North Sea resource distribution and fishery opportunities (NORDFO)

Francois Bastardie, Marie-Christine Rufener, Sieme Bossier, Kirsten B. Håkansson, Asbjørn Christensen, Kasper Kristensen and J. Rasmus Nielsen

North Sea resource distribution and fishery opportunities (NORDFO)

François Bastardie, Marie-Christine Rufener, Sieme Bossier,
Kirsten B. Håkansson, Asbjørn Christensen, Kasper Kristensen
and J. Rasmus Nielsen

DTU Aqua Report no. 402-2022

HAV & FISK

Colophon

Contents

Dansk resumé

Denne undersøgelse viser, at det økonomiske udbytte i dansk fiskeri i Nordsøen risikerer at blive udfordret af klimadrevne forandringer, som påvirker fiskebestandene. Fiskene kan f.eks. vandre til andre områder, som det sker med Nordsø-torsken.

Projektet har udviklet en ny metode til at forbedre forskernes mulighed for at forudsige udviklingen i indbyrdes forbundne fiskebestande og fiskerier under skiftende miljø- og fiskerimæssige forhold. Metoden integrerer data fra det kommercielle fiskeri med uafhængige data fra forsknings-surveys til at beskrive, hvor fiskene er og i hvilke mængder, samt til at udpege områder med særligt mange fisk ("hotspots").

På dette grundlag har projektgruppen evalueret ændringer i fiskebestandenes geografiske udbredelsesmønstre over tid og analyseret, hvor konstante hotspot-områderne er. Undersøgelsen omfatter perioden 2001-2020 og de vigtigste kommercielle fiskebestande i Nordsøen, herunder torsk, ising sej, kuller, atlantisk makrel, rødspætte, tunge, hvilling, brisling og sild.

Projektgruppen har indarbejdet disse oplysninger i en højtopløselig fiskeridynamisk model, der integrerer en avanceret individuel fartøjsbaseret model til benchmarking af fiskerimuligheder. Dette omfatter scenarier begrænset af bestandenes økologiske bæredygtighed og vurdering af den økonomiske levedygtighed og rentabiliteten i fiskeriets udnyttelse af marine levende ressourcer i Nordsøen.

Resultaterne viser, at hotspot-områderne, hvor der er særlig stor tæthed af fisk, var ret stabile i Nordsøen i perioden 2001-2020 for alle de undersøgte kommercielle bestande i Nordsøen, bortset fra for torsken, der viste en markant forskydning østpå. Nordsøtorsken har således bevæget sig længere væk fra den danske kystlinje, men dog uden at det påvirker andelen af bestanden, der er i Storbritanniens eksklusive økonomiske zone (EEZ).

Det er tydeligt, at varierende fordelinger af fisk og manglende viden om vigtige faktorer, der påvirker forekomsten af fisk, kan reducere tilgængeligheden af bestandene for fiskerne. Det kan påvirke rentabiliteten i fiskeriet og omfordele fiskeriets indkomster mellem flåder og nationer givet nationale og EU fiskerizoner. Desuden kan det øge misforholdet yderligere mellem fiskerimuligheder og tildelingsnøgler for EU-kvoter i henhold til den relative stabilitet i kvotefordelingen i EU's fælles fiskeripolitik (Common Fisheries Policy, CFP). Men fordi områderne er ret stabile, er andelen af bestandenes biomasse, der forekommer inden for den britiske EEZ, også fundet stabil.

Videnskabsbaserede tilgange til evaluering og forvaltningsrådgivning kan således hjælpe med at forudse sådanne fordelingseffekter. Dette er ved bedre at kunne forudsige, hvor der er hotspots med mange fisk, og identificere nøglefaktorer, der bestemmer mængden af fisk, og hvor de er, samt hvor fiskene sandsynligvis vil vandre hen, hovedsageligt på grund af påvirkninger forårsaget af klimaforandringer.

English summary

This study has shown that the incomes of Danish fisheries fishing in the North Sea are at risk facing the impact of climate-driven long-term trends when some of the exploited stocks are "on the move" i.e. changing their spatial distribution permanently, as the North Sea cod. The study developed a new methodological approach based on the previous modelling to strengthen our predictive power in anticipating interlinked stocks and fisheries developments under changing environmental conditions or extreme events that would also affect their productivity and spatial distributions.

The method developed a high-resolution integration of fisheries and research survey data to establish and boost the description of fish spatial distribution and abundance fields by combining fisheries and survey catch data. On this basis, we evaluated the changes in fish distribution patterns in time and space and the persistence of density hotspots over the period 2001-2019 for main commercial species, including North Sea cod, dab, saithe, haddock, Atlantic mackerel present in the North Sea, plaice, sole, whiting, sprat, and North Sea herring. We then integrated this information into a high-resolution fisheries dynamics model in a broader fisheries management evaluation framework. This framework integrates an advanced individual vessel-based fisheries model for benchmarking fishing opportunities and scenarios constrained by ecological sustainability and assessing the economic viability and profitability of the use of marine living resources in the North Sea.

We found that the hotspot areas where the main density of stocks distributed, for juveniles and adults fish, and driven by the environmental factors, were quite stable at the scale of the North Sea over the period 2001-2019, for all the examined commercial stocks, except for the North Sea cod that showed a marked movement westwards, making the stock more distant from the Danish coastline, but without affecting the proportion of the stock falling into the UK EEZ (a fraction of the stock that would fall within the UK fisheries legislation). It is apparent that varying fish distributions and lack of knowledge of important factors driving fish occurrence may reduce the accessibility of the stocks to the fishers. This can jeopardize the profitability of the exploitation, redistribute the fisheries incomes among fleets and nations, and further enlarge a mismatch between fishing opportunities and allocation keys for EU quotas according to the EU Common Fisheries Policy (CFP) relative stability of quota distribution. However, because the persistence areas are found quite stable, the proportion of the North Sea stock abundances falling within the UK EEZ is also found stable. Science-based approaches can help anticipate such (re)distributional effects by helping predict where the fish are and the hotspots, that is, where the high concentration of fish are, and identifying key factors determining fish occurrence and abundance, as well as where the fishes are likely to change their distribution areas, mainly from effects on stocks induced by the climate change.

One lesson learnt along the project was the current lack of knowledge to inform the fisheries modelling exercise properly with previous pieces of evidence. Although some aspects of the biology of most stocks were found to be linked to environmental factors, there was a lack of robust statistical models available to describe the likely species-specific linkages between individual biological features (growth, recruits, spatial distribution) and changing environmental conditions in the North Sea. Because of the lack of well-established relationships with environmental variables and climate in some case studies, ad hoc assumptions were made on the magnitude of the changes expected for the different environmental scenarios tested.

Another lesson learnt showed that it is challenging to organize a fine scale coupling between advanced statistical modelling of the spatial distribution of stocks and the dynamic fisheries modelling in the same platform provided the very high computer demand that such an inline, bi-directional coupling would require. Instead, the project implemented a one-way coupling where the fishing in the modelling has been influenced by the fish stock distribution but has not itself influenced the stock distribution. However, spatial distribution patterns may also be affected directly by fishery on different life stages, as well as indirectly by changing fish habitats, for example by altering the physical environment on the seafloor and their benthic community. Explicitly including factors that may influence the spatial and time distribution of the different stocks dynamically. Including these dynamics would then need additional investigations.

Notwithstanding the methodological and available knowledge limitation, the integrative platform and the North Sea application we developed in the project will likely enhance the knowledge on fish stocks dynamics and interlinkage with human (i.e. fisheries, climate change) and environmental factors. The tool is ready to anticipate the effects and stock levels, increasing economic efficiency in exploiting the marine resource on an explicit spatial and temporal scale within the EU CFP and EU Marine Strategy Framework Directive (MSFD) context and objectives. The platform is developed for evaluating the high-resolution social and economic distributional effects induced by the change in stock distribution and availability. The framework can further test how differently the current and new (CFP- or MSFD-related) measures could affect the catches, incomes, fuel consumption and environmental footprint of various fisheries and fishing communities at play.

Catches made by the Danish fleets in North Sea cod distribute over different habitat types. There are likely habitats that will be affected from a displacement of the fishing effort in response to new environmental conditions. Even though extensive spatial scenarios are not tested per fishery the spatial component is accounted for implicitly by locating the abundance hot spots and movements of those stocks in a 20 year period when that is the case (cod). As the hotspots (against expectations) for most species have been rather constant, then it has also limited the possibilities for evaluating effort-re-allocation scenarios. The cod case study has been picked out for further analysis of scenarios for re-allocation of effort - and potential changed pressure on the seafloor induced by the re-allocation in the fishery.

1. Introduction

The purpose of the project was to improve management of valuable Danish fishery resources in the North Sea by describing large and fine-scale spatial, seasonal and annual variation determining the fishing opportunities and caused by physical-biological environmental factors (e.g. temperature) affecting the abundance of certain favorable conditions, stock productivity (growth, recruits) and fisheries dynamics.

This project has evaluated long-term trends and changes in geographical distribution and small scale, short-term spatiotemporal variability in fish stock abundance patterns by applying an advanced statistical modelling framework. This covered 1) high-resolution integration of combined fisheries and research survey data; 2) estimating the predictive effects of high-resolution environmental factors including hydrographical, physical habitats and biological benthic community data; 3) integrating with high-resolution fisheries dynamics in a broader fisheries management evaluation framework for benchmarking fishing opportunities and scenarios constrained by ecological sustainable and economic efficient use of marine living resources. The project has further examined if the spatial distribution could have changed over the 20y period by assessing the centre of gravity of each species distribution and questioning if the core of this distribution has moved toward or within the UK zone now having different fisheries legislation (e.g. technical measures) than the one enforced in EU Waters.

Taking the estimated changes in resource distribution into consideration, the project built upon the knowledge and existing tools developed during previous projects such as EMFF MSP-TOOLS (Nielsen et al. 2019), EU COFASP ECOAST (e.g., Grati et al. 2017) and EU-FP7 BEN-THIS (e.g., Eigaard et al. 2017) to apply specifically to North Sea fisheries and management and support the implementation of a sustainable EU CFP and a sustainable blue economy strategy in North Sea waters. The evaluation framework and the North Sea implementation directly support the implementation of the EU CFP by measuring the past and current natural and fishing pressures on important Danish fisheries resources and on by-catch stocks, as well as on the different EU Marine Strategy Framework Directive (MSFD) relevant benthic habitats.

The project integrates knowledge and dynamics on key factors determining and regulating the abundance and distribution of many important fish stocks in the North Sea ecosystem, and the implications for change in fisheries economic incomes of both offshore and coastal fisheries. We have here improved the coherence in a shared framework for analyzing how data and methods are applied with outcomes presented to a closing workshop.

The project outcome is a methodological and assessment extended and a refined framework applying spatial approaches to fisheries management. It frames fisheries bio-economic assessment methods and integrated data analysis contributing to Technical University of Denmark's (DTU Aqua) strong interdisciplinary and international networks for ensuring an effective implementation to the EU Common Fishery Policy (CFP) and Marine Strategy Framework Directive (MSFD) policy, as well as maritime spatial planning in context of fishery (EU Maritime Spatial Planning Directive, MSPD). Hence, applying the developed framework to the North Sea has been proven useful to investigate the part of the stock and life stages that could lie within the UK EEZ where the UK specific fisheries legislation is in force for non-EU and EU fleets to comply with, and to anticipate with a scenario testing the possible effects induced by a changing climate affecting the exploited stocks in the North Sea.

2. Compilation of fishery-dependent and independent data

Data from commercial fisheries (fishery-dependent) and research survey data (fishery-independent data) were retrieved for the greater North Sea spanning a 20-years period (2001-2019) (Fig. 1).
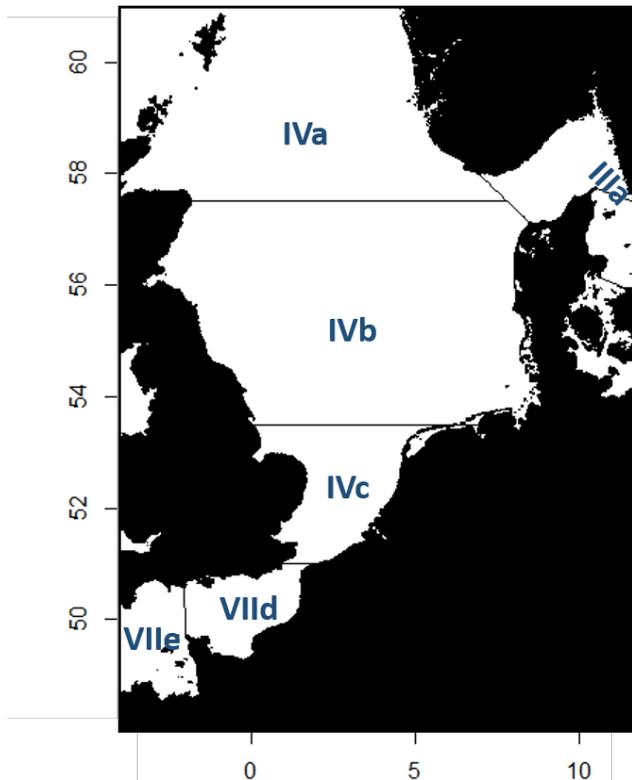
Figure 1. Map of the Greater North Sea highlighting the associated ICES statistical rectangles.

Fishery-dependent data

The fishery-dependent data comprised information from the Danish on-board observers' program, which was provided by the Danish National Institute of Aquatic Resources (DTU Aqua). This database includes information of the total catch (in numbers and weight) on a haul-by-haul basis, in addition to other relevant biological information such as individual fish weight, length and otoliths for age determination (Storr-Paulsen et al., 2012).

The original on-board observers' data (hereafter referred to as OBO data) did not contain information on the fishing gear used, which is an essential information to include in the LGNB model-SDM (Rufener et al. 2021). Thus, information on gear type, mesh size and targeted fish species and sizes (métier) had to be retrieved from the Danish Fisheries Analyses database (DFAD, hereafter referred to as DFADmet) (Fig. 2).

The OBO-DFADmet data coupling is conventionally undertaken through the logbook number, which is a common identifier between the two data sources. However, no logbook numbers were registered in the OBO data for the first ten years (2000-2010), and thus another common identifier had to be created in order to conduct the data coupling according to the LGNB-SDM

model (Rufener et al. 2021) for these set of years. Hence, to mimic the logbook number as close as possible, the vessel ID, year, month and landing date was used to create the new identifier. This identifier was then used to merge the OBO-DFADmet from 2000-2010, and subsequently the logbook number was used to merge the data sources from 2011-2019 (step 1 in Fig. 2).
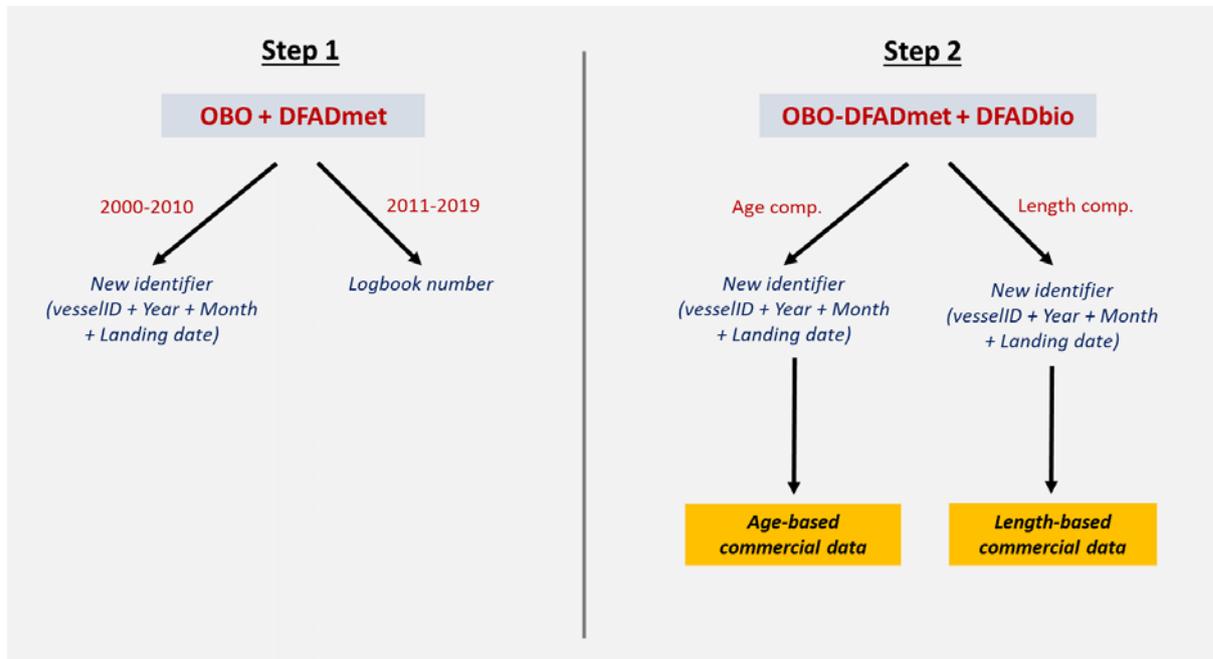
Figure 2. Process of retrieving the métier and biological (age and length composition) information from the DFAD database.

Once the OBO data were merged to the DFADmet data, we had to retrieve information on the age and length composition from the biological database within the DFAD (henceforth DFADbio; step 2 in Fig. 2). Given that several logbook numbers were missing in the DFADbio database, we conducted the data coupling through the previously created identifier. Once the databases were coupled, we had to correct the number of fish individuals for each length/age group for those trips containing more than one haul. In this case, we assumed that the numbers-at-age/length of each haul was proportional to the total catch of the trip.

Fishery-independent data

Fishery-independent data were retrieved from the ICES Database of Trawl Surveys (DATRAS), which is publicly available at http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx. This therefore included information from the International Bottom Trawl Survey (IBTS) and the Beam Trawl Survey (BTS). For the fisheries-dependent data, despite several observers data surveys across the North Sea are conducted in the study area by different countries, only those conducted by Denmark and Danish research vessels were made available for this study.

Both fisheries data and scientific survey catch databases provide information on a haul-by-haul level, whereby the age and length compositions were retrieved by means of the DATRAS R package (Kristensen and Berg, 2018).

Investigated fish species

A preliminary list of commercially important species/stocks from the greater North Sea was retrieved from the most recent reports of the Danish demersal Producer Organisation (DF, 2020) and the Danish statistical accounts (Danmarks Statistik) for Fishery and Aquaculture (DS, 2018). This list was further complemented with the species assessed by the ICES Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK; ICES, 2021).

Overall, the preliminary list comprised a total of 27 stocks spanning 23 species (Table 1). Nevertheless, availability of biological information (age/length composition) and appropriate data coverage for either fishery-dependent or –independent data sources were available for only 10 species (DFADbio database processed by Kirsten Birch Håkansson from DTU Aqua) out of the 23 anticipated (Table 1). Hence, the age and length composition of the landings are the usual missing data. There are length and age samplings during both harbour and at-sea sampling programs. For the port-sampling, there is usually sampling per size sorting category and the extrapolation to the whole catch is therefore much easier. However, for the at-sea sampling program, the sampling is conducted by gear group and is therefore more difficult to extrapolate. The at-sea sampling program also targets very specific vessels/gear groups (those with highest discard rates). Thus, there is for example no sampling for the gillnet fisheries.

Table 1. List of the commercially most important fish species in the greater North Sea, where species with available biological information for the LGNB-SDM model are indicated in bold. The fishery-independent data represents the set of research surveys that are used to assess each species according to the latest stock-specific ICES assessment reports. Species assessed with surveys other than IBTS and BTS were not considered for the analyses. OBO = on-board observers, IBTS = International Baltic Trawl Surveys, BTS = Beam trawl surveys, HERAS = Herring acoustic surveys, Less frequent surveys in NS are EVHOE, SNS, BTS, FGFS, PORC, IFGS, SAMISS, IAMS.

Family	Species	Stock	Fishery-independent data	Fishery-dependent data
Clupeidae	**Sprat (*Sprattus sprattus*)**	**4**	**IBTS, HERAS**	**OBO**
		3a	**IBTS, HERAS**	**OBO**
Gadidae	**Cod (*Gadus morhua*)**	**47d20**	**IBTS**	**OBO**
		7e–k	**EVHOE**	**OBO**
Pleuronectidae	**Plaice (*Pleuronectes platessa*)**	**420**	**IBTS, BTS, SNS**	**OBO**
		7d	**BTS, FGFS**	**OBO**
Soleidae	**Common sole (*Solea solea*)**	**3a47d**	**IBTS**	**OBO**
Clupeidae	**Herring (*Clupea harengus*)**	**3a47d**	**IBTS, HERAS**	**OBO**
Scombridae	**Mackrel (*Scomber scombrus*)**	**3a4bc7d**	**IBTS, CGFS**	**OBO**
Gadidae	**Saithe (*Pollachius virens*)**	**3a46**	**IBTS**	**OBO**
Pleuronectidae	Flounder (*Platichthys flesus*)	3a4	IBTS	OBO
Gadidae	**Haddock (*Melanogrammus aeglefinus*)**	**46a20**	**IBTS**	**OBO**
Merlucciidae	**Hake (*Merluccius merluccius*)**	**3a46-8abd**	**IBTS, EVHOE, PORC, IGFS**	**OBO**
Scophthalmidae	Turbot (*Scophthalmus maximus*)	4	SNS, BTS	OBO
Gadidae	**Whiting (*Merlangius merlangus*)**	**47d**	**IBTS**	**OBO**
Pleuronectidae	**Witch flounder (*Glyptocephalus cynoglossus*)**	**3a47d**	**IBTS**	**OBO**
Gadidae	Norway pout (*Trisopterus esmarkii*)	3a4	IBTS	OBO
Scophthalmidae	Brill (*Scophthalmus rhombus*)	3a47de	NA	OBO
Moronidae	Seabass (*Dicentrarchus labrax*)	4bc7ad-h	CGFS	OBO
Pleuronectidae	**Dab (*Limanda limanda*)**	**3a4**	**BTS**	**OBO**
Pleuronectidae	**Lemon sole (*Microstomus kitt*)**	**3a47d**	**IBTS**	**OBO**
Gadidae	Pollack (*Pollachius pollachius*)	3a4	NA	OBO
		67	NA	OBO
Lotidae	Tusk (*Brosme brosme*)	3a45b6a7-912b	NA	OBO
Triglidae	Grey gurnard (*Eutrigla gurnardus*)	3a47d	IBTS	OBO
Scophthalmidae	Megrim (*Lepidorhombus spp.*)	4a6a	IBTS, SAMISS, IAMS	OBO
Lotidae	Common ling (*Molva molva*)	3a4a6-91214	NA	OBO

Species specific-data coverage

The fishery-dependent data coupling process described in section 2 results in different quality and quantity of information that is available for each species. In general, for all ten species we had the full set of fishery-dependent and –independent data available for (Table 1), we always lost information for the year 2000 only, regarding specifically the fishery-dependent data, given the absence of common identifiers between the OBO and DFADmet datasets (Fig. 1). Thus, to

keep the same year span between the fishery-dependent and –independent data, we selected data from 2001-2019 to conduct the analytical procedures described in sections 3 and 4.

A standard data cleaning procedure was then performed for all species-specific datasets, where we specifically removed dubious outliers related to the fishing time (duration of the haul) and the spatial extent of the haul (for fishery-dependent data), including removal of duplicated rows and hauls positioned on land. For the fishery-independent data, in particular, we selected only valid hauls that lasted 20-40 min, and removed hauls performed with the "BT4S" gear given that it had too few observations and could therefore result in unnecessary noise for the LGNB-SDM model. For the fishery-dependent data, in contrast, we selected only hauls from trawl-related gears (otter bottom trawl OTB, pair bottom trawl PTB, Danish seine SDN, Scottish seine SSC and beam trawl TBB) in order to keep a minimum consistency between the fishery-dependent and –independent datasets. The overall data coverage per species and data type is summarized in Table 2 and Figure 3.

Table 2. Number of hauls per year, species and data type. OBO = on-board observers, IBTS = International Baltic Trawl Surveys, BTS = Beam trawl surveys. Dashed cells represents data that were not available for a given species/year. Note that for Mackerel no fishery-dependent data will be used in the LGNB-SDM model, as the whole time-series had only 82 hauls after the data coupling. Similar reasoning applies to Witch flounder, except in this case the absence of hauls was due to the fact that no common identifier matched between the OBO /DFADmet & DFADbio in the data coupling process.

Year	2001			2002			2003			2004			2005			2006			2007			2008			2009			2010		
Species / Data	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS
Cod	135	685	200	90	669	259	40	657	270	66	627	354	46	637	317	64	622	266	100	606	332	78	609	309	98	589	337	121	628	295
Plaice	138	685	200	52	669	259	18	657	270	60	627	354	27	637	317	55	622	266	97	606	332	84	609	309	86	589	337	113	628	295
Saithe	54	685	-	58	669	-	36	657	-	46	627	-	35	637	-	59	622	-	92	606	-	55	609	-	73	589	-	90	628	-
Haddock	117	685	-	84	669	-	31	657	-	65	627	-	39	637	-	59	622	-	98	606	-	60	609	-	89	589	-	103	628	-
Mackerel	0	685	-	0	669	-	0	657	-	1	627	-	0	637	-	0	622	-	0	606	-	0	609	-	0	589	-	0	628	-
Witch flounder	-	685	-	-	669	-	-	657	-	-	627	-	-	637	-	-	622	-	-	606	-	-	609	-	-	589	-	-	628	-

Year	2011			2012			2013			2014			2015			2016			2017			2018			2019		
Species / Data	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS	OBO	IBTS	BTS
Cod	1	617	303	5	597	317	1	601	325	202	566	271	314	466	271	255	452	275	304	590	298	530	586	330	492	578	311
Plaice	1	617	303	5	597	317	1	601	325	176	566	271	312	466	271	262	452	275	291	590	298	459	586	330	379	578	311
Saithe	-	617	-	5	597	-	1	601	-	166	566	-	224	466	-	219	452	-	222	590	-	403	586	-	439	578	-
Haddock	-	617	-	5	597	-	1	601	-	196	566	-	315	466	-	224	452	-	260	590	-	495	586	-	457	578	-
Mackerel	0	617	-	0	597	-	0	601	-	0	566	-	14	466	-	0	452	-	4	590	-	40	586	-	23	578	-
Witch flounder	-	617	-	-	597	-	-	601	-	-	566	-	-	466	-	-	452	-	-	590	-	-	586	-	-	578	-
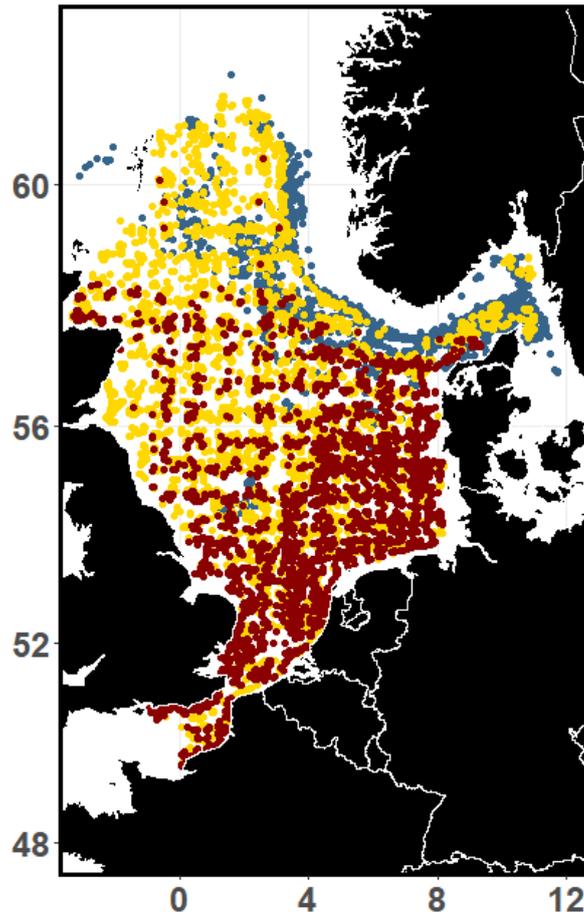
Figure 3. Spatial data haul coverage, where the yellow, red and blue dots refers to scientific survey IBTS and BTS samples (extracted from ICES DATRAS, https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx), and commercial sampling OBO data with hauls. This is an example for North Sea cod, with very similar spatial coverage for the remaining species.

Environmental predictors of spatial distribution and traits data

The LGNB-SDM model (Rufener et al., 2021) allows describing the species abundance dynamics as a function of environmental predictors. Hence, we initially conducted a literature review to investigate which are the main environmental drivers affecting the abundance dynamics of juvenile and adult life stages of each species (See Annexe A, and below Table 3 for an example for the North Sea cod).

Overall, seven environmental predictors were found to be important for at least one of the two life stages, namely:
- Bathymetry (meter)
- Sediment type (EMODNET EUNIS classification)
- Bottom temperature (C^o)
- Bottom salinity (PSU)
- Oxygen concentration (mmol/m^3)
- Seabed shore stress (currents; Newton N/m^2)
- Zooplankton concentration (mg/m^3)

Table 3. Collated information from the literature on the environmental determinants for the North Sea cod. (See Annexe A for other North Sea species).

Species	Environmental effects	Reference
North Sea cod	Widely distributed in a variety of habitats, from the shoreline down to the continental shelf. Juveniles prefer shallow (less than 10-30 m depth) sublittoral waters with complex habitats, such as seagrass beds, areas with gravel, rocks, or boulder, which provide protection from predators. Adults are usually found in deeper, colder waters. During the day, form schools and swim about 30-80 m above the bottom, dispersing at night to feed.	www.fishbase.org
	North Sea cod are omnivorous. Spawning sites are in offshore waters, at or near the bottom, in 50-200 m depth and 0-12 °C (preferred range 0-6°C)	
	depth range 0 - 600 m, usually 150 - 200 m	
	Temp range: -1.5 - 19 °C	Righton et al. 2010
	Optimal Temp: 8 - 10 °C	Righton et al. 2010
	Optimal Sal: 30-35,5 ppt	Hedger et al. 2004
	Depth range: typically found <200m	Hedger et al. 2004
	cod were found throughout the North Sea in either shallower coastal waters or deeper and more oceanic waters (it's possible that separate stocks exist)	Hedger et al. 2004
	most studies to infer species abundance used the following variables: • Water column depth • Bottom temperature • Bottom salinity	Drinkwater 2005 Hedger et al. 2004 Núñez-Riboni et al. 2019 Engelhard et al. 2014
	Optimum temperatures for the development of embryos of North Sea cod, 4°C at 20–33‰ (Von Westernhagen et al., 1970)	Dethlefsen 1996
	warming, winter and summer temperature significant	Perry et al. 2008
	Atlantic embryo range: North Atlantic spawn within a wide range of temperatures, from -1.5 to 9.2°C	Galloway 1998
	Highest percentages of viable hatches occurred in the ranges of 2–10°C and 28–36 ‰ for cod	Laurence and Rogers 1976

The bathymetry layer was extracted from the ocean climate layers for marine spatial ecology (MARSPEC) database, which is publicly available at http://www.marspec.org. MARSPEC constitutes a high resolution dataset for marine climatic and geophysical GIS layers where the spatial resolution is expressed in 30 arc-second (Sbrocco and Barber, 2013). In turn, sediment type was retrieved from the European Nature Information System (EUNIS; https://eunis.eea.europa.eu), which is currently the reference set for European freshwater, marine and terrestrial habitats. The original sediment layer contains 22 levels of habitat types, each being classified as a function of energy regime (e.g., high, moderate and low energy environments), substrate

type (e.g., rock, sand, biogenic reefs) and biological zone (e.g., infralittoral, circalittoral and sub-littoral). Provided that fishes do not generally experience such refined level of sediment type, we aggregated these habitat types into six coarser levels, namely: sand, mud, rock, mixed sediments, coarse sediments and muddy sand.

All other covariates were obtained from the bio-geo-chemical and physical HBM-ERGOM ocean model that is implemented and run by DTU-Aqua (Christensen et al., 2018). Given that each species experiences the surrounding environment differently (see the literature search in Annexe for species specific environmental determinants), we retrieved the covariates for different quantities (average value over the time-series and min-max range) and several spatial and temporal resolutions in an attempt to define the most appropriate quantity and spatio-temporal resolution for each species among 15, 30 and 50 km grid resolution. Because each species has different life-history traits (e.g., benthic/pelagic, small-scale vs. large-scale migrants), the environmental requirements and the spatial and-temporal scales with which they perceive the environment likely differs across species. However, in a lack of time to explore all possibilities, we have chosen the finest grid i.e. 15km (Table 4). As most species are demersal, the HBM-ERGOM model extracted the covariates 3m above the seafloor to mimic the demersal habitat. These covariates were then converted into raster format layers, such that it could be used by the LGNB-SDM model (Rufener et al., 2021), described in the following section. All environmental data were processed through the R programming platform (R Development Core Team, 2018).

Table 4. Environmental covariates retrieved from the HBM-ERGOM model with the final spatial and temporal resolution at which scale the variables were aggregated.

Covariate (3m above seafloor)	Spatial resolution	Temporal resolution
Bottom temperature (average, min-max)	15 km	Weekly, which can be aggregated into coarser a coarser resolution (e.g., monthly, quarterly, yearly)
Bottom salinity		
Oxygen concentration		
Seabed stress (currents)		
Plankton (zooplankton)		

A resolution of 15km has been chosen. However, further work would be to explore, for the LGNB-SDM model, the appropriate spatial and temporal resolution of the environmental covariates for the different life stages in each species.

Bathymetry
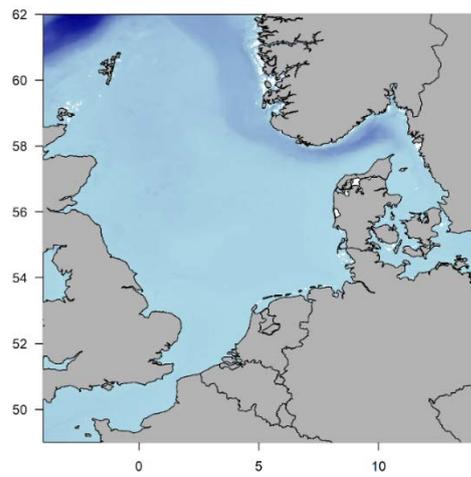
EUNIS habitats
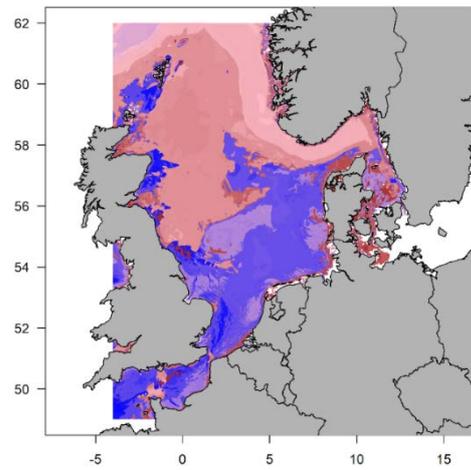
Bottom temperature
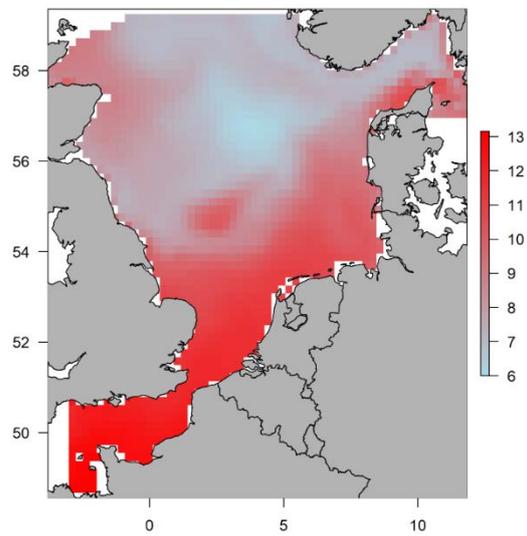
Bottom salinity
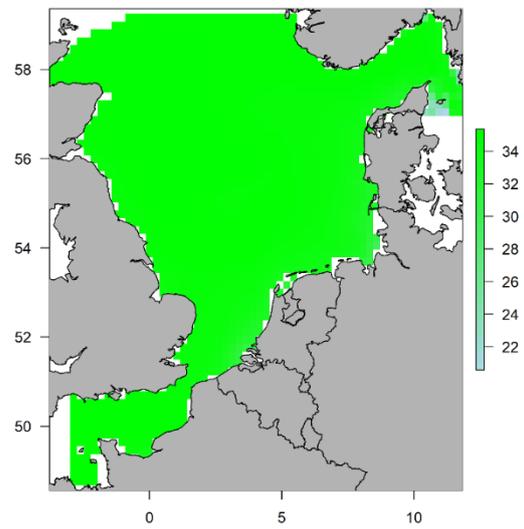
Oxygen concentration
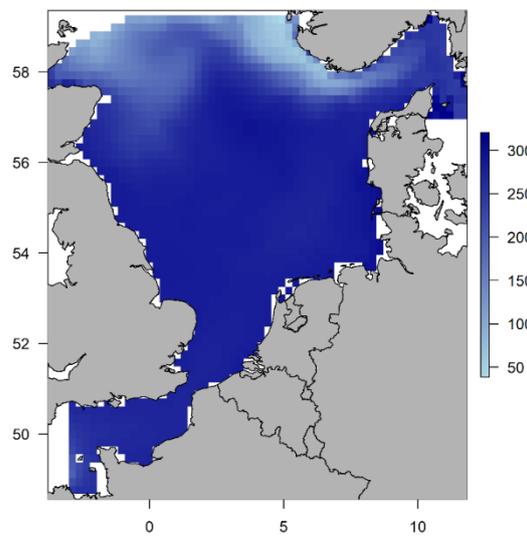
Seabed stress (current velocity)
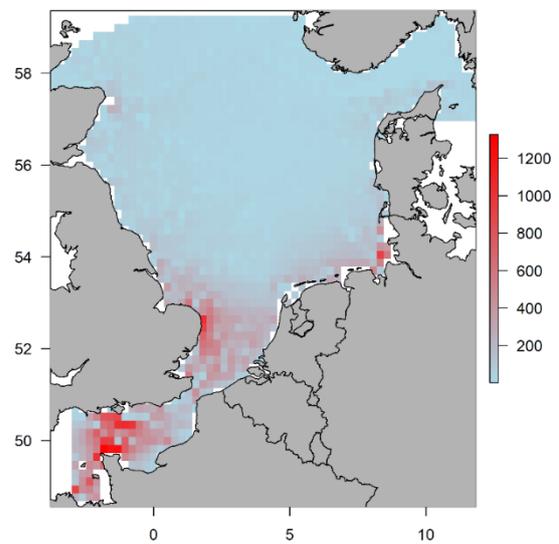
Zooplankton concentration
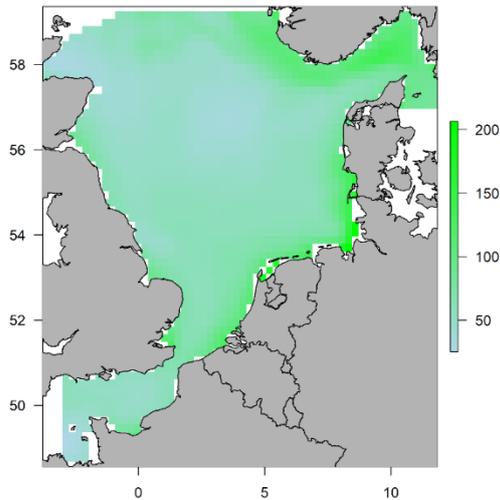
Figure 4. Greater North Sea maps of the covariates used in the LGNB-SDM model to help the fit with the spatial distribution of marine populations, including (from top left to bottom right) bathymetry obtained from the General Bathymetric Chart of Oceans (www.gebco.net), EMODNET EUNIS level 3 seabed habitats, sea bottom temperature (Average Celsius), sea bottom salinity (average PSU i.e. g/kg), sea bottom oxygen concentration (average mmol per m3), seabed stress (average Newton N per m2), and zooplankton concentration (max mg per m3). Bottom temperature, oxygen, zooplankton and shore stress were obtained from extracting daily data modelled with the HBM-ERGOM model for the 2010 year, and further averaged over quarter and grid locations for the use in the model, while an annual aggregation is displayed on the map. (plot code found in covariate_extraction_cod.r)

Irrespective of data source (survey data or fisheries-dependent data), environmental covariates have been used for two different purposes:

1) to account for factors influencing catchability (i.e. efficiency of a fishing operation to catch fish, which depend on the species targeted and their vulnerability to fishing, the gear used, the ability of the fisher, etc.),
2) to account for environmental factors influencing the fish abundance (e.g. sea surface temperature etc.).

The covariates accounting for catchability are attached to "fixed" effects, while the covariates affecting solely abundance are attached to the "random" effects (details at https://github.com/mcruf/LGNB/wiki/model.R:-section-8). When including covariates at the catchability level, the covariates are extracted for the estimation phase, therefore only accounted for in the observation process, i.e. the observed hauls. By contrast, when including covariates at the level of abundance, the values of the covariates extracted are needed at every grid vertex (see the grid on Figure 5) to be further used for the spatial prediction, modelled as a continuous Gaussian Markov Random Field (GMRF).

From environmental covariates listed in our study (bathymetry, sea surface temperature, salinity, etc. see Figure 4), only the bathymetry has the potential for affecting the catchability. To greatly simplify the study, the bathymetry has however not been used as a fixed-effect that would potentially affect the catch observations. Instead, all the environmental covariates including the bathymetry have been included in the environmentally-affected models as covariates to explain levels of abundance in our current outcomes, therefore playing a role in affecting the spatial predictions of stock abundance.

Further investigation will be needed to relate how the projected change in the covariates will affect future distribution of the stock abundance and density. A few projections of environmental variables are available from the CERES project including the Greater North Sea but should refine to downscale to the area of interest, and also include all the relevant variables partly driving the stock distribution.

North Sea spatial resource distribution model calibration (NS-LGNB-SDM)

To estimate and predict the spatio-temporal abundance dynamics of the species selected in Table 1, we used the log-Gaussian negative binomial point process model (LGNB-SDM) that was developed by Rufener et al. (2021). The model was ran on different length groups within each species examined here. Additionally, the model outcomes are separated into two life stages (juveniles and adults) from the different length groups knowing the sex maturity-at-length specific to species and identified in the literature.

The LGNB-SDM model is an advanced Species Distribution Model (SDM; Elith & Leathwick, 2009) that aims to combine both fishery-dependent and –independent data sources, while simultaneously filtering out the data-specific biases. The model incorporates both observation (hereby, the catches retrieved from the fishing hauls) and latent processes (hereby, the abundance field) in a hierarchical structure, where the first stage essentially describes the unobserved abundance field λ as function of space (s) and time (t):

$$\lambda(s, t) = \exp\left(\sum_{k=1}^{K} \beta_k X_k(s, t) + \xi(s, t)\right) \tag{1}$$

where $X_k(s, t)$, $k = 1, \ldots, K$ are a set of explanatory variables with corresponding fixed effect parameters β_k, and $\xi(s, t)$ represents a spatiotemporal structured random effect. Besides a seasonal effect (year-quarter), we used the environmental predictors highlighted in section 2 as fixed effects to describe the abundance fields of the different fish species (section 2 for more details). The spatiotemporal random effect $\xi(s, t)$ is then modelled as a separable process. In particular, the spatial correlation is modelled by means of Gaussian Random Field (GRF), whose precision matrix is described via a first-order conditional autoregressive (CAR) process. This requires the construction of a spatial grid, which herein was given on a 15x15km resolution (2798 grid cells) as it represented the best compromise between computational demand and realism to the biological process being evaluated (Figure 5). Conversely, the temporal correlation is expressed as a first-order autoregressive process (AR1), where we defined a year-quarter time resolution to account for possible seasonal migrations (76 time-steps, from 2001-Q1 to 2019-Q4).
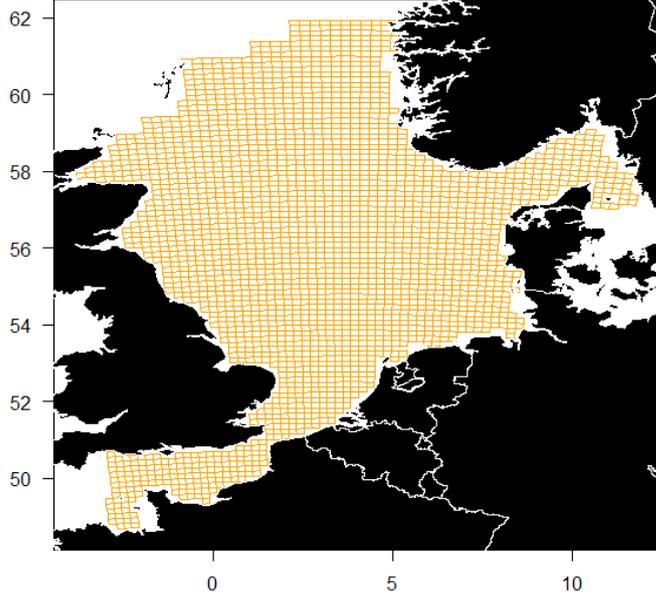
Figure 5. Illustration of the spatial grid (15 km x 15 km) that was used for the North Sea LGNB-SDM model to project the species' spatio-temporal abundance distributions.

Conditional on the abundance field, the second stage of the LGNB-SDM model (Rufener et al. 2021) describes the species abundance (catch in numbers, N) through a negative binomial distribution. Within the LGNB-SDM, the observation process of the fishery-dependent and –independent data are described individually due to the different nature of their sampling designs which, consequently, affects the fishing catchability, fishing effort and spatial extension of the sampling unit (see Rufener et al., 2021 for more details). Overall, both observation processes describe the catch as a function of catchability descriptors:

$$\log(\mu_i^{\mathrm{D}}) = \log(\lambda(s_i, t_i)) + \sum_{k=1}^{K_{\mathrm{D}}} \beta_k^{\mathrm{D}} X_{k,i}^{\mathrm{D}} \qquad (2)$$

where $\log(\mu_i^{\mathrm{D}})$ is the expected catch for data D (fishery-independent or fishery-dependent), $\lambda(s_i, t_i)$ is the unobserved abundance field, $X_{k,i}^{\mathrm{D}}$ is a design matrix quantifying both fixed and random effects of k catchability indicators (e.g., fishing vessel, type of gear, etc.) through a coefficient matrix β_k. We assumed that each data source and species therein had different catchabilities, and therefore we had to calibrate the respective species-specific observation processes individually.

Adjusting species and data-specific catchabilities - Adjusting the species and data-specific catchabilities is a fundamental procedure in the LGNB-SDM model given that the validation of the integrated model is highly dependent on whether the catchabilities among the different data sources are accounted for correctly (see section 5.2 for more details).

