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Dynamic Mapping of North Sea Spawning - Report of the KINO Project

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Tittel (norsk/engelsk):
Kartlegging av gytefelter i Nordsjøen – Rapport fra KINO-prosjektet

Dynamic Mapping of North Sea Spawning- Report of the KINO Project

Hovedforfattere: Svein Sundby, Trond Kristiansen, Richard Nash og Tore Johannessen
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Sammendrag (norsk):
Gyteområder og gyteperioder for 34 fiskearter i Nordsjøen er undersøkt ved kombinert utnyttelse av data, modell og litteratur. Hoveddelen av datatilfanget er fra egg- og larvesurvey. I tillegg er det benyttet data for gytende fisk fra både forskningsfangster og kommersielle fangster. En hydrodynamisk modell med partikkelsporing ble benyttet til å modellere drift av egg og larver fra sentrale gytefelter for utvalgte nøkkelarter og å sammenligne modellresultatene med observasjoner for egg og larver. Til slutt er en omfattende mengde litteratur for gyteadferd, egg og larver syntetisert. Litteraturstudien viste at klimaendringene over de siste 50 år har påvirket fordeling av mange av fiskebestandene, herunder gytefeltene.

Summary (English):
Spawning areas and spawning periods of 34 North Sea fish species have been studied by combining data, models and literature. Major part of data is from eggs and larvae surveys. In addition, data from research vessels and commercial catches on mature (i.e. ripe and running fish) have been applied. A hydrodynamic model including particle-tracking algorithm was applied to trace the drift pattern from the spawning areas. Model results were compared with observations on larval distribution on some selected key species. Finally, a comprehensive literature has been synthesized to include all additional knowledge on spawning activity, and eggs and larval distributions. The literature study revealed that the changing climate over the recent 50 years has influenced distribution of fish stocks and their spawning areas.

Emneord (norsk):	Subject heading (English):
1. Gytefelter	1. Spawning areas
2. Gyteperioder	2. Spawning periods
3. Nordsjøen	3. North Sea

……………………………….. prosjektleder

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Dynamic Mapping of North Sea Spawning – Report of the KINO Project

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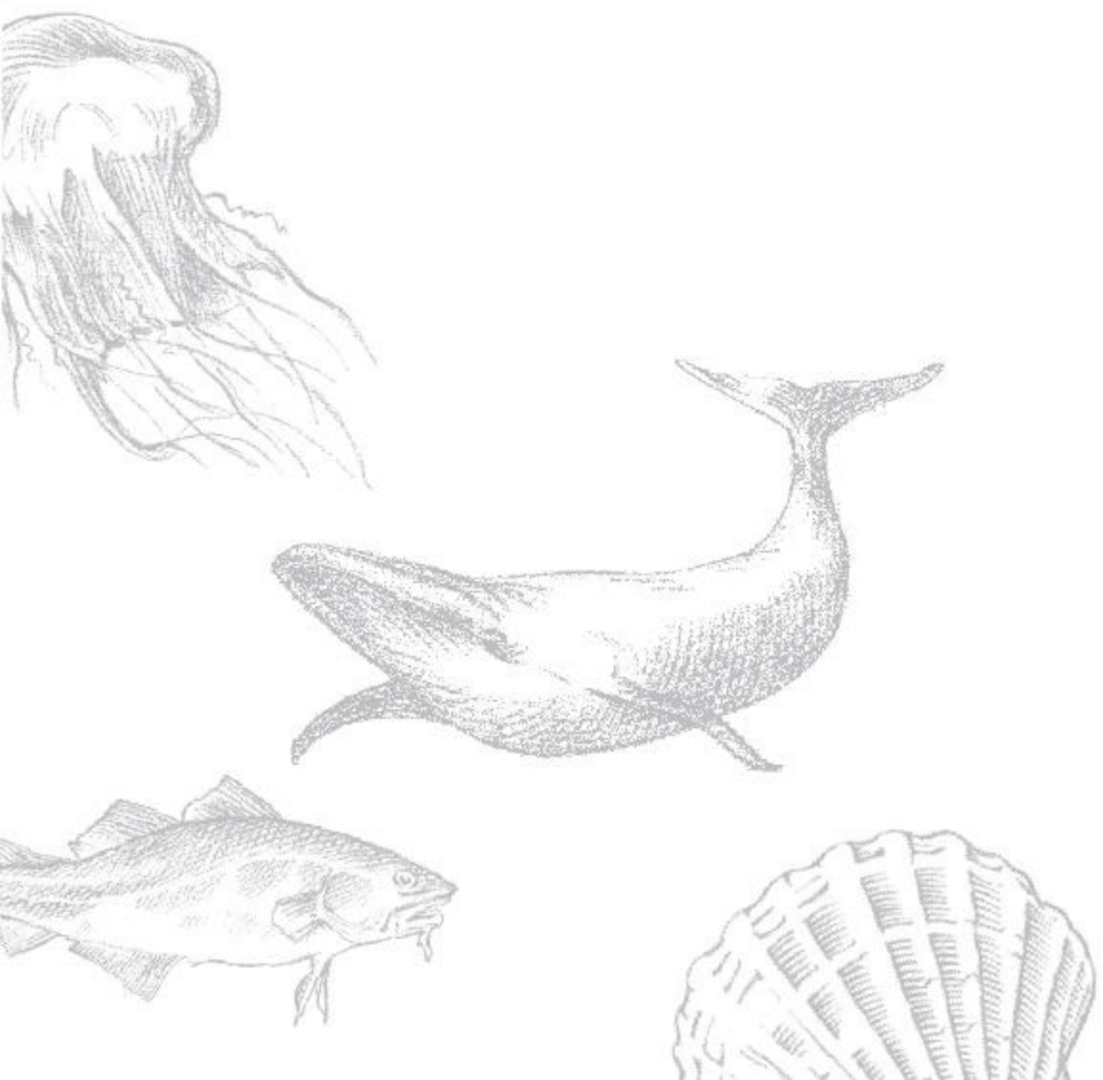

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Dynamic Mapping of North Sea Spawning
The "KINO" Project

Content Page

Page

Preface

The present report consists of the results and conclusions from the project "Dynamic Mapping of North Sea Spawning", funded by Statoil in contract No. 4503121426. The project started in October 2014.

