) and parts of the Arctic Ocean, with 4 km horizontal resolution, 32 vertical layers and output stored daily (Lien, Gusdal, Albretsen, & Melsom, 2013). For downloading options, see http://thredds.met.no/thredds/nansen_daily.html. Further details on the characteristics and limitations of the ELS dispersal model are available in Kvile et al. (2018).

Due to long-term and interannual variation in the relative importance of spawning grounds (González-Irusta & Wright, 2016;Sundby et al., 2017) and the uncertainty in spawning ground locations early in the time series, we released particles representing cod eggs uniformly within the three populations' spatial extent (Figure 1). Although this could reduce the precision of connectivity estimates in some years, we considered this approach as more conservative when modelling larval transport over a long time period including years with unknown spawning ground distribution. To obtain uniform spatial distribution (0.12–0.14 eggs/km$^2$), we set the number of eggs released based on the sizes of the population areas: ~32,400 in the South (~270,000 km$^2$), ~22,950 in the Northwest (~170,000 km$^2$) and ~27,000 in the Viking area (~200,000 km$^2$), for a total of ~91,500 eggs.

We defined the timing of egg release using prior knowledge of the population spawning periods (Brander, 1994, 2005;Fox et al., 2008): between December 15th and April 15th for the South population, between January 1st and May 1st for the Northwest population and between February 1st and May 15th for the Viking population (Figure 2a). The number of eggs released per day followed a Gaussian distribution, $N(\mu, \sigma^2)$, where $\mu = 1$ and $\sigma = 0.25$, scaled to the length of the spawning season and the total number of particles defined per population area and with peaks that approximately matched the spawning peak described by Brander (1994). Setting a broader spawning season than observed in recent years accounts for uncertainty in the spawning season early in the time series. For example, spawning was allowed to start in December for the South population to account for the fact that the Southern Bight component, which spawns earlier than the German Bight and Central-west (Brander, 1994), was more abundant in the past.
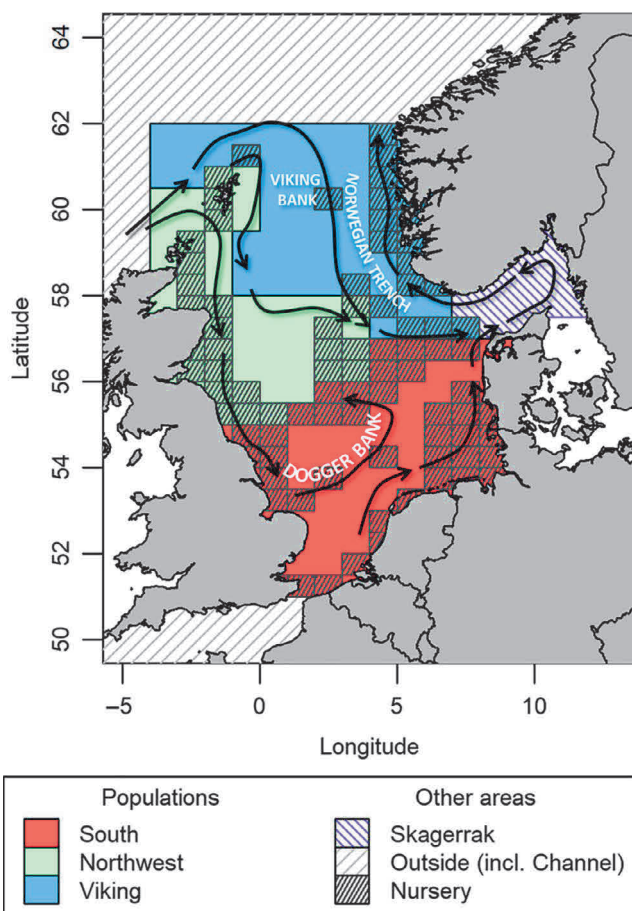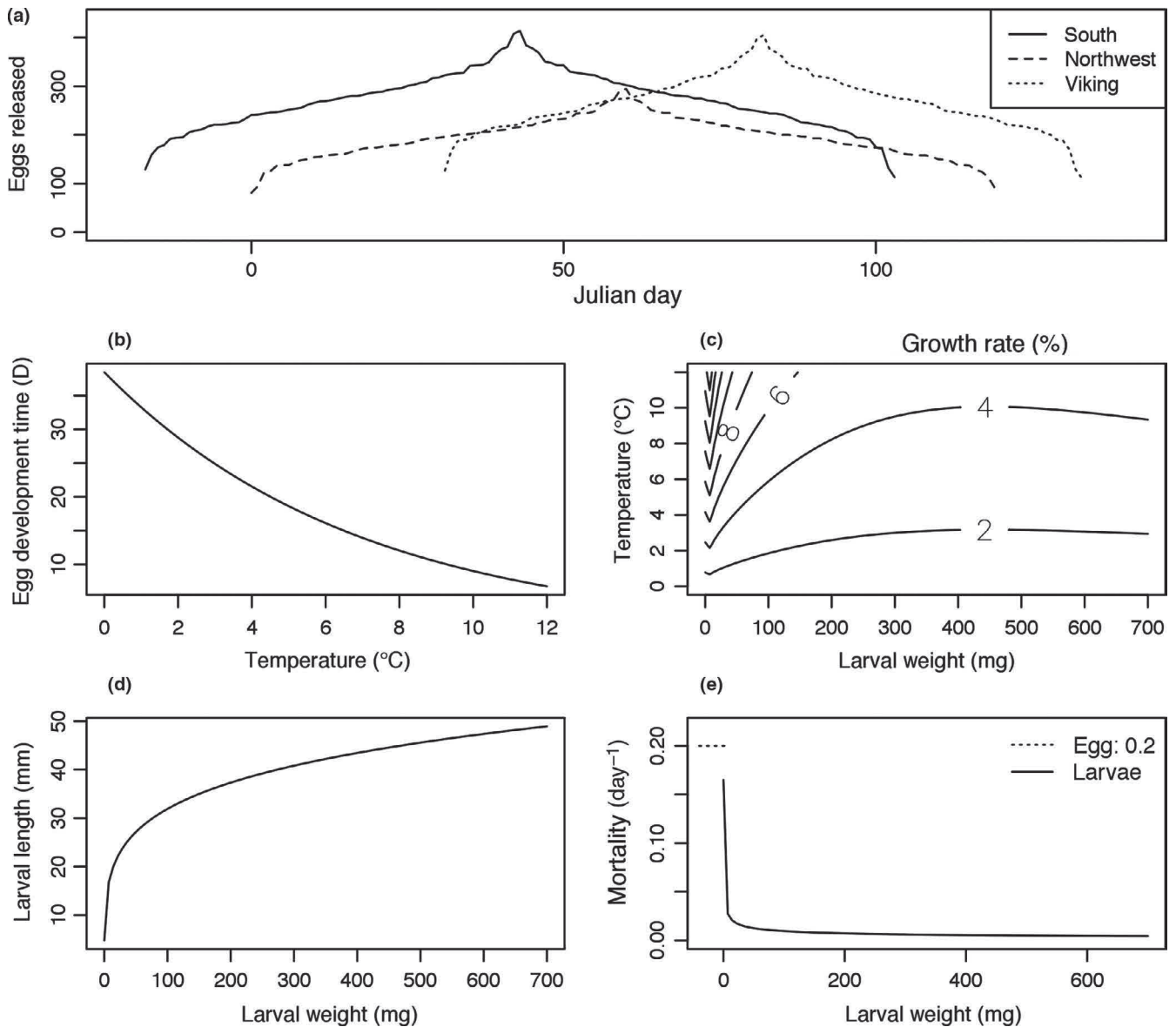
**FIGURE 2** Cod egg and larvae IBM functions. (a) Number of eggs released per Julian day (counting from January 1st) per spawning ground; (b) egg development time (d) as a function of temperature; (c) growth rate of larvae day$^{-1}$ (GR, contours) as a function of larval weight and temperature; (d) larval length (L) as a function of weight; and (e) mortality rate (m, day$^{-1}$) for eggs (fixed at 0.2) and larvae as a function of larval weight