For the present study, the catchabilities of both fishery-independent and –dependent data were described through fixed and random effect terms. The fixed effects, in particular, described the catchability as a function of a seasonal term (both datasets), type of survey (fishery-independent data, whenever $n_{\mathrm{surveys}}>2$) and data-specific gear descriptors (both datasets). These were estimated as separate parameters whereby the first time-step (2001-Q1) and the survey data

were used as reference levels. By contrast, vessel-specific catchabilities were accounted for as random effect as a means to mimic the unobserved skipper effect (Table 5).

The fishery-independent observation process also includes an offset term to account for the different fishing efforts (hereby described by the haul duration in minutes). However, no offset is included for the fishery-dependent observation process as the catches are discretized along the trawled distance (we refer to Rufener et al., 2021 for more details see online https://github.com/mcruf/LGNB and https://github.com/mcruf/gNORDFO).

Table 5. NS-LGNB-SDM model calibration for the different species and the data-specific observation processes therein. The f(·) denotes the function for the vessel-time random term. Note that the mackerel and witch flounder LGNB-SDM model uses only fishery-independent data (i.e. survey data) as input due to the absence of adequate fishery-dependent data (i.e. commercial data). Length groups of total animal length are 5 cm animal body size bins defined as L0:0-5cm, L1 5-10cm, …, L13 65cm+. The missing length groups for some species result from a lack of enough data in the group to make the model converge. Note that for survey the haul duration is known in advance because more or less constant and is therefore inputted as an offset variable, which does not apply for the variable haul duration in the commercial data.

Species / Data		Length Groups L (S: survey, B: both commercial and survey)	Length group stage (Juvenile or Adult)	Fishery-independent	Fishery-dependent	+Environmental variables
Cod (*Gadus morhua*)	Gadoid	L1S, L2S, L3S, L4S, L5S, L6S, L7B, L8B, L9B, L10B, L11B, L12B, L13B	Juv 1 to 6, Adult 7 to 13	Time + Gear + Survey + f(VesselTimeSUR) + offset(log(haul duration))	Time + Metiers + f(VesselTimeCOM)	+ Bathymetry + Sediments + BotTemperature + Salinity + BotOxygen + ShearStress + Zooplankton
Plaice (*Pleuronectes platessa*)	Flatfish	L1S, L2S, L3S, L4S, L5B, L6B, L7B, L8B, L9B, L10B, L11B, L12B, L13B	Juv 1 to 6, Adult 7 to 13	Time + Gear + Survey + f(VesselTimeSUR) + offset(log(haul duration))	Time + Metiers + f(VesselTimeCOM)	+ Bathymetry + Sediments + BotTemperature + Salinity + BotOxygen + ShearStress + Zooplankton
Haddock (*Melanogrammus aeglefinus*)	Gadoid	L1S, L2S, L3S, L4S, L5S, L6B, L7B, L8B, L9B	Juv 1 to 5, Adult 6 to 9	Time + f(VesselTimeSUR) + offset(log(haul duration))	Time + Metiers + f(VesselTimesCOM)	+ Bathymetry + Sediments + BotTemperature + Salinity + BotOxygen + ShearStress + Zooplankton
Saithe (*Pollachius virens*)	Gadoid	L7S, L8B, L9B, L10B, L11B, L12B, L13B	Adult 7 to 9	Time + f(VesselTimeSUR) + offset(log(haul duration))	Time + Metiers + f(VesselTimesCOM)	+ Bathymetry + Sediments + BotTemperature + Salinity + BotOxygen + ShearStress + Zooplankton
Mackerel (*Scomber scombrus*)	Pelagic	L3S, L4S, L5S, L6S, L7S	Juv 3 to 5, Adult 6 to 7	Time + f(VesselTimeSUR) + offset(log(haul duration))	NA	+ Bathymetry + Sediments + BotTemperature + Salinity + BotOxygen + ShearStress + Zooplankton

Species	Type	Levels	Ages	SUR formula	COM formula	Environmental covariates
Dab	Flat-fish	L3S, L4S, L5S	Adult 3 to 5	Time + f(VesselTimeSUR) + offset(log(haul duration))	NA	+ Bathymetry + Sediments + BotTemperature + Salinity + BotOxygen + ShearStress + Zooplankton
Herring (*Clupea harengus*)	Pe-lagic	L1S, L2S, L3S, L4S, L5S, L6S	Juv 1 to 3, Adult 4 to 6	Time + f(VesselTimeSUR) + offset(log(haul duration))	Time + Metiers + f(VesselTimesCOM)	+ Bathymetry + Sediments + BotTemperature + Salinity + BotOxygen + ShearStress + Zooplankton
Sole (*Solea solea*)	Flat-fish	L3S, L4S, L5S, L6S, L7S	Adult 3 to 7	Time + f(VesselTimeSUR) + offset(log(haul duration))	Time + Metiers + f(VesselTimesCOM)	+ Bathymetry + Sediments + BotTemperature + Salinity + BotOxygen + ShearStress + Zooplankton
Sprat (*Sprattus sprattus*)	Pe-lagic	L1S, L2S, L3S	Juv 1, Adult 2 to 3	Time + f(VesselTimeSUR) + offset(log(haul duration))	Time + Metiers + f(VesselTimesCOM)	+ Bathymetry + Sediments + BotTemperature + Salinity + BotOxygen + ShearStress + Zooplankton
Whiting (*Merlangius merlangus*)	Pe-lagic	L2S, L3S, L4S, L5S, L6S, L7S, L8S, L9S, L10S, L11S, L11S, L13S	Juv 2 to 4, Adult 5 to 13	Time + f(VesselTimeSUR) + offset(log(haul duration))	Time + Metiers + f(VesselTimesCOM)	+ Bathymetry + Sediments + BotTemperature + Salinity + BotOxygen + ShearStress + Zooplankton

"Time" is expressed on a year-quarter basis (76 levels, from 2001-Q1 to 2019-Q4)
"Gear" represents the fishing gears deployed by the IBTS and BTS surveys (4 levels: GOV, BT4A, BT7 and BT8)
"Survey" is an indicator variable to account for catchability differences between IBTS and BTS surveys whenever applicable (2 levels: IBTS and BTS)
"VesselTimeCOM/SUR" represents the seasonal vessel-specific catchabilities for each dataset (No of levels depends on the species)
"Metiers" accounts for differences in catchability among the different métiers in the fishery-dependent data (5 levels: OTB, PTB, SDN, SSC, TBB).

3. NS-LGNB-SDM model estimation and validation

All parameter estimates were conducted in the R programming platform (R Development Core Team 2019) through the Template Model Builder R-package (TMB, Kristensen et al, 2016). Within TMB, fixed effects are estimated by maximizing the marginal likelihood, whereas random effects are integrated out and estimated through the Laplace approximation. Model convergence was confirmed by verifying that the Hessian matrix was positive-definite, and by evaluating that the gradient component of the marginal likelihood was < 0.001. A simulation study was then conducted to evaluate the correctness of the estimation method, whereby we specifically used the checkConsistency function that is implemented in the TMB R-package (For more details, we refer to Rufener et al., 2021). Furthermore, we assessed the model's goodness-of-fit by inspecting the residuals' normality both visually (QQ-plots) and quantitatively (Kolmogorov-Smirnov test).

In order to be able to apply the NS-LGNB-SDM model with the two data sources (fishery-dependent and –independent data, whenever applicable), we also had to check whether the fixed and random-effect parameters were consistent across the two data sources. To do so, we used the same approach adopted in Rufener et al. (2021), where a test statistics evaluates whether the parameter estimates from the integrated model are within the 95% confidence interval from the parameters estimated solely by the fishery-independent data. Consistency of the fixed and random effect parameters is confirmed whenever the p-value is greater than the 5% significance level.

4. Model selection

We ran model 1 (i.e. without covariate) and model 2 (i.e. with all covariates; see Table 5) for all species and length groups therein. The computer-demanding fitting prevented us in the timeframe of this project to run additional intermediate model formulations that would for example test for different sets of covariates per length group. Therefore, the exact same model formulation was used across species and length groups, which facilitated the comparison of the goodness-of-fit. To compare the two models for a selected size group in each stage (juvenile and adult), we used the Akaike Information Criterion (AIC; Table 6):

$$AIC = 2k - 2\ln(L)$$

where *k* is the number of parameters, and ln(L) the negative log-likelihood. The best model was selected as the one following the parsimony principle, i.e., the model that fits the best (lowest AIC) with the least amount of parameters. Whenever the AIC difference between the two models was less than five, i.e., $\Delta AIC < 5$ (Burnham and Anderson, 2002), we conducted Likelihood Ratio Test (LRT) to select the best model.

Table 6. Comparing AIC values between species-specific models with or without environmental covariates in the model fitting formulation. The best selected model within each case are highlighted in bold, and were accordingly used to predict the spatio-temporal abundance fields. 'NA' stands for 'non-assigned' given the absence of model convergence in the model fitting for those particular occurrences.

AIC	Juveniles	Adults
Cod (without covariate)	275358	315351
Cod (with all covariates)	**275337**	**272234**
Dab (without covariate)	NA	428705
Dab (with all covariates)	**NA**	**428173**
Haddock (without covariate)	222487	260404
Haddock (with all covariates)	**222353**	**220798**
Herring (without covariate)	328572	325557
Herring (with all covariates)	**327777**	**324711**
Mackerel (without covariate)	200083	196146
Mackerel (with all covariates)	**199926**	**196061**
Plaice (without covariate)	385039	356893
Plaice (with all covariates)	**340952**	**323029**
Saithe (without covariate)	NA	172024
Saithe (with all covariates)	**NA**	**171987**
Sole (without covariate)	NA	271627
Sole (with all covariates)	**NA**	**271439**
Sprat (without covariate)	328347	336735
Sprat (with all covariates)	**NA**	**254674**
Whiting (without covariate)	362509	351331
Whiting (with all covariates)	**361643**	**350372**

For each species investigated here, it is apparent that the best model formulation is the one including the environmental variables as covariates (Table 6). Accordingly, these models were used to predict the species-specific spatial and temporal abundance dynamics that will be used in the bioeconomic modelling (section 8).

5. Spatio-temporal dynamics of juveniles and adults abundance hotspots for main exploited species in the North Sea

The methodology we re-applied to the North Sea case study here is described in full details in Rufener (2020, PhD dissertation), The study identify areas of high concentration of juveniles and adults fish (hereafter named "hotspots"), once all LGNB-SDM models are validated and the predicted abundance maps assembled. If such aggregation likely corresponds to nursery areas, feeding areas or spawning aggregations, the method does not have the power to discriminate these determinants because no sexual status has been tracked in the data. Hence the study assumed the distinction among juveniles from adults based on the typical body size per species reported in the literature.

Defining hotspots often base on a subjectivity where thresholds are used to differentiate hotspots from less concentrated areas (Bartolino et al., 2011; Nelson & Boots, 2008). Recent methods proposed by Bartolino et al. (2011) and Petitgas et al. (2016) could provide more objective measures. Given that the LGNB-SDM already takes into account spatial correlations, there was no need to use geostatistics as described in Petigas et al. (2016) and we therefore used Bartolino et al. (2011) approach to identify juvenile and adult abundance hotspots.

The method use the cumulative relative frequency distribution curve (Bartolino et al., 2011). The curve itself describes the frequency distribution of the abundance (y-axis) as a function of the relative abundance of juveniles/spawners (x-axis), with both axes ranging from 0 to 1. From this curve, the hotspot threshold is then identified as the x-value where the slope of the tangent is 45◦ (Figure 6). Values above this threshold in abundance show a higher rate of change in abundance than the proportional change in surface areas which is a sign of higher species density on this surface (see Bartolino et al. 2011 or Colloca et al. 2009 for details). For both juveniles and adults, we derived monthly thresholds screening the entire time-series of spatial abundance by applying this 45-degree rule on the cumulative distribution (Figure 6). 76 adult thresholds and 76 juvenile thresholds are retrieved along with the 4 quarters a year from 2001-2019.

Once hotspots are identified for each time step the overlap of these hotspots over time would be a sign for persistent hotspots, which is the final information the screening is search for. We used a similar approach as Fiorentino et al. (2003) and Colloca et al. (2009), which, for each cell of the spatial grid calculates an index of hotspot persistence. This index ranges between 0 (grid cell i was never considered as a hotspot) and 1 (grid cell i was consistently identified as a hotspot throughout the time-periods)- Finally, as the EU STECF (2019) recommends, we applied a selecting values of 0.8 to delineate persistent, and very conservative, juvenile and adult concentration areas.

The identified areas are then converted into GIS shapefile layers such that they could be imported as closure areas in the DISPLACE simulations (Bastardie et al., 2014; see next section 8).
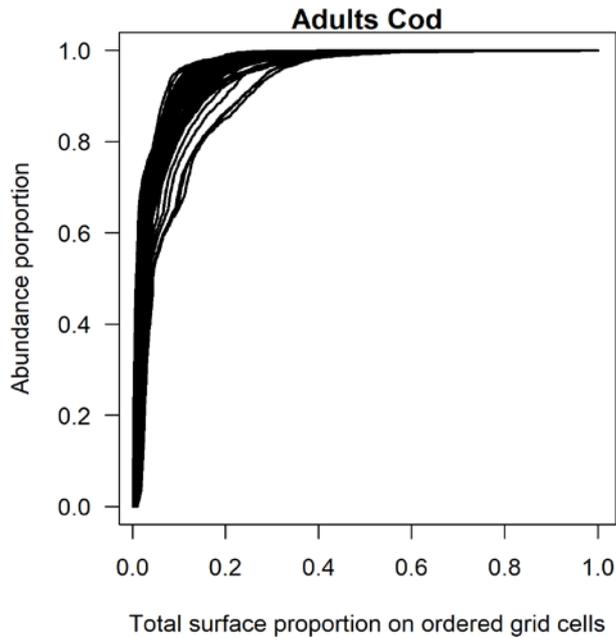
Figure 6. An illustration of the Cumulative Relative Frequency Distribution (CRDF) curves for the adult North Sea cod (there are as many curves as the number of Quarter-Year period during the investigated time span). Similar curves were computed for all other species examined in this study and the two life stages therein.

By applying this methodology described in Rufener (2020), we found that there are consistent hotspots in the Greater North Sea over years and for each studied species (described further below), and having staked all the hotspots together across the different exploited species studied here, it is apparent that some areas are persistently more densely occupied than others (Figure 7). The perception of these persistent areas differs depending on the life stage of the species (juveniles vs adult fish), which support the fact that different areas are visited along the life cycle of a species depending on the physiological needs or the passive movement of larvae, while hotspots for juvenile fishes are less pronounced then for adults in general.

In addition to this, quite different perceptions are obtained for the predicted hotspot fields depending on whether environmental drivers are accounted for or not in the model fitting. Hence, model fitting based on survey or commercial catch data only predict a large hotspot in the vicinity of the Shetlands Island in the Northern part of the North Sea, while accounting for the set of environmental covariates used in the analysis predict the largest hotspot to occur in the Norwegian deep area. Both model formulations agreed however to designate the UK south coastline, south of the North Sea, and part of the Norwegian deep as persistent hotspot for adult fish. Model fitting based on environmental covariates would however likely show the most important (because hosting the greater amount of species persistently) and at the meantime, the most impacted areas (because linked to environmental drivers) in case of climate change affecting the drivers for spatial distribution.

In all description below it is important to keep in mind that the model fit outcome is not incorporating the impact from fisheries in the long run. While the current project is relevant in this context, it is worth mentioning that spatial distribution pattern may also be directly affected by fishery on different life stages as well as indirectly by changing fish habitats, e.g. the benthic community, with potential effects on the stock productivity in the long-run.

Individual species abundance density hotspots stacked over all species studied are shown in Figure 7 below to see the overlap and therefore possible productive areas for several species simultaneously, for models without or with covariates, with a more conservative persistency threshold at 0.5 a year.
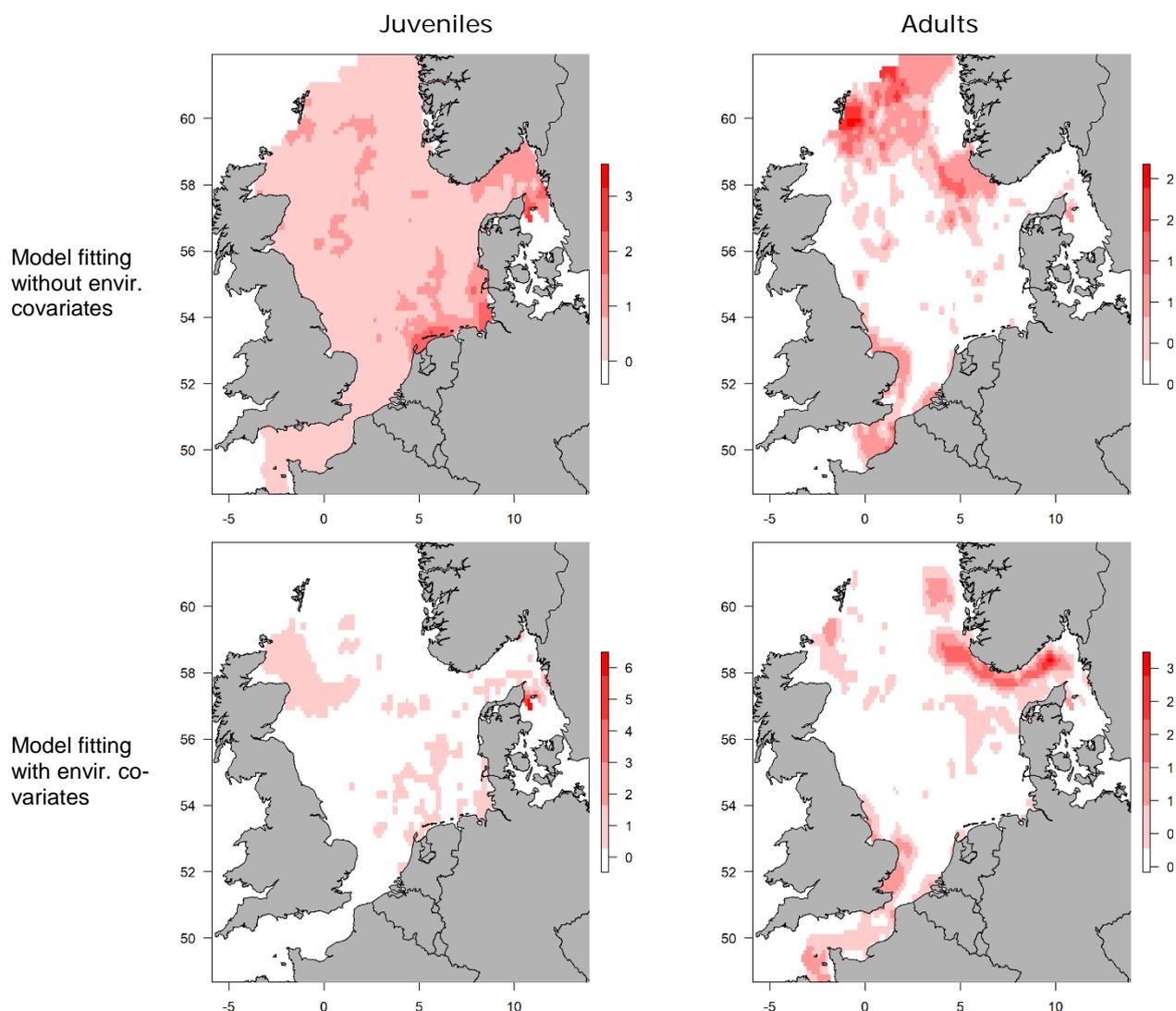
Figure 7. Overall abundance density hotspots per life stage deduced from the LGNB-SDM model fitting, either without or with environmental covariates. All species are stacked, i.e. Cod, Plaice, Haddock, Saithe, Mackerel, Dab, Herring, Sole, Sprat, and Whiting. There was no enough information for juvenile sole, dab and saithe to be accounted for them in the hotspot analysis of juveniles. Note that a widespread color would mean no specific hotspots but an even distribution (e.g. for the juveniles). The scale gives the count of overlapped stocks from 0 to 6.

In the following subsections are presented the hotspots found per species. For all species and life stages we have used the model in which all environmental covariates were used for the fitting aspect. Yet, it is worth noting we have only explored the spatio-temporal predictions of the model's output and we therefore have not explored correlations of abundances with possible environmental drivers as such due to lack of robust time series of environmental drivers at the time of the project.

Abundance hotspots of North Sea cod (*Gadus morhua*)

The key climatic and environmental drivers of the North Sea cod population have been studied across all life history stages, but most have focused on the effect on early life stages before recruitment to fishing, stemming from the dramatic decrease in survival rates (i.e., recruitment per spawning stock biomass) observed over time. These changes have been most often linked to long-term climate change, such as increased temperatures in the North Sea (e.g., Olsen et al. 2011, Akimova et al. 2016). Authors stated that the mechanism of the impact is not clear, however. There is less support for a direct adverse physiological response to increased temperatures. Temperatures may instead positively influence several aspects related to recruitment, including decreased development time in eggs (e.g., McQueen and Marshall 2017), increased growth rates in larvae (e.g., Steinarsson and Björnsson 1999, Fouzai et al. 2015), and faster oocyte development in mature females (e.g., Kjesbu et al. 2010).

Several possible indirect adverse effects have also been postulated, including higher predation rates on eggs, timing mismatches between spawning and suitable planktonic prey (e.g., Beaugrand et al. 2003, Beaugrand and Kirby 2010), and a general long-term northward shift in the habitat and abundance of suitable large-sized zooplankton species, such as *Calanus finmarchicus* (e.g., Heath 1999, Papworth et al. 2016).

Links between short-term interannual variability on recruitment processes are even less conclusive. However, several studies have shown that variability in sea currents and strength of inflowing Atlantic waters likely impact the transport and retention processes of eggs and larvae to important nursery areas (e.g., Jonsson et al. 2016, Kvile et al. 2016). Currents are likely to influence the degree of exchange among sub-populations. For the larger fish (post-recruitment), a northward shift in the spatial distribution has been observed over recent decades (e.g., Engelhard et al. 2014, Nunez-Riboni et al. 2019). This spatial shift could be driven by increasing temperatures in the southern North Sea. Again, the mechanism for the shift is not clear, as it could be due to direct effect affecting cod outside its thermal optima, or indirectly whenever degrading the requirements for their prey.
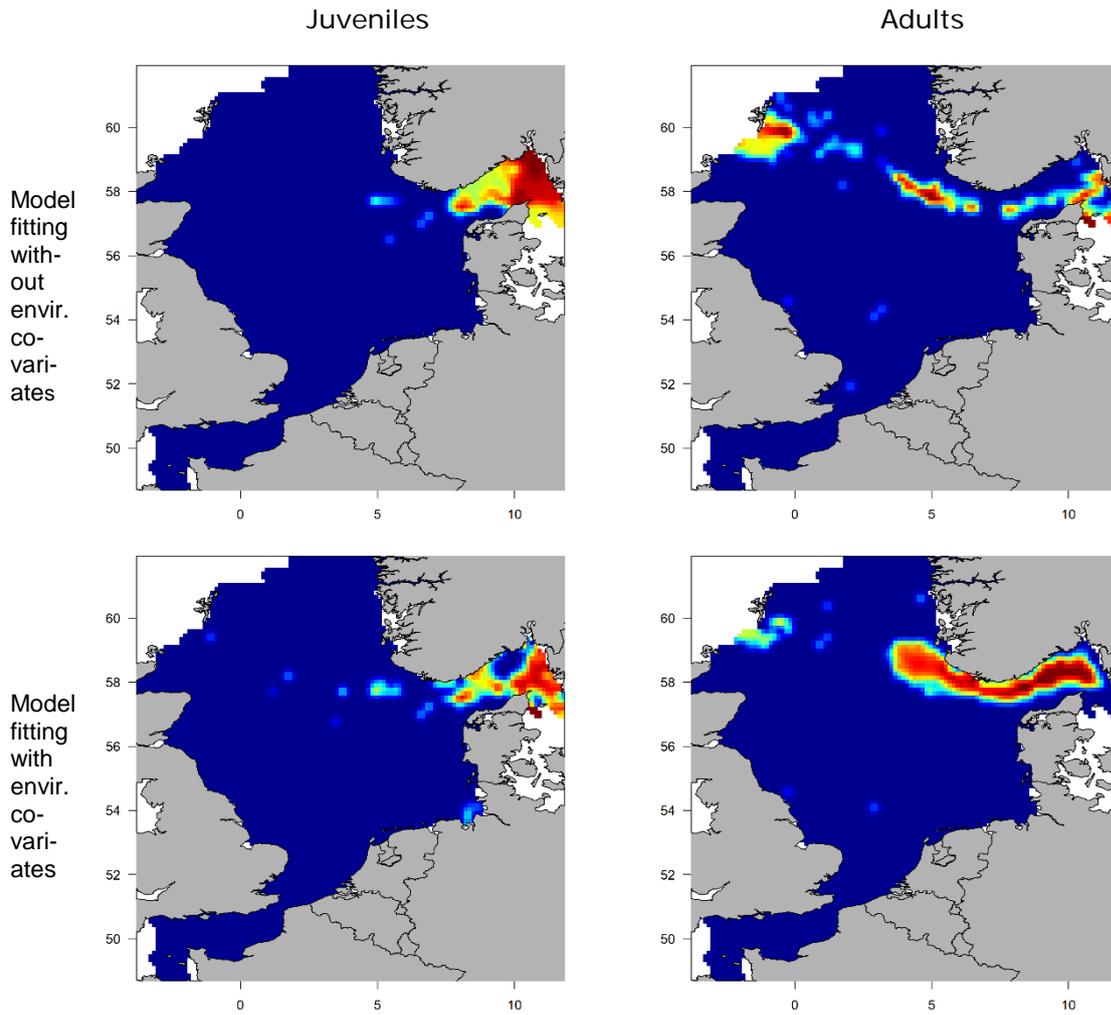
Figure 8. Persistent hotspots during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=7) of the North Sea Cod identified by the hotspot analysis. Top: model m1 no predictor, bottom: model m5 with covariates as predictor.

Our persistence analysis (the one based on fitting accounting for the covariates having the best good-ness-to-fit) shows that juveniles and adult cod persist at the same locations in the North Sea, with a more marked area fidelity for the adult cod, often distributed at the border of the Norwegian deep and close to the UK shore or Shetland highland in the northern part of the North Sea (Figure 8). The grav-ity point tracked during the period 2001-2019 (Figure 9) show a marked westward movement both for adults and juveniles cod, by several degrees in longitude, making the main and persistent cod distri-bution farther from the Danish coastline, but not really changing the overall proportion falling within the UK EEZ (Figure 10). None of the centre of gravity is representative of the distribution however given it makes the average among several disconnected patches.
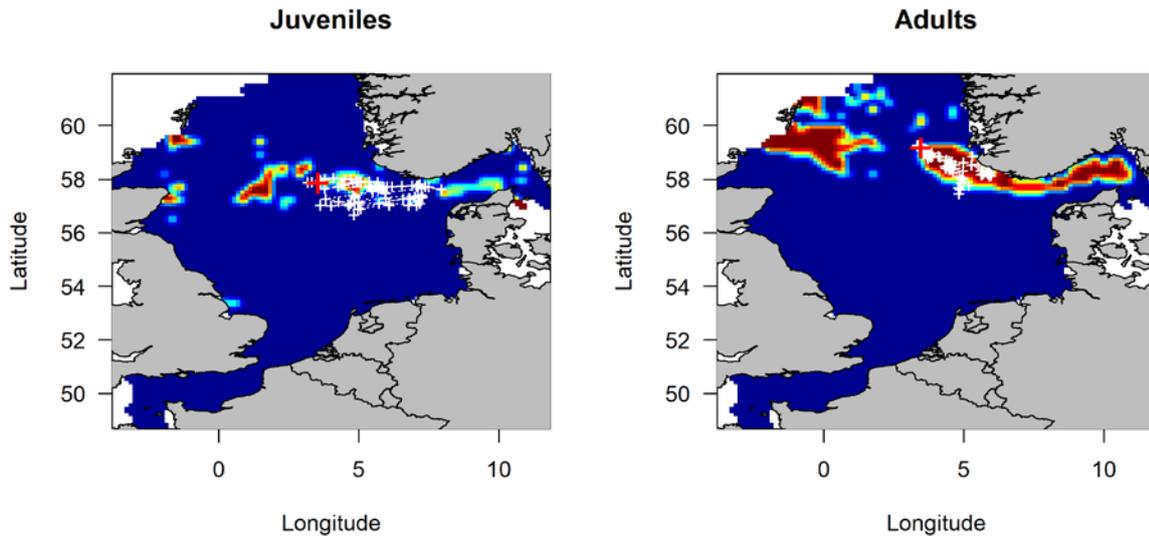
Figure 9. Quarterly centre of gravity of density hotspots for North Sea cod during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=7) identified by the hotspot analysis after fitting model m5 with covariates as predictor. The largest "+" in red symbol marks the gravity point for the last time step, while others are in white. The color levels depict the hotspot areas of the last time step.
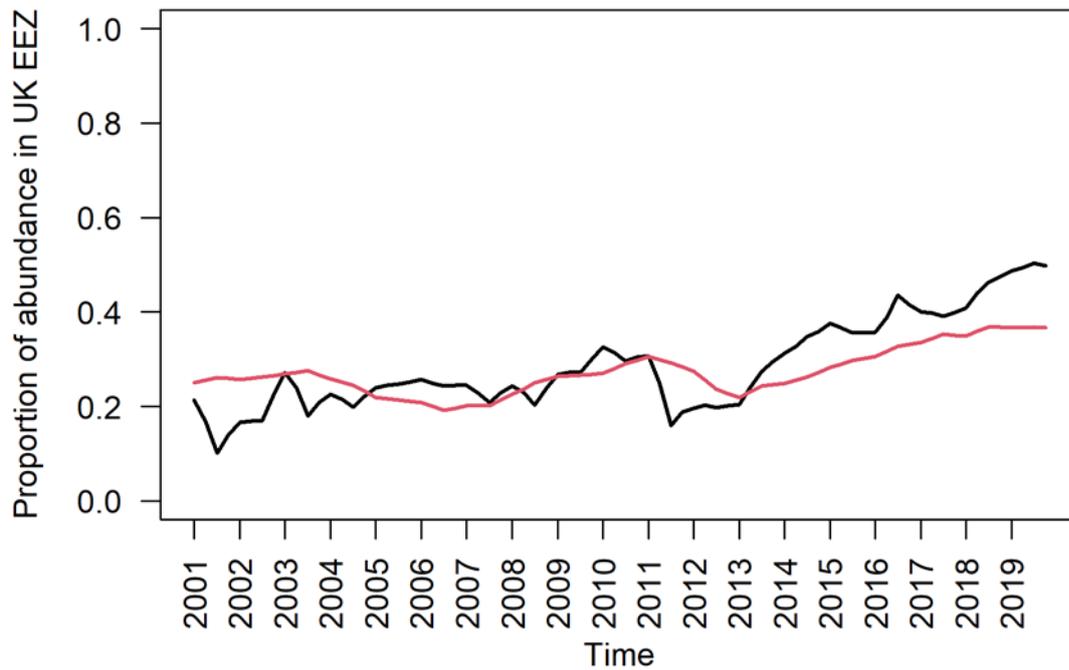
Figure 10. Quarterly based proportion of the abundance of juveniles' fish (in black) and adults (in red) for North Sea cod falling inside the UK EEZ in the North Sea, deduced by the North Sea abundance field reconstruction described here.

Abundance hotspots of North Sea Saithe (*Pollachius virens*)

According to literature, North Sea saithe has so far not been directly influenced by temperature changes (Ottersen et al. 2013, Pecuchet et al. 2015), and also its spatial distribution has not changed within the North Sea (ICES 2017). Neither for recruitment nor for growth direct temperature effects have been observed. However, indirect effects have been described to play an important role. Changes in currents, large scale patterns as the northern annual mode, the composition and timing of phyto- and zooplankton blooms (especially *Calanus finmarchicus* as food for larvae) had likely a negative influence on recruitment over time (Pecuchet et al. 2015, Papworth et al. 2016, Zimmermann et al. 2019).

Although the effect of climate change environmental conditions and their change could not be directly linked so far to any effect on the stocks, the stock has experienced some changes in recent years. According to ICES (ICES 2020), recruitment is on a decreasing trend with the lowest levels in the past 10 years (after 2010). Growth of North Sea saithe may be influenced by density-dependent effects and competition with the northern hake stock (Cormon et al. 2014, 2016). Both species prey on Norway pout as an important item. According to ICES (ICES 2020), mean weight at age has decreased for ages 6+ between the late 1990ies and 2010, but the trend has stopped and has reversed in recent years. Weights-at-age for ages 3–5 have been relatively stable, with some variation over the last decade.
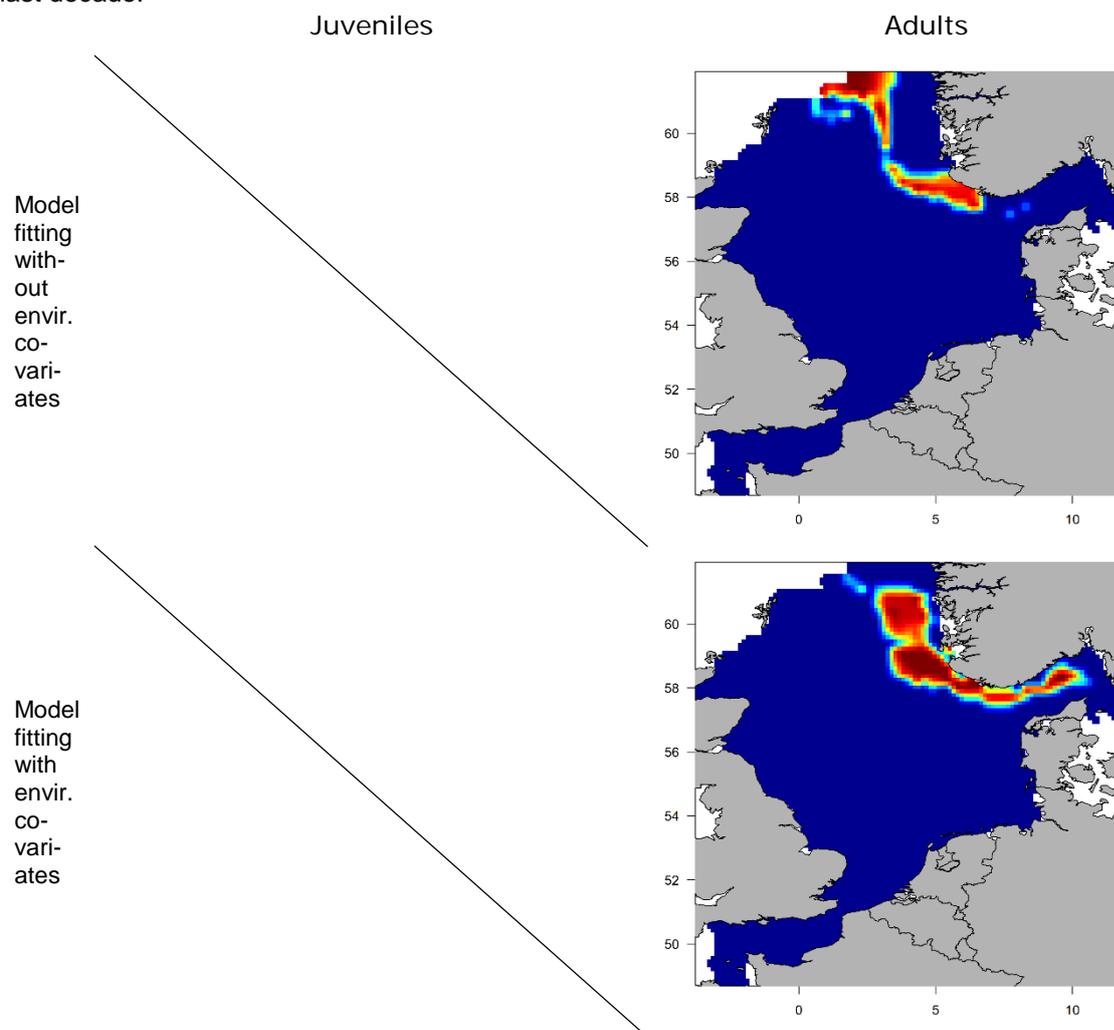
Figure 11. Persistent hotspots during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=7) of the North Sea saithe identified by the hotspot analysis. Top: model m1 no predictor, bottom: model m5 with covariates as predictor.

Our persistence analysis (the one based on fitting accounting for the covariates having the best good-ness-to-fit) shows adult saithe persisting in the Norwegian deep of the North Sea, while no information is available for juvenile fish (Figure 11). The gravity point tracked during the period 2001-2019 (Figure 12) does not show any tendency for adult saithe to adopt a movement of density of fish over time, demonstrating a very stable stock distribution over the 20y period of time, as well as no major change for the proportion of the stock lying within the UK EEZ given the stock is largely outside this area (Figure 13).
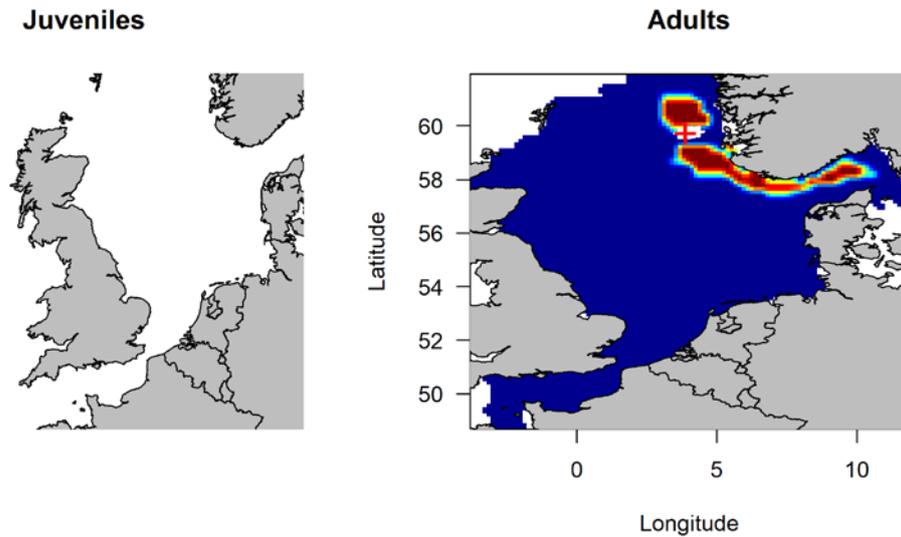
Figure 12. Quarterly centre of gravity of density hotspots for North Sea saithe during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=7) identified by the hotspot analysis after fitting model m5 with covariates as predictor. The largest "+" in red symbol marks the gravity point for the last time step, while others are in white. The color levels depict the hotspot areas of the last time step.
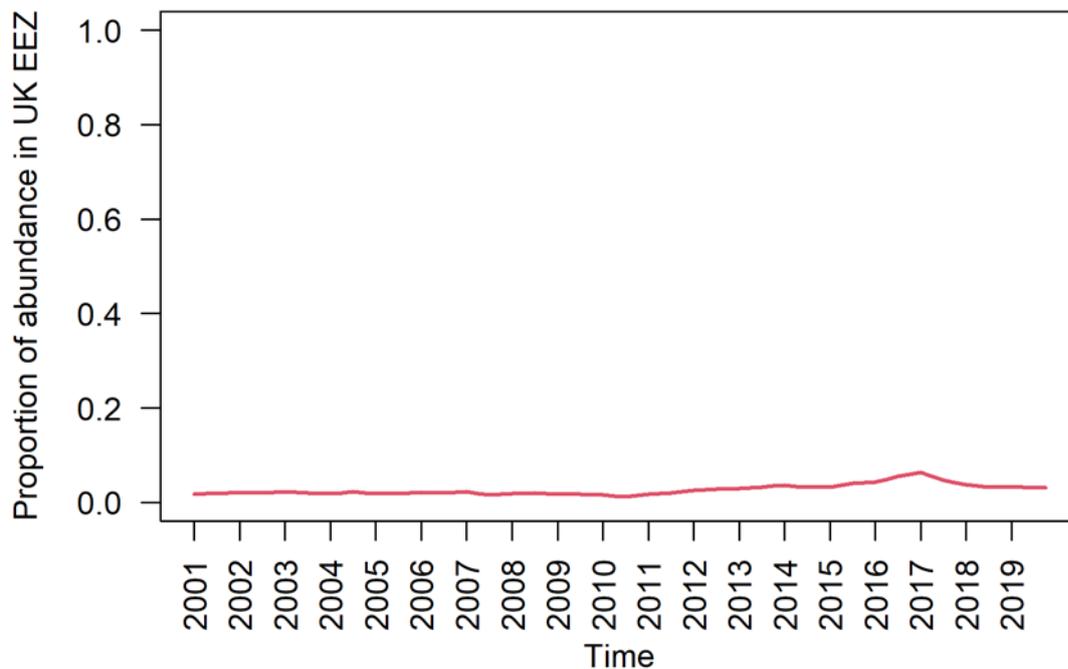
Figure 13. Quarterly based proportion of the abundance of juveniles' fish (in black) and adults (in red) for North Sea saithe falling inside the UK EEZ in the North Sea, deduced by the abundance field reconstruction described here.

Abundance hotspots of North Sea Haddock (*Melanogrammus aeglefinus*)

Previous studies showed that the haddock stock in the North Sea has no apparent relationship to temperature. According to ICES reports, recruitment patterns are marked by exceptionally strong cohorts with lower recruitment in the following years (2021a). Yet, what causes these high numbers is not completely understood. According to literature, recruitment of haddock shows opposite or lagged correlation patterns with sea surface temperature (SST) and no obvious link to the North Atlantic oscillation (Dippner, 1997; Baker et al., 2019). Nevertheless, the egg survival may have its optimum at 7°C, with increasing temperatures likely to accelerate egg development (Laurence and Rogers, 1976; Martell et al., 2005). For the mature haddock, the optimal spawning temperature may coincide with egg survival at 7°C (González-Irusta and Wright, 2016). Overall, the stock is driven largely by outstanding year classes (spikes) that sustain the fishery over many years. The spikes tend to become smaller over time (ICES, 2021a). In the last decades, abundance decreased in areas IVb and IVc, while it stayed constant in the northern part of the North Sea (ICES, 2017).

The growth of haddock larvae could be largest in medium temperature ranges, with a maximum at 8°C (Laurence and Rogers, 1976). Studies have shown that higher temperatures reduce the time haddock spend in different developmental stages, inducing earlier sex maturation (Martell et al., 2005). Therefore, young haddock reach sex maturation at a smaller body size (Baudron et al., 2011). Generally, haddock is reported to benefit from bottom temperatures greater than 6°C in deeper areas with higher salinities (Hedger et al., 2004). During the summer months of quarter three, especially age 0 haddock were located in temperatures less than 11°C mainly in the northern North Sea (Asjes et al., 2016).