The overall goal of the project has been to improve our general knowledge about spawning areas of major North Sea fish stocks, including their spawning behaviour and spawning period in order to optimize the advice on time and regions for seismic surveys, to prevent interference and negative effects on the spawning activities of fishes.

The project was implemented by 1) processing fish plankton samples collected during Institute of Marine Research (IMR) cruises in the North Sea during the years 2009-2013, 2) analyzing available data on the abundance of ripe and running fish caught during scientific trawl surveys during the recent 35 years, 3) developing a high resolution hydrodynamic model for the region to simulated eggs and larval drift patterns from the spawning areas, 4) synthesizing the published literature on spawning periods, spawning behaviour and spawning locations of the North Sea fishes. Finally, 5) we have analyzed changes in spawning areas over the recent 35 years as a result of the changing climate.

The results of the project have improved the scientific knowledge base on spawning in North Sea fish stocks. The main conclusions, i.e. the information on spawning areas and spawning periods for the 34 fish species described in Chapter 5, were submitted to the scientists at IMR who have the stock assessment responsibility for the various stocks during two internal IMR meetings 7 and 8 December 2016. The present version of Chapter 5 is revised accordingly, and the spawning maps, including texts, tables of spawning period, and references tagged to the spawning maps, are made publicly available at http://www.imr.no/temasider/fisk/en.
All other results from the present project are also publicly available.

We want to thank the representatives from Statoil who have provided constructive comments and been good discussion partners at meetings, by emails and telephones throughout the project period. Your true interest in the science, rather than simply ticking off boxes in a table required by the licensing authorities, has been an inspiration in conducting the project and should be an exemplary model for funders of research and science. Special thanks to Finn Roar Aamodt and Rolf Chr. Sundt, Statoil, and Turid Øygard, Norsk olje og gass.

Also, we thank the scientists at IMR responsible for stock assessments of North Sea fishes who have provided input to our report, i.e. Jennifer Devine, Kristin Helle, Espen Johnsen, Cecilie Kvamme, and Arved Staby. Finally, we will thank our colleague Lise Doksæter Sivle who has been a valuable continuous discussion partner during the entire duration of the project.

Bergen, 31 January 2017

Executive summary

The project “Dynamic Mapping of North Sea Spawning” (also called the KINO Project) was initiated in November 2014 to improve the knowledge on spawning areas and spawning periods for key fish species in the North Sea. Spawning behaviour in marine fish is assumed to be disturbed by high-energy acoustic sources, such as those produced from geological surveys where seismic methods are applied. The motivation behind the project was to provide improved and more precise management advice for recommended timing and location of seismic surveys to minimize disturbing the spawning of fishes.

In our work with improving the knowledge on North Sea spawning fish we applied a suit of available sources and methods: 1) data on ripe and running fish held in IMR’s Data Base on commercial and scientific catches, 2) samples of eggs and larvae from fish plankton surveys undertaken in recent years, 3) development of a hydrodynamic circulation model for the North Sea including a particle-tracking model to simulate drift from main spawning areas of key species and compare the particle tracking with observation from the fish plankton surveys, and 4) compilation of a comprehensive and diverse literature on spawning activity in fish and distribution on fish eggs in the sea. These four procedures were compared and synthesized to produce information on spawning areas and spawning periods in 34 North Sea fish species.

The literature on spawning fish in the North Sea is surprisingly, not very comprehensive with a distinct lack of information for the northern North Sea In the present report we have covered spawning in the entire North Sea region to present the relative importance of the various sub regions. We have defined six sub regions in the North Sea based on the specific physical settings and ecosystem productivity of each sub region. More than 140 fish species are found in the North Sea. However, the most economically important fish species account for less than 10 % of the total number of species but they comprise around 80 % of the total North Sea fish catch in terms of biomass. These species are cod, haddock, whiting, saithe, mackerel, herring, sprat, plaice, dab, lemon sole, sandeel, and Norway pout; and they occur throughout the majority of the North Sea.

Due to the increasing temperature in the North Atlantic since the early 1980s, distribution and abundance of the “endemic” boreal species, such as the gadoid species cod, haddock, whiting saithe and Norway pout, have changed in the North Sea. They have experienced decreasing biomass and a distributional shift somewhat more easterly. However, new temperate species have recently started to invade the North Sea. Small pelagic fishes, such as sardine and anchovy, have migrated northwards from the English Channel and increased in abundance. The European hake has migrated into the North Sea from west of the British Isles and into the North Sea from the northern entrance. The hake has shown a dramatic increase in biomass over the recent 10 years. These changes have not only shifted the distribution of the feeding areas, also spawning areas seem to have shifted. Therefore, the older literature on spawning should not necessarily be considered valid for the present climate state of the North Sea ecosystem.

The results on spawning of the 34 fish species are presented in Chapter 5. Each of the species are described with paragraphs on *General stock features*, *Spawning areas*, *Spawning period*, including the associated literature in the *Reference* paragraph. In addition, a table of spawning period and a map for the spawning areas are displayed for each species exemplified below for the North Sea cod:

Spawning table North Sea cod

Viking Bank

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Northwestern North Sea

AN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Southern North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