Eggs were released in equal numbers at 10 m depth intervals between 0 and 50 m (i.e. for a given population, an equal number of eggs was uniformly released at 0, 10, 20, 30, 40 and 50 m). After release, eggs and larvae were advected horizontally at fixed depths using an Euler interpolation scheme without horizontal diffusion and a 1-hr time step. The Euler scheme differed minimally compared to a more computationally costly Runge–Kutta scheme (Kvile et al., 2018). We used different drift depths to represent vertical movement within the depth range typically available in the North Sea, based on the finding that incorporating a more computationally costly vertical movement behaviour had limited effect on connectivity and retention of cod ELS at settlement in the North Sea (Kvile et al., 2018). Development time of planktonic eggs (d, days) was a function of the ambient sea water temperature (T, °C) according to

the ocean model reanalyses, parameterised based on observations for cod eggs (Langangen, Stige, Yaragina, Vikebø, et al., 2014, based on data in Ellertsen, Fossum, Solemdal, Sundby, & Tilseth, 1987, Figure 2b):

$$\ln d = 3.65 - 0.145 \times T \tag{1}$$

After completing the egg stage, the simulated individuals hatch into cod larvae. The simulated cod larvae grew with a growth rate (GR, percentage of larval weight/day) depending on larval weight (W, mg) and ambient temperature (T), as estimated experimentally for Atlantic cod larvae (Folkvord, 2005) (Figure 2c):

$$GR = 1.08 + 1.79 \times T - 0.074 \times T \times \ln W - 0.0965 \times T \times \ln W^2 + 0.0112 \times T \times \ln W^3 \tag{2}$$

Larvae were assumed to feed ad libitum, and their initial weight was set at 0.08 mg. Larval length ($L$, mm) was a function of weight (Folkvord, 2005) (Figure 2d):

$$L = e^{2.296+0.277 \times \ln W - 0.005128 \times \ln W^2} \qquad (3)$$

We assumed that cod larvae had no directional horizontal (swimming) movement. During the simulation, eggs were subject to a fixed daily mortality rate ($m$) of 0.2, which is within the range of mean values estimated in studies of cod eggs (0.1–0.32, Rijnsdorp & Jaworski, 1990; see Table 2 in Langangen, Stige, Yaragina, Vikebø, et al., 2014). For larvae, we set the mortality rate to decrease with weight (Figure 2e) as parameterised for North Sea cod larvae in

Akimova, Hufnagl, Kreus, and Peck (2016), based on the size-spectrum theory (Peterson & Wroblewski, 1984):

$$m = 0.06 \times W^{-0.4} \qquad (4)$$

The survival probability of each individual was updated throughout the simulation according to the mortality rate (i.e. individuals were not removed from the simulation), following a super-individual approach (Scheffer, Baveco, DeAngelis, Rose, & van Nes, 1995).

Larvae settled when reaching a length >49 mm (Bastrikin, Gallego, Millar, Priede, & Jones, 2014). Only larvae settling within known nursery areas for North Sea cod (based on Heath et al., 2014; see Figure 1) were considered to successfully settle and survive; larvae that reached settlement length outside nursery areas were considered dead (hereafter "not settling"). Larvae not reaching settlement length by the end of the simulation (set to 15th August for South and 29th September for Northwest and Viking) were considered dead (amounting to <1% of larvae, not included in the analysis). The juvenile stage was not simulated since cod adopt a demersal lifestyle upon reaching settlement length.

For each population, we estimated the proportion of larvae (a) retained in a nursery area for the given population of origin; (b) drifting into the nursery area of another population; (c) drifting out of the study area (to the Skagerrak or "outside") and (d) reaching settlement size within any population area, but not within a nursery area ("not settling"). Annual values (1971–2014) for these metrics were included in the stock–recruitment analysis (see below). To test the robustness of the results of the stock–recruitment analysis to key assumptions in the larval dispersal model, we performed additional simulations where the mortality rate (for eggs and larvae) was adjusted by ±20% and separate simulations where settlement size was adjusted by ±20%. We ran these additional simulations for 1990 and 2010, two years with different climatic conditions (high and low NAO phase, respectively; Figure 3) and contrasting results of larval dispersal. Parameters included in the ELS model are summarised in Table 1.
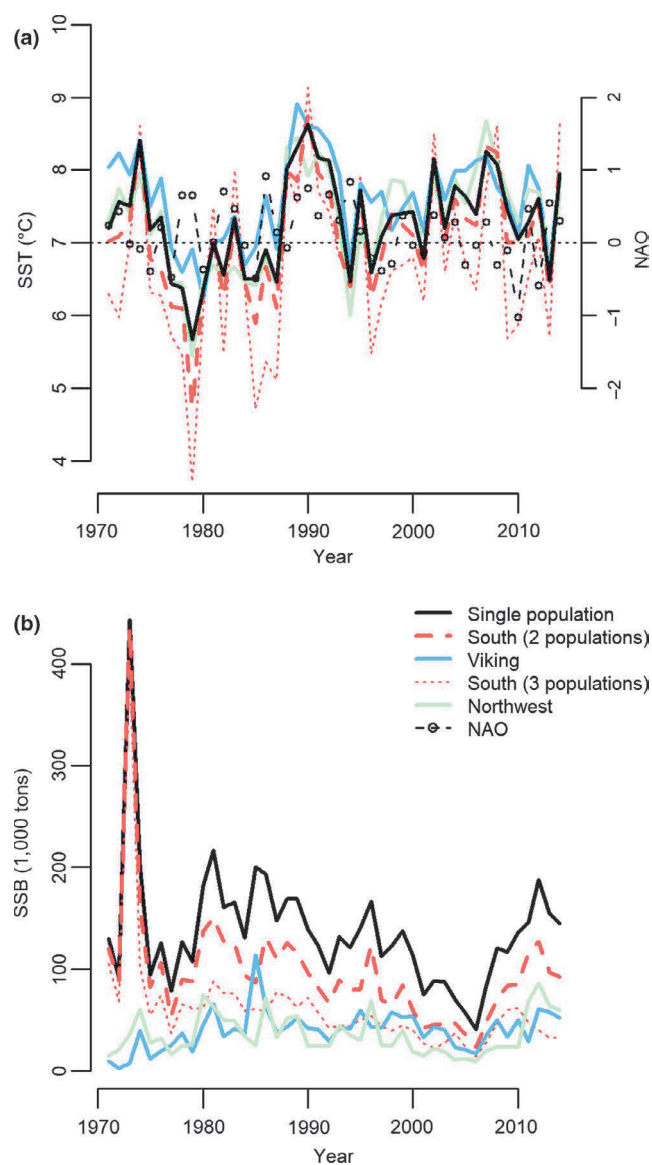


**FIGURE 3** (a) Sea surface temperature (SST) by population area across the three, two and single populations cases, and the NAO index. (b) Spawning stock biomass (SSB) by population area across the three, two and single populations cases

**TABLE 1** Parameters used in the ELS model

| Parameter | Unit | Meaning |
|---|---|---|
| $\mu$ | | Mean of the Gaussian distribution of eggs spawned per day (1) |
| $\sigma$ | | Standard deviation of the Gaussian distribution of eggs spawned per day (0.25) |
| $d$ | days | Development time of planktonic eggs |
| $T$ | °C | Ambient sea water temperature |
| $GR$ | % of larval weight/ day | Larval growth rate |
| $W$ | mg | Larval weight |
| $L$ | mm | Larval length |
| $m$ | day$^{-1}$ | Mortality rate |