Our persistence analysis (the one based on fitting accounting for the covariates having the best goodness-to-fit) shows that juveniles and adult haddock persist at the same locations in the northern North Sea close to the UK coastline, with a more marked area fidelity for the juvenile haddock showing a large persistent patch (Figure 14). The centre of gravity tracked during the period 2001-2019 (Figure 15) show a small vertical oscillation of ca. 1 degree in latitude without a general trend, but an increasing proportion lying with the UK EEZ (Figure 16).
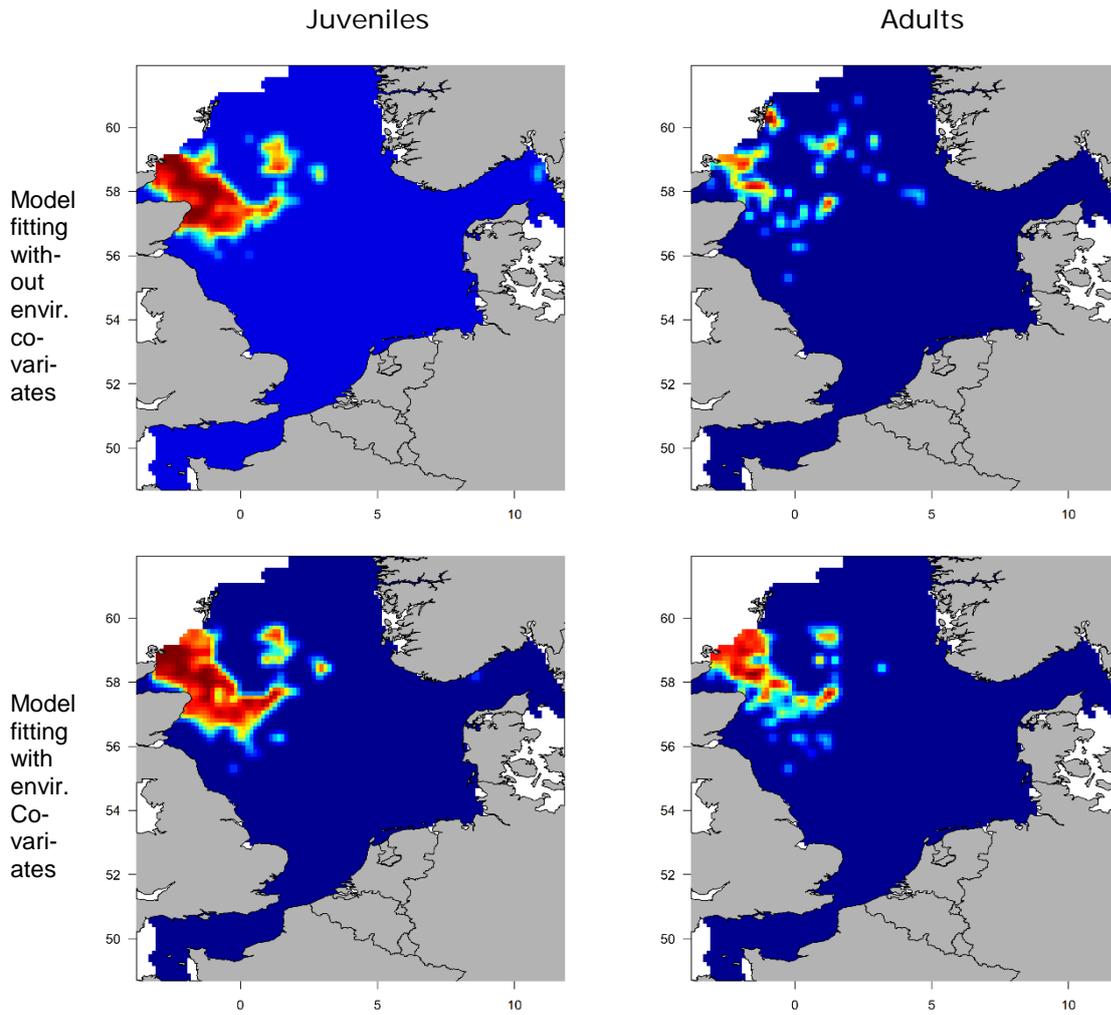
Figure 14. Persistent hotspots during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=6) of the North Sea haddock identified by the hotspot analysis. Top: model m1 no predictor, bottom: model m5 with covariates as predictor.
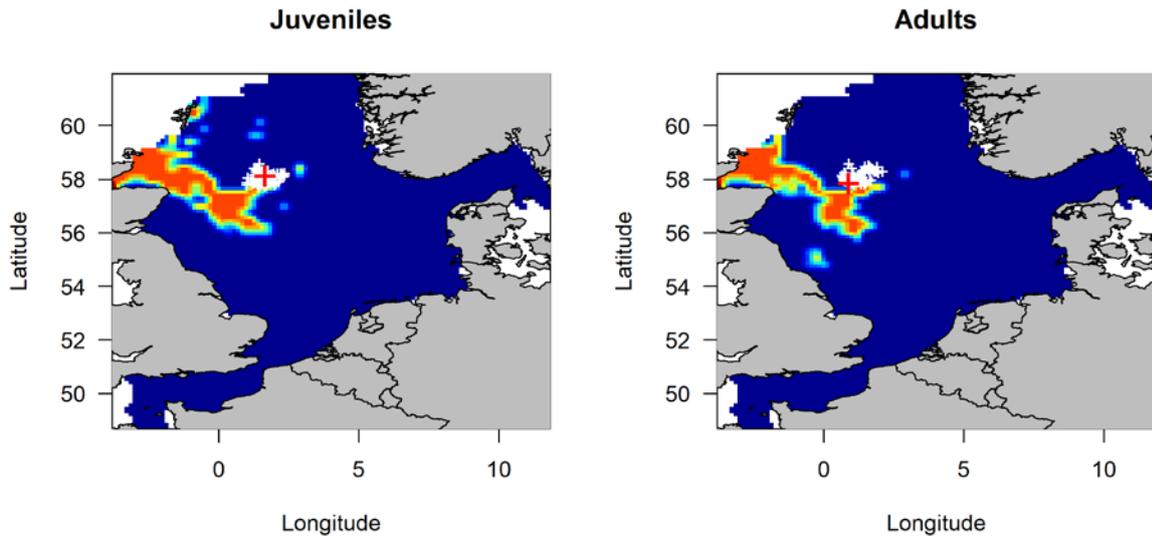
Figure 15. Quarterly centre of gravity of density hotspots for North Sea haddock during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=6) identified by the hotspot analysis after fitting model m5 with covariates as predictor. The largest "+" in red symbol marks the gravity point for the last time step, while others are in white. The color levels depict the hotspot areas of the last time step.
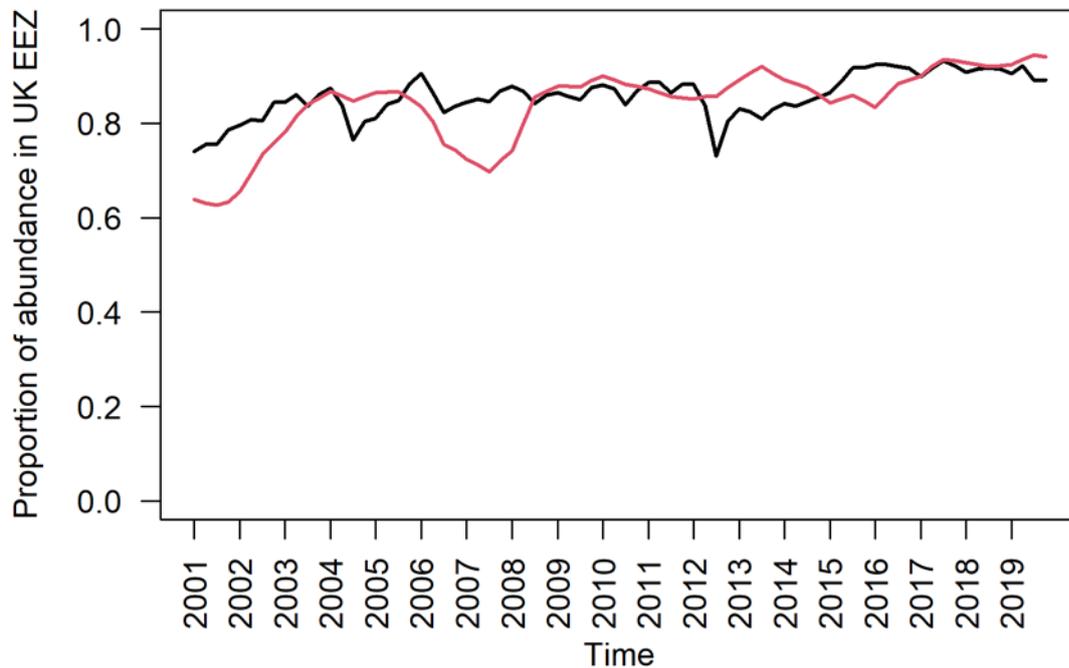
Figure 16. Quarterly based proportion of the abundance of juveniles' fish (in black) and adults (in red) for North Sea haddock falling inside the UK EEZ in the North Sea, deduced by the abundance field reconstruction described here.

Abundance hotspots of North Sea Plaice (*Pleuronectes platessa*)

Recruitment of various stocks of plaice, including the North Sea stock, is negatively correlated to temperature (Fox et al., 2000). For the North Sea stock, year-class strength is mainly determined by the survival during pelagic (egg and larvae) stages (van der Veer et al., 2000) and both egg mortality and larval survival until settlement on nursery grounds is linked to temperature in the spawning season (December to march, van der Land, 1991, van der Veer and Witte, 1999; van der Veer et al., 2000). In addition, in extremely cold years, cold induced mortality of predators on the nursery ground led to high survival of the 0 group and exceptional year classes (van derVeer 2000). Such extremely cold temperatures however caused a high mortality for the older individuals (Woodhead, 1964).

The higher body growth in the 60s and 70s and its reduction in the 80s was related to changes in the nutrient discharge in North Sea marine waters (Rijnsdorp and van Leeuwen, 1996, Rijnsdorp et al., 2004). Temperature positively affects the body growth of early settled young plaice, but negatively at a later stage during the summer (too warm), and its effect is not clear for the older fish (Teal et al., 2008, van Keeken et al., 2007). Body growth in the recent year has been density-dependent limited as there is an inverse relationship between population density and body growth (van der Sleen et al., 2018). Sex maturation is also linked to growth rate and temperature (Rijnsdorp, 1993a).

A shift in the depth distribution of young plaice was reported for the 1990s, whereas a shift to deeper waters of larger plaice (20 – 39 cm) was already apparent before the 1980s (van Keeken et al., 2007). This change in spatial distribution allowed the plaice to follow the ambient temperature that keeps within tolerance range while the North Sea ecosystem temperature increased (van Hal et al., 2016). North Sea coastal areas have become warmer and therefore allows for faster young plaice growth, but with higher energy demands (van der Veer et al., 2011). This increase in energy demands was coupled with a decreased benthic productivity (Tulp et al., 2008) which reinforced the need for plaice individuals to relocate.
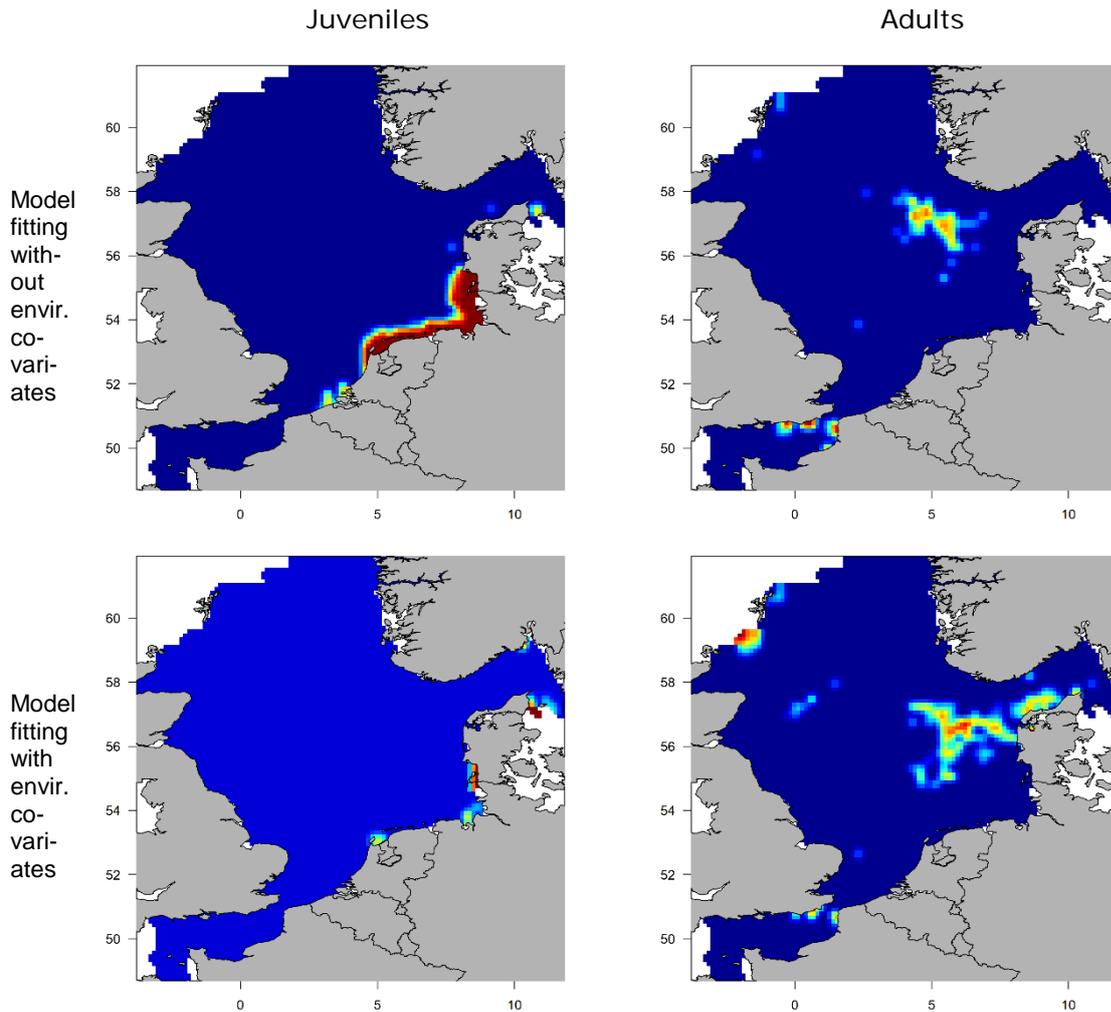
Figure 17. Persistent hotspots during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=7) of the North Sea plaice identified by the hotspot analysis. Top: model m1 no predictor, bottom: model m5 with covariates as predictor.

Our persistence analysis (the one based on fitting accounting for the covariates having the best good-ness-to-fit) shows adult plaice persist in the central North Sea, while juvenile plaice as small fidelity area nearshore (Figure 17). The gravity point tracked during the period 2001-2019 (Figure 18) shows no tendency for juvenile plaice but a westward movement for adult plaice, making the distribution of adult plaice farther over time from the Danish coast, but without clearly affecting the proportion of plaice lying within the UK EEZ (Figure 19).
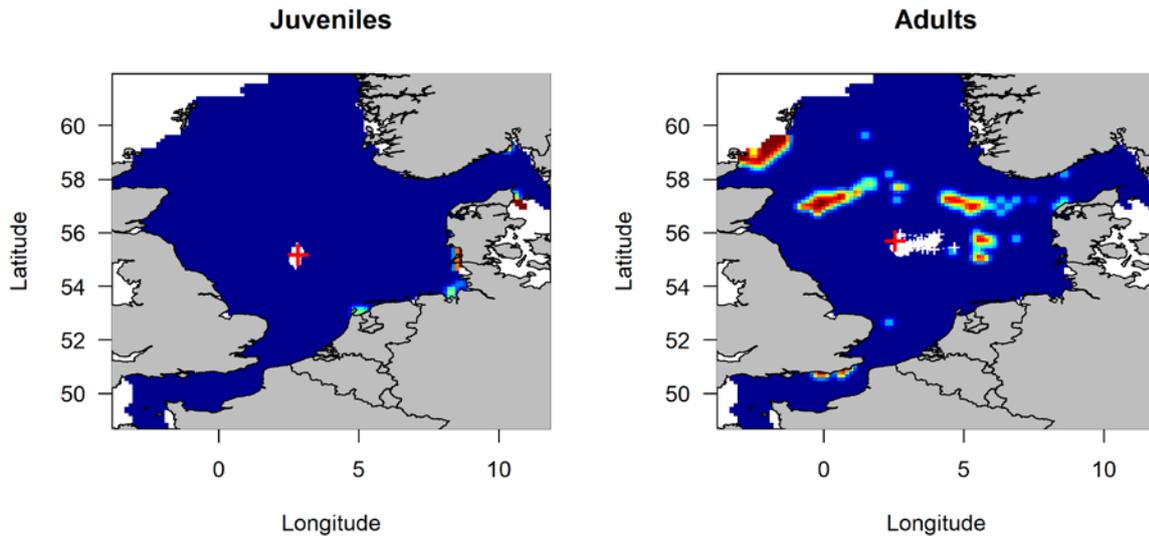
Figure 18. Quarterly centre of gravity of density hotspots for North Sea plaice during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=6) identified by the hotspot analysis after fitting model m5 with covariates as predictor. The largest "+" in red symbol marks the gravity point for the last time step, while others are in white. The color levels depict the hotspot areas of the last time step.
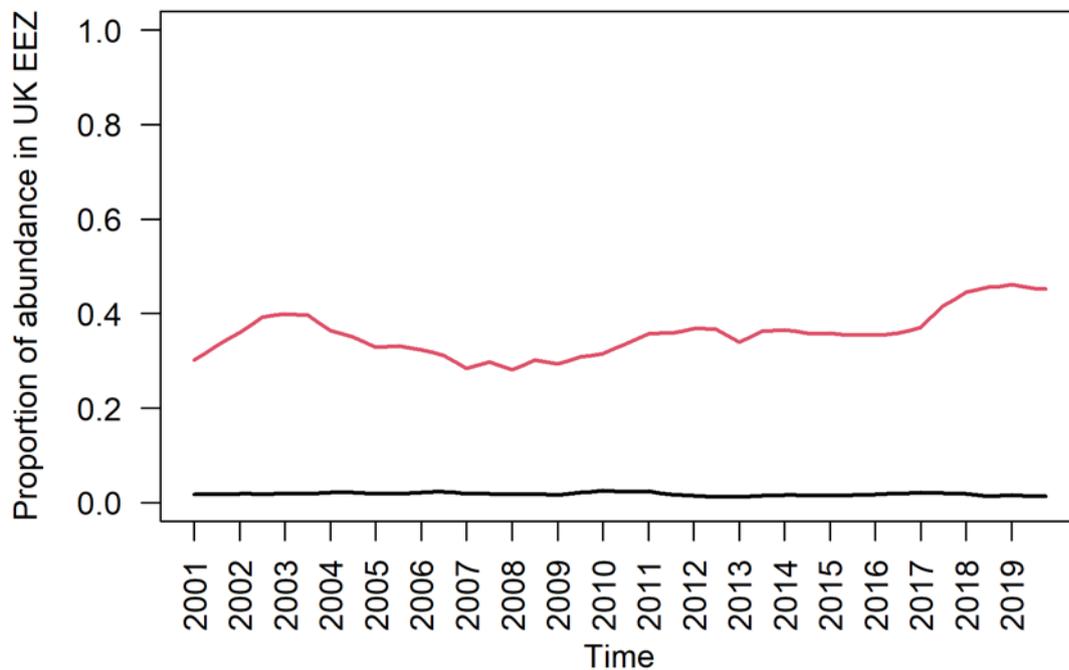
Figure 19. Quarterly based proportion of the abundance of juveniles' fish (in black) and adults (in red) for North Sea plaice falling inside the UK EEZ in the North Sea, deduced by the abundance field reconstruction described here.

Abundance hotspots of North Sea Sole (*Solea solea*)

No relationship between adult growth and temperature has been reported for the North Sea sole stock. On the contrary, for the smaller individuals, earlier spawning may result larvae encountering too low temperature, which reduces larvae survival before the settlement on the nursery grounds (van der Wolfshaar et al., 2022).

Animal body length after its first summer of growth showed an increasing trend in survey data (Teal et al., 2008). Larger body length likely results from both an increase in the growth rate at higher water temperatures and a longer growth period (Teal et al., 2008). The onset of sexual maturity is positively influenced by the growth rate during the juvenile phase (Mollet et al., 2007) and, thus, will also be influenced by temperature. In cold winters, there is higher mortality and sole aggregate in deeper-warmers pits.

Sole distribution has on average shifted to the south North Sea, due to higher winter temperature making the habitat more suitable for sole (Engelhard et al., 2011). However, in recent years, the northern limit of distribution in the North Sea has expanded northwards (Brunel and Verkempynck, 2018).
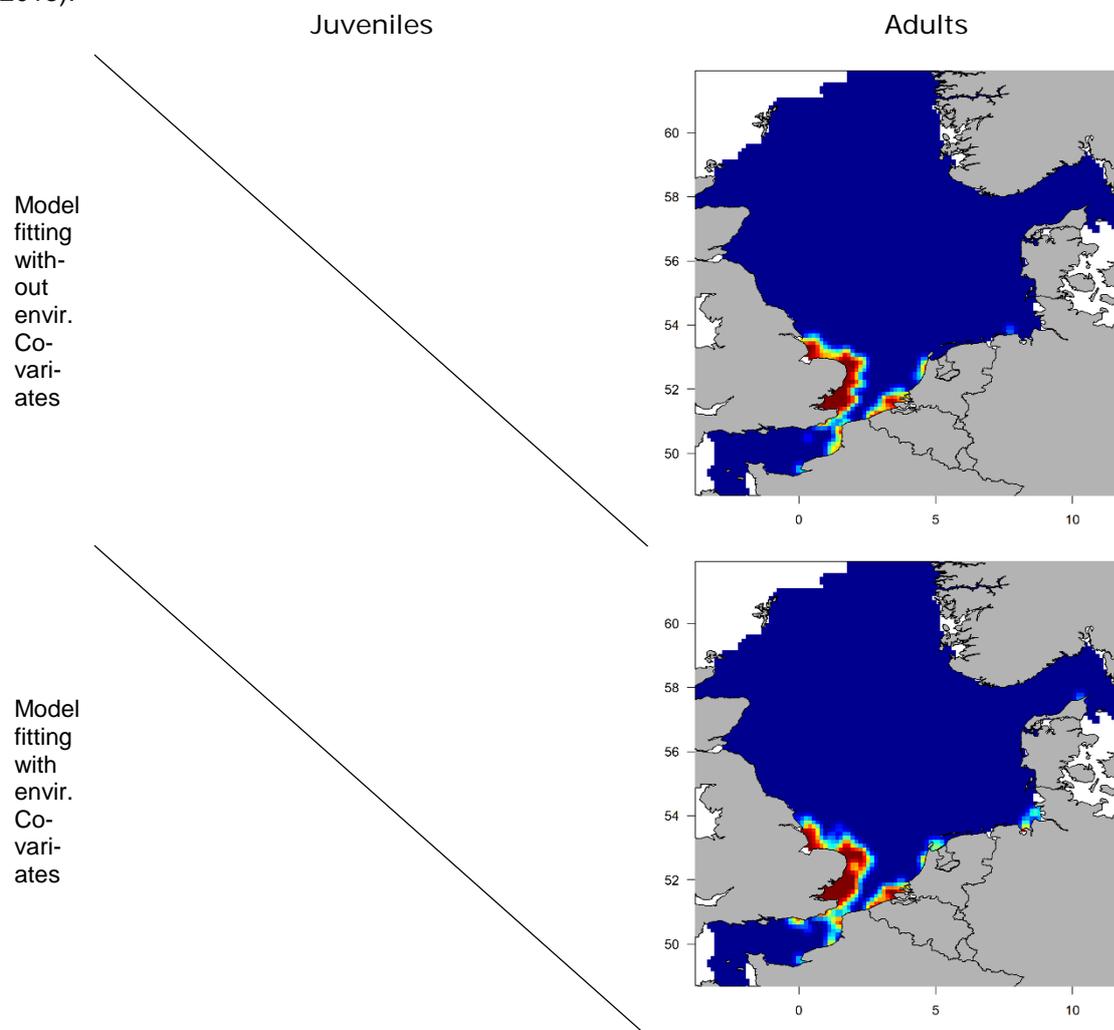
Figure 20. Persistent hotspots during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=3) of the North Sea sole identified by the hotspot analysis. Top: model m1 no predictor, bottom: model m5 with covariates as predictor.

Our persistence analysis (the one based on fitting accounting for the covariates having the best good-ness-to-fit) shows adult sole is persisting in very south North Sea along the coastline, while no infor-mation is available for juvenile fish (Figure 20). The gravity point tracked during the period 2001-2019 (Figure 21) does not show any tendency for adult sole, which demonstrates a very stable stock distri-bution over time for adult fish, and no change is observed in the proportion of the fish lying within the UK EEZ (Figure 22).
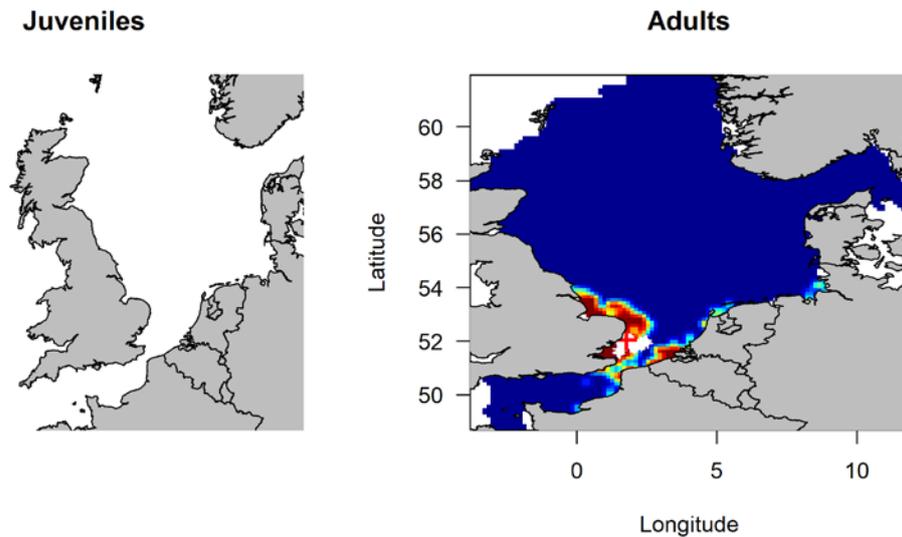
Figure 21. Quarterly centre of gravity of density hotspots for North Sea sole during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=3) identified by the hotspot analysis after fitting model m5 with covariates as predictor. The largest "+" in red symbol marks the gravity point for the last time step, while others are in white. The color levels depict the hotspot areas of the last time step.
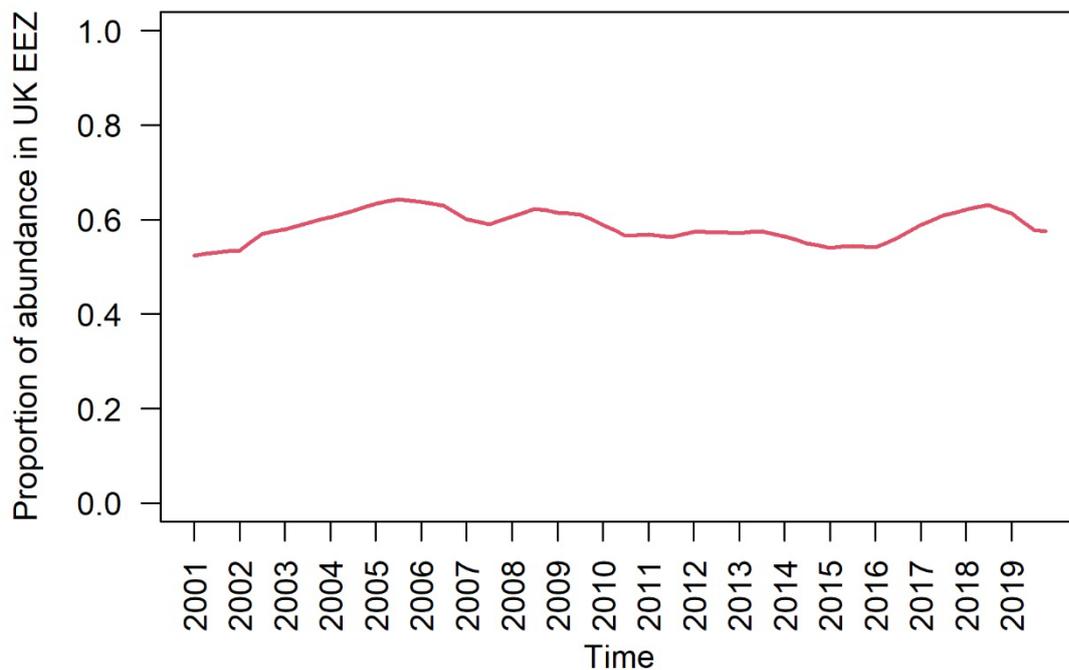
Figure 22. Quarterly based proportion of the abundance of juveniles' fish (in black) and adults (in red) for North Sea sole falling inside the UK EEZ in the North Sea, deduced by the abundance field reconstruction described here.

Abundance hotspots of North Sea dab (*Limanda limanda*)

In the North Sea, it is one of the most abundant species distributed over the whole area in depths down to 100m (fishbase). Dab and flounder are bycatch species of fleets targeting plaice of sole (ices.dk). Nevertheless the information is very seldom on the environmental determinants of this species o the spatial distribution and temporal dynamics (see Annexe), which make the below outcomes even more interesting.

Our persistence analysis shows that adult dab persist on some patches in the central North Sea (Figure 23) that are consistent over time given the centre of gravity tracked during the period 2001-2019 (Figure 24) show almost no displacement over time, and no change in proportion lying within the UK EEZ (Figure 25).
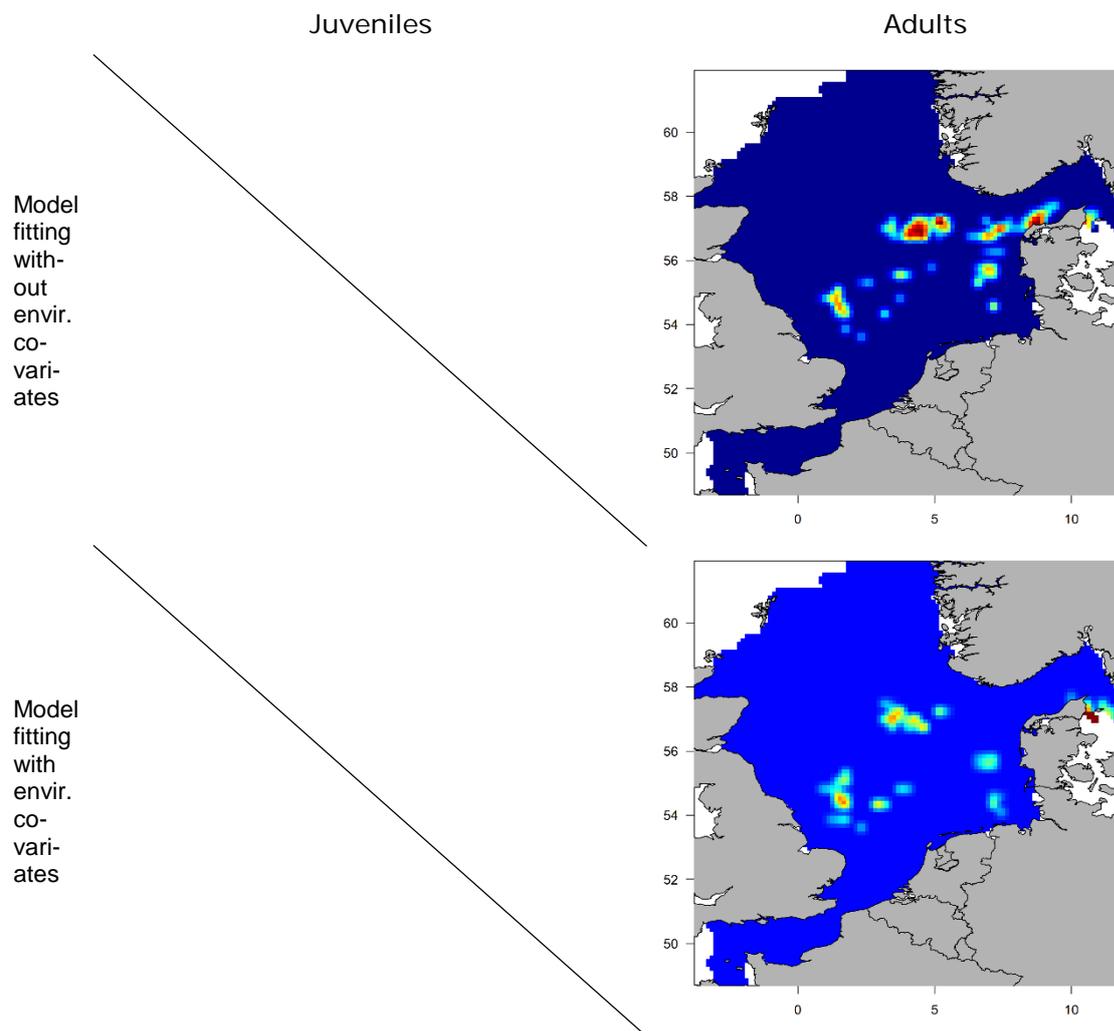
Figure 23. Persistent hotspots during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=3) of the North Sea dab identified by the hotspot analysis. Top: model m1 no predictor, bottom: model m5 with covariates as predictor.
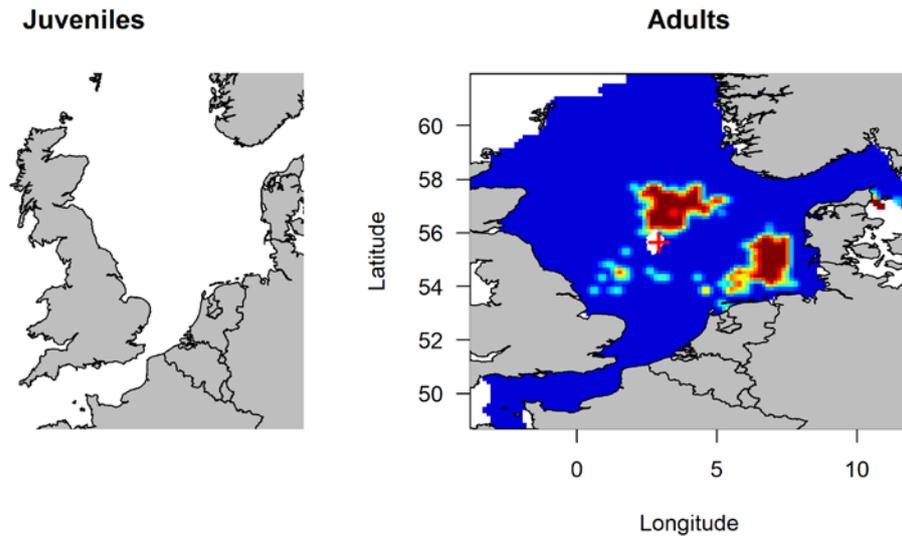
Figure 24. Quarterly centre of gravity of density hotspots for North Sea dab during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=3) identified by the hotspot analysis after fitting model m5 with covariates as predictor. The largest "+" in red symbol marks the gravity point for the last time step, while others are in white. The color levels depict the hotspot areas of the last time step.
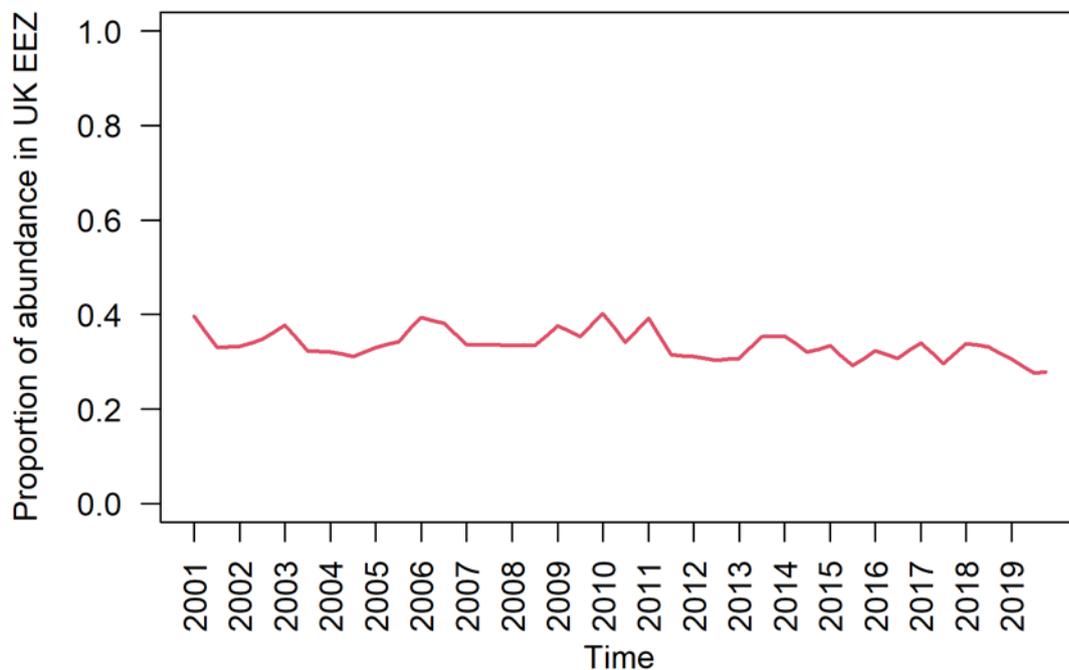
Figure 25. Quarterly based proportion of the abundance of juveniles' fish (in black) and adults (in red) for North Sea dab falling inside the UK EEZ in the North Sea, deduced by the abundance field reconstruction described here.

Abundance hotspots of North Sea Sprat (*Sprattus sprattus*)

Very little research on the relationship between sprat productivity (i.e., recruitment or growth) has been published. Sprat is short-lived and a substantial proportion of a cohort contribute to spawning within the first year of life (ICES 2018a). Sprat recruitment showed no relationship with temperature, but a positive relationship with salinity in Oct-Dec was reported by Akimova et al. (2016). Besides this, sprat larvae might flourish in relatively high salinities, as indicated by a recent un-published larval study, showing a spatial correlation between larval abundance and salinity (EMFF-BEBRIS 2021). However, it is not conclusive yet to what extent the link to salinity is direct (i.e., physiological) or whether salinity is merely an indicator of something else.

Historically, there is some indication that growth and recruitment success (recruitment per spawner biomass, R/S) was on average lower after the mid-1990s than before, indicating a shift for lower productivity (Clausen et al., 2018). However, in the early 1980s productivity was also relatively low, suggesting a temporary peak in productivity (rather than a regime shift) in the late 1980s when the spawner biomass was also low (i.e., density dependent regulation). Recently, a significant relationship between growth of the younger age-classes and stock size has been shown, further supporting of the presence of a density dependence effect in this stock (Lindegren et al., 2020).
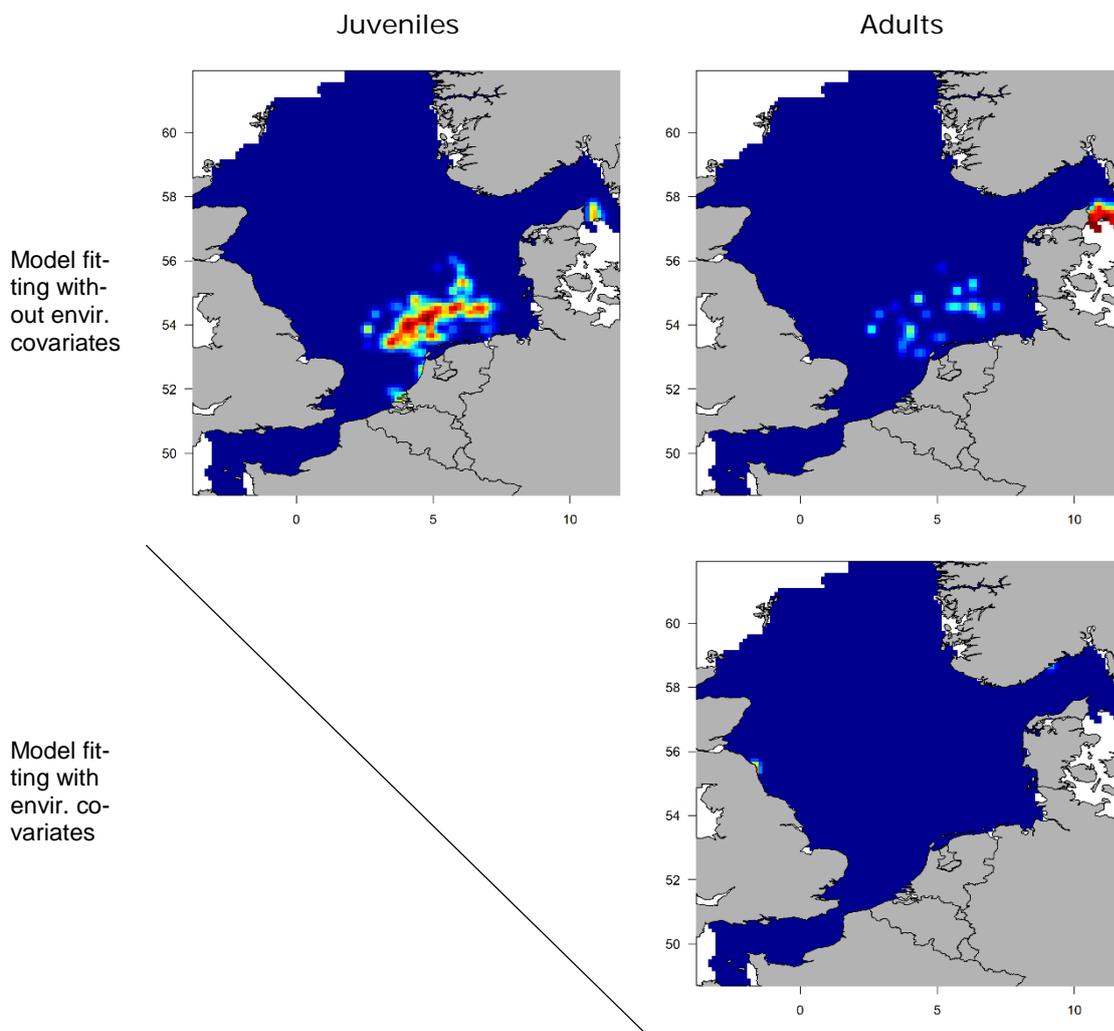
Figure 26. Persistent hotspots during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=2) of the North Sea sprat identified by the hotspot analysis. Top: model m1 no predictor, bottom: model m5 with covariates as predictor.

Our persistence analysis (the one based on fitting accounting for the covariates having the best good-ness-to-fit) shows that there is no obvious persistent area for sprat (Figure 26). The gravity point tracked during the period 2001-2019 (Figure 27) does not show any displacement, which indicates that the stock distributes quite differently across the North Sea over time. Proportion lying within the UK EEZ is however quite fluctuating even if a peak in the UK EEZ (for the only observed adult fish) has appeared during the 20y period during 2010 to 2012 (Figure 28).
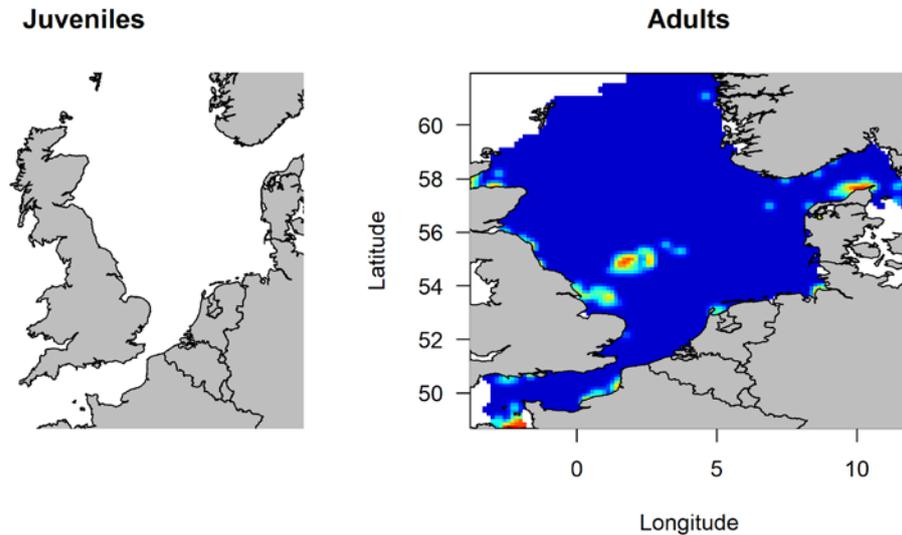
Figure 27. Quarterly centre of gravity of density hotspots for North Sea sprat during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=3) identified by the hotspot analysis after fitting model m5 with covariates as predictor. The largest "+" in red symbol marks the gravity point for the last time step, while others are in white. The color levels depict the hotspot areas of the last time step.
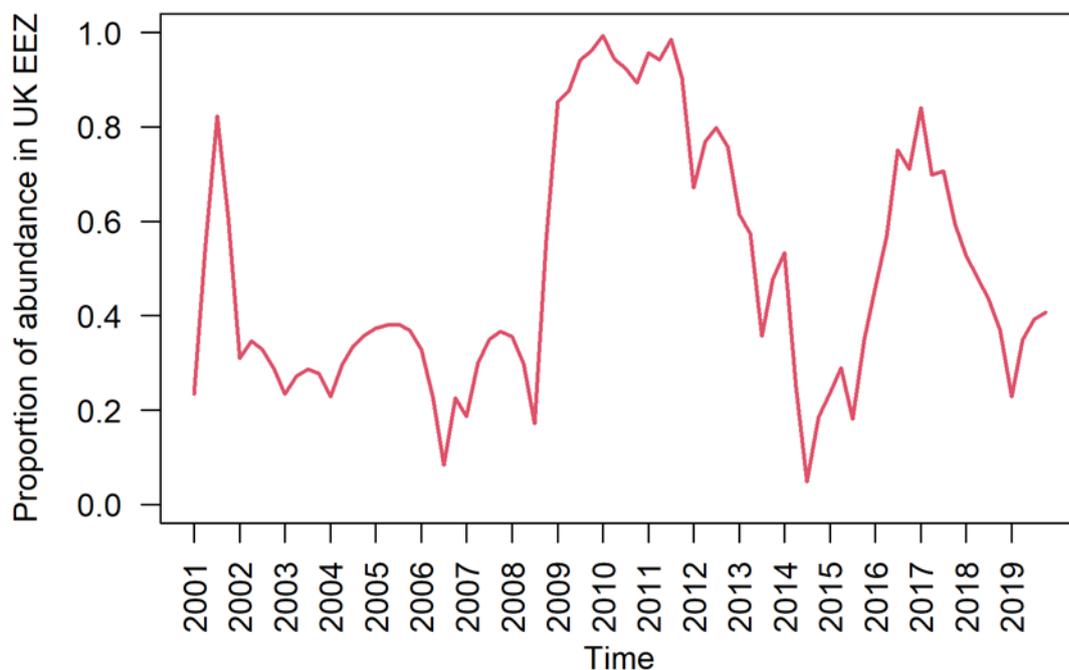
Figure 28. Quarterly based proportion of the abundance of juveniles' fish (in black) and adults (in red) for North Sea sprat falling inside the UK EEZ in the North Sea, deduced by the abundance field reconstruction described here.

Abundance hotspots of North Sea Herring (*Clupea harengus*)

There is a wealth of literature linking climate variables to the potential impact on widely distributed herring stocks. The link with temperature can be variable and is often stock specific. For example, a positive relationship between high temperatures and good recruitment has been observed for the Norwegian Spring Spawning herring stock (Bogstad et al., 2013; Fiksen and Slotte 2002). In contrast, increased temperature could have changed plankton community, decreasing North Sea herring larval survival (Payne et al., 2009). This was suggested to be a driver of the recruitment regime shift observed around the 2000s. Recruitment was also shown to be correlated with the Atlantic multidecadal oscillation (Gröger, Kruse, and Rohlf 2010).

The link between climate change and biological parameters is more tenuous. Brunel and Dickey-Collas (2010) tested the change of van Bertalanffy parameters as a response to climate change across a range of herring stocks. It was found that temperature correlated negatively with von Bertalanfy Linf and positively with k, meaning that the adult body length is reduced but reached earlier in adult life. Clausen et al. (2018) identified a negative of climate change on both recruitment and growth (using *Calanus finmarchicus* abundance as proxy). Hunter et al. (2019) showed significant relationship in specific areas at specific ages for herring for both growth and maturation (L50).
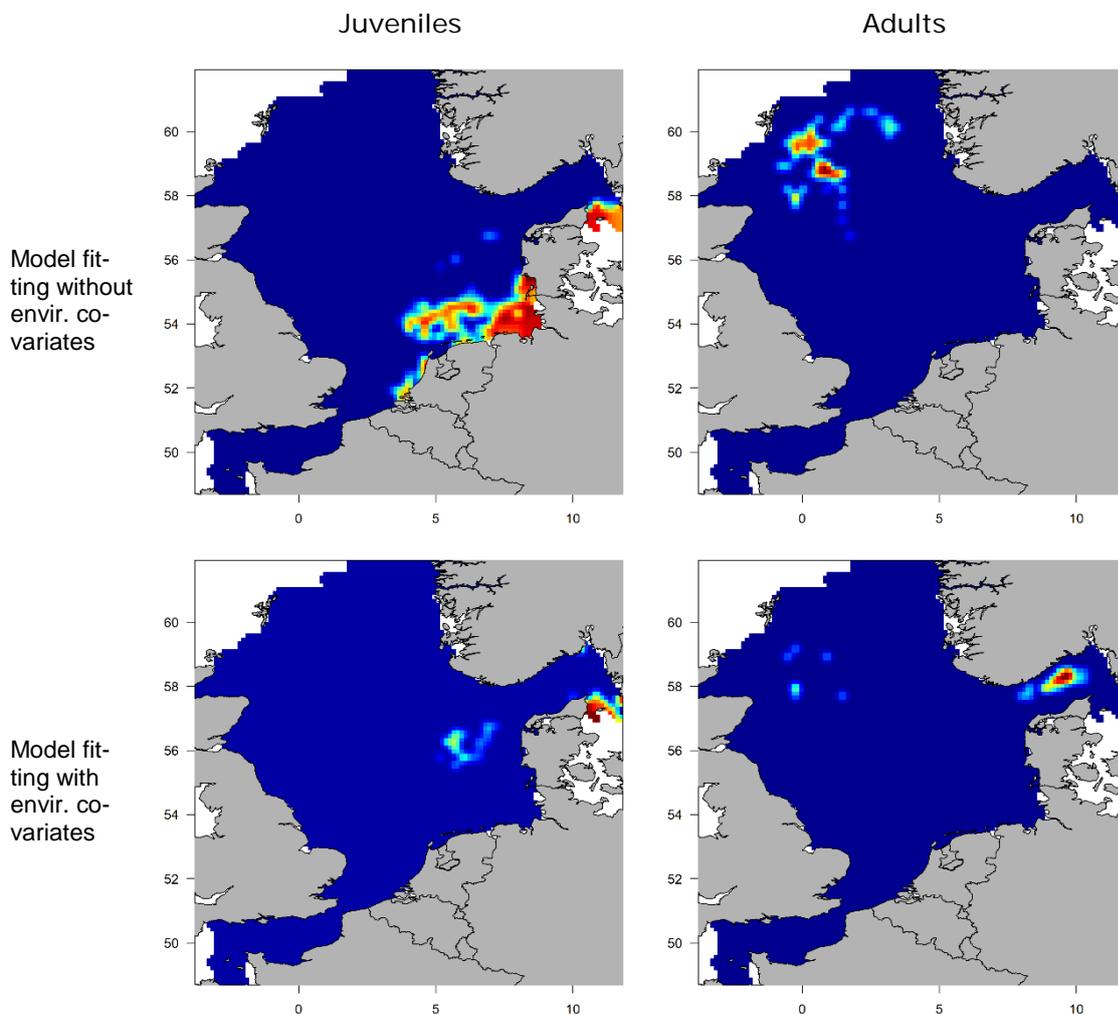
Figure 29. Persistent hotspots during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=4) of the North Sea herring identified by the hotspot analysis. Top: model m1 no predictor, bottom: model m5 with covariates as predictor.