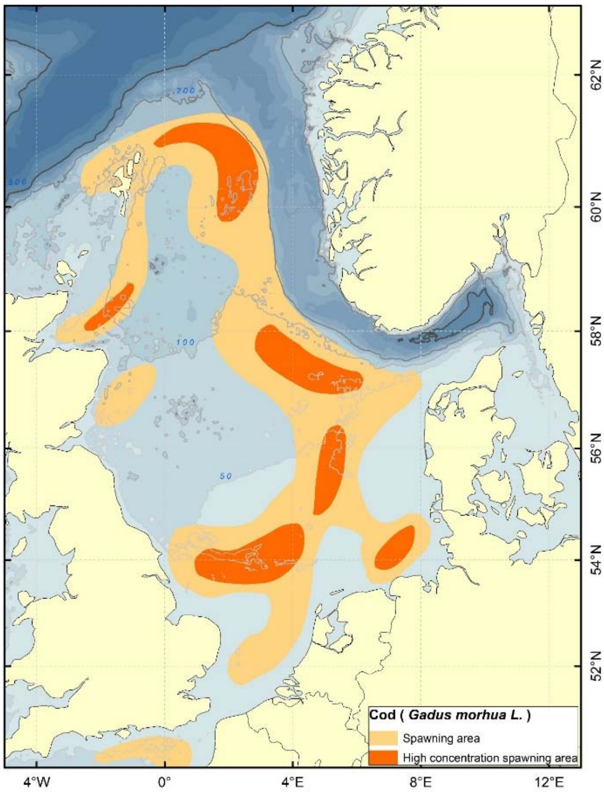

Figure 5.1.1-1. Cod spawning areas in the North Sea mainly based on observations after 2000.

We conclude that our synthesis has considerably improved the information about *spawning areas* of the North Sea, however, this is still not complete. Information about *spawning periods* are still limited. Since such improved spawning period information would be of particular value in the assessment of minimizing potential impacts from seismic survey (both with respect to spatial and temporal aspects), we recommend that spawning period investigation should be initiated.

1. Introduction

There has been a considerable amount of research undertaken on the North Sea and considerable amounts of information gathered on the biology and ecology of fish species in this area. All nations that surround the North Sea have utilised a vast amount of national effort on marine research ranging from the physics, through general ecology to the exploitable renewable and non-renewable resources. Whilst much of the data are housed in national databases there are a number of organisations such as the International Council for the Exploration of the Seas (ICES) (www.ices.dk) that store, archive and make available a wide range of data. ICES has also been responsible for co-ordinating surveys that have primarily been designed to underpin advice on the exploitation and conservation of the natural resources. A number of other institutions e.g. the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) (https://www.sahfos.ac.uk/) through the continuous plankton recorder programme have independently been collecting data on e.g. zooplankton and fish larvae distribution and large and small scale co-ordinated studies through the various European Union (EU) framework research programmes.

In regard to the fish distributions and allied information on their demographies, the largest, standardised data sets are housed in the International Bottom Trawl Surveys (IBTS) (http://www.ices.dk/community/groups/Pages/IBTSWG.aspx). These surveys were standardised across all participating countries in to a collective effort around 1976 and continue to this day and has contributed to a coherent compilation of data on fish species across the national EEZs. Whist the surveys originally covered all quarters of the year, the most recent North Sea IBTS series are centered twice a year on the 1st (January to March) and 3rd (July and August) quarters of the year. The primary objectives of the surveys are to provide abundance data and essential information on sizes, ages etc of commercially exploited species for input to the stock assessments. In more recent years the survey protocols and objectives have been widened to include a greater emphasis on diversity, including information on non-commercially exploited species and other essential information for determining the 'health' of the North Sea Ecosystem. Large sections of these data are held by ICES (http://www.ices.dk/marine-data/dataset-collections/Pages/default.aspx) in the DATRAS database.

A major summary of the distributional data was compiled into a 'Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea' (Heessen et al. 2015). This book also utilises biological and ecological information collected during these surveys and additional information collected by the many experts at the national levels, that worked in the North Sea, to provide comprehensive descriptions of the life histories of the North Sea fishes. Specific to the questions raised for the KINO project, this publication is a very valuable source of the general distribution of each species, variability in annual abundances over time and depth and the average spawning time. However, fine scale distribution patterns and how they vary both interannually and to a certain extent over annual scales are beyond the scope of this publication. In contrast to surveys on adult fish, plankton surveys across the entire North Sea has not yet been organised by the international science community. Hence, we are still left with the cumbersome mosaic work to synthesize data, reports, and publications on spawning in North Sea fishes.

The spawning times of many fish species in the vicinity of the North Sea were compiled into the 'The eggs and planktonic stages of British marine fishes' (Russell 1976). This book was primarily a guide to the identification of fish eggs and larvae, however, also contains much of the information available, up until its publication, on the spawning times of the fishes. A further source of spawning time information is in a more recent book concentrating on North Sea fish egg and larvae identifications (Munk and Nielsen 2005). As with the fish atlas, neither of these books provides detailed spatial and temporal information on the spawning of fishes in the North Sea.

There is a spatial difference in the quantity and quality of detailed information on fish movements and spawning times and locations in the North Sea. There are many more detailed studies in the southern North Sea e.g. south of 56ºN than in the north. The exceptions are possibly the areas just to the east of the Orkney and Shetland islands and there mainly concerning gadoids (Gadidae) and sandeels (Ammodytidae). Working in the northern North Sea on egg and larvae spatial and temporal distributions and responding to requests for the timing and location of significant spawning by commercially important fish species it became apparent how little information was generally available.

As mentioned above SAHFOS holds the most comprehensive times series on plankton, including ichthyoplankton, in the North Sea. The strength of these data is the long and continuous data from the late 1940s, and that they horizontally represent continuous data along the sampling lines. The limitation is that sampling only occurs at one fixed depth in the surface-mixed layer. This has some important implications for the sampling of fish eggs and larvae that have specific vertical distributions depending on the vertical spawning behaviour of the fish, on the buoyancy of the eggs that varies substantially among species, the mixing induced by winds and tides, and the vertical behaviour of the larvae (Sundby and Kristiansen 2015). There is a wide range of plankton equipment for sampling ichthyoplankton, and no international consensus exits for selection of equipment. That depends on the objectives of the investigation, the target species sampled and the stages in focus, the region in focus, and institutional preferences for specific equipment. Hence, the ichthyoplankton data from various data base, institutions, and publications must be interpreted with great care.