## 2.4 | Observational data

We calculated population-specific estimates of SSB and recruitment (age 1) based on abundance data (1971–2014) obtained from the ICES North Sea International Bottom Trawl Survey (NS-IBTS) as catch per unit of effort per ICES statistical sub-rectangle (ICES, 2018a; Figure 3). Although more accurate abundance estimates could be obtained by using standardised indices instead of raw data, these are only available from 1983. We instead used raw data to include a longer time series, spanning years when SSB was higher, to provide robustness to the stock–recruitment estimates. We generated annual data of age-specific abundance to match the ICES statistical sub-rectangle using Catch-Per-Unit-Effort (CPUE) adjusted for swept area and gear catchability, assuming that the sample is representative of fish abundance. The swept area is a function of standardised tow length and net width during towing, which in turn is a function of tow depth (ICES, 2012). Average depth per sub-rectangle (NGDC, 1995) was used as a proxy for tow depth. Catchability coefficient for the survey gear by age (Fraser, Greenstreet, & Piet, 2007) was multiplied by the ratio of the swept area to the whole ICES rectangle area. SSB was calculated as abundance per age multiplied by maturity and weight per age and year, assumed homogeneous between populations lacking population-specific data (ICES, 2017). The recruitment index was estimated by back-calculating abundance of age 1 from averaged age 2 and 3 abundances scaled by the age- and year-specific natural mortality (ICES, 2015). As climate variables, we included sea surface temperature (SST) mean monthly values (ICES, 2018b) for the period February to June (the period of highest sensitivity of cod larvae to temperature in this area, Nicolas et al., 2014), resolved at ICES sub-rectangles and averaged per population area; and monthly means of NAO data (NOAA, 2018) averaged per year (Figure 3).

## 2.5 | Stock–recruitment models

We used the Cushing parametric stock–recruitment model formulation, following recent literature on North Sea cod (Akimova, Núñez-Riboni, et al., 2016). We considered model formulations with (a) drift anomaly included as a covariate or using (b) retention-only SSB (rSSB) or (c) net drift plus retention of SSB (ndSSB) as an alternative predictor for recruitment to SSB. Conceptually, the SSB effectively contributing to recruitment is a fraction of total SSB: rSSB accounts for the proportion of larvae retained within the population of origin after settlement. ndSSB accounts both for the proportion retained and for the number of larvae settling into a population from other populations, quantified as the fraction of other populations' SSB drifted into the population of interest:

$$\mathrm{rSSB}_p = \mathrm{SSB}_p \times D_{p,p} \tag{5}$$

$$\mathrm{ndSSB}_p = \mathrm{SSB}_p \times D_{p,p} + \sum_{p \neq p} \mathrm{SSB}_p \times D_{p,p} \tag{6}$$

For any population $p$ in the pool of all populations $P$, rSSB was calculated as the product of its SSB and the retention proportion $D_{p,p}$. ndSSB was the sum of rSSB and the summed product of the biomass and drift proportion into $p$ for all other populations in $P$ ($D_{P,p}$).

Similarly to the SSB-based models, models with ndSSB and rSSB were fitted with or without climate variables as covariates (Table 2). The models thus took the form (Akimova, Núñez-Riboni, et al., 2016):

$$R = \alpha S^{\gamma} \tag{7}$$

Where recruitment R was calculated as a function of the generic S (either SSB, rSSB or ndSSB). This was extended for inclusion of climate variable $E$ as:

$$R = \alpha S^{(\gamma + \theta E)} \tag{8}$$

$E$ was any climate variable (SST, NAO or retention anomaly, RA). RA was calculated as the annual deviation from the mean larval retention over the whole time series for a given population, determined from the ELS dispersal model.

The linear forms of the models (see Appendix S1) were tested for residuals assumptions, and outliers were removed from the analysis. Commonly used model comparison methods such as AIC and likelihood-based approaches could not be used since models with SSB, ndSSB or rSSB included different data in the predictor variable. Models were therefore compared through their absolute fit to data using adjusted $R^2$, with significance threshold set at .05. Adjusted $R^2$ allows highlighting the combinations of predictor and covariates with highest explanatory power, that is those that improve the model more than expected by chance, with penalisation of additional parameters.

## 3 | RESULTS

We compared the performance of stock–recruitment models for North Sea cod across the three population levels and model formulations (SSB, rSSB, ndSSB, Table 3). At the three populations scale, models including SST as a covariate (models 2, 6 and 9) have

**TABLE 2** Models used in analyses with their predictors and climate variables

| Model | Predictor | Covariate |
|---|---|---|
| 1 | SSB | None |
| 2 | SSB | SST |
| 3 | SSB | NAO |
| 4 | SSB | RA |
| 5 | rSSB | None |
| 6 | rSSB | SST |
| 7 | rSSB | NAO |
| 8 | ndSSB | None |
| 9 | ndSSB | SST |
| 10 | ndSSB | NAO |

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highest fit to data for the South and Northwest populations. In the Northwest population, models with ndSSB have higher fit than their counterparts with SSB when including no covariate or NAO (but not with SST). Model performance is generally low for the Viking population, with only models replacing SSB with ndSSB with or without SST as covariate (models 8 and 9) showing significant fit (p < .05). At the two populations scale, results for the South (including Northwest) unit are similar to the three populations scale,

but with higher overall fit. In the Viking population, models 1–4 and 5–7 in the two and three population cases are fitted to the same data and models 8–10 (with ndSSB) give similar results to the three populations scale. Combining the Northwest and South populations result in slight changes in connectivity values for the Viking population. At the single population scale, model 4 using retention anomaly as covariate shows highest fit, followed by model 2 with SST.

**TABLE 3** Adjusted $R^2$ and $p$-values for each model (Table 2) and population across the three cases of population scale

|  | Predictor | Covariate | South | | Viking | | Northwest | |
|---|---|---|---|---|---|---|---|---|
|  |  |  | Adj. $R^2$ | p | Adj. $R^2$ | p | Adj. $R^2$ | p |
| 1 | SSB | None | .22 | .001 | .04 | .106 | .23 | .001 |
| 2 | SSB | SST | .31 | .001 | .03 | .233 | .35 | .000 |
| 3 | SSB | NAO | .20 | .008 | .05 | .171 | .19 | .011 |
| 4 | SSB | D | .22 | .005 | −.01 | .445 | .19 | .009 |
| 5 | rSSB | None | .21 | .001 | .03 | .121 | .22 | .001 |
| 6 | rSSB | SST | .29 | .001 | .05 | .185 | .33 | .000 |
| 7 | rSSB | NAO | .23 | .005 | .04 | .218 | .18 | .012 |
| 8 | ndSSB | None | .18 | .003 | .11 | .016 | .27 | .000 |
| 9 | ndSSB | SST | .27 | .001 | .15 | .027 | .34 | .000 |
| 10 | ndSSB | NAO | .19 | .010 | .09 | .090 | .25 | .003 |

|  | Predictor | Covariate | South + Northwest | | Viking | |
|---|---|---|---|---|---|---|
|  |  |  | Adj. $R^2$ | p | Adj. $R^2$ | p |
| 1 | SSB | None | .26 | .000 | .04 | .106 |
| 2 | SSB | SST | .36 | .000 | .03 | .233 |
| 3 | SSB | NAO | .24 | .003 | .05 | .171 |
| 4 | SSB | D | .23 | .004 | −.01 | .445 |
| 5 | rSSB | None | .25 | .000 | .03 | .121 |
| 6 | rSSB | SST | .34 | .000 | .05 | .185 |
| 7 | rSSB | NAO | .24 | .003 | .04 | .218 |
| 8 | ndSSB | None | .25 | .000 | .13 | .010 |
| 9 | ndSSB | SST | .32 | .000 | .17 | .018 |
| 10 | ndSSB | NAO | .23 | .004 | .10 | .068 |

|  | Predictor | Covariate | Single population | |
|---|---|---|---|---|
|  |  |  | Adj. $R^2$ | p |
| 1 | SSB | None | .24 | .001 |
| 2 | SSB | SST | .28 | .001 |
| 3 | SSB | NAO | .21 | .006 |
| 4 | SSB | D | .32 | .000 |
| 5 | rSSB | None | .15 | .005 |
| 6 | rSSB | SST | .21 | .007 |
| 7 | rSSB | NAO | .14 | .031 |
| 8 | ndSSB | None | - | - |
| 9 | ndSSB | SST | - | - |
| 10 | ndSSB | NAO | - | - |

*Note:* Darker shades of grey indicate higher adjusted $R^2$ (higher model fit and better model performance).
In the single population case, ndSSB is not calculated.