Our persistence analysis (the one based on fitting accounting for the covariates having the best good-ness-to-fit) shows that both juveniles and adult herring has no obvious persistent density areas in the North Sea but juvenile might persist more likely close to the Danish shore, including the Skagerrak (Figure 29). The gravity point tracked during the period 2001-2019 (Figure 30) oscillate over 2 degree in latitude and might show a trend toward higher latitude over the time period examined (Figure 30). Proportion of herring lying within the UK EEZ shows quite regular oscillations over years, at least for the observed adult fish (Figure 31).
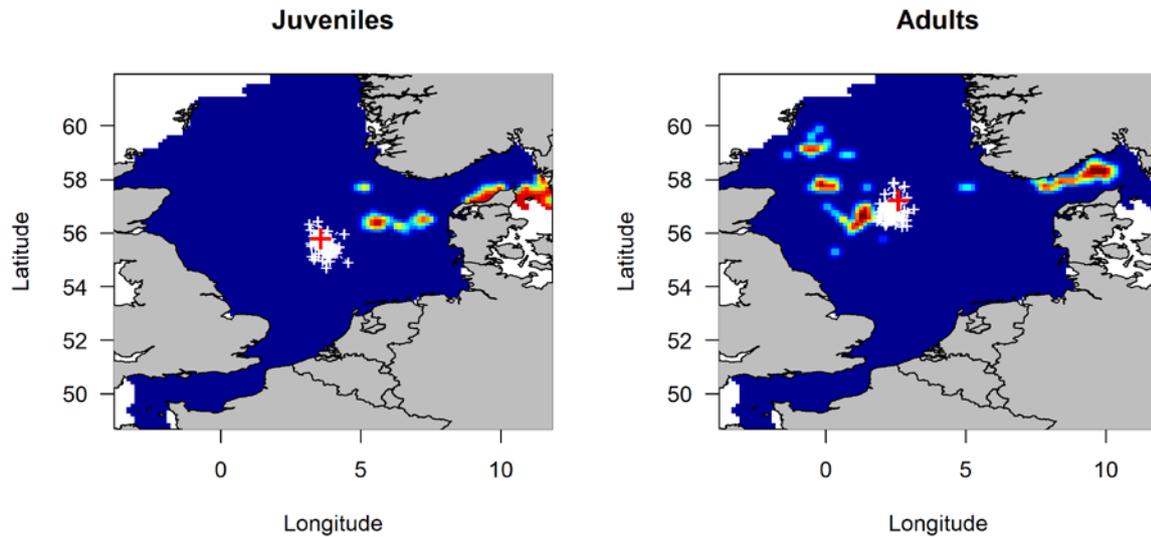
Figure 30. Quarterly centre of gravity of density hotspots for North Sea herring during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=4) identified by the hotspot analysis after fitting model m5 with covariates as predictor. The largest "+" in red symbol marks the gravity point for the last time step, while others are in white. The color levels depict the hotspot areas of the last time step.
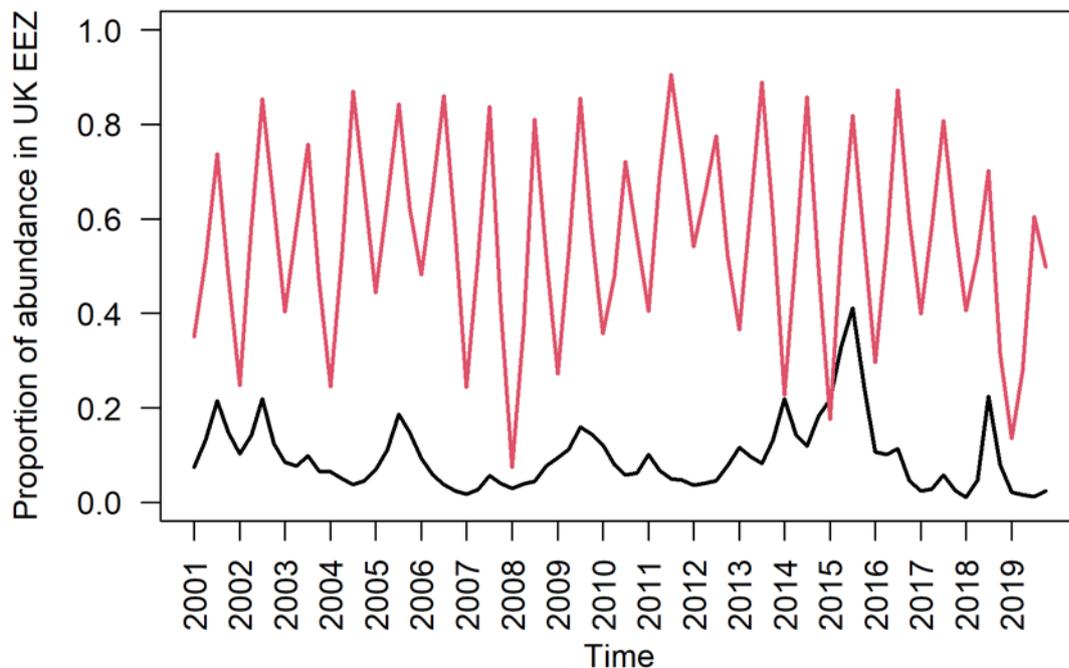
Figure 31. Quarterly based proportion of the abundance of juveniles' fish (in black) and adults (in red) for North Sea herring falling inside the UK EEZ in the North Sea, deduced by the abundance field reconstruction described here.

Abundance hotspots of North Sea Whiting (*Merlangius merlangus*)

Compared to other gadoid stocks like cod and haddock, whiting is reported to benefit from increasing temperatures (Zheng et al. 2002, Loots et al. 2011). Spatial distribution was related to spatial patterns detected for SST, yet changing during the year. During winter and spring, the abundance of whiting was higher within the path of the Atlantic current than in the surrounding areas in the northern North Sea. The longitudinal distribution might change in the future for whiting, and Hadley SST and the Atlantic multidecadal Oscillation (AMO) index were identified to be significant predictors for westward shifts in distribution. Besides this, Whiting recruitment showed a statistically significant positive relationship to temperature.
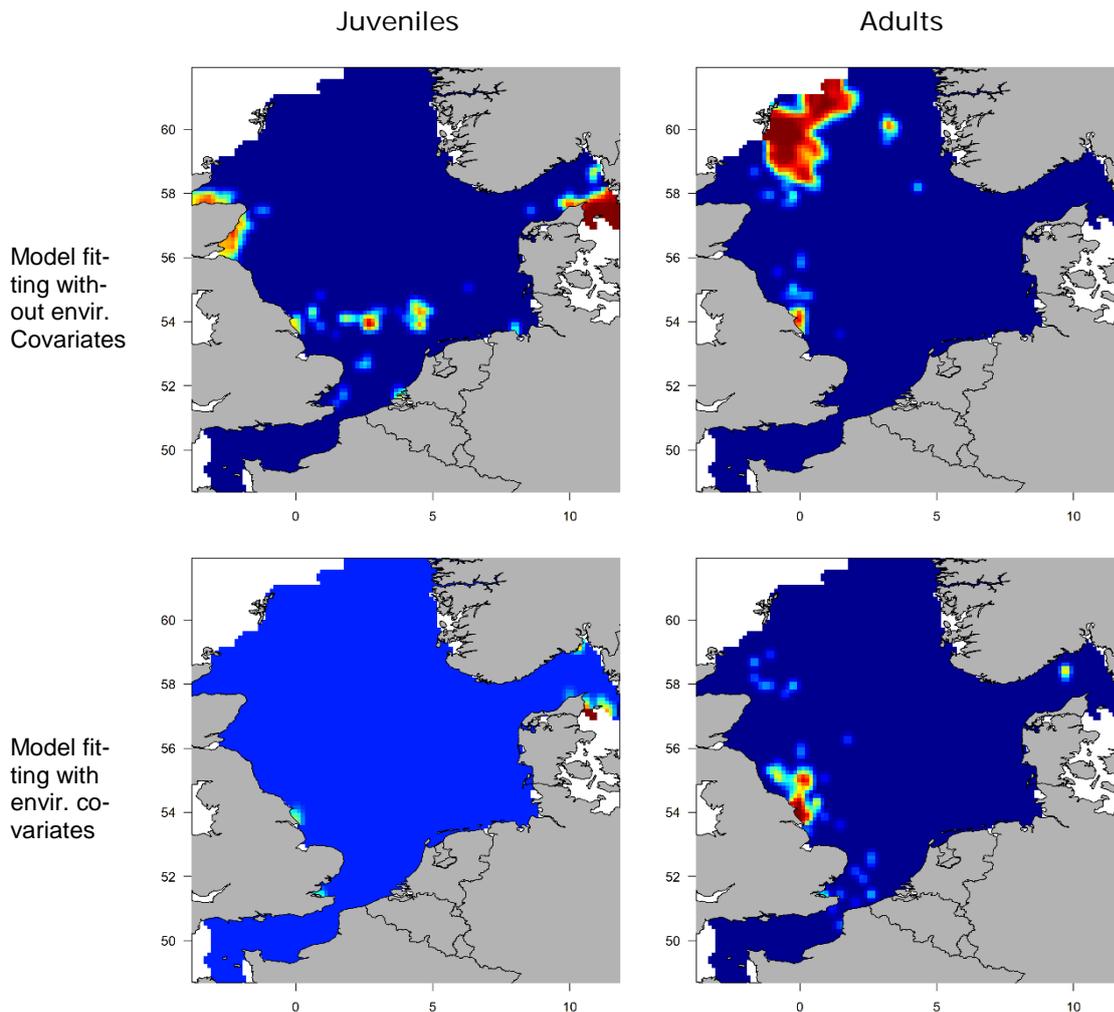
Figure 32. Persistent hotspots during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=5) of the North Sea whiting identified by the hotspot analysis. Top: model m1 no predictor, bottom: model m5 with covariates as predictor.

Our persistence analysis (the one based on fitting accounting for the covariates having the best goodness-to-fit) shows that juveniles does not distribute specifically to the same areas over time. Adult whiting on the contrary distribute persistently to northern part of the North Sea and in some spots on the UK coastline (Figure 32). The gravity point tracked during the period 2001-2019 (Figure 33) does not show a marked movement over time, indicating the hotspots for adult have not moved within the time window examined. Proportion of juveniles and adults fish lying within the UK EEZ has also been

quite constant and high for the adults but increasing for the juvenile fish over the 20y period (Figure 34).
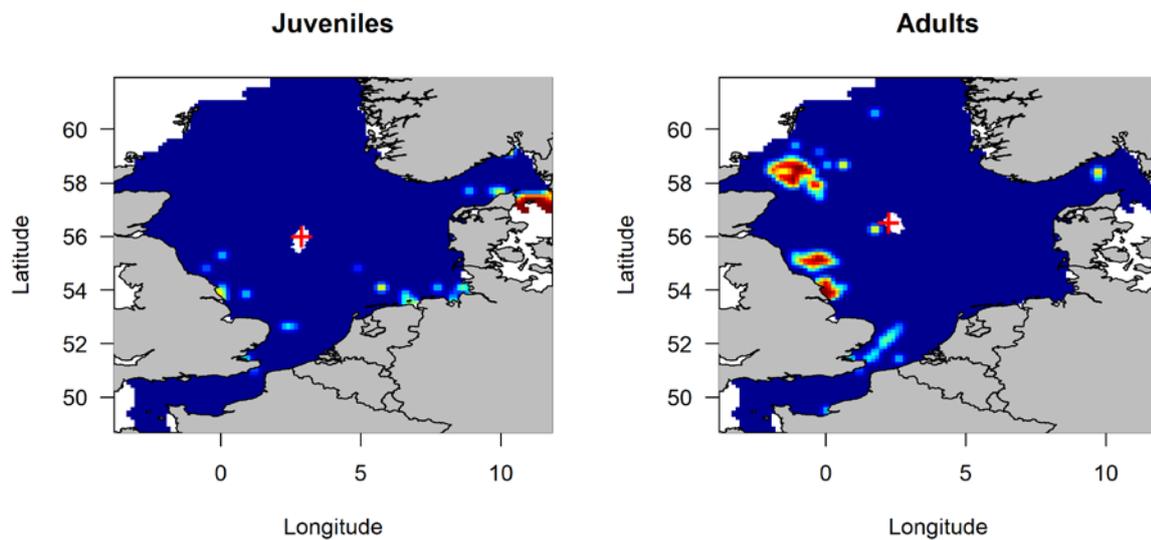
Figure 33. Quarterly centre of gravity of density hotspots for North Sea whiting during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=5) identified by the hotspot analysis after fitting model m5 with covariates as predictor. The largest "+" in red symbol marks the gravity point for the last time step, while others are in white. The color levels depict the hotspot areas of the last time step.
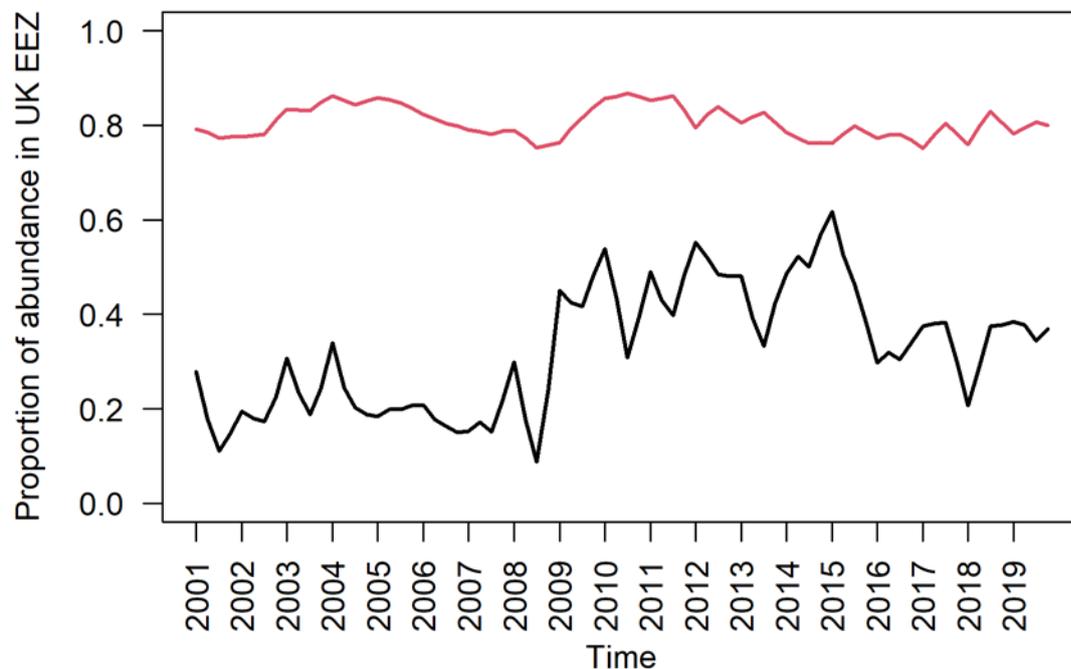
Figure 34. Quarterly based proportion of the abundance of juveniles' fish (in black) and adults (in red) for North Sea whiting falling inside the UK EEZ in the North Sea, deduced by the abundance field reconstruction described here.

Abundance hotspots of North Atlantic Mackerel (*Scomber scombrus*) in the North Sea

Mackerel is not a fish stock attached to the North Sea as such but is a migratory species that distribute widely through the Northeast Atlantic far beyond the North Sea (see the latest data from the IESSNS survey in ICES (2020a). It has been discussed that spawning habitat for mackerel is linked to environmental variables such as temperature and salinity (Bruge et al 2016, Brunel et al. 2017), but there is also a strong geographical attachment (core spawning always around Porcupine and along the shelf edge), suggesting that mackerel spawns in areas associated with particular oceanographic features which have proven to lead to successful recruitment (Brunel et al. 2017).
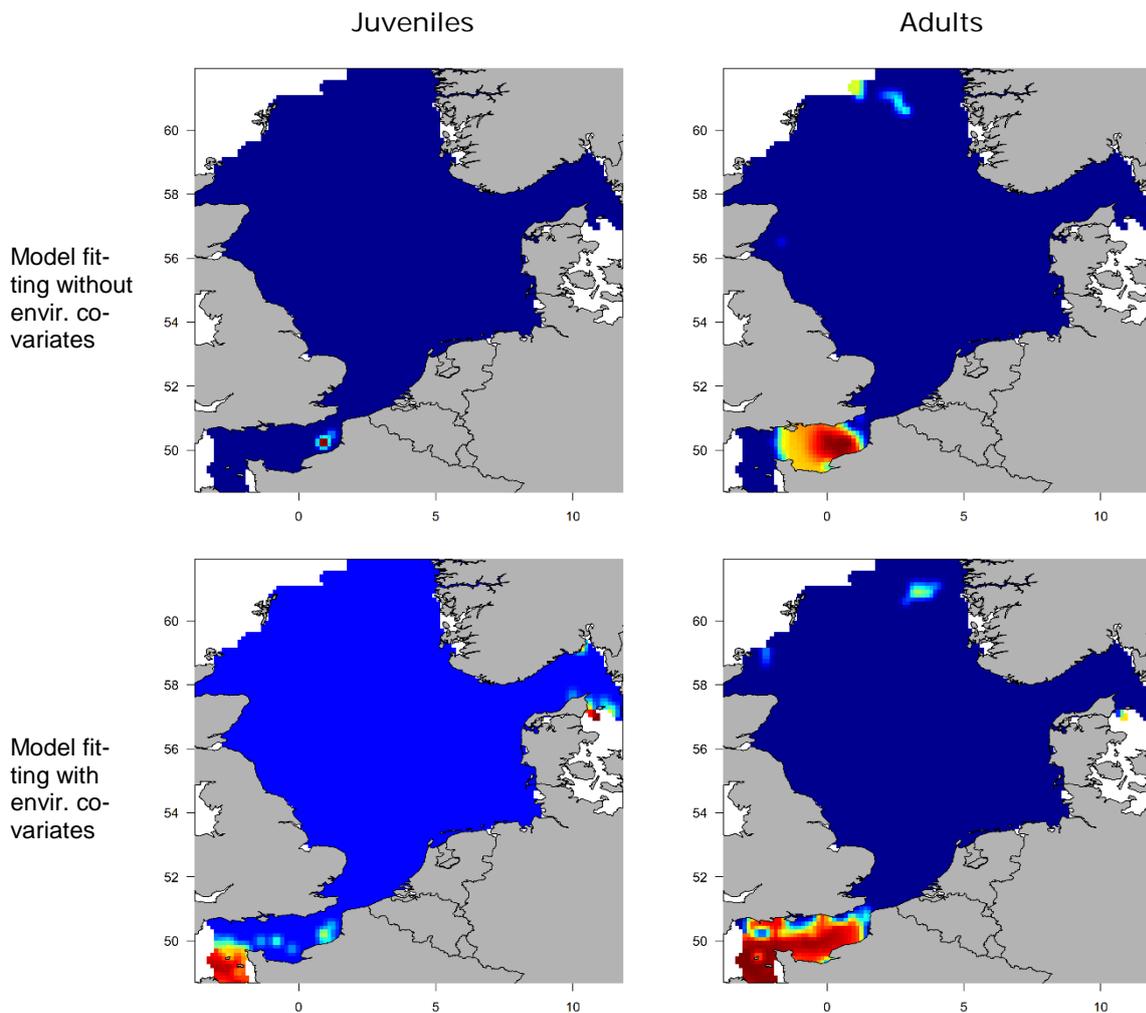
Figure 35. Persistent hotspots during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=6) of the North Sea mackerel identified by the hotspot analysis. Top: model m1 no predictor, bottom: model m5 with covariates as predictor.

Our persistence analysis (the one based on fitting accounting for the covariates having the best goodness-to-fit) shows that juveniles and adult mackerel does not persist in the central North Sea but rather at the limit North and south from the English channel (Figure 35), which is reflected in the gravity point tracked during the period 2001-2019 (Figure 36). The gravity trend is likely an artifact showing a change relative balance between presence of the mackerel north or south the area but mainly outside

the North Sea limits, which makes the indicator not very informative for the current species. The proportion lying within the UK EEZ is not constant and has been at its highest at the start of the time period during the 20y period (Figure 37).
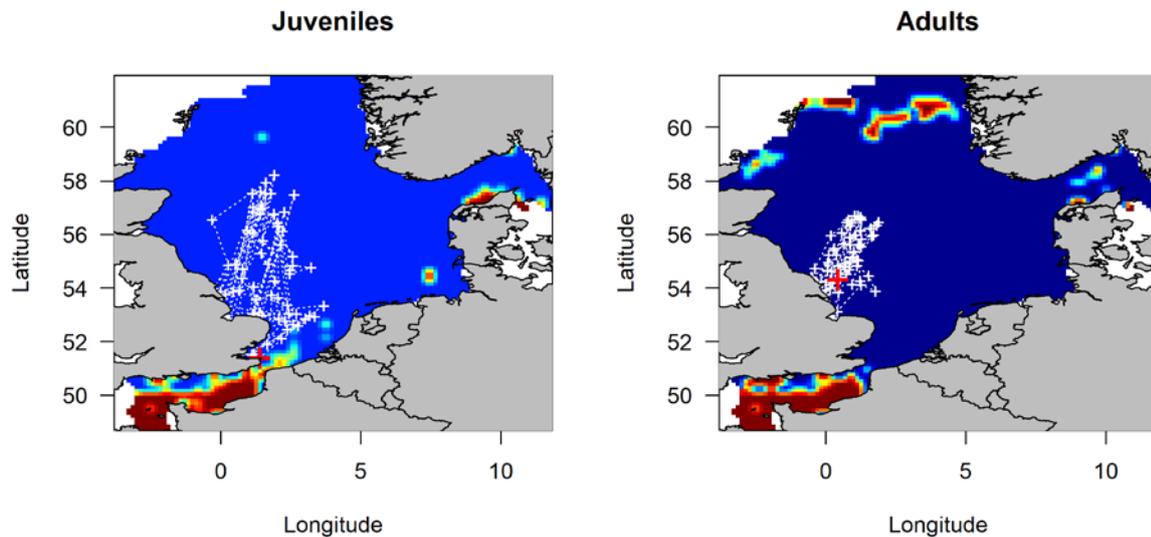
Figure 36. Quarterly centre of gravity of density hotspots for North Sea mackerel during the period 2001 to 2019 of left- juveniles, and right- adults (i.e. LG>=6) identified by the hotspot analysis after fitting model m5 with covariates as predictor. The largest "+" in red symbol marks the gravity point for the last time step, while others are in white. The color levels depict the hotspot areas of the last time step.
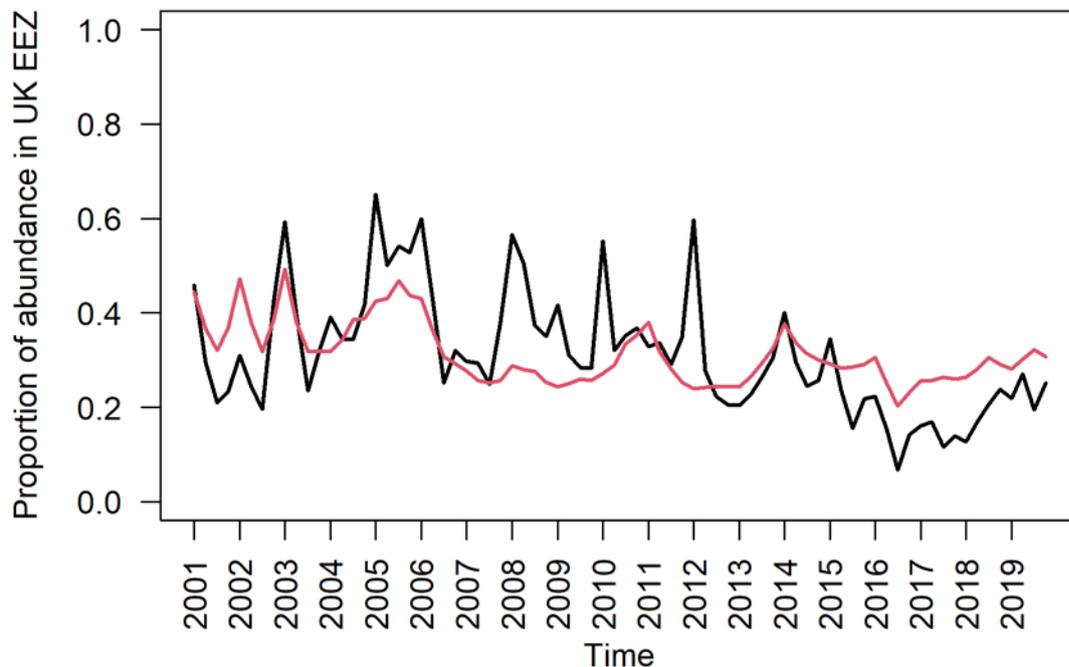
Figure 37. Quarterly based proportion of the abundance of juveniles' fish (in black) and adults (in red) for North Sea mackerel falling inside the UK EEZ in the North Sea, deduced by the abundance field reconstruction described here.

6. Projected changes in the North Sea environment

Extracted from Bastardie et al 2022 CINEA: An international team of 200 climate scientists in different research areas from all countries around the North Sea has recently published a North Sea Region Climate Change Assessment (NOSCCA). This report looked at past changes in the North Sea linked to climate change, and at projections for the next century (Quante and Colijn, 2016 North Sea region climate change assessment). A chapter is dedicated to the projected changes in the North Sea physical environment and lower trophic levels (Schrum et al. 2016 Projected change – North Sea). A comparison of the different projections from a range of studies conducted with different regional models is presented. Coherent findings from the climate change impact studies reviewed in this chapter include overall increases in sea level and ocean temperature, a freshening of the North Sea, an intensification of the ocean acidification and a decrease in primary production. However, the study also points out the variability in the projections across models, regarding the amplitude and spatial pattern of the projected changes in sea level, temperature, salinity and primary production. The report also notes that the large natural variability in the North Sea climate (both interannual variations and multi-decadal climate modes) could have played a prominent role in the projections, in addition to climate change impacts. Especially until 2030, the expected changes are minor and inter-annual variability finally plays a larger role than overall trends.

In the present study, projections of the North Sea environment are only used for illustrative purpose. Due to the lack correlation study for making the linkages between fish stocks and environmental drivers more explicit in our present project, no attempt is made yet to use oceanographic models in background to link to the modelling of future dynamics of fish stocks quantitatively. Instead, in most cases, physical environmental models are used to qualify the more likely direction (increase/decrease), the amplitude and, if available, the spatial heterogeneity of future changes in a set of relevant variables. These have been used as a basis to formulate empirical scenarios for the biology of the fish-stocks (see a CINEA study reported in Bastardie et al 2022).

SST and primary production

The projections available from the CERES project indicate an increase in the North Sea water temperature by 2°C by 2100 for the climate change scenario RCP 8.5 and by 1°C under the scenario RCP 4.5. This would mean an increase of 0.125°C and 0.25°C for the scenarios RCP 4.45 and RCP 8.5 respectively for the simulations in the present study (2020 to 2030).

Projections also indicate a decrease in the primary production in the North Sea (Figure 38) with a more marked reduction in the northern regions. In the coastal areas, especially along the eastern part of the North Sea, projections foresee a slight increase in the primary production, due to an increase in river run-off and an increase in nutrient availability in the marine waters for the primary producers. Overall, until 2030 predictions suggest a somewhat higher variability than the situation between 2000 and 2020, but the overall trend is not evident (Figure 38).
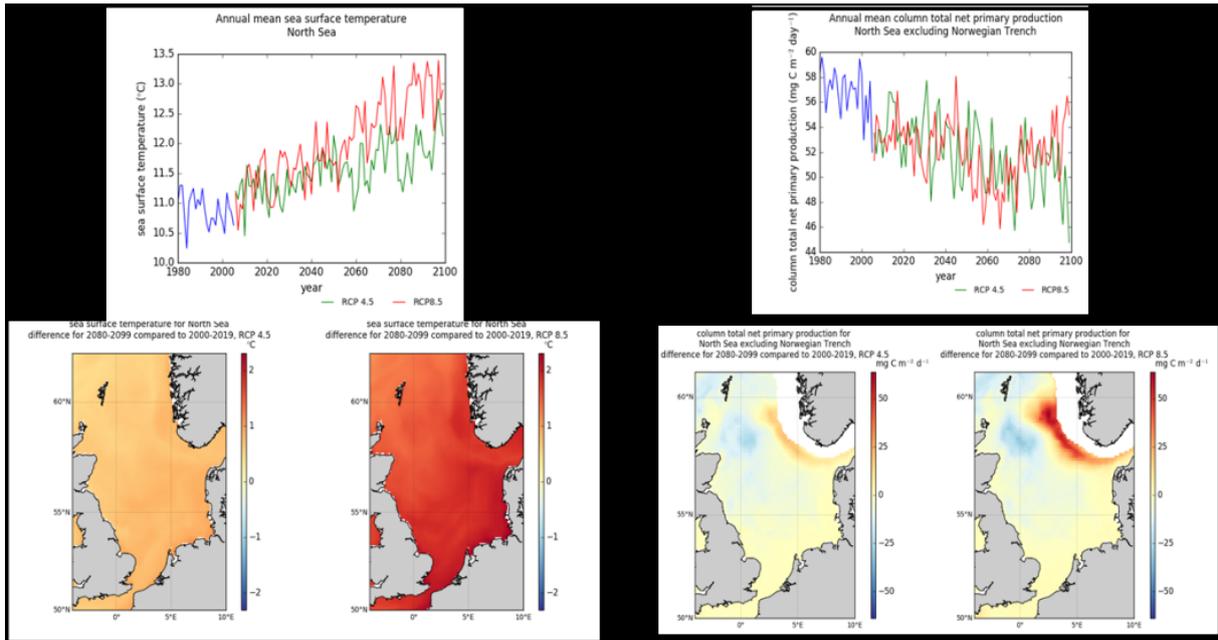
Figure 38. Trend for the average North Sea a) temperature, b) primary production (mgC/m2/day) and their comparison between present and future temperature under both RCP 4.5 and 8.5. (source: CERES project, https://ceresproject.eu/)

Storminess

Regional climate models do not indicate an increase in the frequency of storms, but regional models are quite uncertain. Storms are projected to have more northerly tracks, but the uncertainty is also high. However, it is expected that storms could be of higher intensity, and bring more precipitation in the North Sea catchment area.

Assumption for future changes in fish stock biological features

Given the information collated for each species, it is possible to assume change in biological features (recruit, growth, spatial distribution) induced by the climate change effects (Table 7, from Bastardie et al 2022 CINEA), that will be further used in a subsequent simulation study to anticipate the effect of such changes at the population level.

Table 7. List of possible assumptions for long-term effects on fish stocks induced by a changing climate (extracted from a CINEA study reported in Bastardie et al. 2022)

Stock	Biological function	change	Magnitude of the change	
			Most likely scenario	**Worst case scenario**
Plaice	Recruitment	Decrease in recruitment as higher temperature is associated with higher mortality for early life stages recruitment-temperature correlation published in 2000 was revisited with new data and remains significant	based on a Beverton and Hold stock-recruitment model with temperature as covariate (GLM model). Future recruitment driven with RCP4.5	based on a Beverton and Hold stock-recruitment model with temperature as covariate (GLM model). Future recruitment driven with RCP8.5

	Distribution	All size-ranges continue to move northwards and to deep areas (for adults) to avoid areas that have become too warm		
sole	Growth	Faster growth for young fish due to Longer growing season and higher growth rate. A 1C° increase in temperature leads to a 0.58 cm increase in the body length at the end of the first year, no effect on growth in older ages.	The resulting changes in weight at age over the next 10 years for a temperature increase corresponding to RCP 4.5 are minimal (0.08 cm over 2020-2030) and are negligible, compared to recent interannual variations. Therefore these changes in growth are not implemented	most likely scenario
	maturation	Earlier maturation due to faster growth at young ages	Not implemented since changes in growth are judge negligible based on published correlations	most likely scenario
	Distribution	Centre of gravity moves southwards as habitat improves with the less frequent cold winters range expands to the north (habitat becomes suitable)		
Saithe	Recruitment	No direct temperature effect, but effects of sea currents. Recruitment has shown an overall decreasing trend over time with the lowest levels in the past 10 years.	Environmentally-mediated stock recruitment relationship (EMSRR) linked to patterns in currents and salinity. Future recruitment driven with RCP4.5. EMSRR developed during Pandora.	Environmentally-mediated stock recruitment relationship (EMSRR) linked to pattern in currents. Future recruitment driven with RCP8.5. EMSRR developed during EU PANDORA
	Growth/ Mean weight at age	No direct temperature effects, but density dependent growth rates and competition with hake. Mean weight at age showed a decreasing trend for ages 6 and older between the late 90ies and 2010, but the trend has stopped and has been reversed in recent years. Ages 3-5 stable over time.	Mean weight at age stays at the levels observed in the last 10 years as the northern hake stock seems to stabilize at high level and the saithe stock will likely stay in the next 10 years at levels observed in recent years given its current low productivity.	As worst-case scenario mean weight at age for ages 6+ is scaled downwards to low levels observed between 2000 and 2010 by assuming further increasing competition with hake and associated

				stronger density dependent effects.
Anglerfish	Productivity	Overall, anglerfish has a relatively narrow temperature tolerance but the optimum temperature is higher than for boreal species like herring, cod and haddock. For the southern part of the North Sea (and English Channel) predictions show a decreasing abundance of L. piscatorius in IPCC 4.5 and 8.5 scenarios. However, most of the stock is already now concentrated in the northern part Overall, biomass in the North Sea showed an increasing trend until the 90ies when this trend leveled off. In recent years again an increasing trend is observed with some decline in the last two years. Lophius budegassa that is more associated to southern areas increased in the North Sea in recent years, but still on a low level.	Given that the optimum temperature for anglerfish is higher than for boreal species like herring, cod or haddock and , the most likely scenario for the next 10 years is that in general the current situation prevails in the northern part of the North Sea where most of the anglerfish stock is concentrated already now.	Given that the optimum temperature for anglerfish is higher than for boreal species like herring, cod or haddock, the worst-case scenario for the next 10 years is that that a minor decrease in productivity (-5%) occurs.
Whiting	Recruitment	Increase in recruitment with higher temperatures. Opportunistic predator in larval and juvenile stage (does not much depend on certain prey like cod larvae).	Environmentally-mediated stock recruitment relationship (EMSRR) linked to temperature. Future recruitment driven with RCP4.5. EMSRR developed during Pandora	
Haddock	Recruitment	Stock driven by recruitment spikes. Unclear mechanisms behind these spikes. In general, lower recruitment levels and spikes became lower after 2000.	Recruitment dynamics (frequency of spikes and recruitment level) stay as observed after 2000	See under shock scenarios
Herring	Recruitment	Relationship between surface temperature and recruitment (negatively correlated)	Implement a Ricker formulation with surface temperature as covariate.	
	Growth	Relationship between growth rate and temperature (negatively correlated).	Implement projection with von bertalanffy parameters indexed on surface temperature.	
	Spatial distribution	Decrease in abundance in areas IVb and IVc while remaining constant in the northern part of the North Sea	Indirectly taken into account in recruitment scenarios and low catchability for fleets and metiers mainly operating in the	Indirectly taken into account in recruitment scenarios and lower catchability (-10%) for fleets

			southern part of the North Sea.	and metiers mainly operating in the southern part of the North Sea.
Cod	Recruitment	Clear relationship between temperature and decreased recruitment although likely not a direct physiological effect. Recruitment at low level since 1998 despite some recovery in the northern part of the North Sea. Cod in the southern part of the North Sea depleted.	Environmentally-mediated stock recruitment relationship (EMSRR) linked to temperature. Future recruitment driven with RCP4.5. EMSRR developed during Pandora	Environmentally-mediated stock recruitment relationship (EMSRR) linked to temperature. Future recruitment driven with RCP8.5. EMSRR developed during Pandora
	Spatial distribution	Northward shift of cod in the North Sea	Indirectly taken into account in recruitment scenarios and low catchability for fleets and metiers mainly operating in the southern part of the North Sea.	Indirectly taken into account in recruitment scenarios and lower catchability (-10%) for fleets and metiers mainly operating in the southern part of the North Sea.
	Maturity	Strong increase in maturity at age especially for age 2 cod. May be related to temperature but also because of low population size or fisheries induced evolution	Use maturity ogive representing the most recent 10-year period.	Use maturity ogive representing the most recent 10-year period.
North Sea sprat	Recruitment	The published correlation between recruitment and salinity Akimova et al. (2016) was revised, using more recent data (see details in the report). The correlation was no longer significant wih the addition of 3 new years of data.	Since the publish recruitment-salinity correlation was found not to be robust, no long-term climate effect was imposed on recruitment.	Cf. most likely scenario.

7. Modelling the North Sea fisheries with DISPLACE

We used the DISPLACE modelling platform (Bastardie et al., 2014) as a comprehensive management strategy evaluation tool to assess how fish stocks and fisheries are affected by different spatial fishery management options under climate change scenarios. The core of DISPLACE is a spatial bio-economic model for simulating the movement of individual fishing vessel agents combined with an underlying spatial population dynamics model (Figures 39-42). In DISPLACE, individual agents optimize their decision-making on the fly depending on their given catch rates by zones and the expected cost to reach the zone and return to the harbour. Each vessel depletes the target stocks individually, which further depends on the gear type in use.
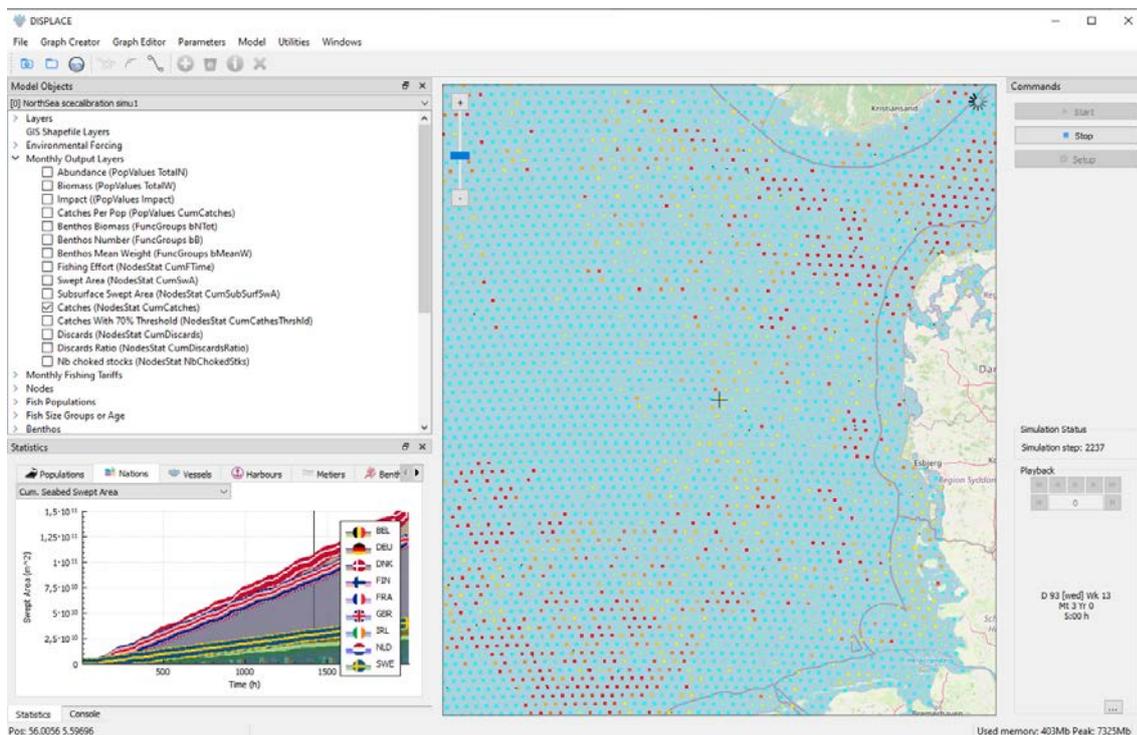
Figure 39. A random snapshot of the DISPLACE North Sea application showing the simulated accumulated catches by different North Sea nations including Denmark over "all species caught" layer on the map.
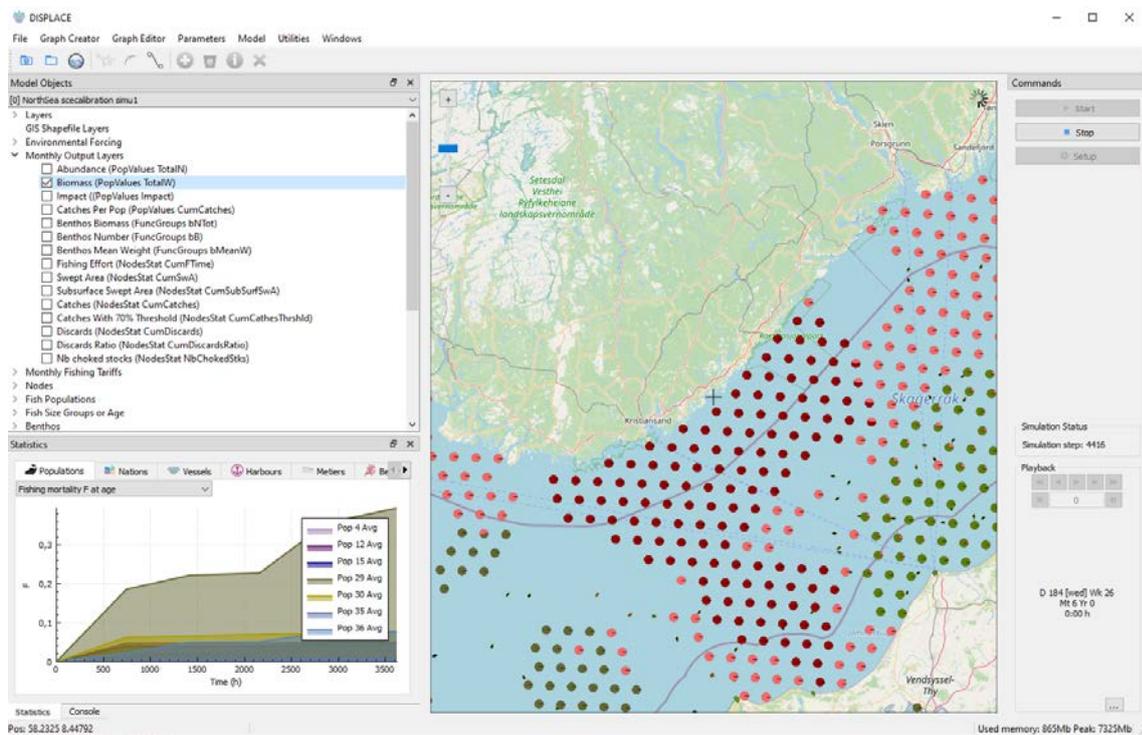
Figure 40. A random snapshot of the DISPLACE North Sea application showing the simulated biomasses (summed over all species simulated) on locations layer as pie charts on the map.
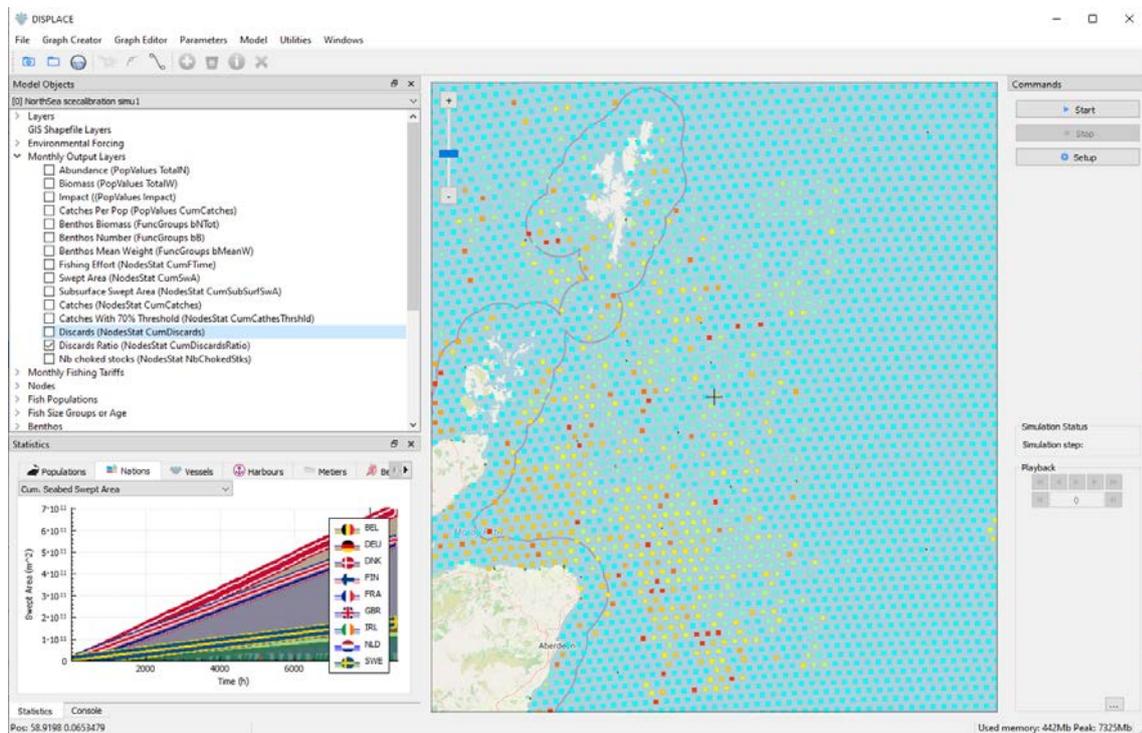
Figure 41. A random snapshot of the DISPLACE North Sea application showing the simulated discard ratio layer (for all simulated fisheries confounded) on the map.
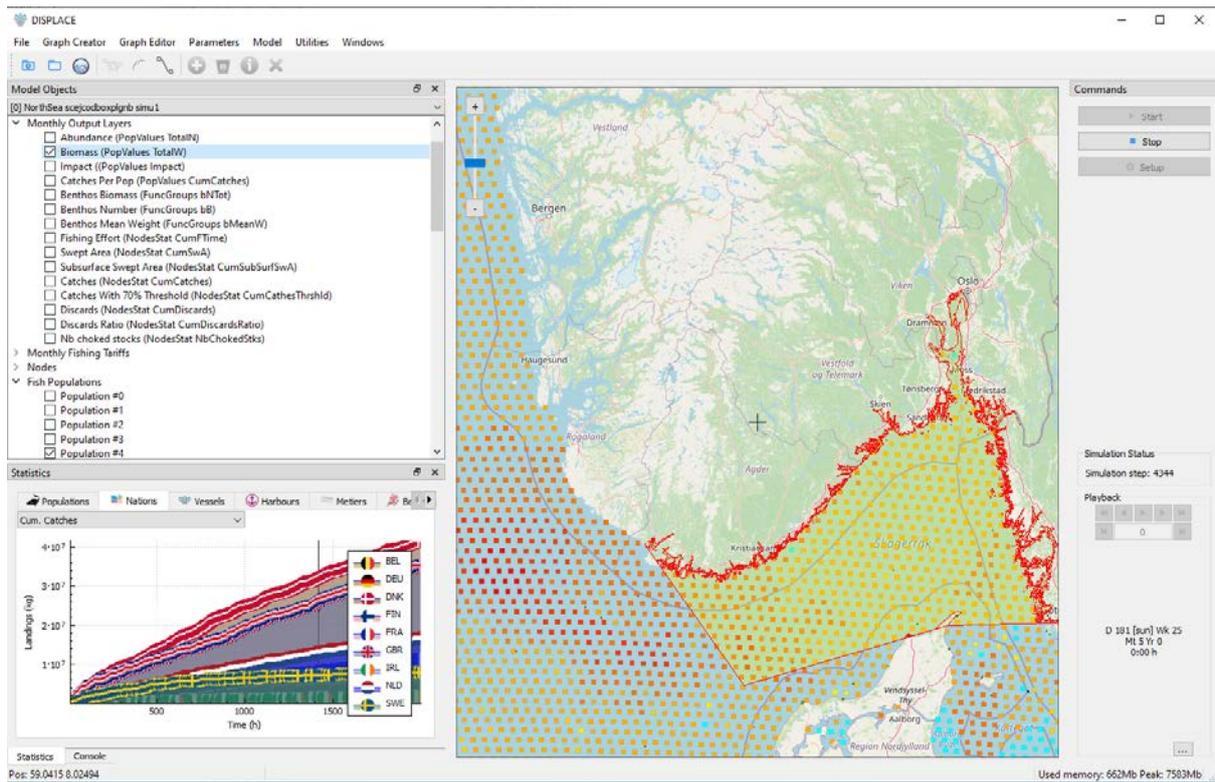
Figure 42. A random snapshot of the DISPLACE North Sea application showing the underlying simulated abundance field of North Sea cod with a scenario on a spatial closure (here a permanent box banning bottom trawling and demersal seines in order to protect juveniles cod in the Skagerrak identified as a persistent hotspot for juvenile cod fish).
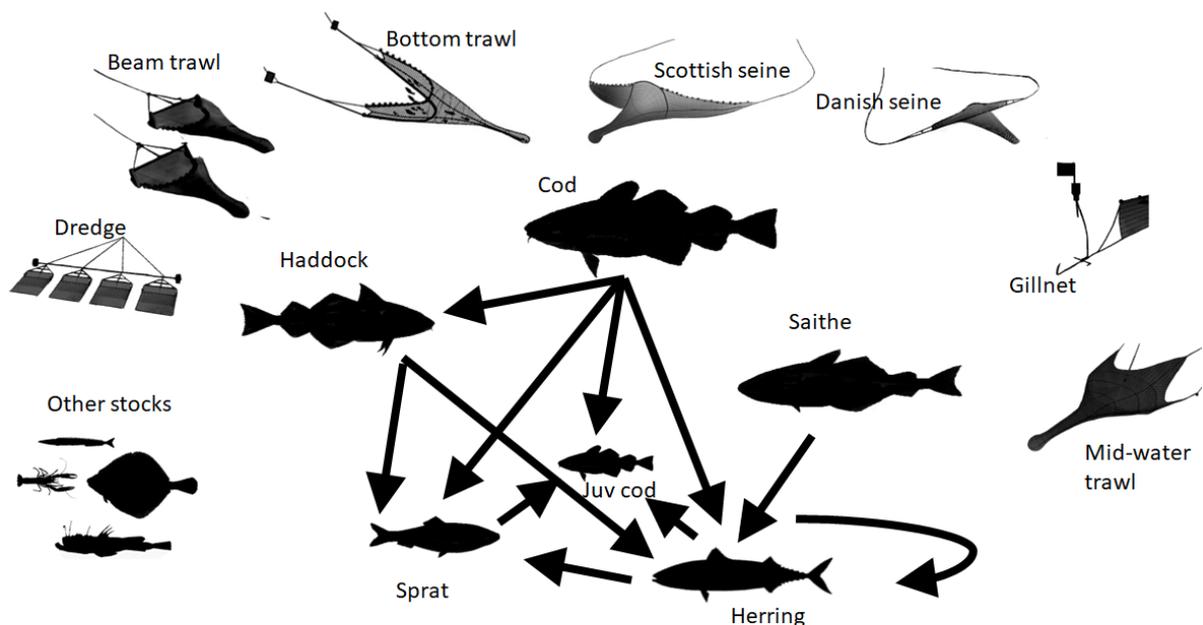
Figure 43. Foodweb modelled in the SizeSpectra DISPLACE module (unpublished but documented on the DISPLACE github repository) informing the adult and juvenile diet matrices preferences with relationships deduced from North Sea SMS model foodweb (ICES 2013), and also showing the various fishing techniques modelled in DISPLACE.