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2. Ecosystem features of the North Sea

The North Sea is the most temperate-influenced ecosystem of the three marine ecosystems of the Norwegian EEZ (North Sea, Norwegian Sea and Barents Sea). All three ecosystems are dominated by boreal (cold-temperate) fish species such as the gadoids cod, haddock and saithe and clupeids like the herring. Annual mean optimal temperatures for such species are typically in the range around 8-10 °C, implying that North Sea has thermal conditions at the upper range for boreal species while the Barents Sea has thermal condition at the lower range. A particular difference between the Barents Sea and North Sea ecosystems is that fish species are mainly spawning outside and south of the feeding habitat of the Barents Sea fish species (i.e. along the coast of Mid Norway and North Norway), while in the North Sea spawning takes place within the feeding habitat of the adult stock component. In addition, habitats of North Sea fish species are much more mixed geographically. Another typical difference is that Barents Sea fish species are all distinct spring spawners, while in the North Sea fish species have variable and protracted spawning periods, particularly in the southern North Sea. Such behavior is adaptation to the plankton dynamics that differs with latitude (Sundby et al. 2016). Hypothetically, it might be expected that northern North Sea fish species have less protracted spawning periods than in the southern North Sea. However, at the present stage this hypothesis has not been validated by observations.

Fish production in the North Sea

The North Sea marine ecosystem has been the most productive ecosystem for fish in the North Atlantic. The entire North Atlantic spring bloom ecosystem, i. e. from north of 30 ºN to the Polar Ocean, has delivered annual average fish catches (1970-2006) of 10.8 million tonnes (Hoegh-Guldberg et al. 2014). Of these catches 26 % has been taken in the North Sea, although a substantial decline occurred over the recent 20 years, most probably in response to climate change. The high fish productivity is based on the high primary production in the North Sea which ranges from 200 to 300 g C m^{-2} yr^{-1} in the highly productive southern and eastern North Sea (Moll 1998) and ranges from 100 to 150 g C m^{-2} yr^{-1} in the northern to central parts of the North Sea. For the period 1970-2010 about 3 million tonnes of fish, distributed over 141 species, were annually caught in the North Sea. However, 11 species comprise 80 % of the total catches (Table 2.1). Sandeel comprised the largest catch in biomass of a single species, 20.4 % of the total catches. In addition, sandeel is also an important prey species. The three pelagic species herring, sprat and Atlantic mackerel comprise nearly 28 % of catches. The five gadoid species cod, haddock, saithe, whiting and Norway pout comprise 23.1 % of the catches. Flatfishes are also important for the fisheries in the North Sea, particularly in the southern and shallow part of the region. Plaice, alone, accounts for 6.1 % of the catches. Finally, shrimps comprise 1.8 % of the total fish catches.

The particular feature of the 10 first fish species listed in Table 2.1 (excluding “Shrimps” and “Others“) is that they are distributed over nearly the entire North Sea. In addition, also a smaller fraction of those in the group “Others” are commercial fished species distributed over the entire North Sea, such as the flatfishes dab, long rough dab, and lemon sole, and the pelagic horse mackerel. Hence, the major part of the commercial catches in the North Sea comprise less than 20 species that are distributed over most of the North Sea ecosystem. A total of 19 fish species occur over the entire North Sea ((see Table 2.2A). It should be noted that a few of these are not commercial fish species, but important components in the ecosystem, for example as forage fish. The majority of fish species, however, i.e. 122 species, are limited in spatial distribution to parts of the North Sea. Some of them are also commercially important, but the majority have an important role as key components of trophic transfer in the food web, and emphasizes the importance of a high biodiversity in the ecosystem. The high diversity is not uniform across the North Sea with selected areas tending to have a higher diversity than others. We have therefore classified the North Sea into six specific sub-regions with their characteristic physical and biological features.

Table 2.1. Average fish catches in the North Sea 1970-2010 in 1000 tonnes and in percent. Data is based on information from ICES Working Group reports and the project The Sea Around Us (http://theseaaroundus.org).

Species	**Catch 1000 tonnes**	**Catch Percent**	**Groups Catch Percent**
Sandeel	614,3	20,4	20,4
Herring	390,4	13,0	
Sprat	241,9	8,1	27,6
Mackerel	196,3	6,5	
Cod	200,1	6,7	
Haddock	140,5	4,7	
Saithe	139,2	4,6	23,1
Whiting	112,6	3,8	
Norway pout	98,8	3,3	
Plaice	181,7	6,1	6,1
Shrimps	55,1	1,8	1,8
Others	633,8	21,1	21,1
SUM	3004,7	100	100

Ecosystem sub-regions of the North Sea

The North Sea and Skagerrak is considered and managed as one marine ecosystem unit. There are, however, distinct physical and biotic features in the various parts of the sea that influence species distribution of plankton and fish including the spawning areas. This makes it natural to divide the North Sea into functional sub-regions that have specific attributes with respect to topography, water masses, current features, tidal mixing, seasonal cycles, ocean climate, plankton productivity, and distributions of fish species. Based on such features we have identified and divided the North Sea into six sub-regions (Figure 2.1). Topography and current features, including the tides and fresh water runoff, (Figure 2.2) are the most important factors structuring the six sub-region features.

The major factors forcing the physics and ecosystem of the North Sea are the inflowing of the saline Atlantic water from north that has two branches (red arrows in Figure 2.2); one flowing in along the western slope of the Norwegian Trench and contains the core and saltiest Atlantic water, and the other one shallower inflow above the shelf east of Shetland. These water masses dominate the northern North Sea comprising the Shetland Banks, Viking Bank, Fladen Ground and Utsira Hight and is here defined as the *Northern Sub Region* (Figure 2.1). The southern boundary of the distribution of the Atlantic water masses is constrained by the bottom topography, particularly the Ling Bank that extends northward towards the Utsira Hight. This topographic feature forms the Dooley Current that connects the two Atlantic inflowing current branches to be joined together as the Atlantic slope current along the southwestern slope of the Norwegian Trench and continues into Skagerrak. The Dooley Current also forms the boundary to the *Central Sub Region*. The dominating role of the Atlantic water in the Northern Sub-Region also implies that the key zooplankton species *Calanus finmarchicus* with its core production region in the central Norwegian Sea has been an important species for ecosystem productivity in this northern part of the North Sea (Sundby 2000). It also influences the species compositions at higher trophic levels, since *C. finmarchicus* is a spring-spawning species. Hence, fish species utilise this spring-spawning behaviour by also spawning in the spring in order to provide their pelagic offspring with appropriate food types (including size ranges) and concentrations during the larval and early juvenile stages. The *Northern Sub-Region* has the highest diversity of fish species. In total, 141 species are identified in the North Sea (Heessen et al. 2015); 96 of these species are abundant in the *Northern Sub-Region* (Table 2.2A-G). The major part of those species absent from the *Northern Sub-Region* are mainly species that are special for *Southern Sub-Region*.