The interannual variation in SSB, rSSB and ndSSB is largest for the Viking and Northwest units (Figure 4). The three indices show similar interannual patterns (but for example the peak around 1985 in Viking SSB Figure missing in rSSB and ndSSB), but can still result in different fit to data (Figure 5b), with, for example, higher fit using ndSSB than rSSB in Viking and Northwest populations (Table 3). Using traditional SSB with retention anomaly (model 4, Table 3), the effect of retention is captured at the single population scale but not at the two or three populations scale. In this case, the effect has a similar magnitude and effect as the inclusion of SST as covariate (Figure 5a,c).

The interannual variation in retention and connectivity is relatively low (Figure 6). Retention is higher in South (0.39 ± 0.08) and Northwest (0.31 ± 0.06) populations compared to the Viking population (0.14 ± 0.04). Connectivity among the three populations is always low. The drift from South to Northwest and Viking populations is comparable (0.02 ± 0.03 and 0.03 ± 0.03, respectively). The drift from the Northwest to South population is slightly higher than to the Viking population (0.07 ± 0.04 and 0.04 ± 0.03, respectively),

while drift from the Viking population is low or close to zero to the Northwest and South populations (0.03 ± 0.05 and 0.01 ± 0.01, respectively). The proportion of larvae drifting to the Skagerrak from the South and Viking populations is similar (0.07 ± 0.07 and 0.07 ± 0.06, respectively) while drift from the Northwest population is lower (0.02 ± 0.03). The proportion of larvae drifting outside of the study area is low for the South (0.03 ± 0.03) and Northwest (0.07 ± 0.05) populations. In contrast, for the Viking population, drift to the outside area is higher than the retention rate (0.39 ± 0.13). The proportion of larvae remaining within the study area but not settling within a nursery area is high for all populations (0.46 ± 0.08, 0.48 ± 0.09 and 0.36 ± 0.08 for South, Northwest and Viking populations, respectively). Only drift from the South to the Viking population and to the Skagerrak and from South to Northwest populations significantly increase or decrease, respectively, in time (Table 4).

The NAO and SST indices are significantly correlated with drift anomalies across population scales (Table 4). SST is positively correlated with drift to the Skagerrak at the single population scale
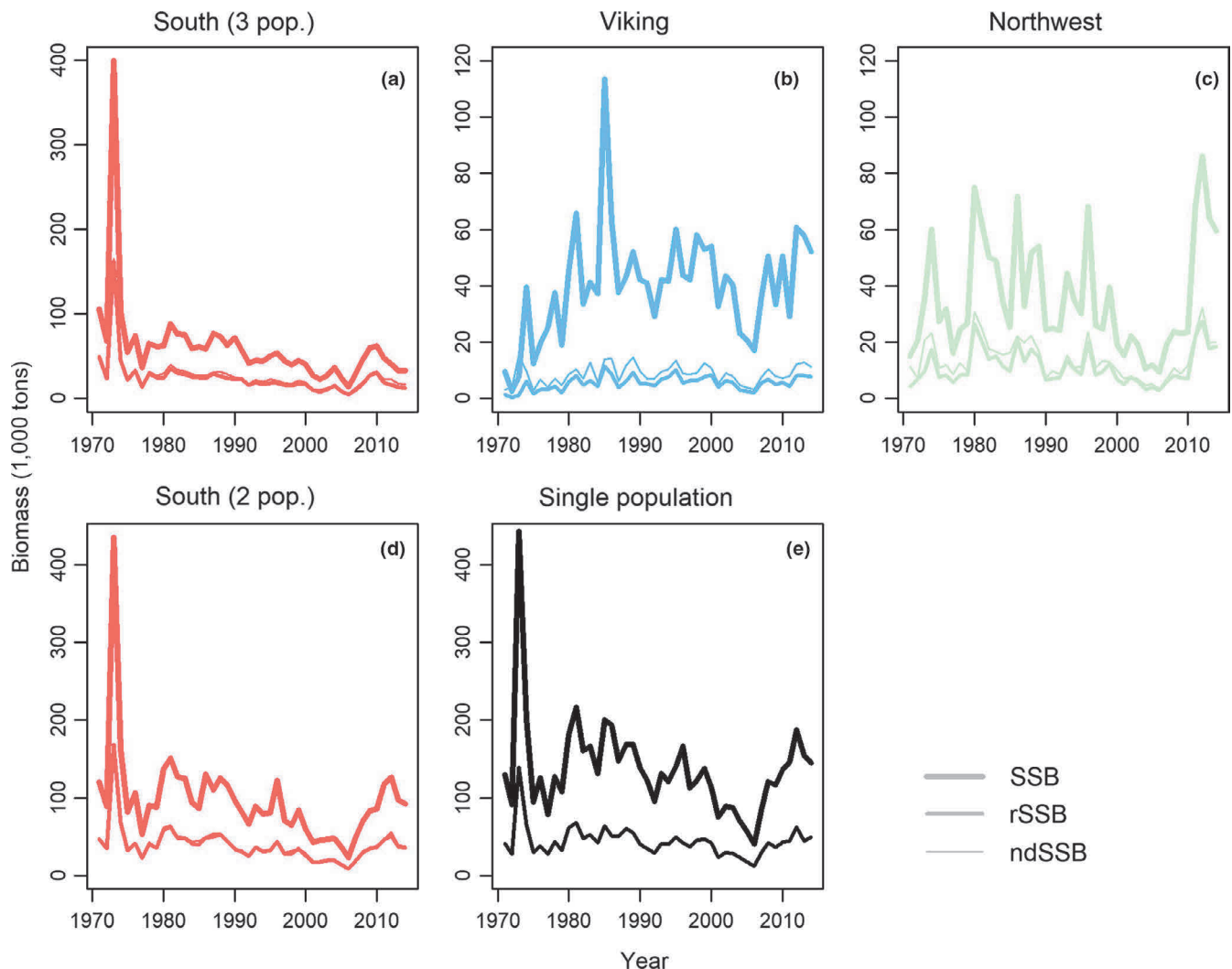