Table 8. Extracted from Rufener (2020, PhD Dissertation). Description of the biological, behavioral and economic indicators informed from ICES stock assessment and STECF database and economic data, tracked in DISPLACE, and used for the evaluation of the effect of climate change in the North Sea. Acronyms stand for: SSB=spawning stock biomass, F=fishing mortality, NPV=net present value, VPUF=value-per-unit-fuel.

Indicators		Description
Biological	SSB	Represents the mature component of the population. Thus, it is used as a proxy for the recruits, whereby higher SSB leads to higher recruitment defined by the stock-recruitment relationship, and ultimately an increase in the exploitable biomass.
	F	Describes the mortality rate that is due to fishing. Lower F values compared to the baseline are indicative of either lowered fishing mortality (hence stock recovery), or change in the selectivity or exploitation pattern for larger fish.
	Total catches	Indicates the overall amount of fish that were caught by the fisheries. Increased catches might indicate that either the fishing effort increased to compensate lower catch (or catch rates), or the exploitable biomass increased due to the management action under concern.
	Total landings	Total landings represent the retained catch brought on-shore.
	Species catches	Species specific catches
	Species landings	As for the total landings, but with focus on WB cod.
Behavioral	Fishing effort	Indicates the amount of fishing hours spent by a fishery, with high effort most likely associated to increased overall catch, although not necessarily. Increased fishing effort might be a response to fisheries closures, where the displacement of the fisheries to more distant grounds can result not only in lower catch rates, as well as higher expenses (e.g., increased fuel consumption). The combination of higher fishing effort and lower economic return indicates that the fishery is operating less efficient, leading to lower VPUFs compared to the baseline.
	Steaming effort	Indicates the amount of time fishers spent at sea heading to the fishing grounds and searching for fish, where most likely higher steaming time, proportionally to the total trip duration, might result in higher fuel consumption for less effective fishing time, thereby possibly lowering the VPUF.
	Trip duration	Indicates the average time sea trip at sea, where longer durations are usually related to increased steaming and, therefore, high fuel consumption.
	Number of trips	Indicates the numbers of time fishers went out at sea in a given fishing season. Higher number of trips can be an indicative of an inefficient fishery whenever fishermen are forced to conduct more trips (hence increased fuel consumption) to compensate for lower catch rates.

8. Coupling reconstruction of spatial stock distribution (LGNB-SDM) to a spatio-temporal bioeconomic model for fisheries (DISPLACE)

The uncertainties associated to the spatio-temporal dynamics of the resources available and vulnerable to fishing is likely to affect the fisheries outcomes (Bastardie et al., 2015), it is expected the simulation study will gain from incorporating more spatially resolved predictions such as the ones deduced from applying the NS-LGNB-SDM (Rufener et al. 2021) (Figure 44). Rufener (2020, PhD Dissertation) tested as a first scenario a case where we coupled the LGNB-SDM model directly to the DISPLACE routine, the case applied to the western Baltic cod. Here we re-use this modelling framework to apply it to the North Sea cod stock. As for the standard scenarios, we simulated this scenario for 10 years at an hourly time interval with 5 stochastic replicates (the time pressure in this project has unfortunately forced this relatively low number of replicates).
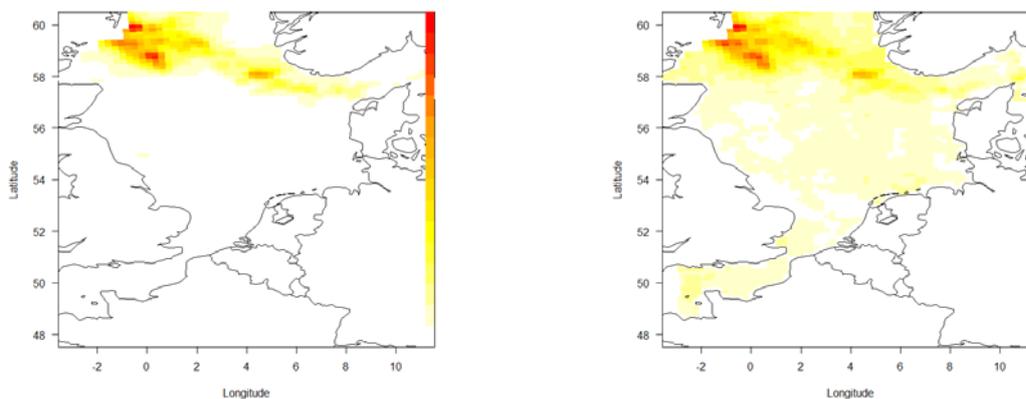
Figure 44. Left: Example of relative cod distribution of abundance modelled in 2019 Q3 applying the LGNB-SDM model. Right: Projecting one time step i.e. Q4 ahead from the left status.

Link to a NS-LGNB-SDM animation, e.g. for Adult cod: https://drive.google.com/drive/folders/1_SKmhpy91eFwcclBY2o82uwB45IVCbGX?usp=sharing
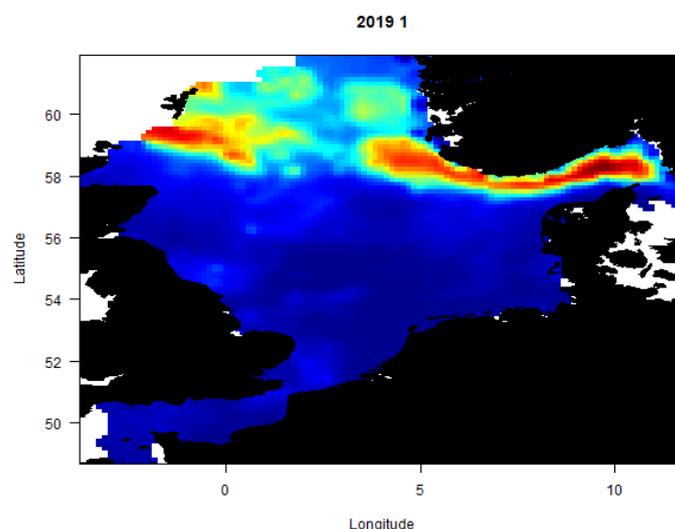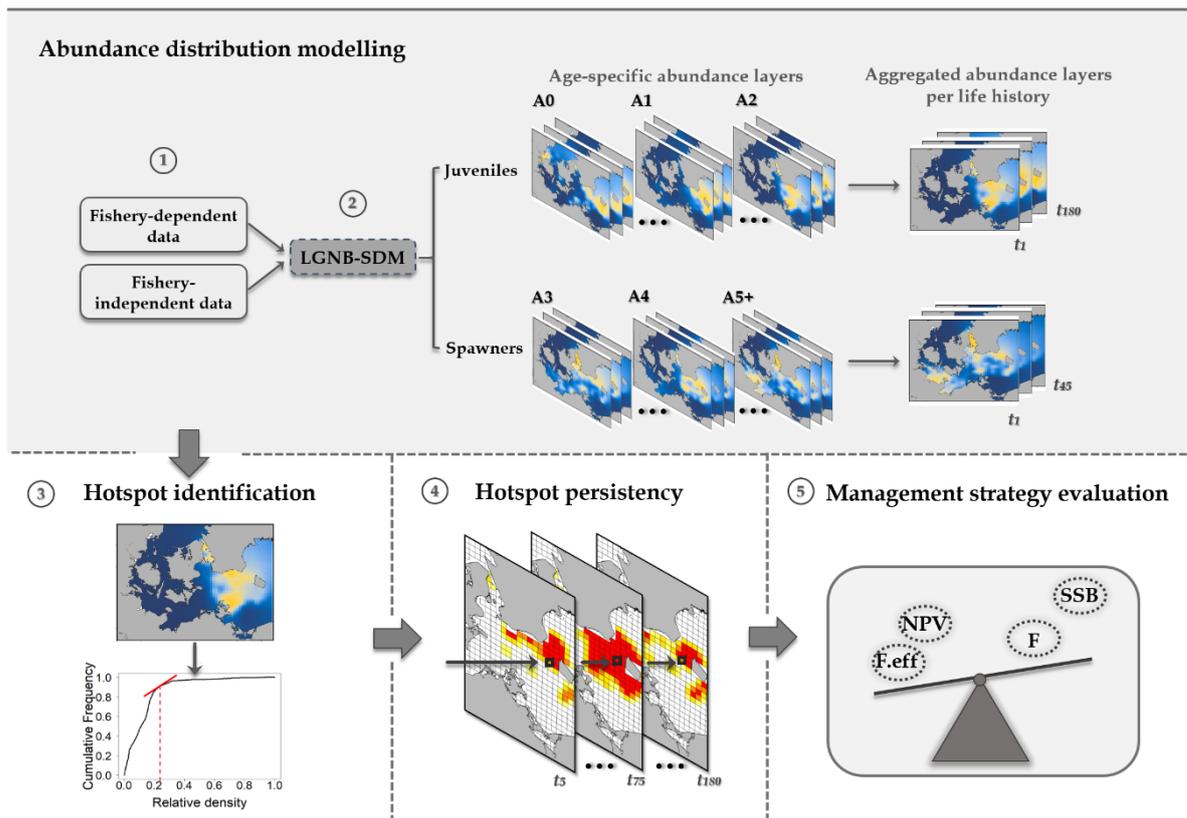
Figure 45. Extracted from Rufener (2020, PhD dissertation). Summary of the approach toward identifying hotspots that can be used in the DISPLACE spatial bio-economic simulations of fisheries.

DISPLACE is built upon a set of interrelated functions that links the fishery resource dynamics to the vessel dynamics (Bastardie et al., 2014). It is built like a management strategy evaluation (MSE) to evaluate fisheries strategies in a controlled, virtual environment. The core assumption is the harvest function, which make the bridge between the fishing process and the underlying stock dynamics by mimicking the vessel-specific stock depletion. DISPLACE is also a behavioral model with individual agents (i.e. the fishing vessels) which make the variation in the abundance of the explicitly modelled species influencing the fishing agents, therefore impacting their next behaviors via a set of decision trees organizing their decision making (Bastardie et al., 2014).

The DISPLACE harvest function includes a term for reflecting the spatial availability of the stocks modelled. This is this terms that is affected by the coupling to the LGNB-SDM. To harmonize with DISPLACE's default configuration, we had to apply the LGNB-SDM model separately for each of the 14 size-groups that are modelled within the simulation framework. We calibrated the LGNB-SDM model exactly as in Rufener et al. (2021), except that here a longer time frame was considered (2001-2019) and the modelling was applied on a size rather than on an age basis.

The LGNB-SDM is applied in simulation mode and used to obtain the abundance predicted for t+1 into the DISPLACE model platform. This predictions follows a multivariate Gaussian random distribution function that randomly draws stock abundance fields based on previously fitted parameters. The function is essentially described by the mean of the predicted abundance field in time t, and the precision ψ of the full space-time field and which is described as:

$$\boldsymbol{\psi} = \boldsymbol{Q}\kappa\sqrt{1-\rho^2}$$
$$\boldsymbol{Q} = \boldsymbol{Q}_0 + \delta\boldsymbol{I}$$

where Q is the sparse precision matrix that is related to the initial sparse matrix $\boldsymbol{Q}_0$, $\boldsymbol{I}$ its diagonal matrix, and δ the spatial correlation delta parameter.

To be applicable in a predictive, simulation mode, the LGNB-SDM model keeps four components for each size group: (i) the space-time abundance fields predicted, (ii) the estimated spatial correlation parameters (described by the delta δ and scale κ parameters), (iii) the estimated temporal correlation parameter (rho ρ), and (iv) the precision matrix $\boldsymbol{Q}$ which corresponds to the inverse of the covariance matrix of the spatio-temporal random effect. These parameters are then linked to DISPLACE to generate the forward-predictions.

9. Conditioning of DISPLACE North Sea and plausible scenarios for a changing climate effects

Conditioning of the spatial modelling platform

This study focuses on the most important species and stocks in terms of fisheries resources for the Danish fleet in the North Sea i.e. cod, haddock, plaice, sole, herring, sprat and other North Sea species (see the online repository for the DISPLACE North Sea application), which constitute most of the total commercial catch of the Danish fleet. The ICES North Sea Fisheries Assessment (ICES WGNSSK 2020) and widely distributed stocks WGWIDE Working Groups focus on assessing 45 stocks that we have integrated into the North Sea DISPLACE model. Besides stock number-at-age issued by the 2020 available ICES analytical assessment estimates (2019), we included fish life-history and ontogenetic growth for modelling the different populations with a body size-based model. Processes affecting population dynamics are often size-dependent (such as growth, mortality, maturity, condition, settling, and recruitment). Fishing is also a selective process that applies differently along with animal body size. Hence, the model handles 14 size groups (5 cm length groups) pooled in 3 size categories (small, medium, and large animals) for describing size-specific spatial distributions and marketable categories (Bastardie et al., 2014). From Von Bertalanffy growth parameters (infinite length Linf, the growth rate K and t0 parameters), we generate stock-specific growth transition matrices (GTM) using the Von Bertalanffy growth curve model for simulating individual stochastic growths (see Bastardie et al., 2014). We run the same procedure to also obtain Age-Length Keys ALKs. In order to account for predator-prey trophic interactions between fish species (Figure 43), we informed the DISPLACE size-spectra model (based on Blanchard et al., 2014) with specific growth parameters, Winf as the asymptotic weight in grams and k as the standard metabolism factor in yr-1, and diet preferences (Jacobsen et al., 2014, 2017). The stochastic trajectories modelled in DISPLACE arise from two additional parameters inducing the stochastic trajectories: CV for lognormal error added on recruits is 0.2, and CV for lognormal error added on quarterly-based growth transition matrix is 0.1.

Defining plausible, contrasted fisheries management scenarios

We defined possible management actions affecting the fisheries in the North Sea region. Indeed, fisheries management can impact fisheries with output control such as setting the TACs and quotas based on different intended fishing mortality, or with input control for controlling the type of gears to be used (especially the mesh size controlling the selectivity of the gears against the body size of the targeted fish), or for controlling where the fishing effort is applied spatially or seasonally. On this basis, we have defined three contrasting management scenarios, to compare against the baseline situation:

- Fishing at FMSY in the lower bound of the FMSY range i.e. FMSYlow (see North Sea EU multiannual management plan)
- Lowering the L50 of selectivity ogives by 10% making fishing gears less selective for smaller fish body length
- Spatial closure to fishing, here as an illustration based on the persistent hotspot identified in the Skagerrak for juvenile North Sea cod.
-

Defining plausible, ecosystem-coherent climate-change induced shock scenarios

We defined two environmental scenarios for the North Sea region (current conditions, and worst-case scenario). These scenarios correspond to particular climatic paths, respectively no further change in the climate, and one pessimistic IPCC scenario (RCP8.5).

The projections available from the CERES project (https://ceresproject.eu/wp-content/up-loads/2020/02/19-Flatfish-in-the-North-Sea-and-north-east-Atlantic_revised.pdf) indicate an increase in the North Sea water temperature by 2°C by 2100 for the climate change scenario RCP 8.5. For the present project, the projection period (2020 to 2030) is roughly 1/8 of the projection period to 2100. This would mean an increase of 0.25°C for the scenarios RCP 8.5 for the simulations in the present study. Projections in CERES also indicate a decrease in the primary production in the North Sea with a more marked reduction in the northern regions. In the coastal areas, especially along the eastern part of the North Sea, projections foresee a slight increase in the primary production, due to an increase in river run-off and an increase in nutrient availability in the marine waters for the primary producers. Overall, until 2030 predictions suggest a somewhat higher variability than the situation between 2000 and 2020, but the overall trend is not evident. Regional climate models do not indicate an increase in the frequency of storms, but regional models are quite uncertain. Storms are projected to have more northerly tracks, but the uncertainty is also high. However, it is expected that storms could be of higher intensity, and bring more precipitation in the North Sea catchment area.

The climatic scenario leads to a series of environmental changes that would affect the individual physiology of the animals impacted and the phenology of the species. In this study, we did not relate the biological impact of these changes on the different stocks considered in a quantitative way due to a lack of empirical observations and evidence relating causal changes to an effect. Information from the literature review has instead been used to assume the nature and direction of the impact of these environmental changes on different stocks. The intensity of this biological response further depends on the scenario (Table 9). Scenarios recognize that life-history parameters are correlated, e.g. faster-growing individuals may mature smaller and be subject to higher natural mortality.

For each scenario and long-term environmental changes (Table 9), assumptions are made on short-term stresses and their impacts on the biology of the stocks induced by a changing climate. The intensity and frequency of these shocks would ideally vary between the two scenarios, however. The first step was to propose plausible, ecosystem-coherent scenarios of biological responses to long-term climate change and short-term stress for the three scenarios. Different assumptions were made for future animal body growth as well, though for a smaller number of stocks. In some instances, a growth model with the influence of temperature was developed, making assumptions on future changes in the von Bertalanffy parameters (Figure 46).

Table 9. A suite of "what if" management combined to climate scenarios affecting the stock productivity and F management of main North Sea Stocks of commercial interest tested with DISPLACE. No environmental forcing is implemented in the model yet (in the absence of proper proportional and correlation relationships). Instead, we tested impact with multipliers on input parameters.

Scenarios	Species	Drivers	Multiplier on SSB-R Ricker alpha	Multiplier on SSB-R Ricker Recru beta	Multiplier on VBGF Linf	Multiplier on VB K	Absolute GFFMSY	Massive M at y=0 (0/1)	Vessel stops if choked (0/1)
Baseline (i.e., FMSY + Landing Obligation LO)	cod, plaice, herring, Sprat	Productivity change	1	1.0	1	1	1	0	1
FMSY + LO + Climate change CC	cod, plaice herring	Productivity change	0.9	1.5	0.8	1.5	1	1	1
	sprat 2	Productivity change	1.1	1.0	0.8	1.5	1	1	1
FMSY low + LO	cod, plaice, herring, sprat	Fmanagement	1	1.0	1	1	FMSYlow	0	1
FMSY low + LO + Climate change CC	cod, plaice, herring,	Productivity change + Fmanagement	0.9	1.5	0.8	1.5	FMSYlow	1	1
	sprat	Productivity change + Fmanagement	1.1	1.0	0.8	1.5	FMSYlow	1	1

NB. SSB-R stands for Spawning stock biomass-Recruit relationships deduced from the Ricker function with the two parameters alpha and beta. VBGF stands for Von Bertalanffy Growth Function with the two parameters Linf and K. M stands for natural mortality. Increase density-dependent effects, e.g., increase of adverse inter-individual interactions from resource scarcity; 2positive effect of warmer water column temperature on sprat.
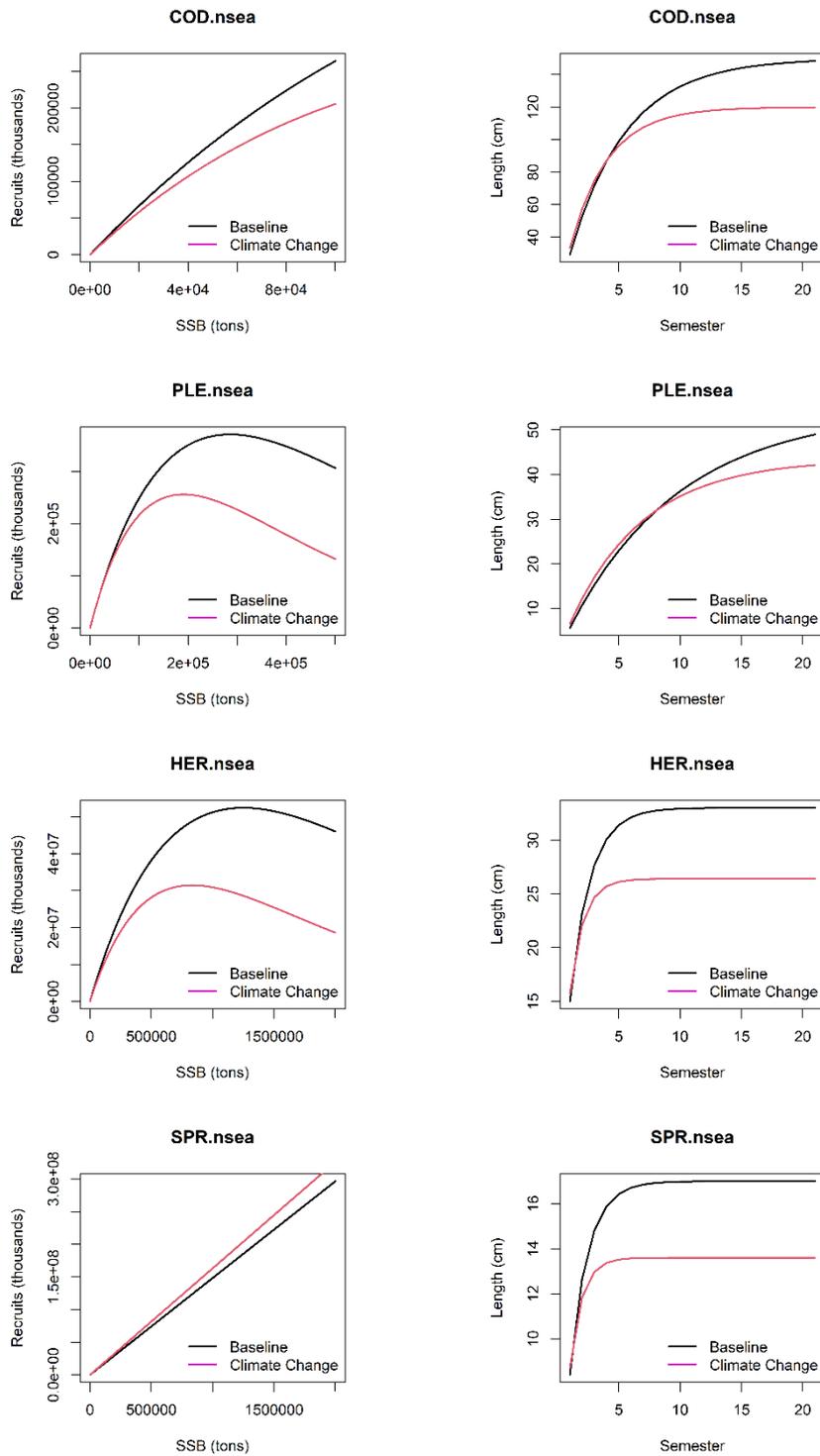
Figure 46. For each of the North Sea stocks assumed affected by the climate scenario (worst-case conditions) compared to a baseline (current conditions) productivity, left: Stock-recruits relationships based on the Ricker model for predicting the number of recruits at y+1 depending on the spawning stock biomass SSB at y; Right: Von Bertalanfy growth curves for predicting the growth of animal body over time for a given cohort in the simulations.

Calibrating the bioeconomic model

Vessel or métier (OTB, GNS etc.) specific catch rates on species are fixed (not depending on the underlying abundance as in previous DISPLACE applications) and calibrated to adjust the overall landings per species to the simulated ones at the end of the first year simulation. Weight at age are calibrated to adjust for the estimated F bar on each stock.

Important effects arise from the vessel behavior facing TACs and quotas (with national allocation key defined by the relative stability). Hence, in the simulation, vessel and stock specific discards could occur each time a fishing event take place as part of the catching process (from a mismatch between the selectivity in use and the MCRS), or if the annual quotas for this vessel is exhausted (possibly the quotas is per nation, vessel size or per vessel). If the stock is then "choking" the vessel by a lack of a remaining quota, then the vessel will stay in port for the rest of the year, unless the Landing Obligation (LO) is not complied with. Discards also could occur for the other landings (i.e. landings resulting from other components than the vessels simulated) that apply on locations where the stock can be found, as soon as there is a mismatch between the MRCS and the selectivity ogive used for simulating the other landings, or when the annual TAC is exhausted for that species.

Spatially, important effects could arise from spatial population mismatch with the vessel effort allocation. A too large mismatch or stock distribution modelled too narrow will induce the under exploitation of the stock and a greatly impaired vessel profitability.

The tropho-dynamics captured by the size spectra modelling on each location where predators and preys overlap may sometime induce large depletion (i.e. large natural predation mortality, i.e. so-called M2) on the smaller size groups of the prey species. In this case, a size spectra scaling factor is used to downscale this effect and let the smaller age groups grow on location for a realistic overall stock level trajectory. The natural "background" mortality (M1) is also a great source of uncertainty in the scaling. The background mortality is not species-specific but is assumed to depend on the animal body size, with smaller sizes suffering more from the natural mortality. The bad scaling of the background mortality at size group is sometime responsible for possibly unrealistic trajectories caused by excessive depletion.

10. Outcomes of the bioeconomic simulation study

Biological indicators

Most fish stocks projection showed spawning biomass SSB stock increased, and mortality F reduced at the horizon 2030 (Figure 47) for the baseline runs applying the current F-MSY strategy to North Sea fisheries defined in multi-annual plan defined in Regulation (EU) 2018/973. North Sea plaice, sole, and sprat are the exception and showed declining trends in SSB compared to the reference points and initial states, even if F is being reduced below the initial one.

There is, however, substantial uncertainty in the future status of North Sea sprat stock. For this stock, the beforehand calibration of the final runs led to downscale the strength of the mortality issued from the predation by top-predators (cod, saithe and haddock) as well as the background natural mortality to ensure the North Sea sprat stock avoids collapsing. Such calibration is a sign of imperfect knowledge on this stock status regarding either L50 Maturity, weight-at-age or estimated N-at age, or a mixture of all these population features in the meantime. Hence, extra caution should also be paid to stock status since we observed this stock could collapse in the simulations when tropho-dynamics occurred at a realistic rate. It also appears the trajectories for North Sea stocks could be overly optimistic in increasing to high levels (i.e. up to 5 times the initial SSB after 10y) due to a lack of a pronounced density-dependence effect in the SSB-R used. For cod for example.

Regardless of these uncertainties, the effect of climate-induced change is estimated low on the short run, apart for North Sea cod. When applying a lower F-strategy facing climate change long term effects or episodic stress, unexpectedly the simulation study anticipates that the regional response to applying FMSY-lower (see Regulation (EU) 2018/973) make little difference and is not beneficial for all stocks to ensure a level above the reference points at the horizon 2030. However the North Sea cod SSB is greatly enhanced if the FMSY low strategy is followed (Figure 48). On the contrary, in case the F-MSY-lower strategy is followed, this will reinforce the declining observed on the flatfish stocks (plaice and sole). Finally, both the effect of using a less selective gear or implement a cod box would be modest on the cod SSB (Figure 50).
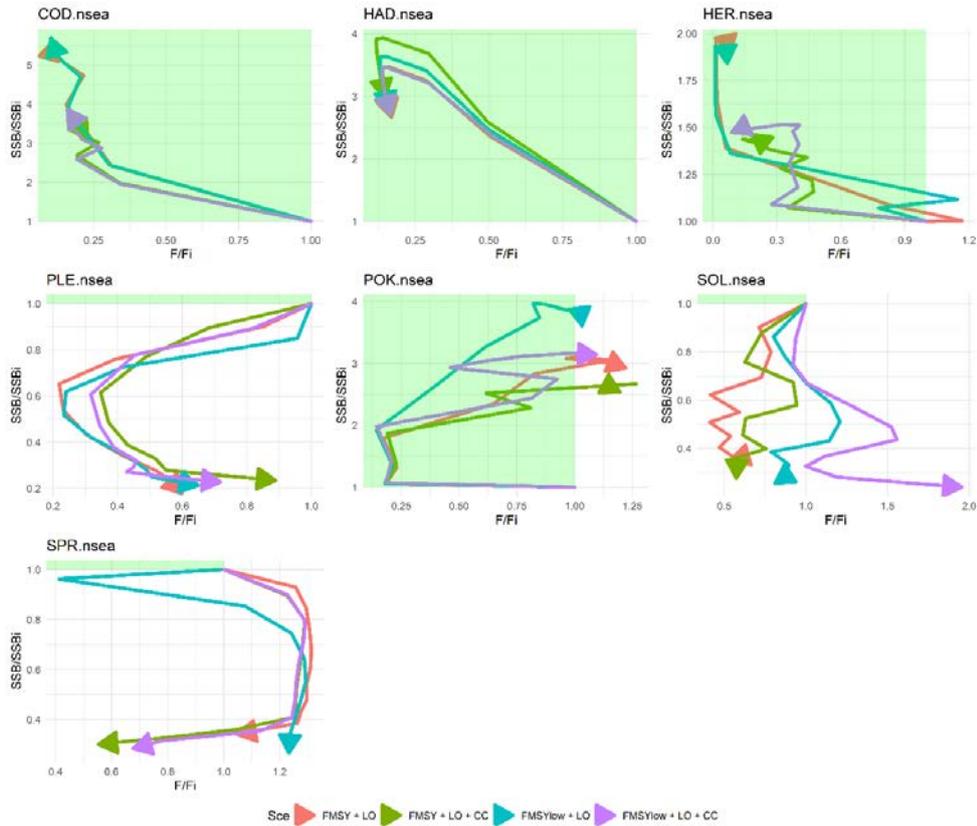
Figure 47. A bi-dimensional plot of average scenario outcomes on F/FMSY and SSB/MSY-B-trigger as simulated temporal trajectories from 2020 to horizon 2030. The wished green corner for the yearly drift of the indicators is the top left (i.e. increase in SSB, reduction in F, compared to initial values). Scenario are applying the FMSY or FMSYlow strategies, assuming the landing obligation (LO) fully complied with, and the presence or absence of climate change (CC) effects.
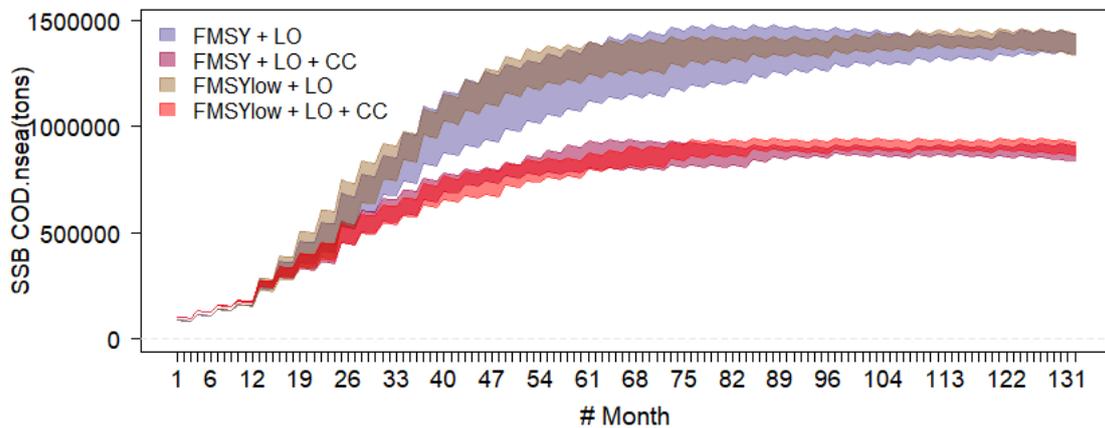
Figure 48. Spawning Stock Biomass (SSB) of the North Sea cod along a 10y projection for a selection of scenarios contrasting the climate change effects.
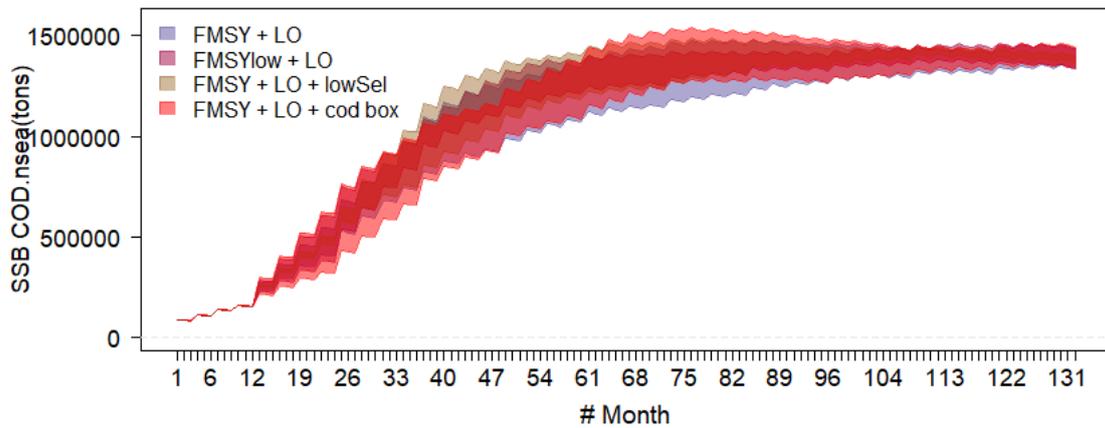
Figure 49. Spawning Stock Biomass (SSB) for the North Sea cod along with a 10y projection for a selection of scenarios contrasting the fisheries management effects ("lowSel" is lowering the L50 of selection ogive, "cod box" is implementing a spatial closure in the Skagerrak; see Table 9).

The effect of less selective fishing gears on stocks trajectories is only significant on increasing the pressure on North Sea sole (Figure 47). In parallel, implementing a cod box does not affect the cod itself but is beneficial for sole, while damaging for plaice. All in all the underlying baseline trajectories is overruling the management effects underlying the importance in the simulations of other variables than fisheries management in directing the population dynamics of exploited stocks.
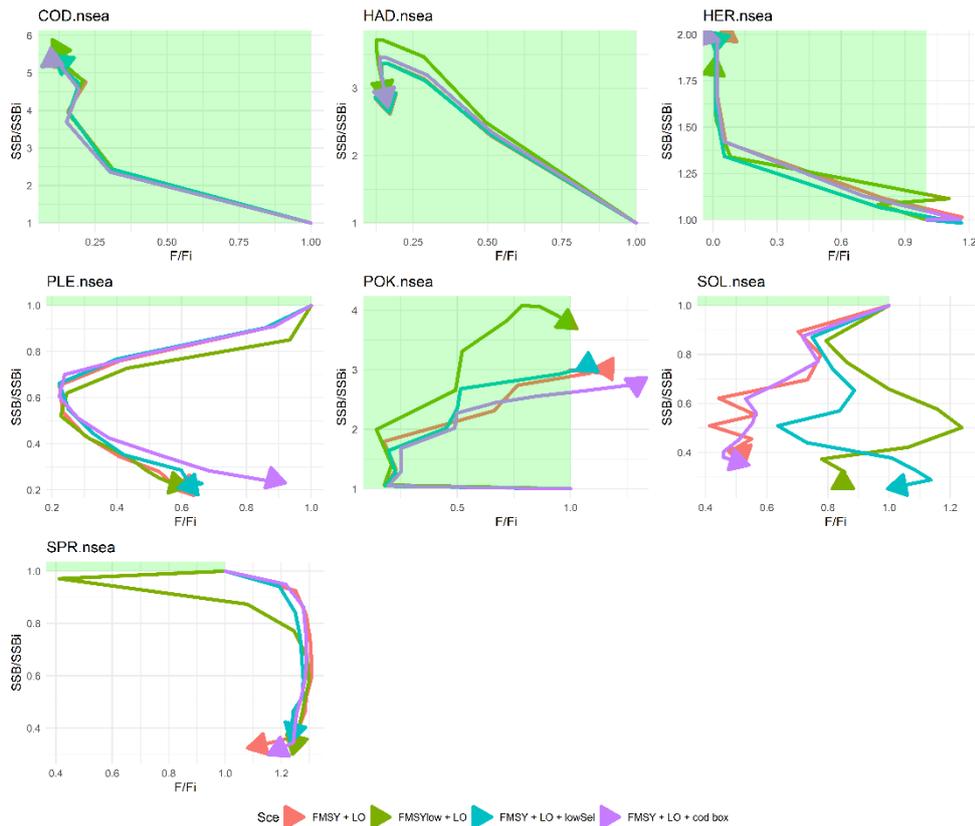
Figure 50. Same as in Fig 47 but for another set of scenarios. A bi-dimensional plot of average scenario outcomes on F/FMSY and SSB/SSBtrigger as simulated temporal trajectories from 2020 to horizon 2030. The wished green corner for the yearly drift of the indicators is the top left (i.e. increase in SSB, reduction in F, compared to initial values). Scenario are applying the FMSY or FMSYlow strategies, assuming the landing obligation (LO) fully complied with, the less selective gears ("lowSel"), or the presence of the cod box ("cod box").

Economic indicators

Applying the FMSY-lower strategy to all stocks simultaneously does not appear beneficial on the fleet indicators leading to a similar accumulated income at the 10y horizon time to the FMSY strategy for both active bottom-contacting gears and passive gears that does not come with more energy-efficient fisheries either (Figure 51). The same effort is applied at sea from a similar number of trips, but each of them may return slight different species composition with a marked increase in sole and plaice landings when the resource levels is better aligned with the TACs, while cod, saithe and haddock landings decreased from lower TACs. Greater short-term opportunities on flatfish stocks induce slightly more revenue for vessels using passive gears as well.

Long-term climate-induced effects on the environmental drivers led to a decreased fleet revenue from landings (expressed as Net Present Value, decreased by ca. 5 to 10%) and energy efficiency (ca. 5%), which decrease is more pronounced for active gears, from lower landings on North Sea cod, herring, plaice and sole; only landings of saithe and Pollock are not affected. Especially North Sea cod stock is seeing its overall abundance decreasing. The FMSY-lower strategy is not correcting for the loss of opportunity induced by the climate change and induced shock but worsen the loss of fishing opportunities on cod instead (Figure 51).