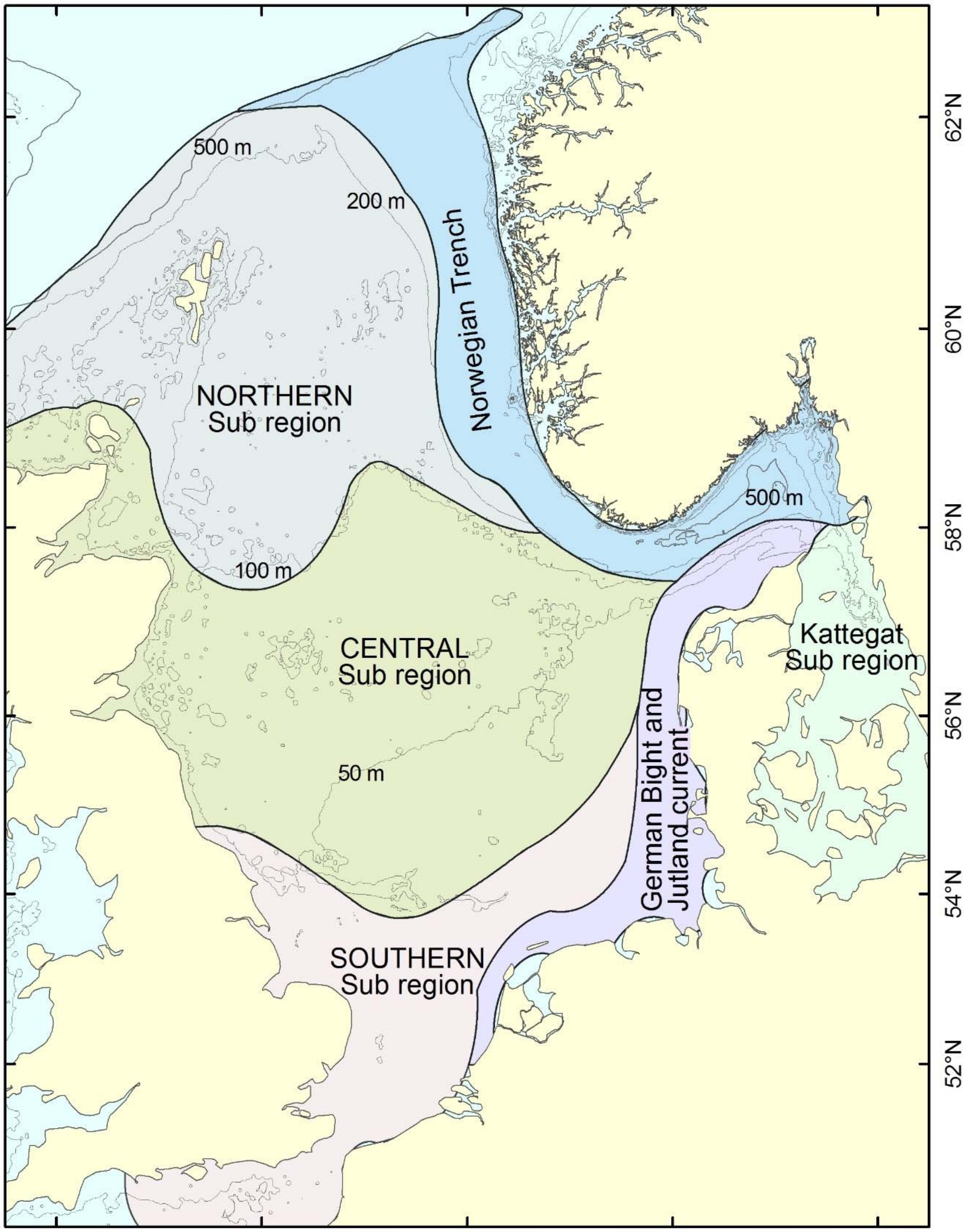

Figure 2.1. Ecosystem sub regions defined in the present report.