**FIGURE 4** Interannual variation in SSB, rSSB and ndSSB (thick, medium and thin lines, respectively) across populations for the three, two and single population cases. Note that rSSB and ndSSB are close, but not identical, for the South population. For the single population case, ndSSB is not calculated
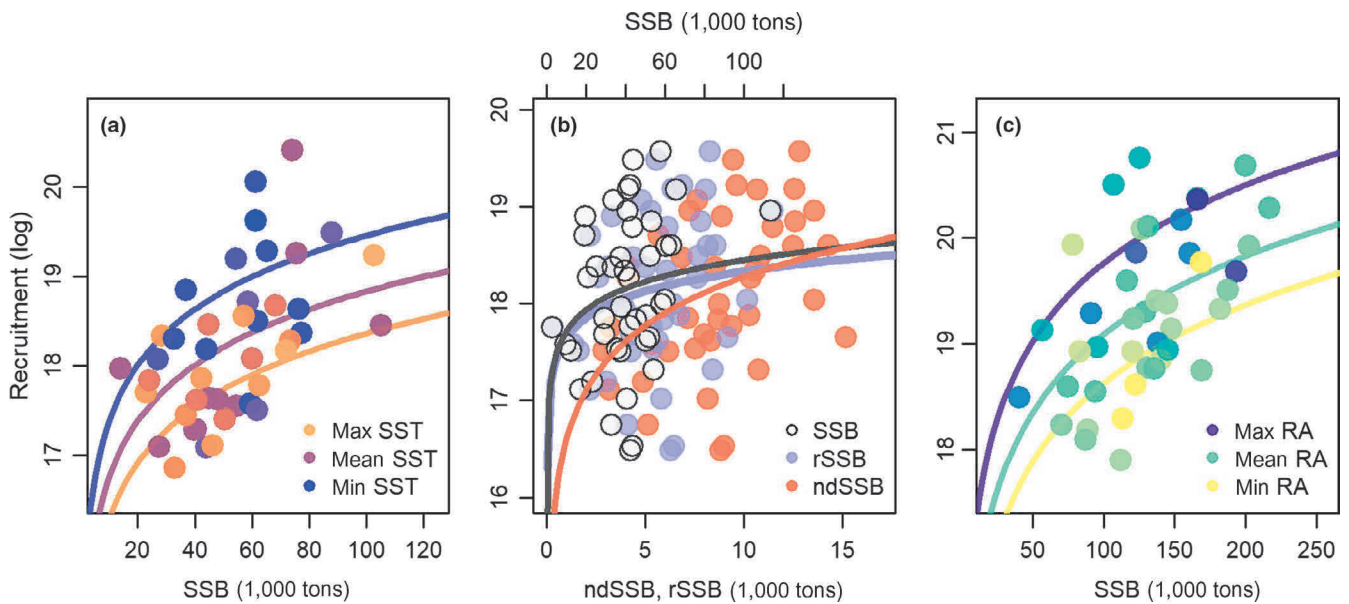
**FIGURE 5** Effects of inclusion of covariates and alternative SSB predictors across populations, spatial scale and predictor variables. Data (dots) and predicted stock–recruitment relationships (lines) for the following: (a) inclusion of SST as covariate (model 2) for the South unit at the three populations scale; (b) three alternative predictor variables with no covariates (models 1, 5, 8) for the Viking unit at the three populations scale; and (c) inclusion of retention anomaly (model 4) in the single population case. In (a) and (c), dots colour scale indicates the covariate anomaly, line colour indicates the model prediction at corresponding maximum, mean and minimum value of the covariate. In (b), SSB scaled by $10^{-1}$ (open dots, dark grey line) is compared to rSSB (purple dots and line) and ndSSB (orange dots and line)

**FIGURE 6** Contribution (retention and proportion of larvae drifted to other areas) from each of the three populations (South in red; Northwest in green; Viking in blue) and numbers of individuals not settled. (Drift to Kattegat is not shown as it was always close to 0). "Not settling" includes larvae that reach settlement length outside of nursery areas, and "outside" includes particles drifting out of the study area (see Figure 1)
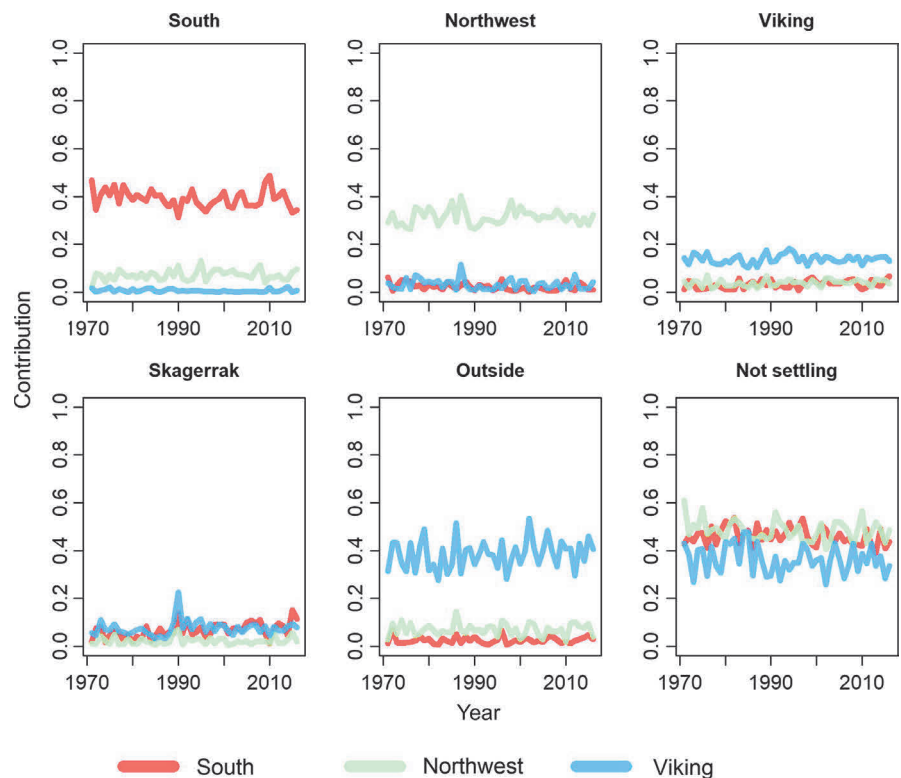


and with drift to the Skagerrak and to the Viking unit from all populations at two and three population scales. SST is negatively correlated with drift from Viking to South populations (at two populations scale) and with retention in South population (also at two populations scale). A high NAO phase corresponds to reduced drift from the Viking to the South populations, reduced retention in the South population at the two populations scale, reduced drift from Viking to Northwest populations and reduced retention in the Northwest population at the three populations scale. The number of individuals not settling in the Viking population is associated

**TABLE 4** Pearson correlation coefficients between indices of drift, climate and year

| | Source | Sink | Years | NAO | SST South | SST Viking | SST Northwest |
|---|---|---|---|---|---|---|---|
| 3 populations | South | South | | | | | |
| | | Northwest | −0.4 ** | | | | |
| | | Viking | 0.42 ** | | 0.43 ** | | 0.43 ** |
| | | Skagerrak | 0.48 *** | | 0.43 ** | 0.37 * | 0.42 ** |
| | | Outside | | | | | |
| | | Not settling | | | | | −0.33 * |
| | Viking | South | | | | | |
| | | Northwest | | −0.42 ** | −0.39 ** | −0.46 ** | −0.33 * |
| | | Viking | | 0.37 * | 0.38 ** | 0.39 ** | |
| | | Skagerrak | | 0.32 * | 0.46 ** | 0.44 ** | 0.33 * |
| | | Outside | | 0.39 ** | | | |
| | | Not settling | | −0.52 *** | −0.29 * | −0.4 ** | |
| | Northwest | South | | | | | |
| | | Northwest | | −0.37 * | −0.3 * | −0.43 ** | |
| | | Viking | | 0.34 * | | 0.3 * | |
| | | Skagerrak | | 0.45 ** | 0.33 * | 0.41 ** | |
| | | Outside | | 0.31 * | | | |
| | | Not settling | | | | | |
| 2 populations | South | South | | −0.48 *** | −0.32 * | −0.53 *** | |
| | | Viking | 0.44 ** | 0.33 * | 0.4 ** | 0.41 ** | |
| | | Skagerrak | 0.39 ** | 0.37 * | 0.48 *** | 0.44 ** | |
| | | Outside | | 0.3 * | | | |
| | | Not settling | −0.37 * | | | | |
| | Viking | South | | −0.44 ** | −0.32 * | −0.45 ** | |
| | | Viking | | 0.37 * | 0.33 * | 0.39 ** | |
| | | Skagerrak | | 0.32 * | 0.45 ** | 0.44 ** | |
| | | Outside | | 0.39 ** | | | |
| | | Not settling | | −0.52 *** | | −0.4 ** | |
| Single population | North Sea | North Sea | | −0.31 * | | | |
| | | Skagerrak | | 0.38 ** | 0.5 *** | | |
| | | Outside | | 0.36 * | | | |
| | | Not settling | | −0.46 ** | | | |

*Note:* "Not settling" represents the proportion of particles that do not reach settlement size within a nursery area and are lost.
Positive correlations are represented in light grey, negative correlation in dark grey.
Asterisks indicate the significance level (***<0.001<**<0.01<*<0.05).
White cells indicate non-significant values at the 0.05 level.

with high NAO. A high NAO is also positively correlated with high drift into the Skagerrak and outside the study area for all populations scales except the South population at the three populations scale.