North Sea resource distribution and fishery opportunities (NORDFO)
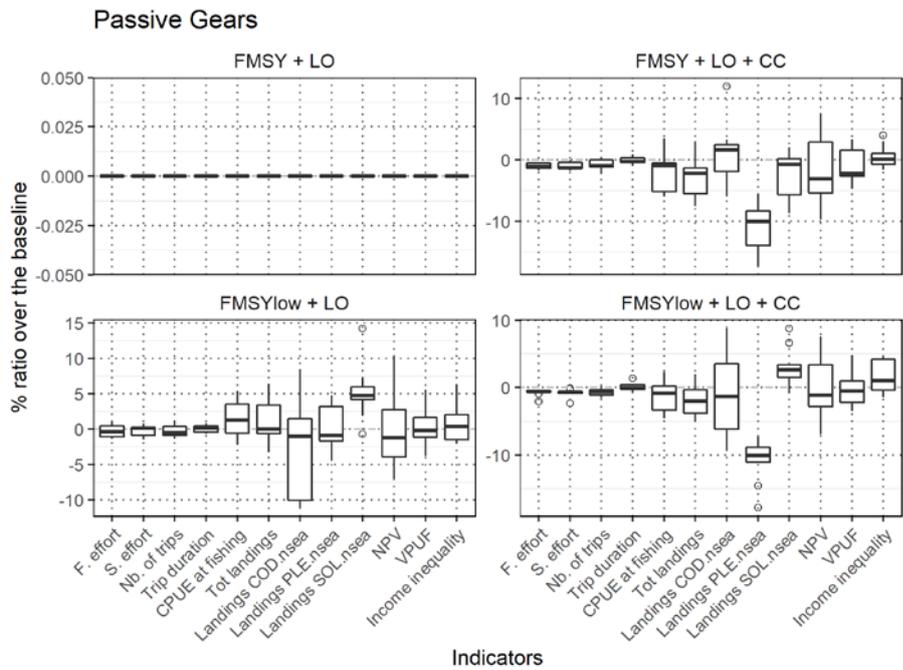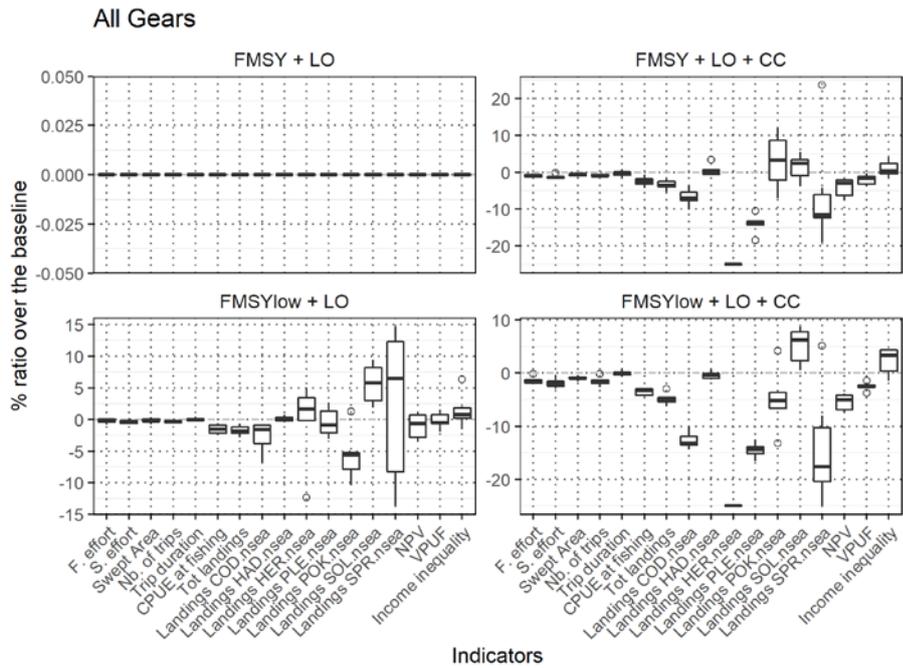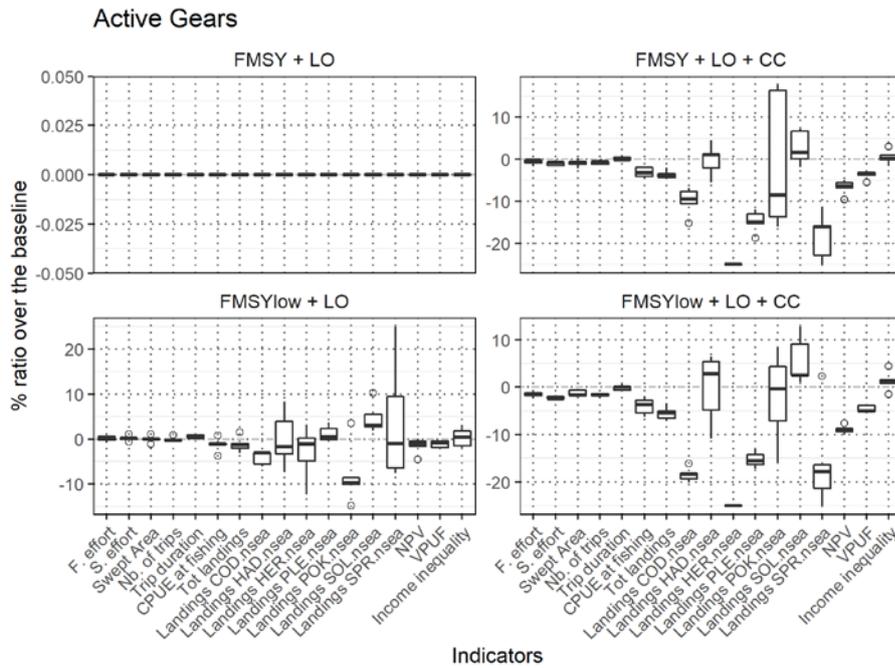
Figure 51. Fleet indicators integrating the differences to baseline (i.e. the FMSY-strategy+LO) over the entire simulation period for selected scenarios. Indicators: Fishing Effort, Steaming Effort, Swept Area by the gear used, Number of Trips, Trip duration, catch rates expressed as CPUE at fishing, Landed kg, Net Present Value (NPV), energy efficiency expressed as Value Per Unit of Effort (VPUF), and Hoover index expressing income inequality (see e.g. Bastardie et al 2020).
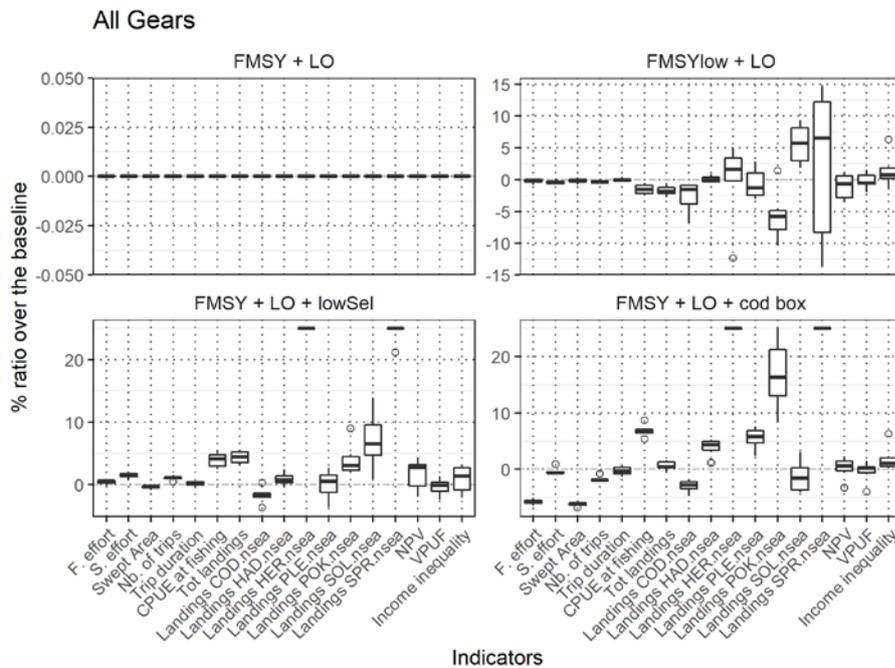
Figure 52. Fleet indicators integrating the differences to baseline (i.e. the FMSY-strategy alone) over the entire simulation period for selected scenarios. Indicators: Fishing Effort, Steaming Effort, Swept Area, Number of Trips, Trip duration, CPUE at fishing, Landed kg, Net Present Value (NPV), Value Per Unit of Effort (VPUF), and income inequality.

Overall effect

At the entire North Sea scale, the overall economic return appears to be less in the long run with the F-MSYlow strategy and opportunities are gained when applying a systematic FMSY-strategy (Figures 53 and 54). The FMSY-low strategy is limiting the fisheries in a situation of increasing stocks (because lower TACs are enforced that choked the mixing fishery), and because of increasing stocks (when not fully exploiting the increasing stocks biomasses). Moreover, the FMSYlow strategy is not correcting for loss induced by the climate change effects. The climate change is in overall negatively affecting the anticipated revenue and the F-MSY-low strategy is not enable to counteract the loss on some stocks.

Simulations shows that long trend in climate change added to shocks may slightly reduce the anticipated revenue. FMSY-strategy is also more rewarding for the fleet economy than the FMSY-lower scenario (Figures 53 and 54). The effect of climate is to reduce these increased opportunities, as well as to reduce the catch-fuel efficiency (Figure 55).

Following the F-MSY-lower strategy under climate change is likely to increase the catches made by fleets fishing upon the north-east corner of the North Sea chasing for cod, and less close to the shore and in the Skagerrak (Figure 56-60, spatial distribution of catches).

It is striking that the simulations anticipate effort and catches to increase over the main fishing grounds visited by the Danish and international fleets in the North Sea over all management tested i.e. when management applied a FMSY low strategy, when the management is less restrictive on the gear selectivity, or when the management applied a spatial closure for cod in the Skagerrak. This increase is the outcomes of three different effects, however. FMSYlow increase the catch on the long run when the stock is temporally underexploited, fishermen using gears with lower selectivity catch more fish but require more effort to exhaust the quota with larger fish, and finally setting a closure does not reduce the overall effort but displace it instead toward the remaining opened areas, increasing the catches there.

Figure 53. Monthly revenue from landings from all simulated vessels fishing in the North Sea combined for a selection of scenarios (first year is removed).
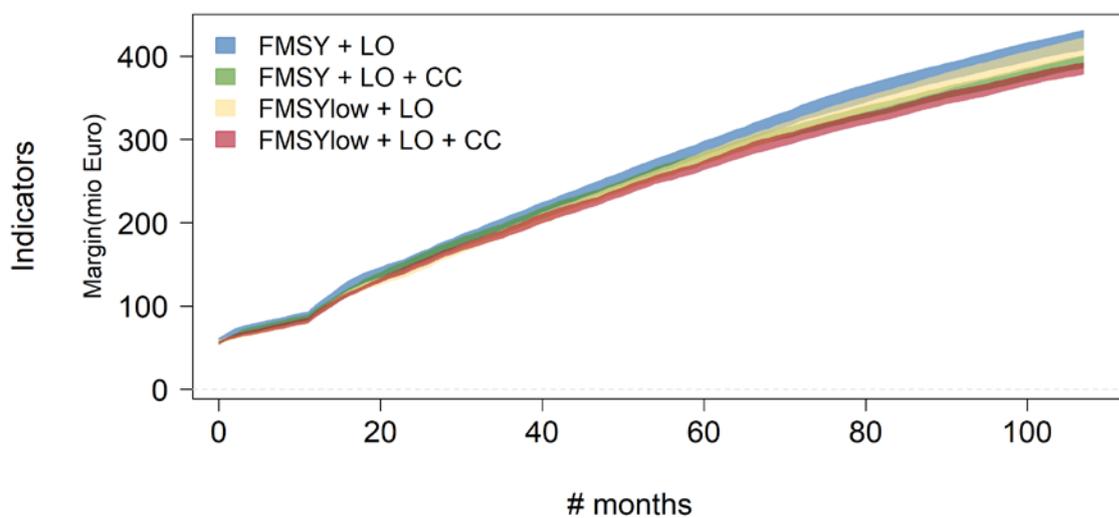
Figure 54. Simulated accumulated contribution margin (revenue minus fuel costs, in millions euros) over the 10y for selected scenarios.
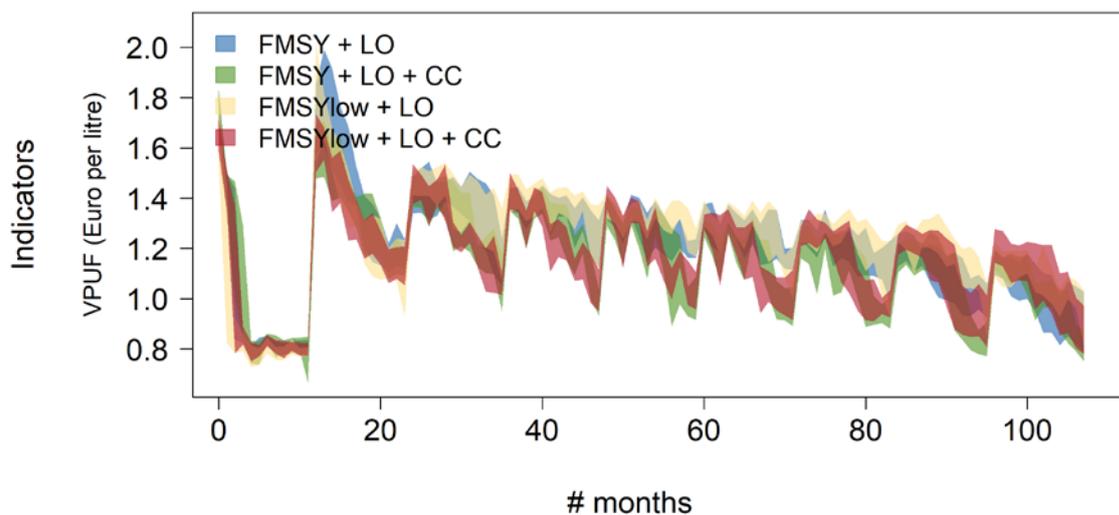
Figure 55. Monthly average of Value Per Unit Fuel (VPUF) as a proxy for energy efficiency calculated as a monthly average per vessel from all vessels fishing in the North Sea combined for a selection of scenarios.
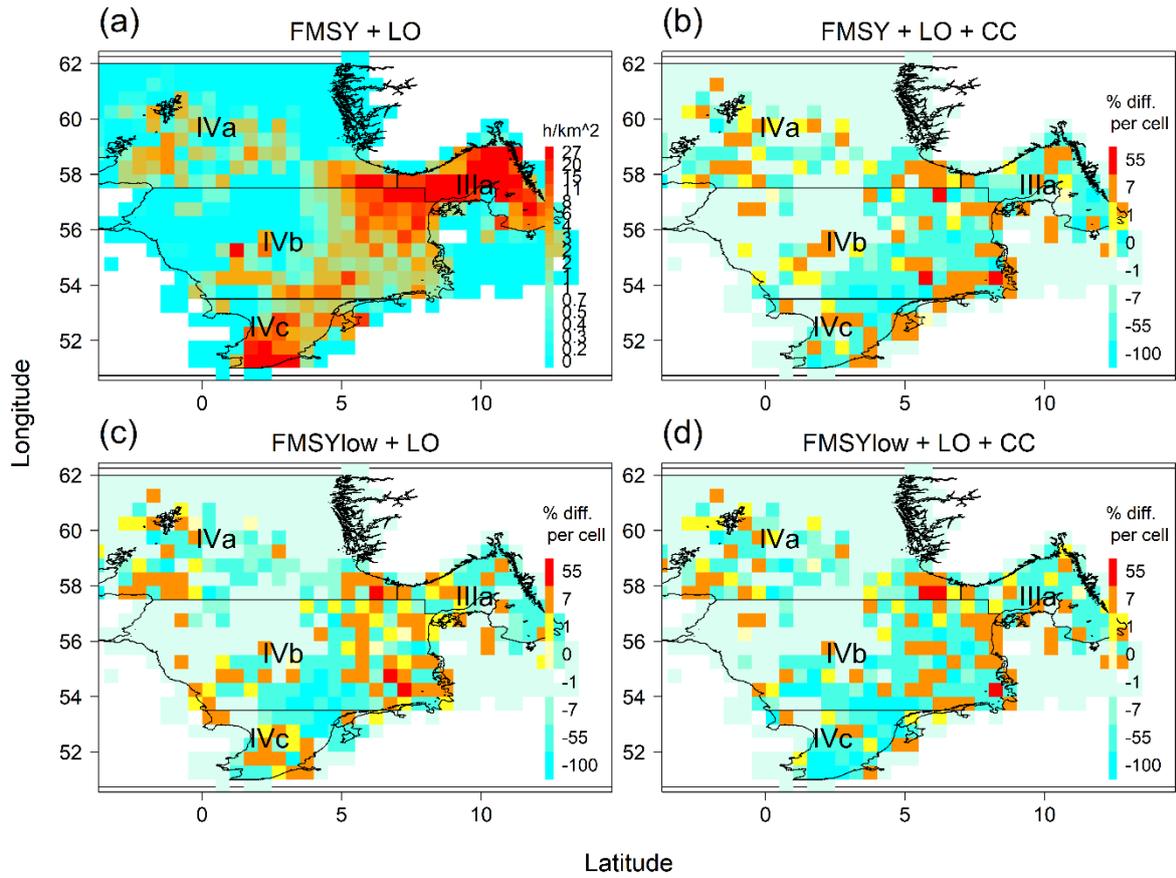
Figure 56. Simulated average spatial distribution of fishing effort (all species confounded, all métiers confounded) at the 2030 horizon time for the baseline scenario in (a) (applying the FMSY strategy + LO), and relative to the baseline for a selection of scenarios (b) to (d). The grid cells are c-squares of 0.5 degree.
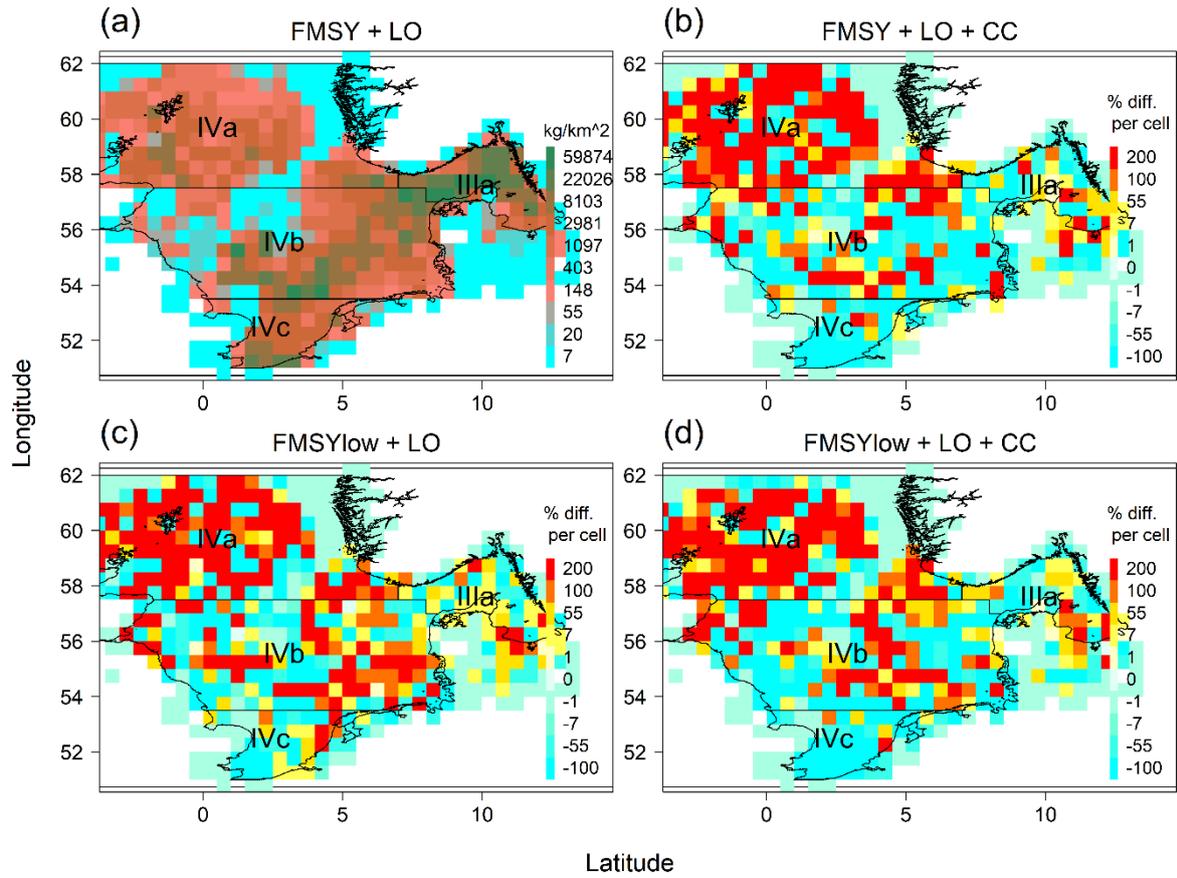
Figure 57. Simulated average spatial distribution of catches (all species, all métiers confounded) at the 2030 horizon time for the baseline scenario in (a) (applying the FMSY strategy + LO), and relative to the baseline for a selection of scenarios (b) to (d). The grid cells are c-squares of 0.5 degree.
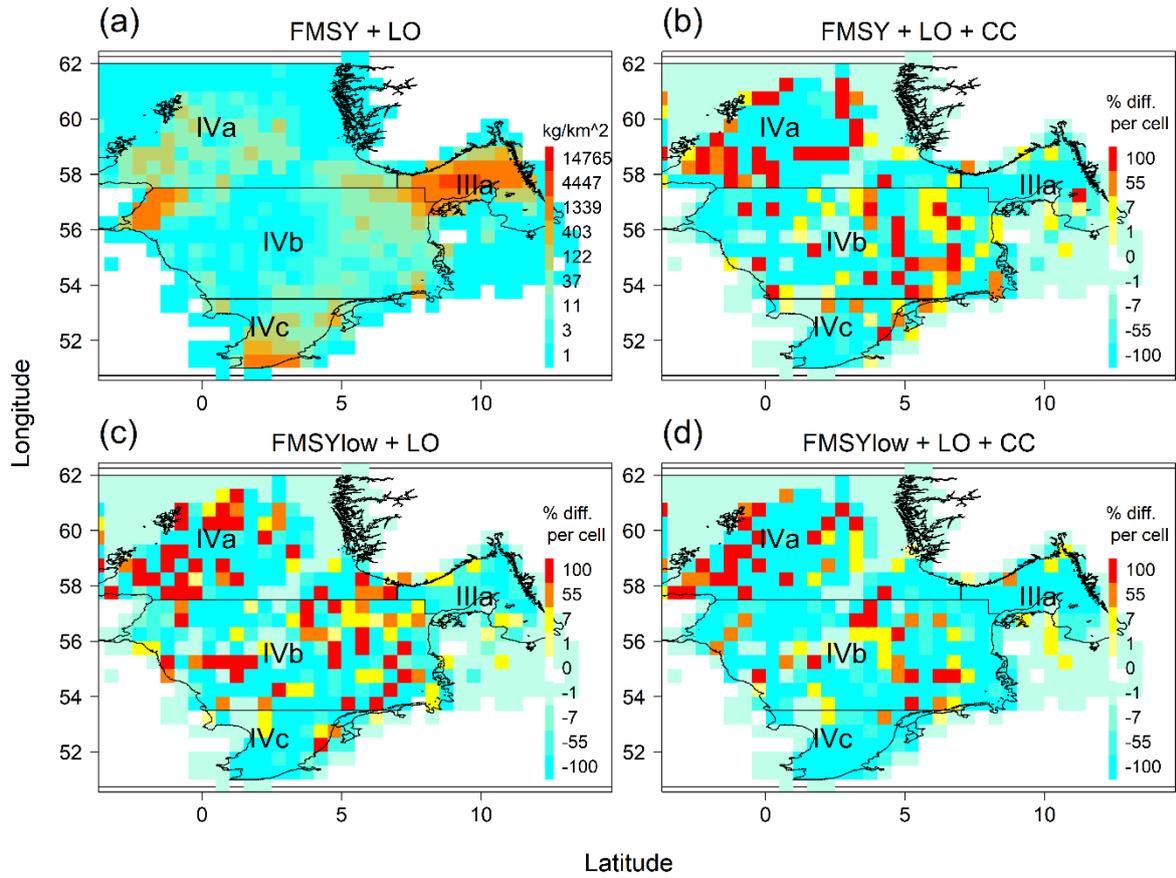
Figure 58. Simulated spatial origin of landings (all species confounded) for North Sea cod at the 10y horizon, and relative change compared to the baseline scenario (i.e. FMSY+LO) in percent for selected scenarios. The grid cells are c-squares of 0.5 degree.
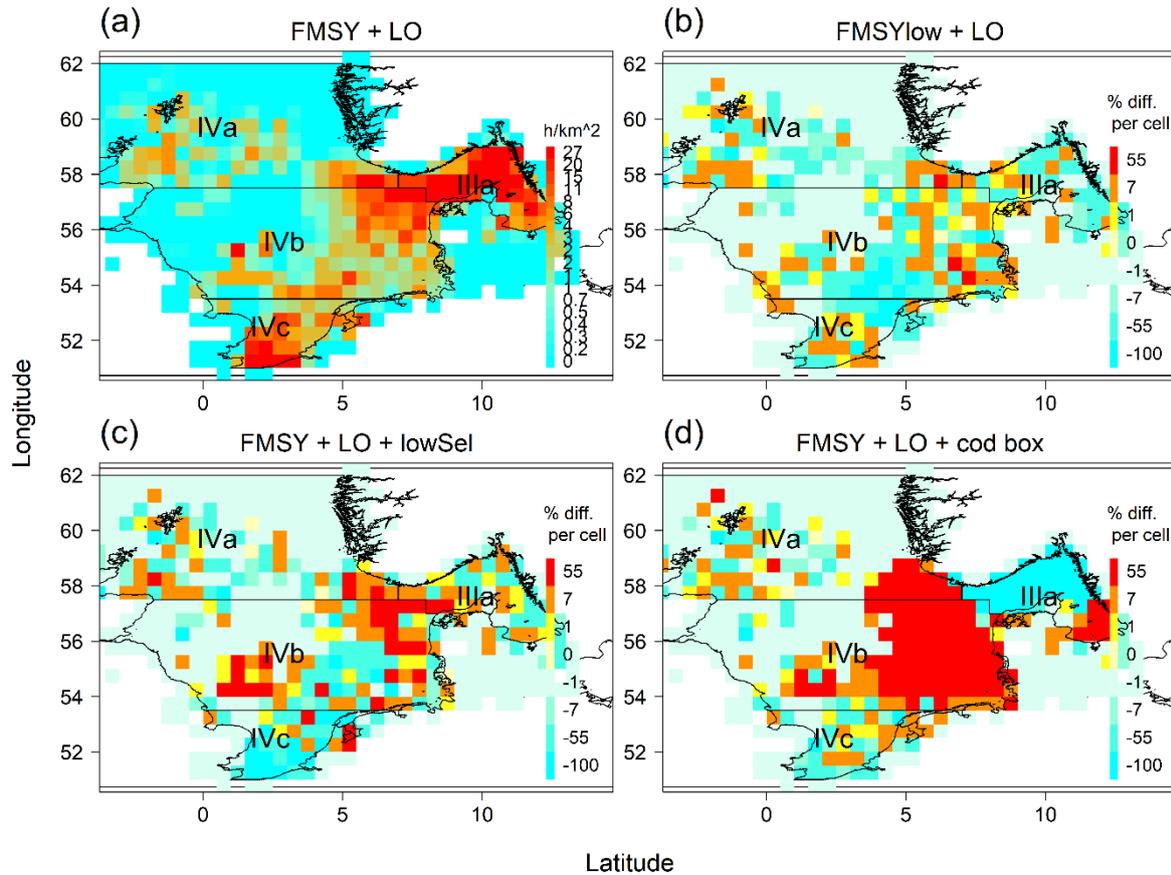
Figure 59. Simulated average spatial distribution of fishing effort (all fleet-segments aggregated) at the 2030 horizon time for the baseline scenario in (a) (applying the FMSY strategy + LO), and relative to the baseline for a selection of scenarios (b) to (d).
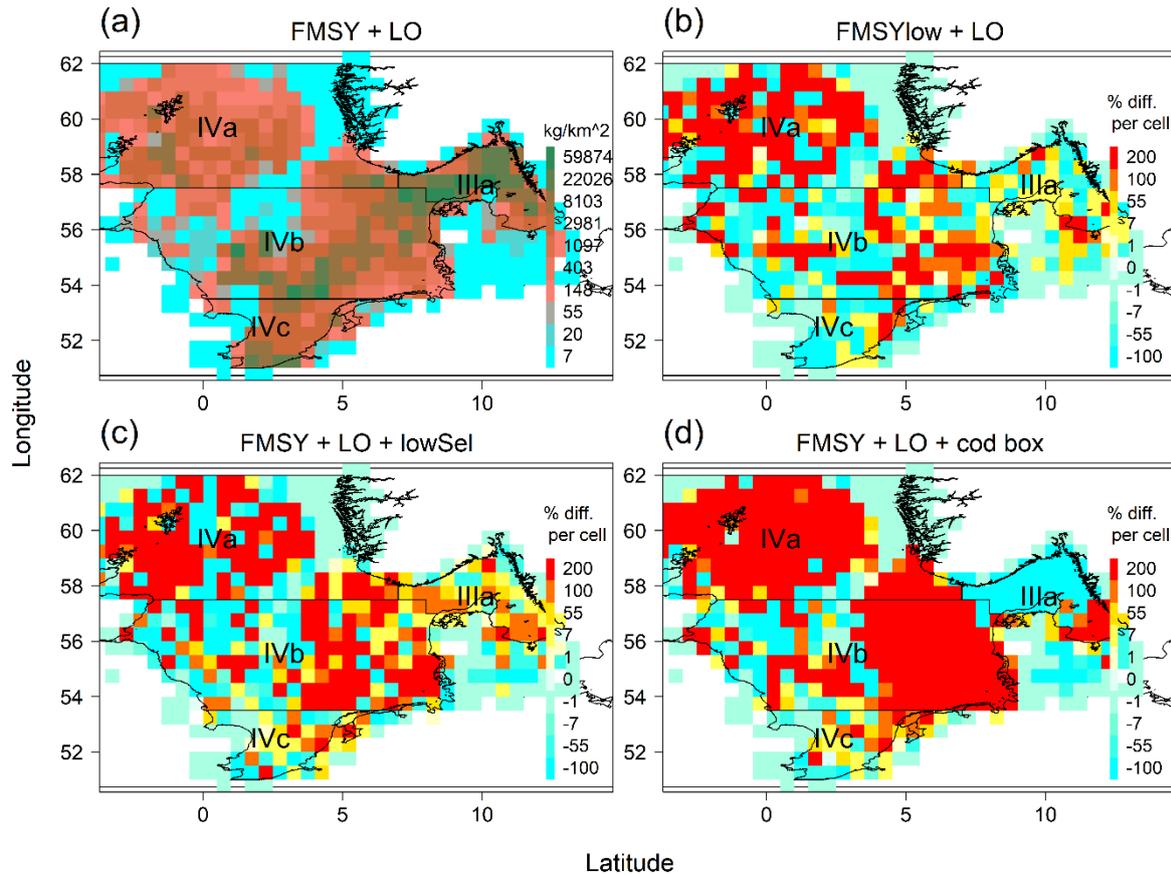
Figure 60. Simulated average spatial distribution of landings (all métiers confounded) at the 2030 horizon time for the baseline scenario in (a) (applying the FMSY strategy + LO), and relative to the baseline for a selection of scenarios (b) to (d).

Fleet-specific effects

Short term climate change effects will likely not affect fleet-specific components differently from their background trajectory changes induced by the long-term climate change trends. The fleet-segments benefiting from the baseline stock developments in the North Sea are the French, and to a less extend the Dutch and the Belgium fisheries. Anticipated effects on stocks from the climate change does not appear to affect with lower revenue or fuel-catch efficiency in future for particular national fleets, apart for the French fleet induced by lower landings on North Sea cod (Figures 61-63).
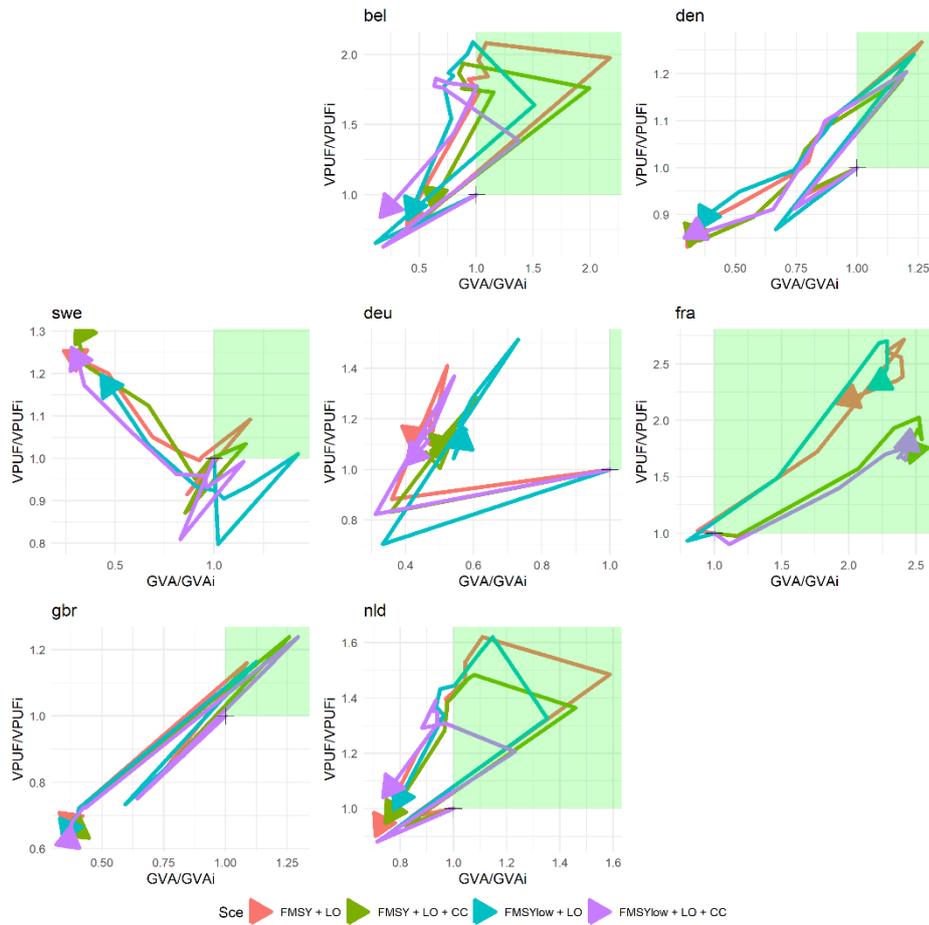
Figure 61. A bi-dimensional plot of average scenario outcomes on country-based (all métier confounded) ratios of VPUF/VPUFi and GVA/GVAi as simulated temporal trajectories from 2020 to horizon 2030. Countries are bel: Belgium, den: Denmark, swe: Sweden, deu: Germany, fra: France, gbr: UK, nld: The Netherlands. The ratio at 1 on both indicators (symbol '+') gives the initial estimates in 2020—the wished green corner for the drift of the indicators in the top right.
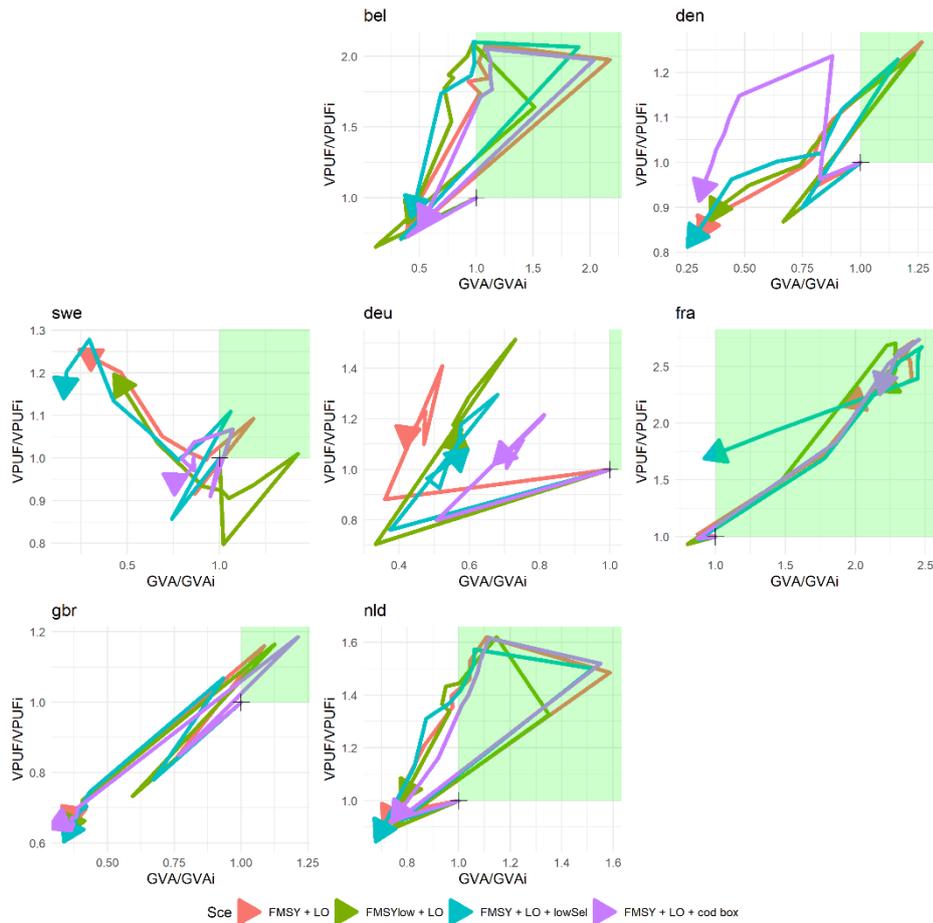
Figure 62. Same as Fig 61 but for another set of scenarios. A bi-dimensional plot of average scenario outcomes on country-based ratios of VPUF/VPUFi and GVA/GVAi as simulated temporal trajectories from 2020 to horizon 2030. Countries are bel: Belgium, den: Denmark, swe: Sweden, deu: Germany, fra: France, gbr: UK, nld: The Netherlands. The ratio at 1 on both indicators (symbol '+') gives the initial estimates in 2020—the wished green corner for the drift of the indicators in the top right.
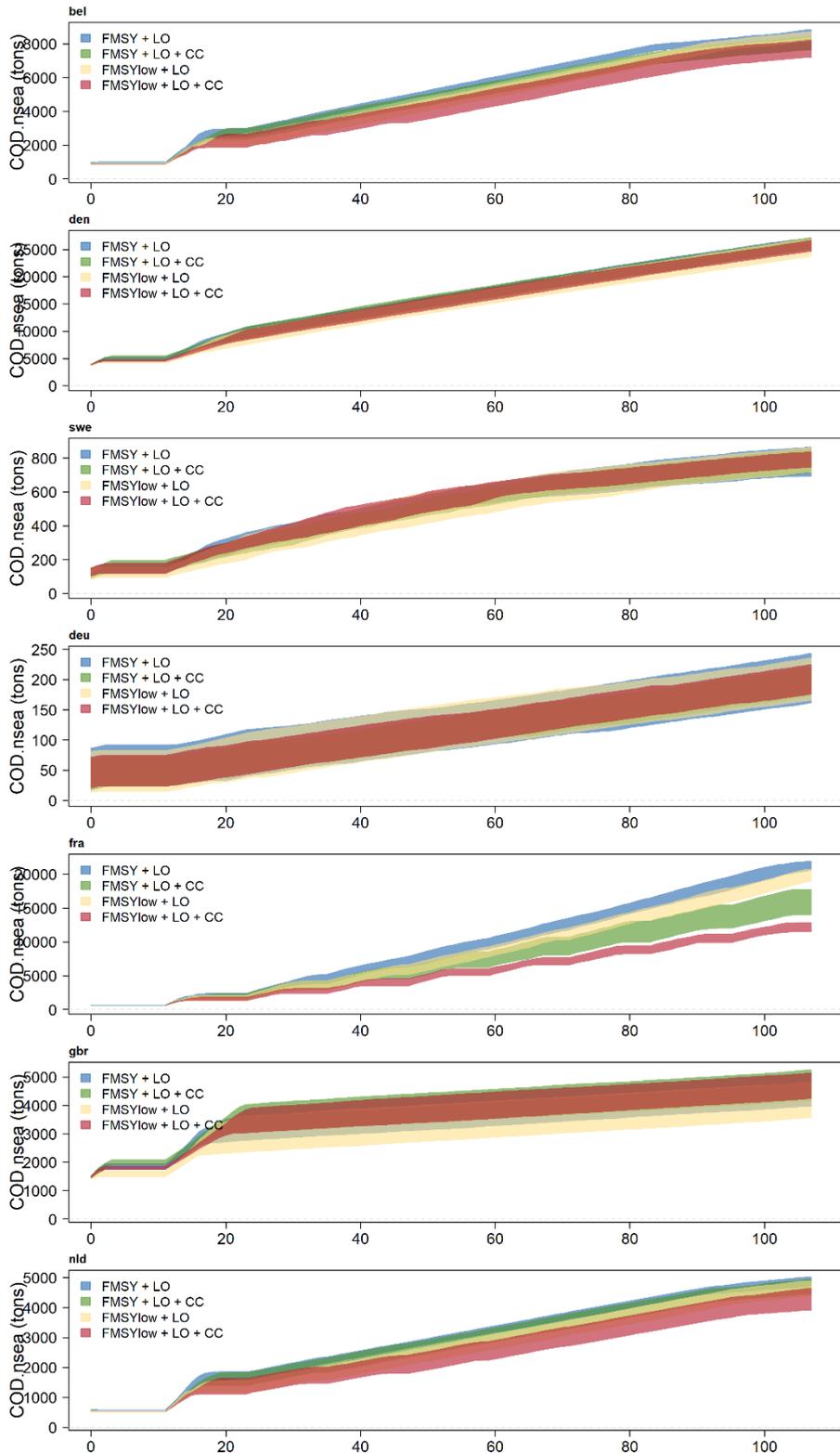
Figure 63. Simulated accumulated cod landings (in millions tons) over months over the 10y for selected scenarios (first y is removed).

The climate change-induced effects on the fleet economy in the North Sea is also likely dependent upon the types of fishing methods (Figure 64). Passive gears (GNS) win both in anticipated revenue

and fuel efficiency in all scenarios. Pelagic, demersal trawlers, and seiners will lose in GVA along with a gain in energy efficiency for pelagics. On the contrary, otter bottom trawls (other than DK) showed a marked improvement of both GVA and energy efficiency following the FMSY strategies which is not really downplayed by the climate-induced effects. Climate effects are not altering these more general trends and differences among fleet-segments.
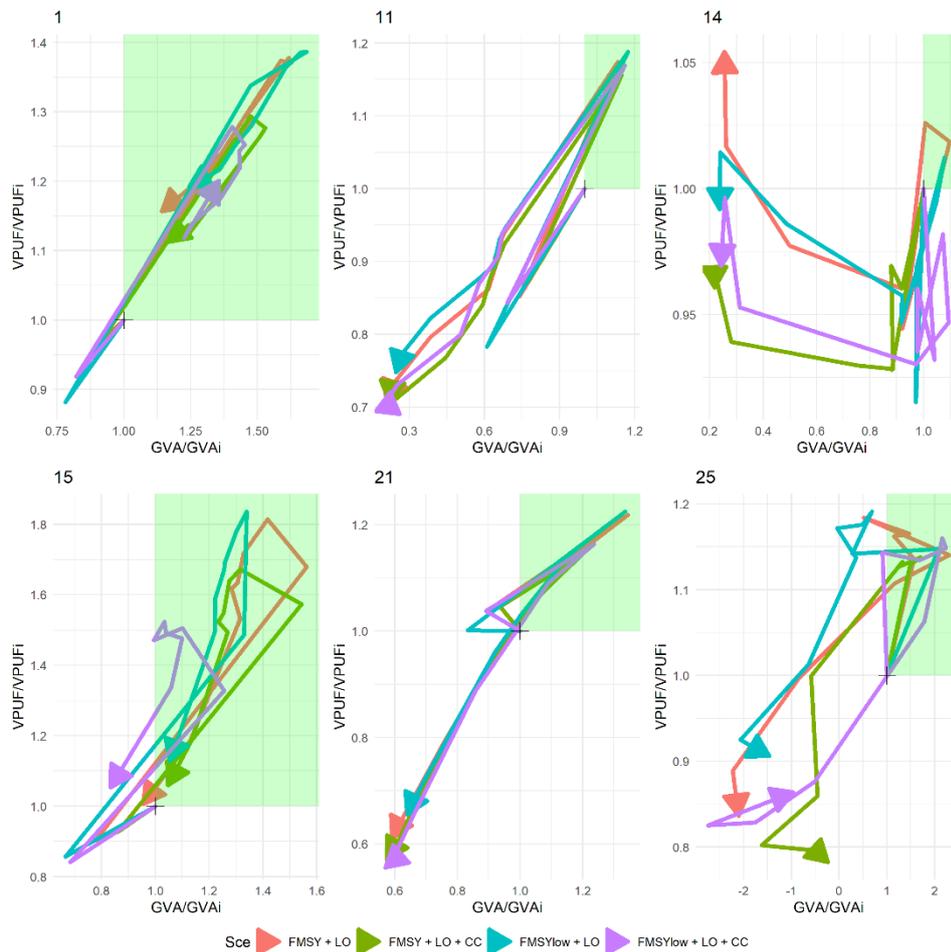
Figure 64. A bi-dimensional plot of average scenario outcomes on metier-based ratios of VPUF/VPUFi and GVA/GVAi as simulated temporal trajectories from 2020 to horizon 2030. Metiers/gear used are 1: GNS, 11: OT_DMF (Danish), 14: OT_SPF, 15: OTB, 21: SDN_DEM (Danish), 25: TBB_DMF (Danish). The wished green corner for the drift of the indicators in the top right.
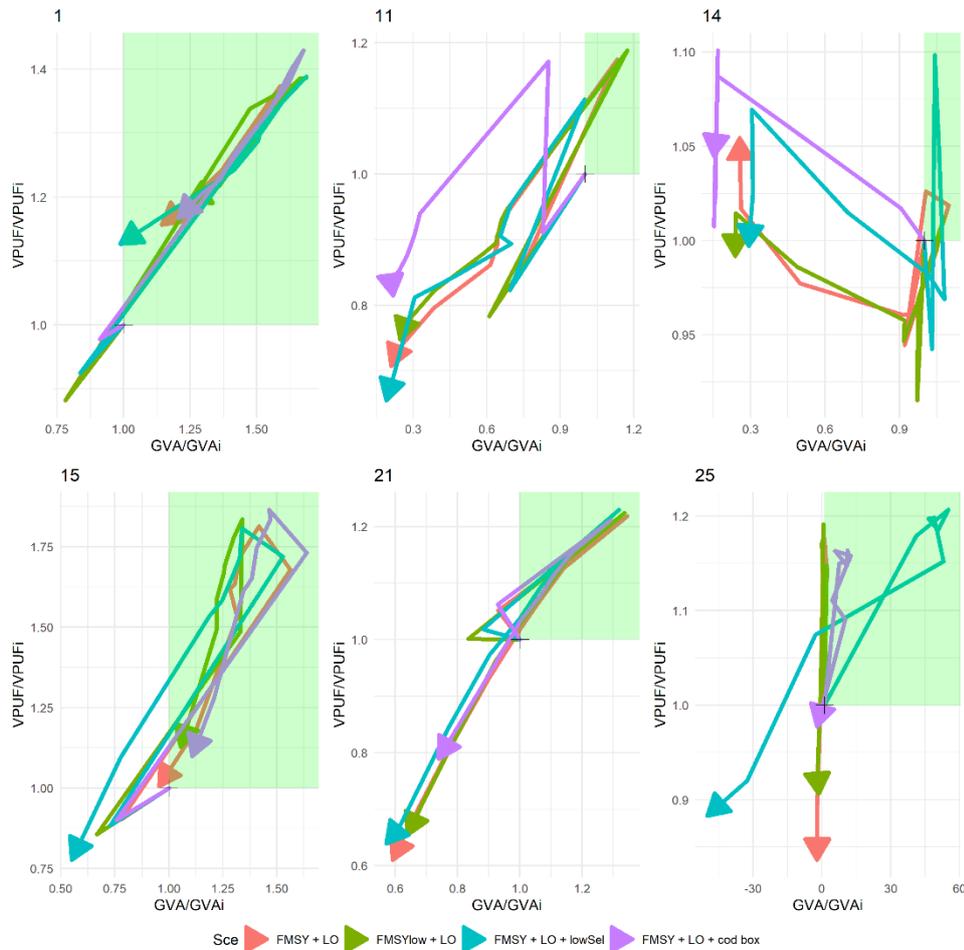
Figure 65. For another set of scenarios. A bi-dimensional plot of average scenario outcomes on metier-based ratios of VPUF/VPUFi and GVA/GVAi as simulated temporal trajectories from 2020 to horizon 2030. Metiers/gear used are 1: GNS, 11: OT_DMF (Danish), 14: OT_SPF, 15: OTB, 21: SDN_DEM (Danish), 25: TBB_DMF (Danish). The wished green corner for the drift of the indicators in the top right.