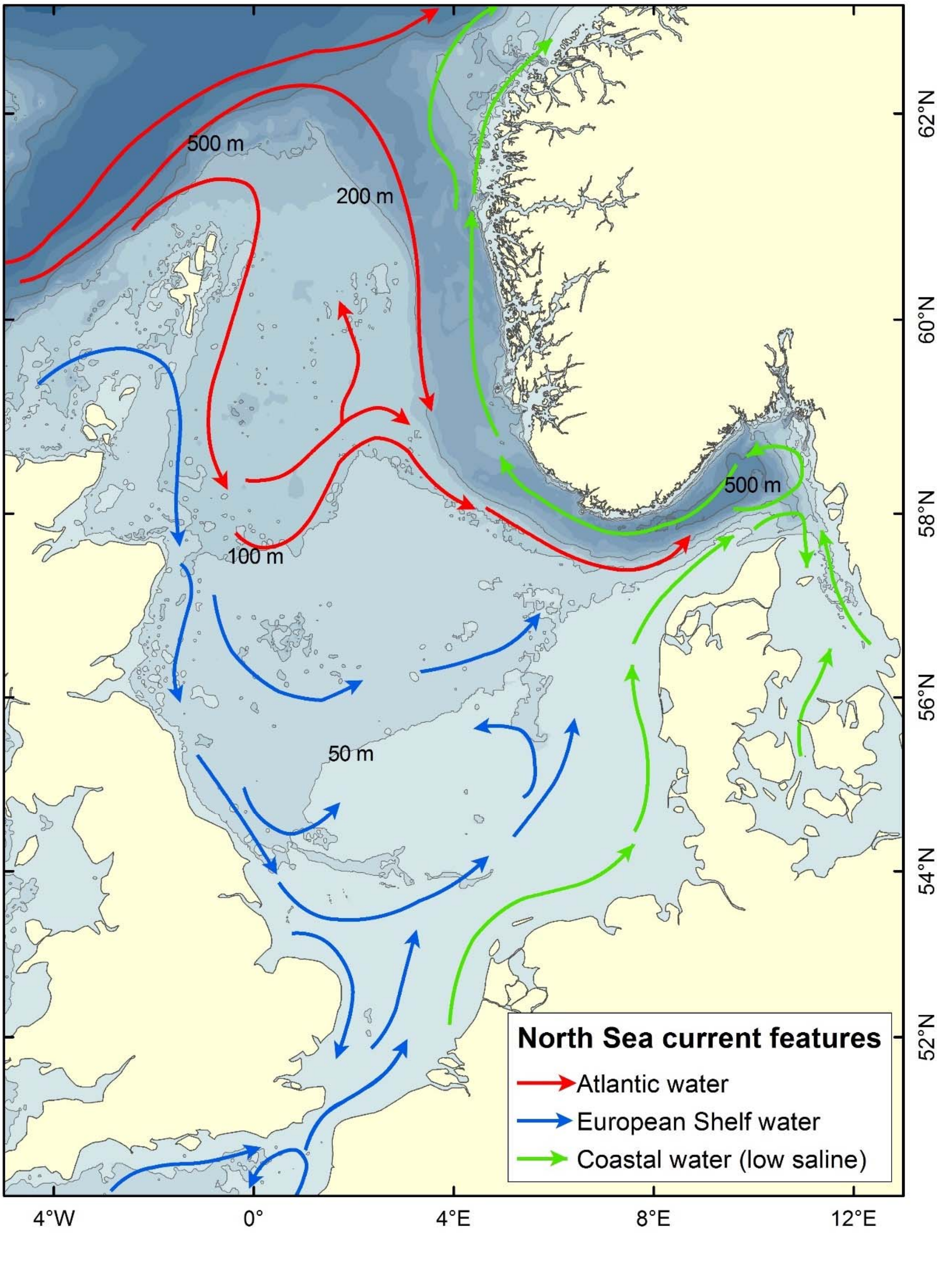

Figure 2.2 Major circulation features of the North Sea

The *Central* and *Southern Sub-Regions* (Figure 2.1) are both dominated by the Atlantic water masses of the European shelf, indicated by blue arrows in Figure 2.2. These water masses are slightly less saline than the core Atlantic water (red arrows) and are interlinked with the Atlantic European Shelf water in which enters the North Sea between Shetland and Scotland, but also to some extent through the English Channel in south. The *Central Sub-Region* is, however, mainly dominated by the northern inflowing branch between Shetland and Scotland and from lateral mixing to Atlantic water in the Northern Sub-Region. *The Central Sub-Region* has the lowest primary production of the North Sea sub-regions, and also tends to be dominated by temperate zooplankton species such as *Calanus helgolandicus* with different life cycle from the *C. finmarchicus*. The difference in life cycle relates to more year-around active herbivorous feeding, whilest *C. finmarchicus* has a more pronounced seasonal life cycle with spawning and grazing during spring-summer and overwintering at depth during winter. Although, in terms of area, it is the largest of the six sub-regions the number of abundant fish species in the *Central Sub-Region* is limited to 84 species (Table 2.2A-G) of the total number of 141 species in the North Sea, i.e. a lower number of species than either the *Northern Sub-Region* (96 species) or the *Southern Sub-Region* (92 species). This is because the deeper-water species, particularly dominating the *Northern Sub-Region* and the *Norwegian Trench Sub-Region*, as well as more temperate species, which are dominant in the *Southern Sub-Region*, are less abundant in the *Central Sub-Region*.

The *Southern Sub-Region* is dominated by European Shelf water, as is the *Central Sub-Region*. However, it differs substantially from the latter region regarding the vertical mixing. Due to the increased tidal mixing and to the shallowness the water masses, the *Southern Sub-Region* is vertically mixed from surface to the sea bed (Pingree and Griffiths 1978). A tidal front forms the boundary with the *Central Sub-Region* in north (Figure 2.3). Here the interaction between the vertical mixing, with enhanced nutrient supply, and the stratification to the north of the tidal front create high primary production. The shallow depth and the higher temperature in this sub-region influences the species diversity. Of the 141 fish species in the North Sea, 82 fish species are abundant here (Table 2.2A-G). The most temperate to subtropical species found in the North Sea are most abundant here.

The three sub-regions *German Bight – Jutland Current, Kattegat*, and *Norwegian Trench* all differ from the three major sub-regions *Northern*, *Central* and *Southern* described above because of the strong influence of fresh water runoff. This structures theirs water masses with low surface salinity and partly high vertical stratification which in turn influences the seasonal cycles in temperature with higher summer temperatures and low winter temperatures than in the regions dominated by oceanic influences.