## 4 | DISCUSSION

In this study, we combined long-term observational data with modelled estimates of larval transport to quantitatively assess the effect of transport on recruitment across spatial scales of observation, and we propose a novel approach for measuring effective biomass contributing to recruitment. While the effect of transport on recruitment has previously been explored using coupled biological-oceanographic models (e.g. Daewel et al., 2015;Hinrichsen et al., 2016), direct inclusion of ELS dispersal model output in stock–recruitment models is less common (but see Hidalgo et al., 2019). Some studies have used proxies for larval transport such as wind speed (e.g. Hare et al., 2015;Köster et al., 2003), water circulation indices (Zimmermann et al., 2019) or cumulative average depth of

modelled particles (Baumann et al., 2006). We instead incorporate estimates of the proportion of cod larvae retained within a population and the influx of larvae from neighbouring populations, that is a more direct proxy for the effect of larval transport (Hidalgo et al., 2019), and apply this approach to the North Sea cod.

Our results suggest that although larval drift appears to play a minor role in the recruitment dynamics of North Sea cod, the effect is comparable in magnitude to the well-established effect of SST on cod recruitment (Beaugrand & Kirby, 2010;Nicolas et al., 2014). Similarly, Daewel et al. (2015) found that although correlations between modelled larval survival and observed recruitment of North Sea cod were variable and periodically low, effects of transport processes and temperature on larval survival were of comparable importance. Comparing different model formulations and population scales, our analysis captures the interplay between oceanographic drift and temperature on recruitment patterns across spatial scales of observation (Figure 7). Specifically, the importance of considering larval drift depends on the spatial scale of analyses. At the population scale, larval transport between populations and larval loss due to transport affect the recruitment in Viking and Northwest populations. When aggregating all populations at the basin scale these effects are diluted, but not dissipated, and are captured through the retention anomaly (Figure 7).

## 4.1 | Effective biomass

Estimating effective biomass is a novel approach to account for larval transport compared to using SSB with additive covariates. In traditional stock–recruitment models, a covariate allows higher (lower) asymptotic value, that is higher (lower) expected recruitment at a given SSB value, while maintaining the shape of the curve (Figure 5a, c). Incorporating retention anomaly as a covariate, the interpretation is that a positive anomaly (higher than usual retention) results in higher level of recruitment compared to the same level of SSB with a lower drift anomaly. Subbey et al. (2014) point out that model forms with environmental covariates are generally linear approximations of non-linear environmental effects, approximations that might be unreliable or inaccurate. In our case, the linear approximation at the single population scale captures an overall effect that encompasses multiple mechanisms operating at finer scale. Conversely, the inclusion of drift as effective biomass allows estimating the contributing biomass to an observed recruit value and re-designing the curve altogether (Figure 5b), permitting higher flexibility to data compared to the traditional SSB.

Spawning stock biomass is a suboptimal variable for predicting recruitment, since it does not capture biological aspects such as age and size structure, sex ratio, total egg production, skipped spawning or interannual variability in fecundity or condition (Köster et al., 2003; Marshall et al., 2003; Marshall, Needle, Thorsen, Kjesbu, & Yaragina, 2006; Marteinsdottir & Begg, 2002; Mintevera et al., 2019). Marshall et al. (2006) and Köster et al. (2003) show that female-only spawner biomass and predicted potential egg production are better predictors of realised egg production than SSB in Northeast Arctic and Baltic cod stocks. Similarly, our study shows that effective SSB might be a better predictor at population scale for some populations, such as the Viking unit, characterised by large drift to other areas and low retention rate. A similar result was observed by Hidalgo et al. (2019) who found that retention influenced recruitment in European Hake populations characterised by high drift to and from other areas in the northwest Mediterranean.
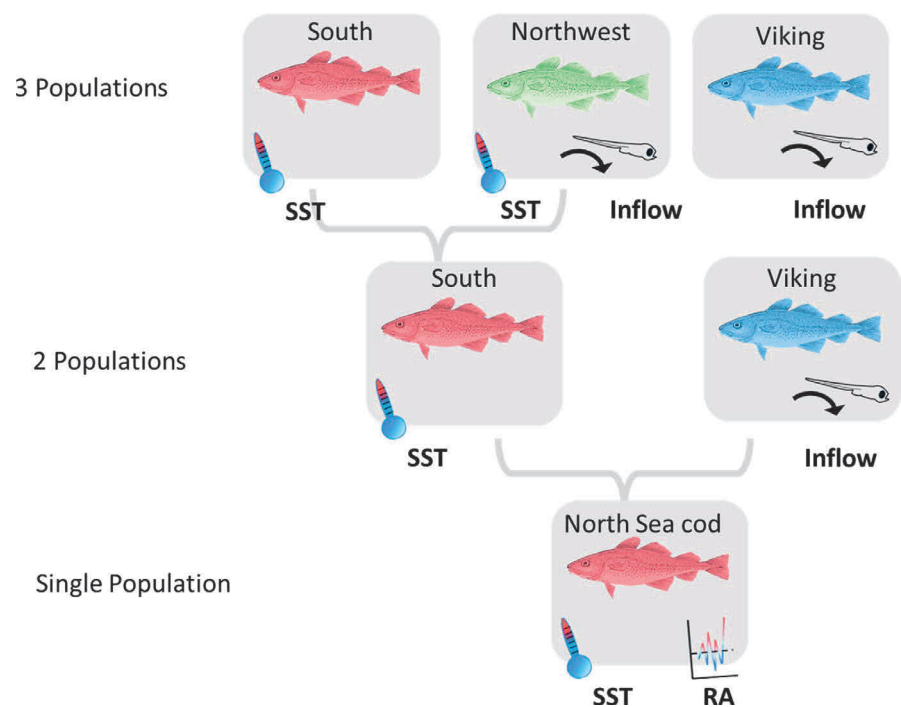


FIGURE 7 Graphical scheme summarising the key factors influencing recruitment of the different populations across spatial scales: sea surface temperature (SST), larval inflow (through connectivity with other populations) and retention anomaly (RA)

## 4.2 | Effects of drift and climate variables on recruitment

We investigated the emergent relationships between climate variables (SST and NAO), connectivity and retention metrics and recruitment. High SST can influence recruitment through faster development and thus increased retention and survival to settlement (Heath, Kunzlik, Gallego, Holmes, & Wright, 2008). Additionally, both SST and NAO could be proxies for other phenomena acting at local scales, such as food availability (Capuzzo et al., 2018;Nicolas et al., 2014) and flow regimes (Henriksen et al., 2018). NAO and SST can furthermore be correlated to connectivity and retention (Table 4). However, these relationships do not necessarily affect recruitment dynamics. For example, NAO is correlated with retention and connectivity across populations and scales, but including NAO as a covariate in the stock–recruitment model does generally not improve model fit (Table 3). NAO as a proxy thus captures the phenomena influencing circulation patterns, but not those affecting actual survival to recruitment.

Sea surface temperature interacts with each population in different ways. For the South population, increased SST is correlated with increased outflow to the Viking and Skagerrak populations; however, accounting for drift does not improve the stock–recruitment model fit. This might be due to the limited outflow and high retention in the South population. The observed effect of SST on recruitment could therefore be due to other mechanisms: for example food availability (Nicolas et al., 2014), physiological constraints (Butzin & Pörtner, 2016;Nunez-Riboni, Taylor, Kempf, Pu, & Mathis, 2019) and predation by warm-water predators (Akimova, Hufnagl, et al., 2016). For the Viking population, our results suggest that SST could influence recruitment through drift both positively and negatively. In fact, higher SST is associated with increased retention and inflow, but also increased outflow to Skagerrak. At present, the two effects seem to counterbalance each other: SST does not influence recruitment according to our model results. However, with increasing SST this equilibrium, which currently masks the underlying relationships, might break down with unforeseeable outcomes in terms of magnitude and direction. Recruitment in the Northwest population is negatively associated with increased SST via reduced drift from the Viking population. The effects of both SST and inflow on recruitment are strong but not additive (indicated by similar fit of model 2 and of model 8 and 9), and likely reflect the same phenomenon: increasing temperature corresponds to decreasing inflow, resulting in lower recruitment for the Northwest population.