Environmental indicators

The scenarios on fleet or métier specific behaviour, F management strategies and the short-term climate change-induced stresses and long-term effects were at the origin of some relative change in the spatial effort allocation (Figure 59) and the related catches, e.g. on North Sea cod (Figure 66), which distribute over different habitat types. The largest habitat in proportion in the North Sea is A5.2 "Sublittoral Sand" followed by the A5.3. "Sublittoral mud" where it is anticipated the effort could slightly reduce by a few percent when applying scenarios, while the same scenarios could induce more effort on locally distributed rocky habitats (Figure 66).
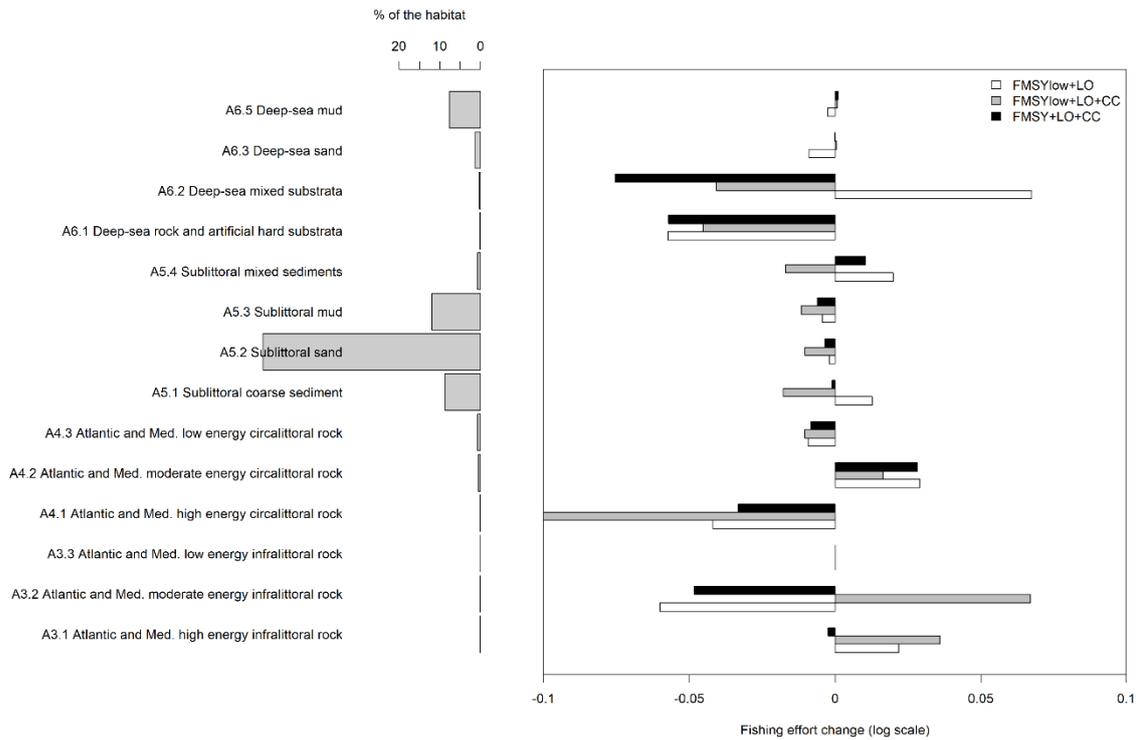
Figure 66. Relative change of fishing effort applied on EUNIS habitat types in the North Sea for selected scenarios. A value of -0.1 in logscale corresponds to exp(-.1)=0.90 in natural scale i.e. 90% of the effort compared to the baseline scenario, which is FMSY+LO. The fishing effort is the effort of all fleets pooled together. The percentage of habitat type is also given as an indication of the importance of each habitat in the North Sea in terms of overall surface area.

The simulation study also anticipated that, along with an overall catch reduction on North Sea cod compared to the baseline, the catch could be evenly reduced across the different habitats where the cod is been caught, with very minor gain on rocky and deep sea fishing grounds that represent a very small area in proportion of the overall North Sea area (Figure 67).
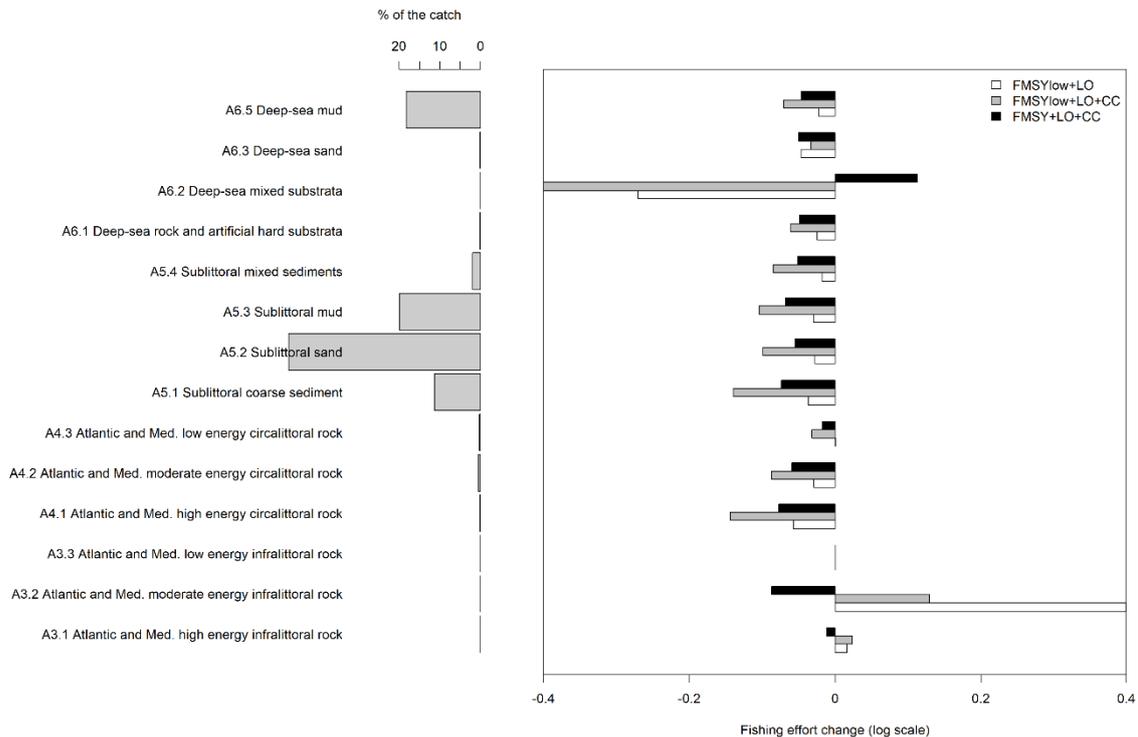
Figure 67. Relative change of North Sea cod landed amount applied on EUNIS habitat types in the North Sea for selected scenarios. A value of -0.1 in logscale corresponds to exp(-.1)=0.90 in natural scale i.e. 90% of the effort compared to the baseline scenario, which is FMSY+LO.

Concluding remarks on the bioeconomic simulation study and recommendations

The simulation study aims at extrapolating the stock trajectories to domains where there is some uncertainty about the central parameter values (i.e. future stock productivity and spatial distribution), and describing possible courses of the system, depending upon a choice of parameter values that are likely to be impacted by the climate change effects. As described by Harfoot et al. (2014) in Mouquet et al. (2015), these anticipatory predictions are therefore not meant to represent the actual future but mimic changes in a integrated evaluation. The fact that the projection do not match reality does not count against the validity of the underlying hypotheses. Instead, the simulation study should be regarded as a guide for present action.

Simulations showed that climate change effects we tested (i.e. a change in productivity) might have limited effects only in the 10 years' time horizon from now on the North Sea on fisheries. However, this would be possibly different if the climate-induced change on the harvested stocks would translate into a contraction, a westward or a northward move of the stock distributions (from some signals caught with the LGNB-SDM). We have not been able to test spatial distribution change within the frame of the project but we have on this aspect got some outcomes in the Baltic Sea (Bastardie et al. 2022). Hence, it is likely that the gross value added might become negative due to fixed and variable costs exceeding landings incomes and other revenues. The fishery energy efficiency might also be severely affected by longer trip duration and lower catch rates. This would be the likely result of some part of the stocks becoming out of range of small coastal fisheries. Besides this, if non-compliance to the LO might increases catch-fuel efficiency, other studies showed dramatic consequences on the gross value added induced by a long-term stock declining developments a non-compliance would induce (see Bastardie et al. 2022).

All the simulation outcomes and graphics can be retrieved from an R Shiny application delivered online (http://ono.dtuaqua.dk:8282/DISPLACE_RShiny_plots_NorthSea). This eases the exploration of the outcomes across the species, fleets and scenarios. Probability plots to exceed or keep below references points are not shown because the simulation outcomes show that the system derives towards new levels below or above the references. Equally, no estimates are provided in terms of per cent change for both stock development and fleet economy, and time for recovery, as no recovery is observed at the scale of the study, but diverging paths instead (i.e. not returning to initial states). The methodology and workflow developed during this project is particularly relevant for:

- Keeping the socio-ecosystems dynamics in the green zone: The purpose of the fisheries management is primarily to implement rules that should keep the system in the green area (see the Kobe plots). Given that the FMSY approach is implemented in the current CFP, it is also questionable if it is sufficient to face new challenges such as climate change or if climate-aware fisheries management/harvest control rules should be added, including a revision of the reference points before they go outdated.

- Testing the robustness of F-strategies: Overall, the simulation study shows that the F-MSY-lower strategy in the North Sea does not provide better pathways for future stock developments compared to F-MSY and is also surprisingly not adding any robustness against climate change effects. However, the simulations showed that the conditioning of the stocks in the model might provide overly optimistic stock levels and trajectories making the stock projection mediated by the trophic interactions quite uncertain. It also does not mean that a higher F-level should be advised. Because FMSY should be considered a limit and not a target per se, fishing at FMSY up to Fupper has regularly been criticized for putting future stocks at risk. The rationale for Fupper is to help the fishing sector to cope with possible choke species by mitigating the mixed fisheries issue often ignored. Here it is shown that indeed some TACs might choke some fisheries from time to time. Our findings also show that sticking to F-MSY lower is not rewarding for fishing in the short to medium term because limiting the fishing opportunities with early closure. It does not appear that following an F-MSY strategy in the ac-tual FMSY ranges is sufficient to counteract the risk induced by a changing climate. The undesired trajectories are even more pronounced when vessels are not complying with the LO (i.e. GVA declines along with stock developments on collapse trajectories if vessels continue fishing after being choked). It comes as no surprise for modellers that it is indeed not coherent to increase the fishing pressure be-yond FMSY and the associated operating variable costs to likely achieve poor yield and put some of the stocks (especially the short-lived ones like the pelagic herring and sprat) at risk of collapse (see, e.g. the discussion in Earle (2021), as the North Sea MAP would allow.

- Documenting a fleet-based approach: When the LO is fully enforced, the simulations suggest that the most significant uncertainty for the stocks and fisheries facing climate change would arise from how the stock distribution would react spatially to a change in environmental driv-ers and tolerance limits. The loss or the redistribution of fishing areas and opportunities might not be compensated for, even if the stock is developing better under the FMSY-lower strat-egy. Hence, it is required to follow a fleet-based approach to identify who might be impacted and who contribute the most to degradation or who will be hit the most by the management or climate change.

- Keeping aware of the interlinked dynamics: Unfortunately, even in a simulation study, the in-terpretation of anticipated benefits is still uncertain because possible opportunity loss may

arise either from degraded and degrading stocks or, on the contrary, from improved and improving stocks when some of the TACs are choking the fishing fleets. Therefore it appears that the best management is to match opportunities with the catch allowances and stock levels, which is mainly a challenge when technical and biological interactions are ruling.

- Account for collateral effects: Fishing to FMSY should address other environmental concerns, i.e. "collateral" effects, i.e. on the ecosystem. Target/optimisation is of no use there, and the thinking is better on finding the way forward for minimizing the impacts of fisheries as the CFP specify it. This would require coherence among references levels to manage the fisheries. This includes fishing impacts on the seafloor and the benthic habitats, especially removing contradiction between the ones for sensitive species and habitat and the ones for commercially exploited species. Such evaluation requires additional information to ensure the sustainability of the impact, as different fishing methods combined with the habitat's vulnerability and the fishing intensity. We first expected the energy efficiency to be related to the fishing footprint on such other ecosystem components of the marine ecosystem. However, our simulation study shows that the link is not straightforward, as saving fuel might sometimes lead some vessels to spend more time at sea instead of less. Hence, it is not apparent to the scientific community what is the best scientific rationale in advising special fishing gears in different areas. It might also be recognized that ten times fishing with less impacting gears might be just as harmful as one time fishing with more impacting fishing gear, which requires the trade-offs in fisheries management to be made well explicit. It is expected that evaluating the respective energy efficiency of different types of gears might help reconcile this apparent dilemma as, for now, the more energy-efficient fishing methods are also likely the less impacting gears. To minimize such effects, (e.g. the harmful fishing gears are also the ones spending more fuel at sea), management should also ideally account for spatial (e.g. closed areas) and non-spatial effort management (e.g. effort reduction plans) besides the output control TAC management.

- Organizing model coupling: To ease accounting for ecosystem models beyond single stocks or fleet-based approach is required to use more than one model and more strategic models (i.e. ecosystem models). Because one big complex model can quickly become untractable, a way forward is to arrange model coupling. Hence, the present simulation study could pass some viability check for the ecosystem by using its outcomes for informing the input of ecosystem models (e.g. use the effort time series or the exploitation patterns from different scenarios as input to ecosystem models).

- Supporting more investigation on the fuel use intensity: The simulation shows no apparent link with the energy use intensity apart from saving on costs that benefit the economy of fishing. There are likely dominating compensatory/rebound effects that prevent saving fuel from stocks in better shape. We, however, showed a possible indirect effect arising from saving energy on fished stocks levels, including more time spent at sea or redirecting fishing toward areas that become attractive when fuel use is less limiting, which is possibly unwished side effects.

Finally, there are important limitations of the present simulation study as the study is not addressing possible important drivers in population dynamics, including:
- Predictions of harmful algal blooms and eutrophication zones;
- Identification of the impact of climate change on species diversity;
- A possible effect of a change in land use in the North Sea catchment area including effects of pollution;

- Possible helpful management options such as the design of marine protected areas and other management measures;
- Understanding seasonal patterns of fish spawning and spatial migration.

The study is not addressing possible important drivers in fleet dynamics, including:
- Possible different fishing styles (e.g., risk-takers vs risk-averse fishers etc.)
- Profitability at the company level (possibly owning several vessels)
- Insurance against risks provided by POs or fishing communities, or quota swapping
- Fishing outside the known historical footprint
- An abrupt change in catching power from technological innovations
- Market integration and prices dynamics from external markets

11. Workshop with the fishing industry

The 7th of April 2022 we held a workshop initially plan to be attended by the Danish POs representative in order to collect their feedback on our scientific outcomes. However, none of them was able to attend the meeting due to urgent matters on the political agenda. The WK has however be maintained so that scientists exchanged on the project findings. The first hour of the meeting was dedicated to present the outcomes with the support of the presentation attached in Annexe. In the follow-up, scientists reflected on involve POs and engage them to react to the methodology and give their views on the findings. Scientist agrees that the POs representative would be asked to fill out a short questionnaire survey to inform on possible response of the sector to an array of change induced by a changing climate.

Box 1. Questionnaire survey to investigate Possible response of the fishing sector to climate change induced effects (inspired by Fulton et al. 2020) collected via a questionnaire survey to POs representatives.

Fishery Adaptation Survey – Workshop with the fishing industry – April 2022 – Lyngby
In the context of the EMFF projected named "North Sea resource distribution and fishery opportunities (NORDFO)" EMFF Contract number 33113-B-19-128

Abstract of the NORDFO project
This study has shown that the Danish fisheries fishing in the North Sea are at risk facing the impact of climate-driven short-term stresses when some of the exploited stocks are on the move, as the North Sea cod. The study developed a new methodological approach based on the previous modelling to strengthen our predictive power in anticipating interlinked stocks and fisheries developments under changing conditions.

Aim of the short survey (1 hour)
Understanding the adaptive responses available to fishers, whether there really is the capacity to change operations or whether social, financial or regulatory barriers exist, and under what conditions they would implement this adaptive response (i.e. the level of change in catch or physical conditions needed before an adaptive behavioural change is made).

Please score between 0 to 5 in the below table in each cell
(do not try to scale or rank by row or column, just use values for all cells independently).
0: Fishers will not do this
1: unlikely
2: somewhat likely
3: likely
4: very likely
5 Fishers will do this certainly

Please consider fill out the last column (i.e. the blue field) with your comments

---

Possible response of the fishing sector to climate change induced effects (inspired by Fulton et al. 2020) collected via a questionnaire survey to POs representatives	A change in number of fish	A change in where the fish can be found	A change in when the fish move or spawn	A change in the quality of the product	A change in how variable the accessible fish is year to year	Comments on your possible response (for example, the direction of your response, that is, decrease/increase)
Change the amount of quota trade						
Change the amount of fishing effort						
Move to another fishing location						
Switch to different target species						
Invest in new technology or assets						
Change the sale price of fish						
Change supply chain management						
Improve fish handling methods						
Diversify markets						
Value add to the product						
Seek information about adaptation options						
Communication with concerned stakeholders						
Comments on each pressure						

12. General conclusion

We have applied an advanced statistical method to reconstruct the past dynamic of the spatial distribution of the most important commercial stocks in the North Sea from both scientific survey data and commercial fisheries data, with a special focus on cod.

Based on the statistical reconstruction we have identified the persistent areas of abundance density for each stock as well as the gravity point of these hotspots areas and the tendency of this average geographical position over the period examined, and the consequences regarding the change in the distance to the Danish coastline.

We have identified plausible scenarios for a change in productivity of the stocks induced by climate change effects on those stocks at the horizon 2030. These effects were the basis for conditioning a spatial modelling of fisheries platform to project, under the current FMSY-strategy implemented in the EU CFP, the anticipated stock developments and likely economic income including change in operating costs for the international North Sea fleets including the Danish fleet fishing in the North Sea.

Our findings showed that stock distribution have been stable over the 2001-2019 period with the same repeated seasonality effect. The only exception among the stock examined is the North Sea cod, which might have shifted westward, farther from the Danish coastline, with possible implication to access its fishing opportunity (require large range vessels, and access to UK EEZ). Stable concentration of fish to the same areas ("persistent hotspots"), especially juvenile undersized fishes, suggest the possible use of area-based management such as closed areas to fishing to limit the unwanted catches. Our bio economic impact assessment modeling the international fisheries in the North Sea showed that long-term climate-induced effects on the environmental drivers led to a decreased fleet revenue (NPV ca. 5 to 10%) and energy efficiency (ca. 5%), which is more pronounced for active gears, from lower landings on North Sea cod, herring, plaice and sole; only landings of saithe and pollock are not affected. Especially North Sea cod stock is seeing its overall abundance decreasing. The FMSY-lower strategy is not correcting for the loss of opportunity induced by the climate change and shock but worsen the loss of fishing opportunities on cod instead. It is striking that the simulations anticipate effort and catches to increase over the main fishing grounds visited by the Danish and international fleets in the North Sea over all management tested i.e. when management applied a FMSY low strategy, when the management is less restrictive on the gear selectivity, or when the management applied a spatial closure for cod in the Skagerrak. This increase is the outcomes of three different effects, however. FMSYlow increase the catch on the long run when the stock is temporally underexploited, fishermen using gears with lower selectivity catch more fish but require more effort to exhaust the quota with larger fish, and finally setting a closure does not reduce the overall effort but displace it instead toward the remaining opened areas, increasing the catches there.

Simulations showed that climate change might have limited effects only in the 10 years' time horizon from now on the North Sea on fisheries. However, this would be possibly different if the climate-induced change on the harvested stocks would translate into a contraction or a northward move of the stock distributions. In this latter case, the gross value added might become negative due to fixed and variable costs exceeding landings incomes and other revenues. The energy efficiency might also be severely affected by longer trip duration and lower catch rates. This would be the likely result of some part of the stocks becoming out of range of small coastal fisheries.

These anticipatory predictions are therefore not meant to represent the actual future. The fact that the projection do not match reality does not count against the validity of the underlying hypotheses. Instead, the simulation study should be regarded as a guide for present action. Hence, the project outcomes can be of use directly in the evaluation of suggested spatial management measures intended to protect specific aspects such as bycatch species or intended to avoid choke species issues to fulfilling the continuous need of supporting the implementation of a sustainable CFP with knowledge and scientific work. In this context, the evaluation framework and the outcomes for its North Sea implementation could be of use by EU STECF, ICES, OSPAR and regional ACs. The evaluation framework solution and application to the North Sea marine ecosystem developed in this project can measure the past and current pressures the fishing induced and exert on important Danish fisheries resources and on the by-catch stocks, as well as on the different benthic habitats. The framework integrates knowledge and dynamics of key factors determining and regulating the occurrence and distribution of many important fish stocks in the North Sea marine ecosystem, and ultimately the social, environmental and economic implications in changing the fisheries economic incomes that a change in pressure could create, e.g. induced by the climate change. These knowledge and analyses should support the current North Sea and future other case studies implementation of a sustainable CFP also including landing obligation related issues.

13. References

Ahrens, R.N.M., Walters, C.J., Christensen, V., 2012. Foraging arena theory. Fish Fish 13, 41–59. https://doi.org/10.1111/j.1467-2979.2011.00432.x.

Akimova, A., Nunez-Riboni, I., Kempf, A., and Taylor, M. H. (2016). Spatially-resolved influence of temperature and salinity on stock and recruitment variability of commercially important fishes in the North Sea. PloS one, 11(9), e0161917.

Asjes, A., González-Irusta, J., and Wright, P. 2016. Age-related and seasonal changes in haddock Melanogrammus aeglefinus distribution: implications for spatial management. Marine Ecology Progress Series, 553: 203–217.

Baker, H. S., Woollings, T., Forest, C. E., and Allen, M. R. 2019. The Linear Sensitivity of the North Atlantic Oscillation and Eddy-Driven Jet to SSTs. Journal of Climate, 32: 6491–6511.

Bastardie, F., Nielsen, J. R., & Miethe, T. (2014). DISPLACE: a dynamic, individual-based model for spatial fishing planning and effort displacement - integrating underlying fish population models. Canadian Journal of Fisheries and Aquatic Sciences, 71(3), 366-386. https://doi.org/10.1139/cjfas-2013-0126

Bastardie, F., Nielsen, J. R., Eero, M., Fuga, F., & Rindorf, A. (2017). Effects of changes in stock productivity and mixing on sustainable fishing and economic viability. ICES Journal of Marine Science, 74(2), 535-551.

Bastardie et al. 2022. Scientific advice in support of the CFP in the Baltic Sea and North Sea EU waters: Climate change and the common fisheries policy adaptation and building resilience to the effects of climate change on fisheries and reducing emissions of greenhouse gases from fishing

Blanchard, J.L., Andersen, K.H., Scott, F., Hintzen, N.T., Piet, G. and Jennings, S. (2014), Evaluating targets and trade-offs among fisheries and conservation objectives using a multispecies size spectrum model. J Appl Ecol, 51: 612-622. https://doi.org/10.1111/1365-2664.12238

Baudron, A. R., Needle, C. L., and Marshall, C. T. 2011. Implications of a warming North Sea for the growth of haddock Melanogrammus aeglefinus. Journal of Fish Biology, 78: 1874–1889.

Beaugrand, G., Brander, K. M., Alistair Lindley, J., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. Nature, 426: 661–664.

Bogstad, B., Dingsør, G. E., Ingvaldsen, R. B., and Gjøsæter, H. 2013. Changes in the relationship between sea temperature and recruitment of cod, haddock and herring in the Barents Sea. Marine Biology Research, 9: 895–907.

Bruge, A., Alvarez, P., Fontán, A., Cotano, U., and Chust, G. 2016. Thermal Niche Tracking and Future Distribution of Atlantic Mackerel Spawning in Response to Ocean Warming. Frontiers in Marine Science, 3. http://journal.frontiersin.org/article/10.3389/fmars.2016.00086 (Accessed 26 April 2022).

Brunel, T, and M Dickey-Collas. 2010. "Effects of Temperature and Population Density on von Bertalanffy Growth Parameters in Atlantic Herring: A Macro-Ecological Analysis." Marine Ecology Progress Series 405: 15–28. http://www.int-res.com/abstracts/meps/v405/p15-28/ (March 17, 2021).

Brunel T, Verkempynck R. 2018. Variation in North Sea sole distribution with respect to the 56°N parallel perceived through scientific survey and commercial fisheries. Report number: Wageningen Marine Research report C087/18

Brunel, T., van Damme, C. J. G., Samson, M., and Dickey-Collas, M. 2018. Quantifying the influence of geography and environment on the northeast Atlantic mackerel spawning distribution. Fisheries Oceanography, 27: 159–173.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York

Carton, J.A., G.A. Chepurin, and L. Chen (2018), SODA3: a new ocean climate reanalysis, J. Climate, 31, 6967-6983, https://doi.org/10.1175/JCLI-D-18-0149.1 - downloaded May 2021

Christensen, V, C.J. Walters and D. Pauly. 2005. Ecopath with Ecosim: a User's Guide. Fisheries Centre, University of British Columbia, Vancouver. November 2005 edition, 154 p.

Christensen, A., Mariani, P., Payne, M.R., Dias, J.M. 2018. A generic framework for individual-based modelling and physical-biological interaction. P L o S One, vol. 13, no. 1, pp. e0189956

Clausen, L. W., Rindorf, A., van Deurs, M., Dickey-Collas, M., and Hintzen, N. T. (2018). Shifts in North Sea forage fish productivity and potential fisheries yield. Journal of Applied Ecology, 55(3), 1092-1101.

Cormon, X., Kempf, A., Vermard, Y., Vinther, M., and Marchal, P. 2016. Emergence of a new predator in the North Sea: evaluation of potential trophic impacts focused on hake, saithe, and Norway pout. ICES Journal of Marine Science, 73: 1370–1381.

Danmarks Statistik, 2018. Account Statistics for Fishery and Aquaculture, 73 pp. Url: https://www.dst.dk/Site/Dst/Udgivelser/GetPubFile.aspx?id=28174&sid=fisk2018, accessed on August, 2020.

Danmarks Fiskeriforening, 2020. Fiskeri i tal 2020: TAC og kvoter 2020 og statistik om dansk erhvervsfiskeri, 24 pp. Url: https://fiskeriforening.dk/media/7154/fiskeri_i_tal_2020.pdf, accessed on August, 2020.

Dippner, J.W, (1997). SST anomalies in the North Sea in relation to the North Atlantic Oscillation and the potential influence on the theoretical spawning time of fish, Dt. Hydrogr. Z., 49, 267-275.

Elith, J. and Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annual review of ecology, evolution, and systematics, 40, 677-697.

Earle, M., 2021. Maximum sustainable yield in the EU's Common Fisheries Policy - a political history, ICES Journal of Marine Science, Volume 78, Issue 6, September 2021, Pages 2173–2181

Eigaard, O. R., Bastardie, F., Hinzen, N. T., Buhl-Mortensen, L., Mortensen, P. B., Catarino, R., Dinesen, G. E., Egekvist, J., Fock, H., Geitner, K., Gerritsen, H., González, M. M., Jonsson, P., Kavadas, S., Laffargue, P., Lundy, M., Gonzalez-Mirelis, G., Nielsen, J. R., Papadopoulou, N., ... Rijnsdorp, A. D. (2017). The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES Journal of Marine Science, 74(3), 847-865. https://doi.org/10.1093/icesjms/fsw194

EMFF 2021. grant ID: 33113-B-17-091; project: Maintaining a sustainable sprat fishery in the North Sea, BEBRIS: https://backend.orbit.dtu.dk/ws/portalfiles/portal/246745647/382_2021_Bevarelse_af_et_baeredygtigt_industrifiskeri_BEBRIS.pdf

Engelhard, G. H., Pinnegar, J. K., Kell, L. T., and Rijnsdorp, A. D. 2011. Nine decades of North Sea sole and plaice distribution. ICES Journal of Marine Science, 68: 1090–1104.

Engelhard, G. H., Righton, D. A., and Pinnegar, J. K. 2014. Climate change and fishing: a century of shifting distribution in North Sea cod. Global Change Biology, 20: 2473–2483.

Fiksen, Øyvind, and Aril Slotte. 2002. "Stock-Environment Recruitment Models for Norwegian Spring Spawning Herring (Clupea Harengus)." Canadian Journal of Fisheries and Aquatic Sciences 59(2): 211–17.

Fouzai, N., Opdal, A., Jørgensen, C., and Fiksen, Ø. 2015. Effects of temperature and food availability on larval cod survival: a model for behaviour in vertical gradients. Marine Ecology Progress Series, 529: 199–212.

Fox, C. J., Planque, B. P., and Darby, C. D. 2000. Synchrony in the recruitment time-series of plaice (Pleuronectes platessa L) around the United Kingdom and the influence of sea temperature. Journal of Sea Research, 44: 159–168.

Fulton EA, van Putten EI, Dutra LXC, Melbourne-Thomas J, Ogier E, Thomas L, Murphy RP, Butler I, Ghebrezgabhier D, Hobday AJ, Rayns N (2020) Adaptation of fisheries management to climate change Handbook, CSIRO, Australia.

González-Irusta, J. M., and Wright, P. J. 2016. Spawning grounds of Atlantic cod (Gadus morhua) in the North Sea. ICES Journal of Marine Science: Journal du Conseil, 73: 304–315.

Grati, F., Bolognini, L., & Bastardie, F. 2017. Spatial Planning for Fisheries in the Adriatic Sea, – the ECOAST project. Abstract from International Symposium: Protection of the Black Sea Ecosystem and Sustainable Management of Maritime Activities, PROMARE, Constanta, Romania.

Gröger, Joachim P., Gordon H. Kruse, and Norbert Rohlf. 2010. "Slave to the Rhythm: How Large-Scale Climate Cycles Trigger Herring (Clupea Harengus) Regeneration in the North Sea." ICES Journal of Marine Science 67(3): 454–65. https://academic.oup.com/icesjms/article/67/3/454/732742 (March 16, 2021).

Heath, M. 2000. Winter distribution of Calanus finmarchicus in the Northeast Atlantic. ICES Journal of Marine Science, 57: 1628–1635.

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A., and Andrews, J. 2004. Analysis of the spatial distributions of mature cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) abundance in the North Sea (1980–1999) using generalised additive models. Fisheries Research, 70: 17–25.

Hunter, A., Speirs, D. C., and Heath, M. R. 2019. Population density and temperature correlate with long-term trends in somatic growth rates and maturation schedules of herring and sprat. PLOS ONE, 14: e0212176.

ICES. 2020. Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). ICES Scientific Reports. 2:61. 1140 pp. http://doi.org/10.17895/ices.pub.6092

ICES. 2020a. Working Group on Widely Distributed Stocks (WGWIDE). ICES Scientific Reports. 2:82. 1019 pp. http://doi.org/10.17895/ices.pub.7475

ICES (2018b) https://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2018/WKspratMSE/WKspratMSE%20Report%202018.pdf

Idongesit E. Ikpewe, Alan R. Baudron, Aurore Ponchon, Paul G. Fernandes 2020 Bigger juveniles and smaller adults: Changes in fish size correlate with warming seas

Jacobsen, N. S., Gislason, H., & Andersen, K. H. (2014). The consequences of balanced harvesting of fish communities. Proceedings of the Royal Society B-Biological Sciences, 281(1775). https://doi.org/10.1098/rspb.2013.2701

Jonsson, P.R., Corell, H., André, C., Svedäng, H., & Moksnes, P. (2016). Recent decline in cod stocks in the North Sea–Skagerrak–Kattegat shifts the sources of larval supply. Fisheries Oceanography, 25, 210-228.

Jungclaus, J. H., N. Fischer, H. Haak, K. Lohmann, J. Marotzke, D. Matei, U. Mikolajewicz, D. Notz, and J. S. vonStorch, 2013. Characteristics of the ocean simulations in MPIOM, the ocean component of the MPI-Earth system model, J. Adv. Model.Earth Syst., 5, 422–446, doi:10.1002/jame.20023

Kjesbu, O. S., Thorsen, A., and Fonn, M. 2011. Quantification of Primary and Secondary Oocyte Production in Atlantic Cod by Simple Oocyte Packing Density Theory. Marine and Coastal Fisheries, 3: 92–105.

Kristensen, K., Berg, C. 2018. Datras: Read and convert raw data obtained from http://datras.ices.dk/dataproducts/download/downloaddatapublic.aspx [R package version 1.01].

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. M. 2016. TMB: Automatic differentiation and Laplace approximation. Journal of Statistical Software 70: 1-21.

Kvile, K. Ø, Giovanni Romagnoni, Knut-Frode Dagestad, Øystein Langangen, Trond Kristiansen, 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*, Volume 75, Issue 7, December 2018, Pages 2413–2424

Lindegren, M., Rindorf, A., Norin, T., Johns, D., and van Deurs, M. (2020). Climate-and density-dependent regulation of fish growth throughout ontogeny: North Sea sprat as a case study. ICES Journal of Marine Science, 77(7-8), 3138-3152.

Mollet, F., Kraak, S., and Rijnsdorp, A. 2007. Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole Solea solea. Marine Ecology Progress Series, 351: 189–199.

Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., et al. (2015). Predictive ecology in a changing world. J. App. Ecol. 52, 1293–1310. doi: 10.1111/1365-2664.12482

Nielsen, J. R., Rufener, M-C., Kristensen, K., & Bastardie, F. (2019). The correlation between spatial distribution of fisheries and resources – integrated spatial and bio-economic fisheries management evaluation (MSPTOOLS). DTU Aqua. DTU Aqua-rapport No. 355-2019

Núñez-Riboni, I., Taylor, M. H., Kempf, A., Püts, M., and Mathis, M. 2019. Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (Gadus morhua) under climate change. ICES Journal of Marine Science, 76: 2389–2403.

Núñez-Riboni, I., and Akimova, A., 2015. Monthly maps of optimally interpolated in situ hydrography in the North Sea from 1948 to 2013. Journal of Marine Systems, 151(Suppl. C): 15–34.

Olsen, E. M., Ottersen, G., Llope, M., Chan, K.-S., Beaugrand, G., and Stenseth, N. Chr. 2011. Spawning stock and recruitment in North Sea cod shaped by food and climate. Proceedings of the Royal Society B: Biological Sciences, 278: 504–510.

Ottersen, G., Stige, L.C., Durant, J.M., Chan, K., Rouyer, T., Drinkwater, K.F., & Stenseth, N.C. (2013). Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. Marine Ecology Progress Series, 480, 205-225.

Papworth, D. J., Marini, S., and Conversi, A. 2016. A Novel, Unbiased Analysis Approach for Investigating Population Dynamics: A Case Study on Calanus finmarchicus and Its Decline in the North Sea. PLOS ONE, 11: e0158230.

Payne, Mark R. et al., 2009. "Recruitment in a Changing Environment: The 2000s North Sea Herring Recruitment Failure." ICES Journal of Marine Science 66(2): 272–77. https://academic.oup.com/icesjms/article/66/2/272/595050 (March 17, 2021).

Pécuchet, L., Nielsen, J. R., and Christensen, A. 2015. Impacts of the local environment on recruitment: a comparative study of North Sea and Baltic Sea fish stocks. ICES Journal of Marine Science, 72: 1323–1335.

Püts, M., Taylor, M., Núñez-Riboni, I., Steenbeek, J., Stäbler, M., Möllmann, C., Kempf, A., 2020. Insights on integrating habitat preferences in process-oriented ecological models – a case study of the southern North Sea. Ecol. Modell. 431, 109189. https://doi.org/10.1016/j.ecolmodel.2020.109189

Quante, M.; Colijn, F. (Ed.) (2016). North Sea region climate change assessment. Regional Climate Studies. Springer: Switzerland. ISBN 978-3-319-39743-6. xlv, 528 pp.

R Development Core Team, 2019. R: a language and environment for statistical computing. http://.R-project.org/

Rijnsdorp, A.D., O.A. van Keeken and L.J. Bolle. 2004. Changes in the productivity of the southeastern North Sea as reflected in the growth of plaice and sole. ICES CM 2004/K:13.

Rijnsdorp, A. 1996. Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. ICES Journal of Marine Science, 53: 1054–1062.

Rufener, M-C. 2020. Integrating commercial fisheries and scientific survey data: Advances, new tools and applications to model the fish and fishery dynamics, PhD Dissertation, DTU-Aqua.

Rufener, M-C., Kristensen, K., Nielsen, J. R., & Bastardie, F. (2021). Bridging the gap between commercial fisheries and survey data to model the spatiotemporal dynamics of marine species. Ecological Applications, 31(8), [e02453]. https://doi.org/10.1002/eap.2453

Sbrocco, E.J., Barber, P.H., 2013. MARSPEC: Ocean climate layers for marine spatial ecology. Ecology 94: 979.

Schrum, Corinna, et al. "Projected change—North sea." North Sea region climate change assessment (2016): 175-217.

Stäbler, M., Kempf, A., Mackinson, S., Jaap, J., Garcia, C., Temming, A., 2016. Combining efforts to make maximum sustainable yields and good environmental status match in a food-web model of the southern North Sea. Ecol. Modell. 331, 17–30. https://doi.org/10.1016/j.ecolmodel.2016.01.020

Stäbler, M., Kempf, A., Temming, A., 2018. Assessing the structure and functioning of the southern North Sea ecosystem with a food-web model. Ocean Coast. Manag. 165. https://doi.org/10.1016/j.ocecoaman.2018.08.017

Storr-Paulsen M., Håkansson K. B., Egekvist J., Degel H., and Dalskov, J. 2012. Danish Sampling of Commercial Fishery: Overview with special attention to discards 2010 data. DTU Aqua Report No 250-2012. National Institute of Aquatic Resources, Technical University of Denmark.

Steinarsson, A., and Bjornsson, B. 1999. The effects of temperature and size on growth and mortality of cod larvae. Journal of Fish Biology, 55: 100–109.

Teal, L. R., van Hal, R., van Kooten, T., Ruardij, P., and Rijnsdorp, A. D. 2012a. Bio-energetics underpins the spatial response of North Sea plaice (Pleuronectes platessa L.) and sole (Solea solea L.) to climate change. Global Change Biology, 18: 3291–3305.

Teal, L. R., van Hal, R., van Kooten, T., Ruardij, P., and Rijnsdorp, A. D. 2012b. Bio-energetics underpins the spatial response of North Sea plaice (Pleuronectes platessa L.) and sole (Solea solea L.) to climate change. Global Change Biology, 18: 3291–3305.

Tulp, I., Bolle, L. J., and Rijnsdorp, A. D. 2008. Signals from the shallows: In search of common patterns in long-term trends in Dutch estuarine and coastal fish. Journal of Sea Research, 60: 54–73.

Van der Veer HW, Witte JIJ (1999) Year-class strength of plaice Pleuronectes platessa in the Southern Bight of the North Sea: a validation and analysis of the inverse relationship with winter seawater temperature. Mar Ecol Prog Ser 184:245-257

van der Veer, H. W., Geffen, A. J., & Witte, J. IJ. (2000). Exceptionally strong year classes in plaice Pleuronectes platessa: are they generated during the pelagic stage only, or also in the juvenile stage? Marine Ecology Progress Series, 199, 255–262.

Van Keeken, O.A., Van Hoppe, M, Grift, R. E., Rijnsdorp, A. D., 2007. Changes in the spatial distribution of North Sea plaice (Pleuronectes platessa) and implications for fisheries management. J. Sea Res. 57, 187-197.

Van der Veer, H., J. Koot, G. Aarts, R. Dekker, W. Diderich, V.Freitas & J. Witte, 2011. Long-term trends in juvenileflatfish indicate a dramatic reduction in nursery function ofthe Balgzand intertidal, Dutch Wadden Sea. MarineEcology Progress Series 434: 143–154

van de Wolfshaar, K. E., Barbut, L., and Lacroix, G. 2022. From spawning to first-year recruitment: the fate of juvenile sole growth and survival under future climate conditions in the North Sea. ICES Journal of Marine Science, 79: 495–505.

Van der Land, M. A. 1991. Distribution of flatfish eggs in the 1989 egg surveys in the southeastern North Sea, and mortality of plaice and sole eggs. Netherlands Journal of Sea Research, 27: 277–286.

van Hal, R., Griffioen, A. B., and van Keeken, O. A. 2017. Changes in fish communities on a small spatial scale, an effect of increased habitat complexity by an offshore wind farm. Marine Environmental Research, 126: 26–36.

Woodhead, P. M. J. 1964. Changes in the behaviour of the sole,Solea vulgaris, during cold winters, and the relation between the winter catch and sea temperatures. Helgoländer Wissenschaftliche Meeresuntersuchungen, 10: 328–342.

Zimmermann, F., Claireaux, M., and Enberg, K. 2019. Common trends in recruitment dynamics of north-east Atlantic fish stocks and their links to environment, ecology and management. Fish and Fisheries, 20: 518–536.

Annexe A. Literature study on the environmental determinants of selected North Sea fish stocks

Species	Environmental effects	Reference
North Sea cod	Widely distributed in a variety of habitats, from the shoreline down to the continental shelf. Juveniles prefer shallow (less than 10-30 m depth) sublittoral waters with complex habitats, such as seagrass beds, areas with gravel, rocks, or boulder, which provide protection from predators Adults are usually found in deeper, colder waters. During the day, form schools and swim about 30-80 m above the bottom, dispersing at night to feed	www.fishbase.org
	North Sea cod are omnivorous Spawning sites are in offshore waters, at or near the bottom, in 50-200 m depth and 0-12 °C (preferred range 0-6°C)	
	depth range 0 - 600 m, usually 150 - 200 m	
	Temp range: -1.5 - 19 °C	Righton et al 2010
	Optimal Temp: 8 - 10 °C	Righton et al 2010
	Optimal Sal: 30-35,5 ppt	Hedger et al. 2004
	Depth range: typically found <200m cod were found throughout the North Sea in either shallower coastal waters or deeper and more oceanic waters (it's possible that separate stocks exist)	Hedger et al. 2004 Hedger et al. 2004
	Most studies used the following environmental variables: • Water column depth • Bottom temperature • Bottom salinity	Drinkwater 2005 Hedger et al. 2004 Núñez-Riboni et al. 2019 Engelhard et al. 2014
	Optimum temperatures for the development of embryos of North Sea cod, 4°C at 20–33‰ (Von Westernhagen et al., 1970)	Dethlefsen 1996
	Warming, winter and summer temperature significant	Perry et al. 2008
	Atlantic embryo range: North Atlantic spawn within a wide range of temperatures, from -1.5 to 9.2°C	Galloway 1998
	Highest percentages of viable hatches occurred in the ranges of 2–10°C and 28–36 ‰ for cod	Laurence and Rogers 1976
North Sea sole	Adults occur at a temperature range of 8.0-24.0°C; They burrow into sandy and muddy bottoms. Retreat to deeper water during winter Adults feed on worms, mollusks and small crustaceans at night. Waden sea is the most important nursery area.	www.fishbase.org

Juveniles are found during the first 2 to 3 years in coastal nurseries (bays and nurseries) before migrating to deeper waters
Spawning takes place in shallow coastal waters at temperatures of 6 - 12°C. Reproduction starts after 3-5 years of age, when 25-30cm size is reached.

Depth range is 0 - 150 m, usually 10 - 60 m
As only one hypoxia event was recorded in the 1990s (in 1994, OSPAR, 2000), hypoxia does not seem to have played a role in the changes in plaice distribution since the mid 1990s.

van Keeken et al., 2007

Maximum growth rate is at about 18-20°C, values at 22°C were similar to those at 18°C. At temperatures higher than 22°C feeding and growth will decline strongly, since 26-27°C is the upper lethal temperature limit for both
species

Fonds et al., 1992

juvenile Dover sole are thermo-sensitive; they are capable of detecting temperature differences and behavioural thermoregulation.

Schram et al. 2013

According to our growth experiment the optimal growth temperature of juvenile Dover sole (30–50 g) is 22.7°C. This result corresponds very well to, and provides further refinement of the previously reported optimal temperature range of 20 to 25°C

Juvenile sole are generally found on muddy or sandy substrate in shallow and sheltered areas ; The juvenile sole have a significant preference for fine sediments.

Marchand 1988; Post et al. 2017

Sole larvae showed a tolerance to high salinities and no clear effect of the diet was evidenced.

Rueda-Jasso et al. 2005

Exposed to moderate hypoxia (80 to 20% air saturation), sole reduce their routine locomotor activity

Via et al. 1997

In the English Channel, sole (<23 cm) were observed in sediment types ranging from muddy to sandy substrata, but seemed to avoid sediments with high gravel content (Hinz et al. 2006). Highest abundances of adult sole (>23 cm) were primarily observed in depths of 20-30 m, temperatures of 18-19 °C and salinity of 33.8-34.6 (Hinz et al., 2006).

Støttrup et al. 2019

Sole habitat is defined by the environmental parameters salinity and current speed.
The spatial distribution of sole is thus known to be influenced by sediment structure, bathymetry and estuarine influence.

Muddy sediment is highly important and increasing granule size render the habitat less important for sole. YOY (41 -91mm length) preferred very fine (63-180 um) and fine (150-250 um) sediment irrespective of temperature (11 and 20°C) in experimental laboratory studies (Post et al., 2017).