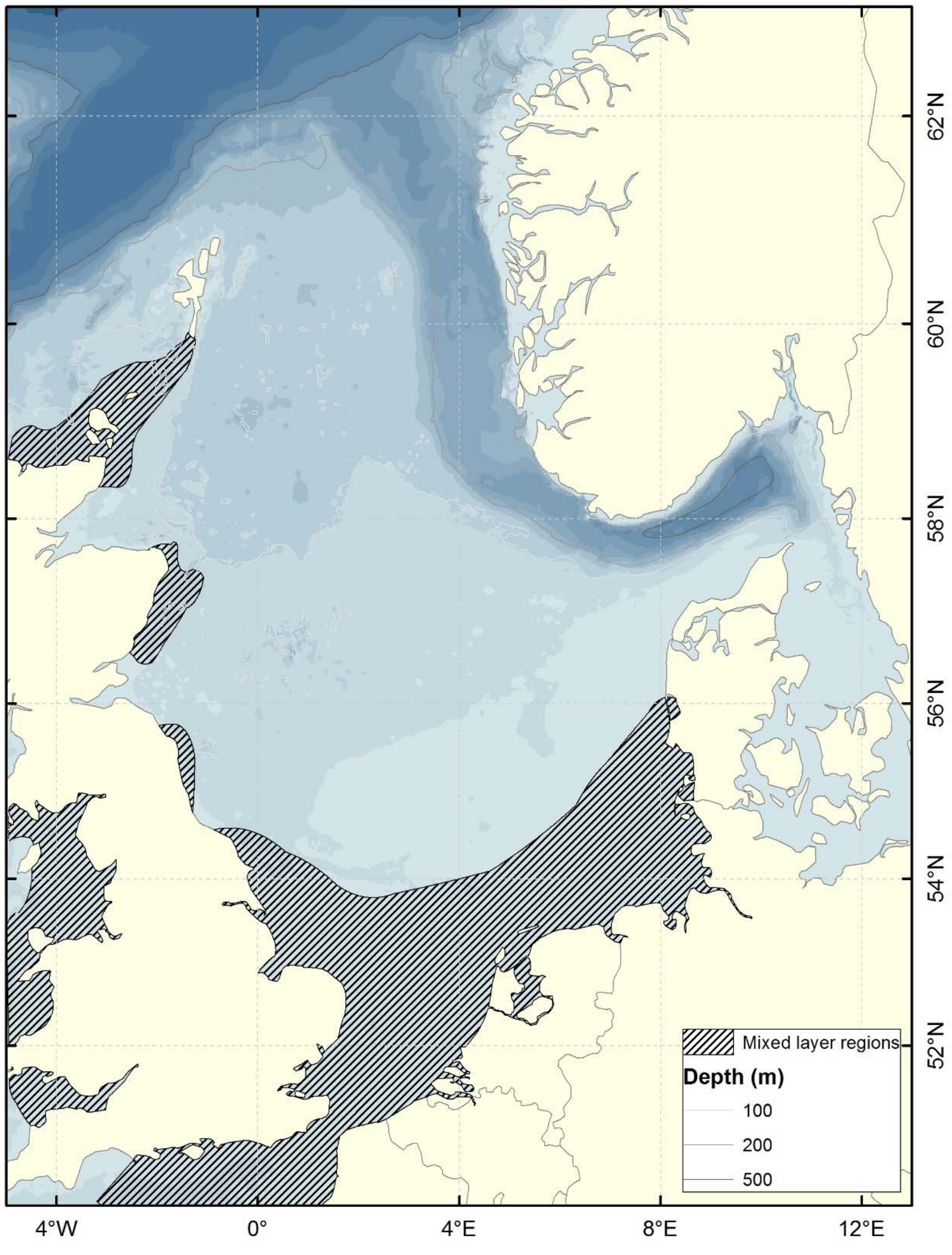

Figure 2.3. Tidally mixed regions of the North Sea. After Pingree and Griffiths 1978.

The southern part of the *German Bight-Jutland Current Sub-Region* is strongly influenced by tidal mixing, similar to the *Southern Sub-Region*. However, the low salinity from the large European rivers, such as the Rhine and Elbe makes the environmental conditions different. Large amounts of silt and nutrients are supplied from the runoff. Therefore, primary production is the highest in the North Sea, and the area is generally shallow. Flat fishes dominate the commercial fisheries. It has the lowest number of fish species (64 species) of the North Sea sub-regions (Table 2.2A-G) which is probably due to the shallow depth and the low salinity that restricts the number of species that can occupy the region.

The *Kattegat Sub-Region* is shallow like the German Bight – Jutland Current area but the fresh water supply origins from the outflow of brackish water from the Baltic Sea. Moreover, a deeper trough from the Skagerrak region allows higher salinity water to intrude the bottom layers. Hydrographic variability is strongly influenced by the pulsed outflow of the brackish water that is largely forced by atmospheric processes, and the saltier water at the bottom overflows irregularly across the sill to the Baltic Sea and renews the deep water there. The region has lower winter temperatures, and species composition of fish is more influenced by boreal species from Skagerrak in north and other boreal species from the Baltic in the south. Hence, the Skagerrak region has a relatively high diversity of fish species; 82 of the 141 North Sea fish species are abundant in Kattegat (Table 2.2A-G).

The *Norwegian Trench Sub-Region*, including Skagerrak, differs the most from the other five sub regions. The Norwegian Coastal Current, which is the continuation of the Kattegat brackish water outflow and the brackish Jutland Current, flows around the southern coast of Norway and northward along the Norwegian west coast. More fresh water is supplied to the Norwegian Coastal Current from the fjords along the Norwegian coast. Along the western slope of the Norwegian Trench the core of the high-saline Atlantic water is flowing southward. Mesoscale eddies are formed in response to the strong current shear between the northward-flowing Norwegian Coastal Current and the southward-flowing Atlantic Current. The strong contrast in environmental conditions are also reflected in the species composition of fish. Deepwater fish species are characteristic for this sub-region, species that are not found in any of the other North Sea regions. All together, 71 fish species are found here (Table 2.2A-G), and 22 of them are only found in this sub-region or at the boundary to the *Northern Sub-Region*.

Table 2.2A. 19 fish species are distributed in all six ecosystem sub regions of the North Sea. Information on the distribution of the fish species is extracted from the species maps on catch distribution in “Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea” (Heessen et al. 2015).