For the South population, the importance of SST for recruitment and its correlation with drift patterns are similar in the three- and two population scales, indicating that effects of SST (but not of NAO) on the dynamics of retention, connectivity and recruitment are dominated by the South component in the combined unit. At the single population scale, the association between SST and drift is reduced: SST is correlated with flow into the Skagerrak but not with retention. At this scale, however, recruitment is affected by SST and, importantly, by drift. Here the retention anomaly (model 4), but

not rSSB, improves the stock–recruitment model fit. The two models involve the same variable (retention), but differing mechanisms, as described in the section "Effective biomass" above.

Overall, our results indicate that the key mechanisms affecting recruitment (summarised in Figure 7) include: SST in the South population through processes unrelated to larval transport, SST and transport through the same underlying phenomenon in the Northwest population, with inflow from the Viking population and retention being higher in low SST years, and inflow from other populations into the Viking population (Figure 5b; Table 3).

## 4.3 | Drift patterns, retention and population connectivity

The retention and connectivity patterns estimated here broadly reflect known patterns for the area. The southern North Sea is characterised by a generally retentive system (Henriksen et al., 2018), while in the northern area there is a strong flow to the Skagerrak and the Norwegian Sea (Huserbråten et al., 2018). Consequently, the South and North populations are generally isolated, with limited connectivity (Heath et al., 2008). According to our results, connectivity between the Northwest and South units is higher, but declined from the 1970s to present, while connectivity between South and Viking units increased.

Drifting into a suitable nursery area, however, is not enough for granting survival to recruitment, as density dependence and predation after settlement might influence successful recruitment into the new populations (Akimova, Hufnagl, et al., 2016;Heath et al., 2014). Some studies discriminate potential connectivity (estimated from modelled particle drift) from effective connectivity using genetic methods (e.g. Bode et al., 2019;Jahnke et al., 2017). In our study, effective connectivity is an emerging result of fitting stock–recruitment models to data after inclusion of drift anomaly. Our results highlight that effective connectivity only affects the Viking and Northwest populations.

Notably, we assess how larval drift influences recruitment, irrespective of whether individuals merge with the host population or return to the natal population after being accounted as recruits. For example, our results indicate that larvae from the South unit enter the Viking area and survive until being accounted as recruitment of the Viking population (shown by higher fit with ndSSB than rSSB or SSB). However, the Viking and South units show genetic differences, generally considered incompatible with interbreeding between populations (Heath et al., 2014). We therefore speculate that juveniles from the South unit settle in the Viking area and survive until age 1, to then return to the population of origin. This mechanism, known as homing behaviour and site fidelity, is known for cod in the North Sea (Neat et al., 2014) and between the North Sea and Skagerrak (André et al., 2016;Jonsson, Corell, André, Svedäng, & Moksnes, 2016), and is suggested for larvae drifting from the Norwegian Trench (within our Viking area) to the Norwegian Sea (Huserbråten et al., 2018).

Although drift between the North Sea and Skagerrak is well known (Jonsson et al., 2016), we show here for the first time, to our knowledge, that larval drift from the Viking and South units into the Skagerrak is potentially of the same order of magnitude, showing an increasing trend in time and positive correlation with SST (Table 4). Although the effective contribution cannot be determined in this study, trends in larval influx from the North Sea might have implications for management and recovery of cod in offshore and coastal areas of the Skagerrak.

Our results are influenced by the assumptions and simplifications of the ELS dispersal model. However, in a previous study, Kvile et al. (2018) showed that the present model configuration yields comparable results to a more realistic but computationally costly alternative. Specifically, both the inclusion of vertical swimming behaviour and the use of a higher resolution ocean model that resolves tidal circulation had limited effects on larval drift patterns compared to interannual variations in ocean dynamics. Since our aim here was to quantify long-term interannual variation in population connectivity, we opted for a less computationally costly representation of vertical movement using fixed drift depths, and applied the coarser ocean model that was available for 44 years. Additionally, sensitivity analyses of the parameterisation of ELS mortality and settlement size, the latter related to temperature-dependent growth, confirmed the robustness of the results to these key parameters (Tables A2 and A3 in the Appendix S1). Finally, factors such as spatially explicit predation pressure and prey fields, variability in fecundity, juvenile mortality through predation and density dependence upon settlement might all affect recruitment dynamics, but are not accounted for in this study. These caveats need to be considered in the interpretation of results.

## 4.4 | Implications for management

Despite the relatively low prediction power and major assumptions (Subbey et al., 2014), stock–recruitment models are routinely applied in management for short-term advice (e.g. Punt, 2019), and there is increasing interest in including spatial structure in recruitment dynamics in stock assessment (Cadrin et al., 2019;Hidalgo et al., 2019;Punt, 2019). Although reliable ocean current forecasts are not available in advance, estimates of larval drift can be useful to inform short-term forecasts (Henriksen et al., 2018;Hidalgo et al., 2019). This effort is however constrained by the availability and rapid applicability of ocean models in the context of operational fisheries oceanography (Hidalgo et al., 2019).

We find relatively low fit to data in the stock–recruitment models for North Sea cod, and inclusion of indices for larval drift results in relatively small improvements. Considering the computational cost of running ELS dispersal models, one must therefore carefully consider the benefits of this approach for the specific case at hand. Regardless, our study highlights a novel approach for accounting for connectivity in stock–recruitment dynamics, with potential applications for fisheries assessment and management in stocks characterised by highly dynamic oceanographic conditions. Adopting spawning output metrics that account for effective connectivity, for example, could affect the determination of biological reference points (Minte-vera et al., 2019), with direct implications for management. For example, relationships between drift, temperature and recruitment across populations (Figure 7) have implications for management of the North Sea cod population complex in the context of a changing climate (Nunez-Riboni et al., 2019).

Future research should focus on how climate change can influence larval transport, survival of larvae drifting between units and homing behaviour. Understanding these aspects, and developing operational fisheries oceanography and its application to management, will improve our capacity to tailor management to the population structure in the context of a changing climate.

## CONFLICT OF INTERESTS
The authors declare to have no conflict of interest.

## AUTHOR CONTRIBUTIONS
GR, KK, ØL and AME conceived the research idea; GR and KK ran data analyses and wrote the manuscript; KFD, TK, ØL, AME and NCS participated in discussions of the results and critically reviewed the manuscript.

## DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Influence of larval transport and temperature on recruitment dynamics of North Sea cod (*Gadus morhua*) across spatial scales of observation

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**Appendix S1: Linearised stock-recruitment functions**

The corresponding linear formulas to the Cushing stock-recruitment model (Akimova *et al.*, 2016) is:

$$Log(R) = Log(\alpha) + \gamma Log(SSB)$$

and

$$Log(R) = Log(\alpha) + \gamma Log(SSB) + Log(SSB) \times \theta E$$

Subbey *et al.* (2014) point to the need to correct recruitment for the bias introduced by log-transforming the recruitment. Sensitivity test (table A1) shows that the results when such correction is included differ minimally from the non-corrected recruitment, thus for the main analysis the dataset was not corrected for the bias.