	In normoxia, sole (ca 10g in weight) settled preferentially on sand whereas under hypoxic conditions, sole settled preferentially on the muddy substratum.	
	Estuarine influence (river plume) is also considered important habitat characteristic for YOY sole, probably due to a high productivity of invertebrate prey.	
	sole densities were positively correlated with salinity and negatively correlated with temperature. Thus salinity and temperature best explained the distribution of YOY sole (Brown et al. 2019). The abundance of YOY sole was correlated with an index of the benthic invertebrate biomass and, more specifically, with the biomass of suspension feeders.	
	Inter-annual variations of abundance and distribution of juveniles were synchronous with those of the macrobenthos. A further study by Vinagre (2006) also on habitat suitability modelling showed that amphipod abundance together with abiotic variables were good in predicting sole abundance. For this work the author used abundance of amphipod, polychaetes and bivalves together with abiotic variables such as salinity, temperature, substrate, depth and intertidal. The areas identified were located in the upper estuary, which is dominated by large extensions of intertidal mudflats (Bay of Biscay).	
	The environmental variables predicting sole juvenile habitat were salinity and oxygen.	
	Winter and summer temperature has a significant role	Perry et al., 2008
Saithe	An active, gregarious fish occurring inshore and offshore waters. Usually enters coastal waters in spring and returns to deeper waters in winter Smaller fish in inshore waters feed on small crustaceans (copepods, amphipods, euphausiids) and small fish, while larger fish prey predominantly upon fishes	www.fishbase.org
	depth range 37 - 364 m	
	selected variables: - prey overlap - sediment type - average temperature - average bathymetry - bathymetry is more important for saithe - temperature is less important for saithe presence	Cormon et al. 2014 Cormon et al. 2014
	saithe spawn at various temperatures. Thus, spawning in the North Sea was observed at	Lukmanov and Mukhina 1989

surface temperatures of 7.5-8.4°C
(Berenbeim and Golubyatnikova, 1984)

North Sea Haddock	Adults are found more commonly from 80 to 200 m, over rock, sand, gravel or shells, usually at temperatures between 4° and 10°C. Feed mainly on small bottom-living organisms including crustaceans, mollusks, echinoderms, worms and fishes (sand lance, capelin, silver hake, American eels, herring and argentines)	www.fishbase.org
	depth range 10 - 450 m, usually 10 - 200 m	
	- An optimum temperature for spawning of 7 ◦C - Spawning haddock preferred high salinity waters in northern North Sea and shelf edge waters to the west of Scotland - tended not to aggregate on mud-rich sediments GAM: - depth, - distance to coast, - springtide, - sediment type, - temperature near bottom - salinity near bottom - maximum temperature	González-Irusta and Wright 2016
	Mature sized haddock did not occur in temperatures >13 ◦C (Hiddink et al. 2005)	González-Irusta and Wright 2016
	Atlantic embryo range: Highest percentages of viable hatches occurred in the ranges of 4–10°C and 30–36 ‰ for haddock	Laurence and Rogers 1976
	Temperature accounted for ca 56% of the observed variance in developmental rates and increased temperature also resulted in a significantly greater hatch (Bay of Fundy)	Martel et al. 2005
North Sea Whiting	More commonly found from 30 to 100 m, mainly on mud and gravel bottoms, but also on sand and rock. Feed on shrimps, crabs, mollusks, small fish, polychaetes and cephalopods. Migrate to the open sea only after the first year of life.	www.fishbase.org
	Larvae and juveniles are associated with jellyfish.	
	depth range 10 - 200 m, usually 30 - 100 m	
	Adults are predominantly found in shallow waters, at temperatures between 6 and 9°C	Loots et al. 2011
	No eggs survived to hatch at incubation temperatures above 14.5°C	

Determining environmental conditions:
• sea surface temperature (SST),
• sea bottom temperature (SBT),
• depth

The spatial pattern of SST apparently has an important influence on the spatial distribution

Zheng et al. 2002

Five environmental variables were used:
• depth (m),
• bottom temperature (°C),
• salinity,
• seabed stress (N m-2)
• sediment type

Loots et al. 2011

Although environmental factors such as temperature and salinity may play a role in the location and extent of whiting distribution, year-to-year persistence in the spatial distribution allows North Sea whiting to buffer against short-term environmental variations. Therefore, as long as changes in present environmental conditions remain within the fundamental niche of whiting, it should be expected that the geographical configuration of spawning areas will vary little

Loots et al. 2011

Perry et al. 2008

Warming is a significant effect (see the PCA)

Witch flounder		www.fishbase.org
	Inhabits soft mud bottoms in fairly deep water	
	Feeds on crustaceans, polychaetes, brittle stars and fish	
	depth range 18 - 1570 m, usually 45 - 366 m	
	2°C - 6°C	
	Optimum temperatures for the development of embryos of North Sea flounder, 4°C at 33‰ (Von Westernhagen et al., 1970)	Dethlefsen 1996
Norway Pout		www.fishbase.org
	Mostly found between 100 and 200 m. Feeds mostly on planktonic crustaceans (copepods, euphausiids, shrimps, amphipods) but also on small fish and various eggs and larvae	
	Depth range 50 - 300 m, usually 100 - 200 m	

	The species is preyed upon by cod (Gadus morhua), whiting (Merlangius merlangus), saithe (Pollachius virens) and other fish in the North Sea	Huse et al. 2008
	The analyses indicate a negative impact by herring on recruitment of Norway pout, the most plausible cause for this being herring predation on Norway pout larvae, but field studies are needed to verify such predation	
	warming, winter and summer temperature significant	Perry et al. 2008

Lemon sole		www.fishbase.org
	Lives most often on stony bottoms.	
	Feeds on a variety of small invertebrates, but polychaetes seem to dominate.	
	Spawning is mainly confined to depths of 55-91 m in the northwestern North Sea and commences at a minimum temperature of 6.5 °C in Scottish waters.	
	depth range 10 - 200 m, usually 10 - 150 m	
	no significance with warming, winter and summer tempereature	Perry et al. 2008

Sprat	Usually inshore schooling, sometimes entering estuaries (especially the juveniles) and tolerating salinities as low as 4 ppt.	www.fishbase.org
	Shows strong migrations between winter feeding and summer spawning grounds. Moves to the surface at night.	
	Feeds on planktonic crustaceans	
	Spawns at depths of 10-20 m. Some spawn almost throughout the year, mainly in spring and summer, near the coast or up to 100 km out to sea, the young drifting inshore.	
	depth range 10 - 150 m	
	Little information is available on the biology and ecology of this species;	Støttrup et al. 2019

North Sea herring	Juveniles (up to 2 years) shoal close inshore, while adults are found more offshore	www.fishbase.org
	Adults spend the day in deeper water, but rise to shallower water at night	
	Light is an important factor in controlling their vertical distribution.	
	A facultative zooplanktivorous filter-feeder, i.e., it can switch to filter-feeding if the food density and particle size are appropriate. Feed mainly on copepods finding food by visual sense.	

Herring populations are known to use traditional spawning grounds, many of which are along shallow coastal areas (15-40 m depth) or on offshore banks down to 200 m
Spawning usually occurs on gravel or rock bottoms, with the exception of Baltic populations which show a preference for shallow (less than 10 m depth) sea-weed beds

depth range 0 - 364 m, usually 0 - 200 m

1°C - 18°C
The environmental variables predicting adult herring habitat were salinity, temperature, oxygen and depth.   Støttrup et al. 2019

Mackerel	Abundant in cold and temperate shelf areas, forms large schools near the surface. They overwinter in deeper waters but move closer to shore in spring when water temperatures range between 11° and 14°C.	www.fishbase.org

Mainly diurnal, it feeds on zooplankton and small fish. Eggs and larvae are pelagic

depth range 0 - 1000 m, usually 0 - 200 m

mackerel mainly spawn in waters warmer than 12°C
mackerel eggs in the North Sea were normally most abundant in waters warmer than 12°C and occasionally in waters as cold as about 10°C
survival range: 9.7°C-15.1°C

lower treshold of temperature 11-12°c at 10 m depth   Iversen and Ljøen 1985

analyses have demonstrated a strong relationship between sea surface temperature in the North Sea, the timing of spawning of the North Sea mackerel and the timing of the post-spawning migration. Sea surface temperature was shown to be strongly positively related to the temperature at the depth of spawning and egg development.   Jansen and Gislason 2011

All the evidence from both horizontal and vertical profiles of temperature suggest that the mackerel were concentrated in the area of the Norwegian Trench with the highest temperatures.   Reid et al. 2001
mackerel would be expected to move from the areas of low water temperature and to concentrate in the areas of highest water temperature. Anecdotal information from fishermen have suggested that the mackerel concentrate in such an area of the North   Reid et al. 2001

Sea every year prior to migration. The present study has confirmed this and also shows that the mackerel are, as hypothesised, concentrated in the warmest areas.

	Atlantic: Development of North-east Atlantic mackerel (Scomber scombrus) eggs from the Bay of Biscay, Celtic Sea and West of Ireland at temperatures ranging from 7.4 to 17.8 ∘C.	Mendiola et al. 2006
Plaice	Adults live on mixed bottoms, the older the deeper the occurrence; small individuals are usually seen on bathing beaches Occurs on mud and sand bottom from a few meters down to about 100 m, at sea, estuaries and rarely entering freshwaters	Fishbase
	Feed mainly on thin-shelled mollusks and polychaetes.	
	depth range 0 - 200 m, usually 10 - 50 m	
	2°C - 15°C Adults feed mainly on fish (small hakes, anchovies, pilchard, herrings, cod fishes, sardines and gadoid species) and squids. The young feed on crustaceans (especially euphausiids and amphipods).	
	depth range 30 - 1075 m, usually 70 - 400 m	
	Optimum temperatures for the development of embryos of North Sea plaice, 6°C at 20‰ (Von Westernhagen et al., 1970).	Dethlefsen 1996
	embryo temperature range of North Sea Plaice: range 4.1-10.5 "C median temperatures of 6.5-8.0 "C are most efficient	Ryland and Nichols 1975
	Spawning adults seemed to prefer areas with very weak seabed stress	Loots et al. 2010

	· First quarter of the International Bottom Trawl Survey (IBTS)
	· Abundance data on plaice spawners in IBTS first quarter data
	· Five environmental variables were used in the analysis:
	  o Depth (m)
	  o bottom temperature (8°C)
	  o bottom salinity
	  o seabed stress (N m-2)
	  o sediment type
	· GAM
	· The stock distribution itself is the driving feature for the life cycle
	rather than a response to environmental constraints
		Loots et al. 2010b

	interannual variability in environmental factors such as	
	temperature and salinity are poorly related to the interannual	
	variations in the spawning areas of plaice	
	The results from this study show depth and salinity to be of high importance for habitat choice in adult plaice.	Støttrup et al. 2019
	Adult plaice (>26 cm) inhabit primarily sandy sediments and seem to avoid sediments with either a high gravel or mud content (Hinz et al., 2006).	
	In laboratory experiments juvenile plaice (1-11 cm in length preferred the finest sediment type presented (<0.5 mm grain size).	
	Presence of food and predators may also affect habitat choice. For visual predators such as plaice, benthic habitats with emergent epifauna are preferred as these habitats provide higher habitat complexity and prey diversity (i.e. predation avoidance and prey abundance).	
	Plaice occurrence decreased with increasing site salinity whereas growth rates increased.	
	The results from this study show depth, salinity and oxygen to be of high importance for habitat choice in juvenile plaice	
Hake	Found usually between 70 and 370 m depth. Adults live close to the bottom during day-time, but move off-bottom at night.	
	selected variables:	
	- prey overlap	
	- sediment type	
	- average temperature	Cormon et al. 2014
	- average bathymetry	
	- hake presence variations are generally less explained by bathymetry	
	- temperature is more important for hake presence	Cormon et al. 2014
Red mullet	Adults occur on broken and rough grounds but also found over sand and soft bottoms at depths less than 100 m. Depth range from 5-60 m	www.fishbase.org
	Feed on benthic organisms such as shrimps and amphipods, polychaetes, mollusks, and benthic fishes.	
	There is certainly a connection between higher sea surface temperature and the presence of red mullet around Scottish coasts.	Baere et al. 2005
	One possibility is that the red mullet migrate into the northern	

	North Sea: from the southern North Sea during winter to escape lower temperatures. This is because the North Sea is warmer in the north during wintertime than it is in the south due to the influence of the North Atlantic current.	
	Mediterranean: depth: 28-300 m temperature: 13.6-23.8 salinity: 38.12-39.75	Machias et al. 1998
Dab	Adults live mainly on sandy bottoms, from a few me-ters to about 100 m. Feed mainly on crustaceans and small fishes. depth range 20 - 150 m	www.fishbase.org

Beare, D., Burns, F., Jones, E., Peach, K., and Reid, D. 2005. Red mullet migration into the northern North Sea during late winter. Journal of Sea Research, 53: 205–212.

Cormon, X., Loots, C., Vaz, S., Vermard, Y., and Marchal, P. 2014. Spatial interactions be-tween saithe (Pollachius virens) and hake (Merluccius merluccius) in the North Sea. ICES Journal of Marine Science, 71: 1342–1355.

Dethlefsen, V. 1996. Malformations in North Sea pelagic fish embryos during the period 1984–1995. ICES Journal of Marine Science, 53: 1024–1035.

Drinkwater, K. F. 2005. The response of Atlantic cod (Gadus morhua) to future climate change. ICES Journal of Marine Science, 62: 1327–1337.

Engelhard, G. H., Righton, D. A., and Pinnegar, J. K. 2014. Climate change and fishing: a century of shifting distribution in North Sea cod. Global Change Biology, 20: 2473–2483.

Fonds, M., Cronie, R., Vethaak, A. D., and Van Der Puyl, P. 1992. Metabolism, food consump-tion and growth of plaice (Pleuronectes platessa) and flounder (Platichthys flesus) in re-lation to fish size and temperature. Netherlands Journal of Sea Research, 29: 127–143.

Galloway, T.F., E. Kjorsvik and H. Kryvi. 1998. Effect of temperature on viability and axial muscle development in embryos and yolk sac larvae of the northeast Atlantic cod. Gadus morhua.Mar. Biol. 132: 559-567

González-Irusta, J. M., and Wright, P. J. 2016. Spawning grounds of haddock (Melanogram-mus aeglefinus) in the North Sea and West of Scotland. Fisheries Research, 183: 180–191.

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A., and Andrews, J. 2004. Analysis of the spatial distributions of mature cod (Gadus morhua) and haddock (Mela-nogrammus aeglefinus) abundance in the North Sea (1980–1999) using generalised ad-ditive models. Fisheries Research, 70: 17–25.

Huse, G., Salthaug, A., and Skogen, M. D. 2008. Indications of a negative impact of herring on recruitment of Norway pout. ICES Journal of Marine Science, 65: 906–911.

Iversen, S.A. and R. Ljøen, 1985. The spawning and distribution of mackerel eggs in the North Sea related to the hydrography. ICES: C.M. H(37).

Jansen, T., and Gislason, H. 2011. Temperature affects the timing of spawning and migration of North Sea mackerel. Continental Shelf Research, 31: 64–72.

Laurence, G. C. and Rogers, C. A. 1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (Gadus morhua L.) and haddock (Mel-anogrammus aeglefinus L.). J. Cons. int. Explor. Mer, 36: 220-228.

Loots, C., Vaz, S., Planque, B., and Koubbi, P. 2010. What controls the spatial distribution of the North Sea plaice spawning population? Confronting ecological hypotheses through a model selection framework. ICES Journal of Marine Science, 67: 244–257.

Loots, C., Vaz, S., Planque, B., and Koubbi, P. 2011. Understanding what controls the spawning distribution of North Sea whiting (Merlangius merlangus) using a multi-model approach: Spatial distribution of whiting population. Fisheries Oceanography, 20: 18–31.

Lukmanov, E. G., & Mukhina, N. V. (1989). Some aspects of saithe (Pollachius virens L.) abundance dynamics during early life stages in relation to the effect of biotic and abiotic environmental factors during the formation of year classes. Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer, 191, 319-323.

Machias, A., Somarakis, S., and Tsimenides, N. 1998. Bathymetric distribution and movements of red mullet Mullus surmuletus. Marine Ecology Progress Series, 166: 247–257.

Marchand, J. (1988). Seasonal distribution, growth and ecological role of the juvenile sole, Solea solea L., population in the Loire estuary, France. Journal of Fish Biology, 33, 229-229.

Martell, D. J., Kieffer, J. D., and Trippel, E. A. 2005. Effects of temperature during early life history on embryonic and larval development and growth in haddock. Journal of Fish Biology, 66: 1558–1575.

Mendiola, D., Alvarez, P., Cotano, U., Etxebeste, E., and de Murguia, A. M. 2006. Effects of temperature on development and mortality of Atlantic mackerel fish eggs. Fisheries Research, 80: 158–168.

Núñez-Riboni, I., Taylor, M. H., Kempf, A., Püts, M., and Mathis, M. 2019. Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (Gadus morhua) under climate change. ICES Journal of Marine Science, 76: 2389–2403.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate Change and Distribution Shifts in Marine Fishes. Science, 308: 1912–1915.

Post, M. H. M., Blom, E., Chen, C., Bolle, L. J., and Baptist, M. J. 2017. Habitat selection of juvenile sole (Solea solea L.): Consequences for shoreface nourishment. Journal of Sea Research, 122: 19–24.

Reid, D. G., Walsh, M., and Turrell, W. R. 2001. Hydrography and mackerel distribution on the shelf edge west of the Norwegian deeps. Fisheries Research, 50: 141–150.

Righton, D., Andersen, K., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H., Michalsen, K., et al. 2010. Thermal niche of Atlantic cod Gadus morhua: limits, tolerance and optima. Marine Ecology Progress Series, 420: 1–13.

Rueda-Jasso, Rebeca A., & Rees, Jean Francois, & De Coen, Wim, & Conceição, Luis E.C., & Sorgeloos, Patrick (2005). Diet and weaning age affect the growth and condition of Dover sole (Solea solea L.). Ciencias Marinas, 31(3),477-489

Ryland, J. S., and Nichols, J. H. 1975. Effect of temperature on the embryonic development of the plaice, Pleuronectes Platessa L. (teleostei). Journal of Experimental Marine Biology and Ecology, 18: 121–137.

Schram, E., Bierman, S., Teal, L. R., Haenen, O., van de Vis, H., and Rijnsdorp, A. D. 2013. Thermal Preference of Juvenile Dover Sole (Solea solea) in Relation to Thermal Acclimation and Optimal Growth Temperature. PLoS ONE, 8: e61357.

Støttrup, J. G., Kokkalis, A., Brown, E. J., Vastenhoud, B., Ferreira, S., Olsen, J., & Dinesen, G. E. (2019). Essential Fish Habitats for commercially important marine species in the inner Danish waters. Technical University of Denmark. DTU Aqua-rapport No. 338-2019 https://www.aqua.dtu.dk/-/media/Institutter/Aqua/Publikationer/Forskningsrapporter_301_350/338-2019-Essential-Fish-Habitats.ashx?la=da&hash=4BD61604CE09E708D8D739ED4E7D287C9917E0AA

van Keeken, O. A., van Hoppe, M., Grift, R. E., and Rijnsdorp, A. D. 2007. Changes in the spatial distribution of North Sea plaice (Pleuronectes platessa) and implications for fisheries management. Journal of Sea Research, 57: 187–197.

Via, J. D., van den Thillart, G., Cattani, O., & Cortesi, P. (1997). Environmental versus functional hypoxia/anoxia in sole Solea solea: the lactate paradox revisited. Marine Ecology Progress Series, 154, 79–90. http://www.jstor.org/stable/24857845

Zheng, X. 2002. Does the North Atlantic current affect spatial distribution of whiting? Testing environmental hypotheses using statistical and GIS techniques. ICES Journal of Marine Science, 59: 239–253.

Annexe B. "Workshop with POs" presentation
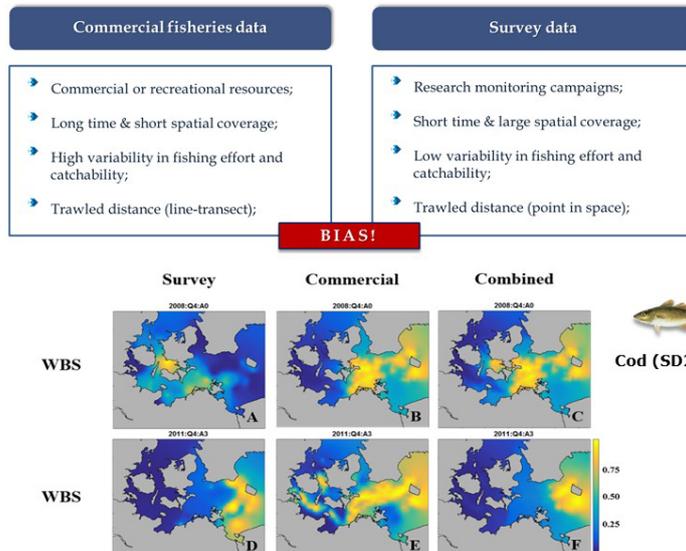
Using & generating fishing intensity, spatial footprint & Population fields
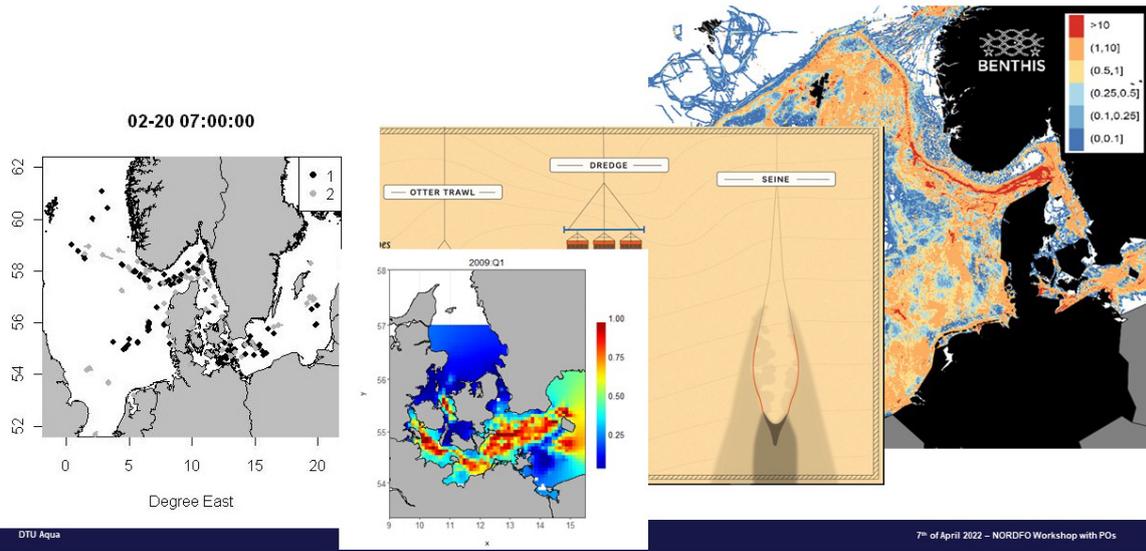
DISPLACE
A spatial model of fisheries to help sustainable fishing and maritime spatial planning

Home   Job Offer   Download   Tutorials   Contact & Apps   Code repository   Wiki   Outreach   Overview   About

How individual fishermen´s micro-decision-making affects the overall performance of fisheries

Growing network of fisheries modelling using DISPLACE

National fishing fleet economic performance and sustainable use of the ocean

Spatial multi-agents bioeconomic model combined to spatial population dynamics and other activities

Support achieving economically viable, profitable fisheries (CFP)

Approaches that allow spatial upscaling of local findings to regional scale

Management actions/plans (MSFD) that reduce the footprint of human activities or establish trade-offs between impact and economic revenue

DISPLACE building a case

Norwegian Fjord CS
Spatial conflicts between fisheries and aquaculture

Portuguese Waters CS
Multiple sea uses in a narrow space

International North Sea CS
Mixed fisheries and spatial exclusion effects

Romanian & Bulgarian Black Sea CS
Impact assessement of top down decisions for spatial reservation

Irish fleet Celtic Sea CS
Annual decisions on TACs and problems of quota underutilization from choked species

Greek Ionian Sea CS
Spatial conflicts / define priority sites also ensuring the sustainable use of the seas

Italian & Croatian Adriatic Sea CS
Spatial conflicts between mutually exclusive gears and conservation areas

International Baltic Sea CS
Spatial conflicts between mutually exclusive gears and conservation areas, effects on benthic habitats, bycatching

Wheel segments: MSPD SCENARIOS, DATA COLLATION, CONDITIONING, BASELINE RUNS, CFP SCENARIOS, MSFD SCENARIOS

Spatial multi-agent bioeconomic model combined to spatial population dynamics and other activities

Tracking Economic-Ecological indicators per

- Fishing Nations
- Fleet-segments
- Harbour communities
- Fish communities
- Benthic communities

Accounting for real-case **individual footprints** & using best available fisheries-related science

DISPLACE Impact Evaluation of Alternative Spatial Plans & Policies
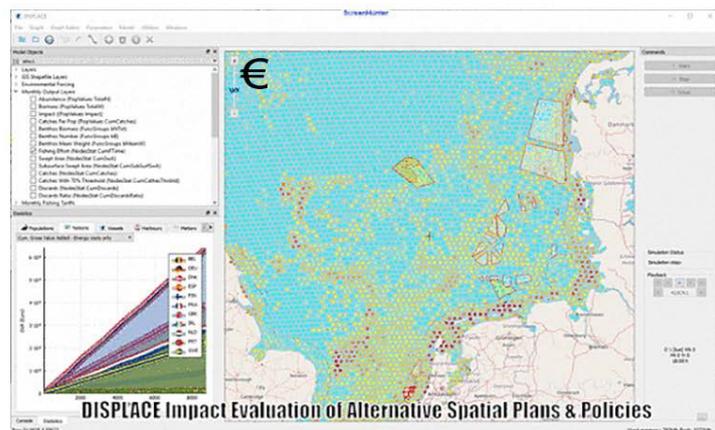
Hidden tasks: Dynamic coupling with fine-resolved predictions of fish abundance fields, dynamic coupling with benthos dynamics, Management Strategy Evaluation

North Sea Resource Distribution & Fishery opportunities (NORDFO)

- Follow-up EMFF MSPTOOLS and document ways to increase fishing opportunities, in the crowded and changing North Sea

- Integrate knowledge & dynamics of key factors determining and regulating the distribution of many important fish stocks to the Danish fleet

- Evaluate the social, economic & environmental implications in changing the fisheries economic incomes

- Consolidate the CFP with supportive information for sustainable & profitable fisheries

- Be relevant for spatial management in a CFP, MSFD and MSPD context

North Sea Resource Distribution & Fishery opportunities (NORDFO)

- WP1 – High resolution integration of fisheries & research survey data
  - Task 1.1 Data collation of the North Sea fish & fisheries data
  - Task 1.2 Application of the LGNB framework to combind fisheries & survey data
  - Task 1.3 Maps production and time series analysis of fish abundance fields and change in fish assemblages

- WP2 – High resolution correlations to marine environmental factors
  - Task 2.1 Data collation of the North Sea environmental data
  - Task 2.2 Expanding the LGNB framework to include environmental data
  - Task 2.3 Predicting historical fish abundance field under influence of environment

- WP3 – Applied management evaluation framework with implementation in the North Sea
  - Task 3.1 Conditioning LGNB-DISPLACE platform to North Sea
  - Task 3.2 Designing the fish & fisheries baseline scenario
  - Task 3.3 Evaluating the suite of CFP, MSFD and MSPD-related scenarios

Family	Species	Stock	Fishery-independent data	Fishery-dependent data
Clupeidae	Sprat (Sprattus sprattus)	4	IBTS, HERAS	OBO
		3a	IBTS, HERAS	OBO
Gadidae	Cod (Gadus morhua)[1]	47d20	IBTS	OBO
		7e–k	EVHOE	OBO
Pleuronectidae	Plaice (Pleuronectes platessa)[1]	420	IBTS, BTS, SNS	OBO
		7d	BTS, FGFS	OBO
Soleidae	Common sole (Solea solea)	3a47d	IBTS	OBO
Clupeidae	Herring (Clupea harengus)	3a47d	IBTS, HERAS	OBO
Scombridae	Mackrel (Scomber scombrus)[1]	3a4bc7d	IBTS, CGFS	OBO
Gadidae	Saithe (Pollachius virens)[1]	3a46	IBTS	OBO
Pleuronectidae	Flounder (Platichthys flesus)	3a4	IBTS	OBO
Gadidae	Haddock (Melanogrammus aeglefinus)[1]	46a20	IBTS	OBO
Merlucciidae	Hake (Merluccius merluccius)	3a46-8abd	IBTS, EVHOE, PORC, IGFS	OBO
Scophthalmidae	Turbot (Scophthalmus maximus)	4	SNS, BTS	OBO
Gadidae	Whiting (Merlangius merlangus)	47d	IBTS	OBO
Pleuronectidae	Witch flounder (Glyptocephalus cynoglossus)[1]	3a47d	IBTS	OBO
Gadidae	Norway pout (Trisopterus esmarkii)	3a4	IBTS	OBO
Scophthalmidae	Brill (Scophthalmus rhombus)	3a47de	NA	OBO
Moronidae	Seabass (Dicentrarchus labrax)	4bc7ad-h	CGFS	OBO
Pleuronectidae	Dab (Limanda limanda)	3a4	BTS	OBO
Pleuronectidae	Lemon sole (Microstomus kitt)	3a47d	IBTS	OBO
Gadidae	Pollack (Pollachius pollachius)	3a4	NA	OBO
		67	NA	OBO
Lotidae	Tusk (Brosme brosme)	3a45b6a7-912b	NA	OBO
Triglidae	Grey gurnard (Eutrigla gurnardus)	3a47d	IBTS	OBO
Scophthalmidae	Megrim (Lepidorhombus spp.)	4a6a	IBTS, SAMISS, IAMS	OBO
Lotidae	Common ling (Molva molva)	3a4a6-91214	NA	OBO

Figure xx. Spatial data haul coverage, where the yellow, red and blue dots refers to scientific survey IBTS, and BTS data (extracted from ICES DATRAS), and commercial sampling OBO data with hauls. This is an example for North Sea cod, with very similar spatial coverage for the remaining species.

Environmental covariates in NORDFO

Covariate (3m above seafloor)	Spatial resolution	Temporal resolution
Bottom temperature (average, min-max)	15, 30, 50 km	Weekly, which can be aggregated into coarser a coarser resolution (e.g., monthly, quarterly, yearly)
Bottom salinity		
Oxygen concentration		
Seabed stress (currents)		
Plankton (zooplankton)		

Etc.

The Spatial Distribution Model SDM-LGNB

The model incorporates both observation and latent processes in a hierarchical structure, where the first stage essentially describes the unobserved abundance field $\bar{\lambda}$ (latent process) as function of space (s) and time (t):

$$\lambda(s,t) = \exp\left(\sum_{k=1}^{K} \beta_k X_k(s,t) + \xi(s,t)\right)$$

where $Xk(s,t)$, $k=1,...,K$ are a set of explanatory variables with corresponding fixed effect parameters βk, and $\xi(s,t)$ represents a spatiotemporal structured random effect. Besides a seasonal effect (year-quarter), we used the environmental predictors highlighted in section 4 as fixed effects to describe the abundance fields of the different fish species
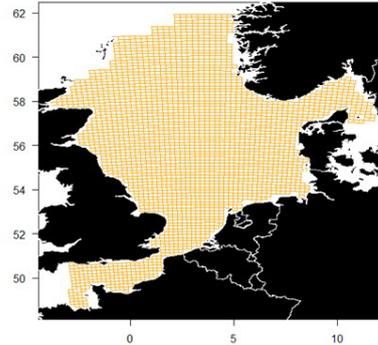
Figure. Illustration of the spatial grid (15 km x 15 km) that was used for the North Sea LGNB model to project the species' spatio-temporal abundance distributions.

Quartely spatial dynamics of North Sea stocks reconstructed (2001-2019) – GIF Animations
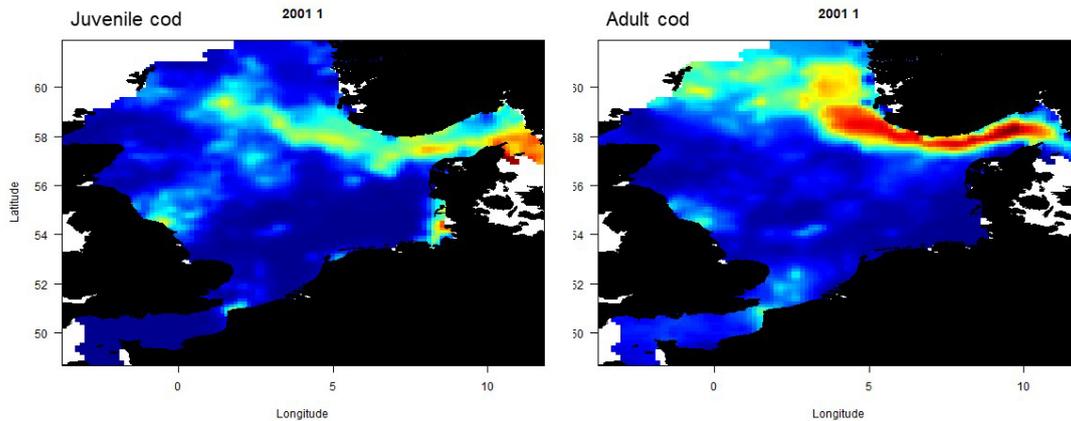
Quartely spatial dynamics of North Sea stocks reconstructed (2001-2019)

Juvenile haddock — 2001 1

Adult haddock — 2001 1

Quartely spatial dynamics of North Sea stocks reconstructed (2001-2019)

Juvenile herring — 2001 1

Adult herring — 2001 1
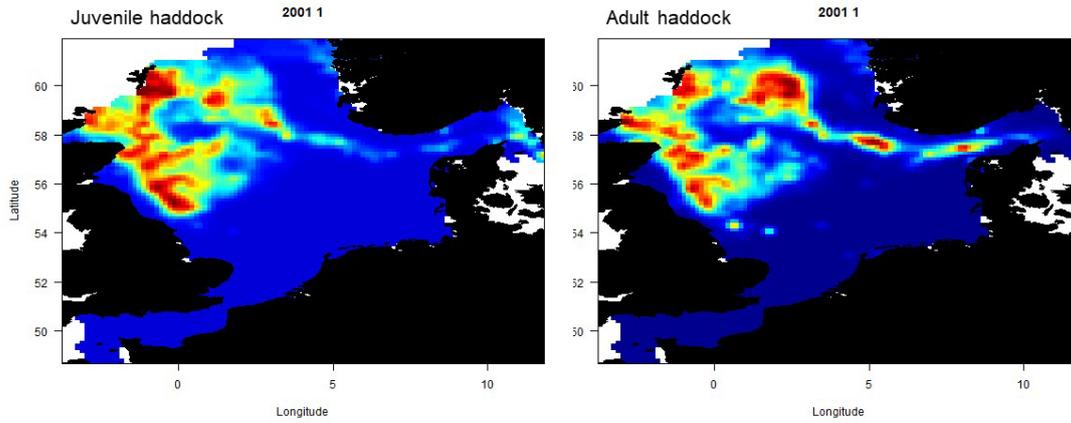
Spatial Abundance field (2001-2019)
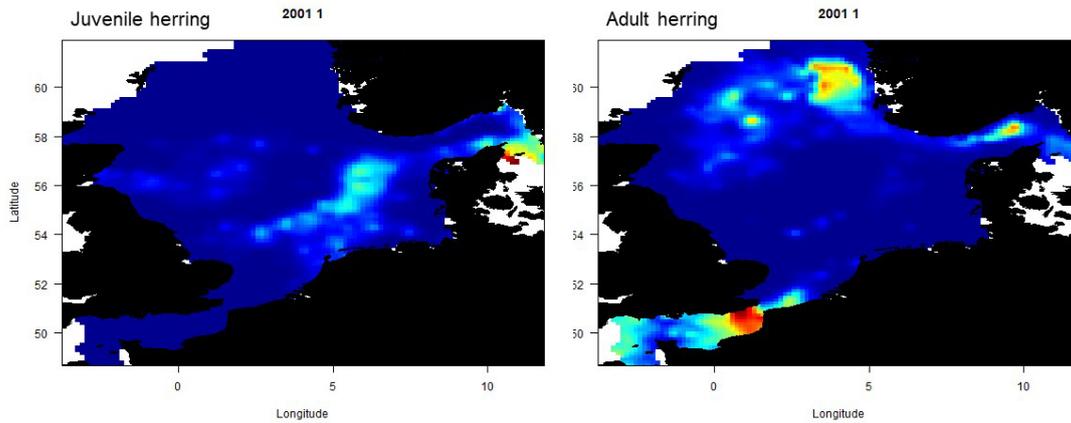
Figure xx. Quarterly based proportion of the abundance of cod juveniles' fish (in black) and adults (in red) for North Sea cod falling inside the UK EEZ in the North Sea, deduced by the abundance field reconstruction described here.

...ot persistency over time (2001-2019)

...concentration of fish
...persistent over time
...rsistent areas

Figure xx. Overall abundance density hotspots per life stage deduced from the model fitting, either without or with environmental covariates. All species are stacked, i.e. including, for adults, Cod, Plaice, Haddock, Saithe, Mackerel, Dab, Herring, Sole, Sprat, and Whiting. There was no enough information for juvenile sole, dab and saithe to be accounted for them in the hotspot analysis of juveniles. Note that a widespread color would mean no specific hotspots but an even distribution (e.g. for the juveniles).

Juveniles   Adults
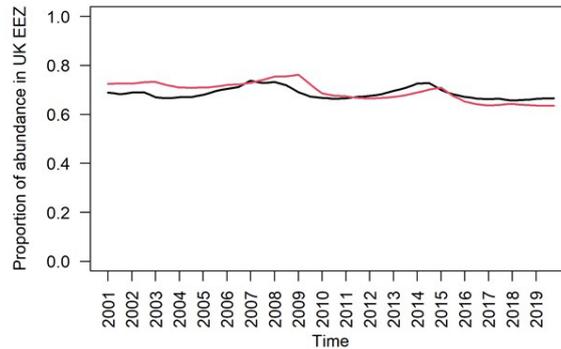
Model fitting without *envir.* covariates

Model fitting with *envir.* covariates

Hotspot persistency over time (2001-2019)

AIC	Juveniles	Adult fish
Cod (without covariate)	275358	315351
Cod (with all covariates)	275337	272234
Dab (without covariate)	NA	426705
Dab (with all covariates)	NA	426173
Haddock (without covariate)	222487	260404
Haddock (with all covariates)	222353	220798
Herring (without covariate)	328572	325557
Herring (with all covariates)	327777	324711
Mackerel (without covariate)	200083	198146
Mackerel (with all covariates)	199926	198061
Plaice (without covariate)	385039	356893
Plaice (with all covariates)	340952	323029
Saithe (without covariate)	NA	172024
Saithe (with all covariates)	NA	171987
Sole (without covariate)	NA	271827
Sole (with all covariates)	NA	271439
Sprat (without covariate)	326347	336735
Sprat (with all covariates)	NA	254874
Whiting (without covariate)	362506	351331
Whiting (with all covariates)	361643	350372

For each species investigated here, it is apparent that the best model formulation is the one including the environmental variables as covariates
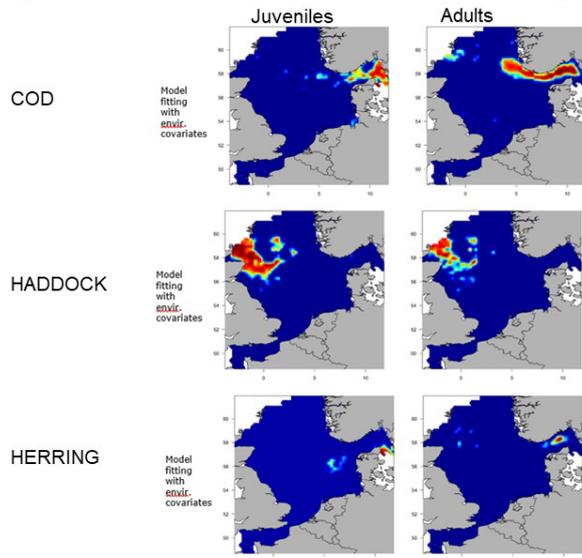
Modelling North Sea fisheries with DISPLACE

International fisheries in the North Sea with more than 30 stocks simulated spatially. Individual vessels from all harbours around the North Sea.
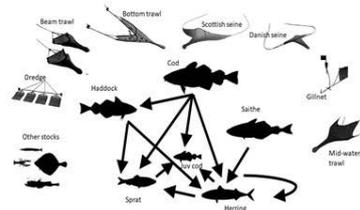
Figure xx. A random snapshot of the DISPLACE North Sea application showing the simulated accumulated catches by different North Sea nations including Denmark over all species caught layer on the map.
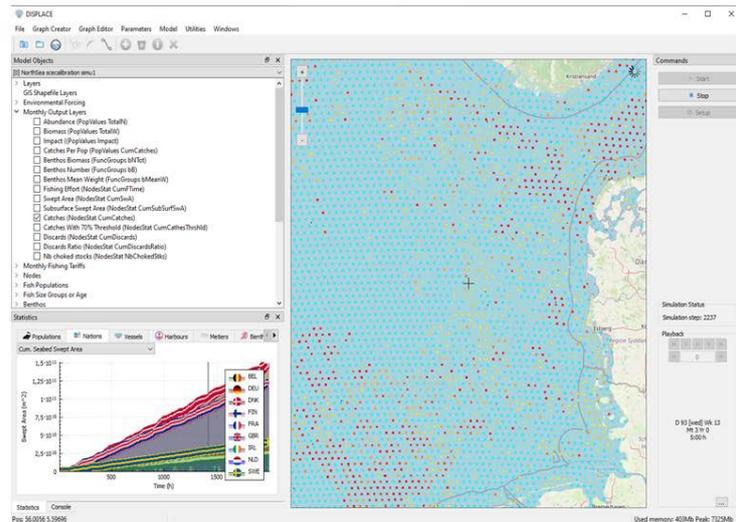
Spatial scenario testing with DISPLACE

Testing the bioeconomic effect of a spatial closure scenario based on documentation provided by the spatial distribution model fitting
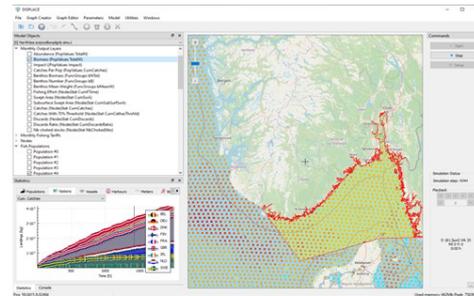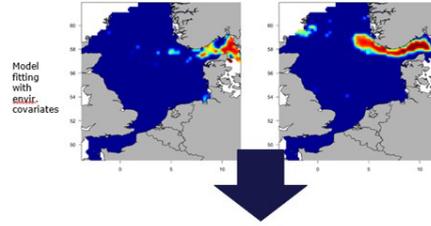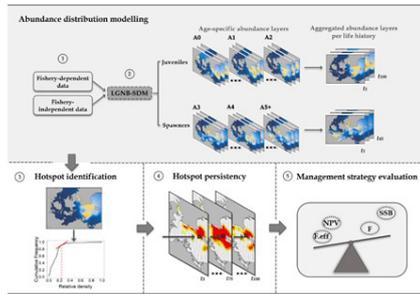
Figure xx. A random snapshot of the DISPLACE North Sea application showing the underlying simulated abundance of North Sea cod with a scenario on a spatial closure (here a permanent box banning bottom trawling and demersal seines in order to protect juveniles cod in the Skagerrak identified as a persistent hotspot for juvenile cod fish).

Climate scenarios testing with DISPLACE

Testing the bioeconomic effect of a spatial and climate scenarios based on assumed relationships between drivers and effects on the populations productivity (growth, recruits)

Figure xx. For each of the North Sea stocks assumed affected by the climate scenario compared to a baseline productivity, left: Stock-recruits relationships based on the Ricker model for predicting the number of recruits at y+1 depending on the spawning stock biomass SSB at y; Right: Von Bertalanfy growth curves for predicting the growth of animal body over time for a given cohort in the simulations.
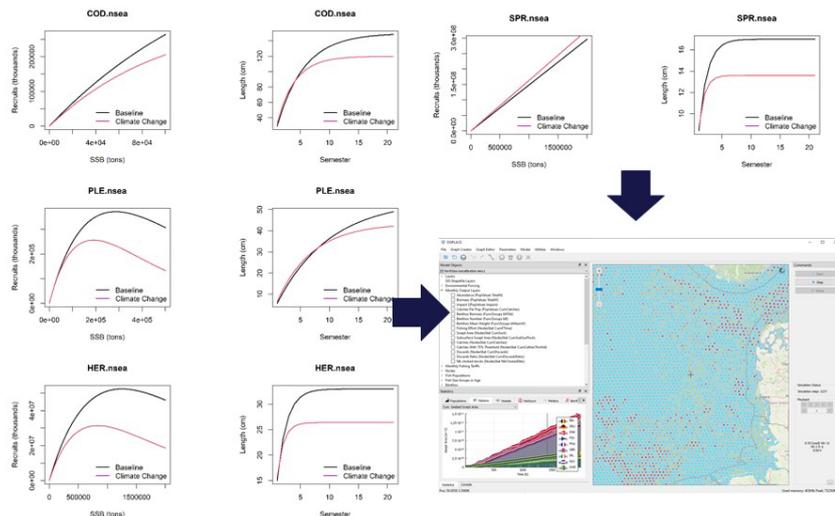
Climate scenarios testing with DISPLACE

Figure xx. A bi-dimensional plot of average scenario outcomes on F/FMSY and SSB/SSBtrigger as simulated temporal trajectories from 2020 to horizon 2030. The wished green corner for the yearly drift of the indicators is the top left (i.e. increase in SSB, reduction in F, compared to initial values). Scenario are applying the FMSY or FMSYlow strategies, assuming the landing obligation (LO) fully complied with, and the presence or absence of climate change (CC) effects.
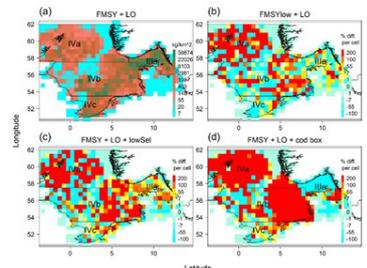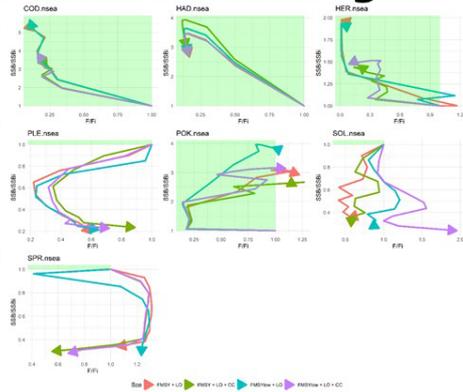
Figure xx. Simulated average spatial distribution of fishing effort at the 2030 horizon time for the baseline scenario in (a) (applying the FMSY strategy + LO), and relative to the baseline for a selection of scenarios (b) to (d).
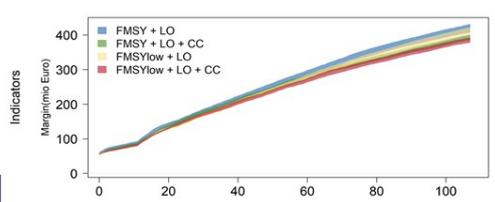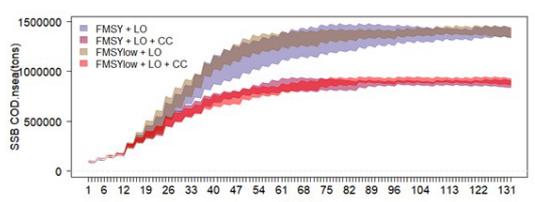
Lessons learnt

- Combining scientific data with fisheries-dependent commercial data is useful to map the stock distribution over time
- There are persistent areas of high fish concentration in the North Sea
- No detected change in the centre of gravity apart for the North Sea cod moving eastwards, farther form the coastline, and possibly within the UK EEZ
- Environmental covariates have some explanatory power
- Modelling fisheries is a challenging task, but spatial fisheries modelling platform can help anticipate some effects
- Spatial closure can help when there are evidence of persistent high concentration of juvenile fish (i.e. essential fish habitats)
- Climate change will affect the future stock distribution with incidence on the fisheries profitability, especially affecting small scale fishers when stock distribution is changed

Questionnaire survey to POs

Aim of the survey: Understanding the adaptive responses available to fishers – whether there really is the capacity to change operations or whether social, financial or regulatory barriers exist – and under what conditions they would implement this adaptive response (i.e. the level of change in catch or physical conditions needed before an adaptive behavioral change is made).

Possible response	A change in number of fish	A change in where the fish can be found	A change in when the fish move or spawn	A change in the quality of the product	A change in how variable the accessible fish is year to year	Comments (for example, the direction of your response, that is, decrease/increase)
Change the amount of fishing effort						
Move to another fishing location						
Switch to different target species						
Stop fishing for the target species						
Invest in new technology or assets						
Change the amount of quota trade						
Change the sale price of fish						
Change supply chain management						
Improve fish handling methods						
Diversify markets						
Value add to the product						
Seek information about adaptation options						
Communication with concerned stakeholders						

Annexe C. Software dissemination

SDM-LGNB repository wiki website: https://github.com/mcruf/LGNB
NS- LGNB-SDM repository: https://github.com/mcruf/gNORDFO
DISPLACE website: https://displace-project.org/blog/
DISPLACE github repository: https://github.com/frabas/DISPLACE_GUI
DISPLACE RShiny and github repository: https://github.com/frabas/DIS-
PLACE_RShiny_plots_NorthSea

Technical
University
of Denmark