| | Predictor | Covariate | South adjR2 | South Pval | Viking adjR2 | Viking Pval | Northwest adjR2 | Northwest Pval |
|---|---|---|---|---|---|---|---|---|
| 1 | SSB | None | 0.22 | 0.001 | 0.04 | 0.106 | 0.23 | 0.001 |
| 2 | SSB | SST | 0.31 | 0.001 | 0.03 | 0.233 | 0.35 | 0.000 |
| 3 | SSB | NAO | 0.20 | 0.008 | 0.05 | 0.171 | 0.19 | 0.011 |
| 4 | SSB | RA | 0.22 | 0.005 | -0.01 | 0.445 | 0.19 | 0.009 |
| 5 | ndSSB | None | 0.18 | 0.003 | 0.11 | 0.016 | 0.27 | 0.000 |
| 6 | ndSSB | SST | 0.27 | 0.001 | 0.15 | 0.027 | 0.34 | 0.000 |
| 7 | ndSSB | NAO | 0.19 | 0.010 | 0.09 | 0.090 | 0.25 | 0.003 |
| 8 | rSSB | None | 0.21 | 0.001 | 0.03 | 0.121 | 0.22 | 0.001 |
| 9 | rSSB | SST | 0.29 | 0.001 | 0.05 | 0.185 | 0.33 | 0.000 |
| 10 | rSSB | NAO | 0.23 | 0.005 | 0.04 | 0.218 | 0.18 | 0.012 |

| | Predictor | Covariate | South adjR2 | South Pval | Viking adjR2 | Viking Pval |
|---|---|---|---|---|---|---|
| 1 | SSB | None | 0.26 | 0.000 | 0.04 | 0.106 |
| 2 | SSB | SST | 0.36 | 0.000 | 0.03 | 0.233 |
| 3 | SSB | NAO | 0.24 | 0.003 | 0.05 | 0.171 |
| 4 | SSB | RA | 0.24 | 0.004 | -0.01 | 0.445 |
| 5 | ndSSB | None | 0.25 | 0.000 | 0.13 | 0.010 |
| 6 | ndSSB | SST | 0.33 | 0.000 | 0.17 | 0.018 |
| 7 | ndSSB | NAO | 0.23 | 0.004 | 0.10 | 0.068 |
| 8 | rSSB | None | 0.25 | 0.000 | 0.03 | 0.121 |
| 9 | rSSB | SST | 0.34 | 0.000 | 0.05 | 0.185 |
| 10 | rSSB | NAO | 0.24 | 0.003 | 0.04 | 0.218 |

| | Predictor | Covariate | South adjR2 | South Pval |
|---|---|---|---|---|
| 1 | SSB | None | 0.24 | 0.001 |
| 2 | SSB | SST | 0.28 | 0.001 |
| 3 | SSB | NAO | 0.22 | 0.005 |
| 4 | SSB | RA | 0.32 | 0.000 |
| 5 | ndSSB | None | - | - |
| 6 | ndSSB | SST | - | - |
| 7 | ndSSB | NAO | - | - |
| 8 | rSSB | None | 0.16 | 0.005 |
| 9 | rSSB | SST | 0.21 | 0.007 |
| 10 | rSSB | NAO | 0.14 | 0.029 |

*Table A1. Values of Adjusted $R^2$ and respective P-values including correction from the bias introduced by log-transformation of the recruitment data (see Table 2 in main text) for each model and population across the three cases of population scale. Darker shades of grey indicate higher Adjusted $R^2$ (higher model fit and better model performance). For single population ndSSB is not calculated.*

| | 20% decrease | | default | | 20% increase | |
|---|---|---|---|---|---|---|
| **South** | | | | | | |
| | **1990** | **2010** | **1990** | **2010** | **1990** | **2010** |
| South | 0.30 | 0.49 | 0.31 | 0.49 | 0.32 | 0.48 |
| NW | 0.01 | 0.06 | 0.01 | 0.05 | 0.01 | 0.04 |
| Viking | 0.06 | 0.01 | 0.05 | 0.01 | 0.05 | 0.01 |
| Skagerrak | 0.16 | 0.02 | 0.14 | 0.01 | 0.12 | 0.01 |
| Outside | 0.04 | 0.02 | 0.04 | 0.02 | 0.03 | 0.02 |
| Not settling | 0.43 | 0.40 | 0.45 | 0.42 | 0.47 | 0.44 |
| **Viking** | | | | | | |
| | **1990** | **2010** | **1990** | **2010** | **1990** | **2010** |
| South | 0.00 | 0.02 | 0.00 | 0.02 | 0.00 | 0.02 |
| NW | 0.01 | 0.03 | 0.01 | 0.03 | 0.01 | 0.03 |
| Viking | 0.12 | 0.11 | 0.13 | 0.11 | 0.13 | 0.11 |
| Skagerrak | 0.22 | 0.05 | 0.23 | 0.04 | 0.23 | 0.04 |
| Outside | 0.37 | 0.43 | 0.34 | 0.41 | 0.32 | 0.38 |
| Not settling | 0.27 | 0.36 | 0.29 | 0.39 | 0.31 | 0.41 |
| **Northwest** | | | | | | |
| | **1990** | **2010** | **1990** | **2010** | **1990** | **2010** |
| South | 0.11 | 0.06 | 0.11 | 0.06 | 0.11 | 0.07 |
| NW | 0.27 | 0.30 | 0.27 | 0.30 | 0.26 | 0.30 |
| Viking | 0.03 | 0.04 | 0.03 | 0.04 | 0.03 | 0.04 |
| Skagerrak | 0.07 | 0.01 | 0.07 | 0.01 | 0.07 | 0.01 |
| Outside | 0.06 | 0.02 | 0.06 | 0.02 | 0.06 | 0.02 |
| Not settling | 0.44 | 0.57 | 0.46 | 0.57 | 0.47 | 0.57 |

*Table A2. Sensitivity of connectivity to setting of mortality parameter. Connectivity at settlement for the three populations for two years with contrasting oceanographic patterns for default value and +/-20%*

| | South | | | | | |
|---|---|---|---|---|---|---|
| | 20% decrease | | default | | 20% increase | |
| | 1990 | 2010 | 1990 | 2010 | 1990 | 2010 |
| South | 0.34 | 0.47 | 0.31 | 0.49 | 0.32 | 0.47 |
| NW | 0.00 | 0.06 | 0.01 | 0.05 | 0.01 | 0.05 |
| Viking | 0.04 | 0.01 | 0.05 | 0.01 | 0.06 | 0.01 |
| Skagerrak | 0.13 | 0.01 | 0.14 | 0.01 | 0.13 | 0.01 |
| Outside | 0.03 | 0.02 | 0.04 | 0.02 | 0.05 | 0.02 |
| Not settling | 0.45 | 0.43 | 0.45 | 0.42 | 0.43 | 0.44 |

| | Viking | | | | | |
|---|---|---|---|---|---|---|
| | 20% decrease | | default | | 20% increase | |
| | 1990 | 2010 | 1990 | 2010 | 1990 | 2010 |
| South | 0.00 | 0.02 | 0.00 | 0.02 | 0.00 | 0.02 |
| NW | 0.01 | 0.03 | 0.01 | 0.03 | 0.01 | 0.03 |
| Viking | 0.10 | 0.12 | 0.13 | 0.11 | 0.13 | 0.11 |
| Skagerrak | 0.22 | 0.04 | 0.23 | 0.04 | 0.23 | 0.05 |
| Outside | 0.33 | 0.37 | 0.34 | 0.41 | 0.36 | 0.43 |
| Not settling | 0.34 | 0.42 | 0.29 | 0.39 | 0.27 | 0.37 |

| | Northwest | | | | | |
|---|---|---|---|---|---|---|
| | 20% decrease | | default | | 20% increase | |
| | 1990 | 2010 | 1990 | 2010 | 1990 | 2010 |
| South | 0.12 | 0.04 | 0.11 | 0.06 | 0.12 | 0.07 |
| NW | 0.27 | 0.31 | 0.27 | 0.30 | 0.27 | 0.30 |
| Viking | 0.02 | 0.03 | 0.03 | 0.04 | 0.04 | 0.05 |
| Skagerrak | 0.07 | 0.01 | 0.07 | 0.01 | 0.08 | 0.02 |
| Outside | 0.06 | 0.02 | 0.06 | 0.02 | 0.07 | 0.02 |
| Not settling | 0.45 | 0.59 | 0.46 | 0.57 | 0.43 | 0.53 |

*Table A3. Sensitivity of connectivity to setting of settlement size parameter. Connectivity at settlement for the three populations for two years with contrasting oceanographic patterns for default value and +/- 20%*

**References:**

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Subbey, S., Devine, J. A., Schaarschmidt, U., and Nash, R. D. M. 2014. Modelling and forecasting stock–recruitment: current and future perspectives. ICES Journal of Marine Science, 71: 2307–2322.

# Paper IV

*"…E quindi uscimmo a riveder le stelle."*

*Dante, Inferno XXXIV, 139*