Species	Southern Sub Region	German Bight-Jutland	Central Sub Region	Northern Sub Region	Norwegian Tr. Sub Region	Kattegat Sub Region	SUM Sub Regions
Plaice	1	1	1	1	1	1	6
Lemon sole	1	1	1	1	1	1	6
Dab	1	1	1	1	1	1	6
Long rough dab	1	1	1	1	1	1	6
Saithe	1	1	1	1	1	1	6
Whiting	1	1	1	1	1	1	6
Haddock	1	1	1	1	1	1	6
Cod	1	1	1	1	1	1	6
Poor cod	1	1	1	1	1	1	6
Four-bearded rockling	1	1	1	1	1	1	6
Mackerel	1	1	1	1	1	1	6
Horse mackerel	1	1	1	1	1	1	6
Herring	1	1	1	1	1	1	6
Sprat	1	1	1	1	1	1	6
Anchovy	1	1	1	1	1	1	6
Lumpsucker	1	1	1	1	1	1	6
Grey gurnard	1	1	1	1	1	1	6
Snake pipefish	1	1	1	1	1	1	6
Striped red mullet	1	1	1	1	1	1	6

Table 2.2B. 25 fish species are distributed in 5 ecosystem sub regions of the North Sea. Information on the distribution of the fish species is extracted from the species maps on catch distribution in "Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea" (Heessen et al. 2015).

Species	Southern Sub Region	German Bight-Jutland	Central Sub Region	Northern Sub Region	Norwegian Tr. Sub Region	Kattegat Sub Region	SUM Sub Regions
Turbot	1	1	1	1		1	5
Small gobies	1	1	1	1		1	5
Transparent goby	1	1	1	1		1	5
Dragonet	1	1	1	1		1	5
Sandeels	1	1	1	1		1	5
Pogge	1	1	1	1		1	5
Bullrout	1	1	1	1		1	5
Tub gurnard	1	1	1	1		1	5
Other pipefish	1	1	1	1		1	5
Three-spined stickleback	1	1		1	1	1	5
John Dory	1		1	1	1	1	5
Garfish	1	1	1	1	1		5
Bib	1	1	1	1		1	5
Norway pout	1		1	1	1	1	5
Pollack	1		1	1	1	1	5
Gaidropsarus sp.	1	1		1	1	1	5
Tadpole fish	1	1	1	1		1	5
Thornback ray	1		1	1	1	1	5
Pilchard	1	1	1	1		1	5
Lesser-spotted dogfish	1	1	1	1		1	5
European hake		1	1	1	1	1	5
Shad	1	1	1	1		1	5
European eel	1	1	1		1	1	5
Starry ray	1		1	1	1	1	5
Spurdog	1		1	1	1	1	5

Table 2.2C. 23 fish species are distributed in 4 ecosystem sub regions of the North Sea. Information on the distribution of the fish species is extracted from the species maps on catch distribution in “Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea” (Heessen et al. 2015).

Species	Southern Sub Region	German Bight-Jutland	Central Sub Region	Northern Sub Region	Norwegian Tr. Sub Region	Kattegat Sub Region	SUM Sub Regions
Sole	1	1	1			1	4
Solenette	1	1	1			1	4
Flounder	1	1	1			1	4
Halibut			1	1	1	1	4
Witch			1	1	1	1	4
Scaldfish	1	1	1			1	4
Brill	1	1	1			1	4
Large gobies	1	1	1			1	4
Crystal goby	1	1		1		1	4
Spotted dragonet		1	1	1		1	4
Greater weever		1	1	1		1	4
Butterfish	1	1	1			1	4
Snake blenny			1	1	1	1	4
Sea-snails	1	1	1			1	4
Anglerfish			1	1	1	1	4
Blue whiting	1		1	1	1		4
Ling			1	1	1	1	4
Northern rockling	1	1	1	1			4
Spotted ray	1		1	1	1		4
Pearlside			1	1	1	1	4
Sea trout	1	1	1			1	4
Silver smelt	1			1	1	1	4
Hagfish			1	1	1	1	4

Table 2.2D. 27 fish species are distributed in 3 ecosystem sub regions of the North Sea. Information on the distribution of the fish species is extracted from the species maps on catch distribution in “Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea” (Heessen et al. 2015).

Species	Southern Sub Region	German Bight- Jutland	Central Sub Region	Northern Sub Region	Norwegian Tr. Sub Region	Kattegat Sub Region	SUM Sub Regions
Thickback sole	1		1	1			3
Norwegian topknot			1	1		1	3
Megrim			1	1		1	3
Transculent gobies	1	1				1	3
Lesser weever	1	1	1				3
Atlantic wolffish			1	1		1	3
Yarrell's blenny	1		1		1		3
Viviparous blenny	1	1				1	3
Vahl's eelpout				1	1	1	3
Moustache sculpin			1	1	1		3
Long-spined sea scorpion	1	1	1				3
Red gurnard	1		1	1			3
Norway haddock			1	1	1		3
Bluemouth redfish			1	1	1		3
Sandsmelt	1	1					2
Five-bearded rockling	1	1				1	3
Silvery pout			1	1	1		3
Blonde ray	1		1	1			3
Cuckoo ray	1		1	1			3
Greater-spotted dogfish	1			1		1	3
Common skate complex	1			1	1		3
Starry smooth-hound	1		1	1			3
Sea lamprey	1	1				1	3
Smelt	1	1				1	3
Common stingray	1			1	1		3
Tope	1	1	1				3
Lampern	1	1				1	3

Table 2.2E. 31 fish species are distributed in 2 ecosystem sub regions of the North Sea. Information on the distribution of the fish species is extracted from the species maps on catch distribution in "Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea" (Heessen et al. 2015).

Species	Southern Sub Region	German Bight-Jutland	Central Sub Region	Northern Sub Region	Norwegian Tr. Sub Region	Kattegat Sub Region	SUM Sub Regions
Imperial scaldfish	1			1			2
Common topknot			1			1	2
Fries's goby				1		1	2
Reticulated dragonet	1	1					2
Spotted wolffish				1	1		2
Spotted snake blenny					1	1	2
Sars's eelpout				1	1		2
Corkwing	1					1	2
Ballan wrasse	1					1	2
Goldsinny	1					1	2
Black sea-bream	1		1				2
Sea bass	1					1	2
Atlantic hook-ear sculpin			1		1		2
Redfish				1	1		2
Fifteen-spined stickleback		1				1	2
Black-bellied anglerfish			1	1			2
Pearlfish				1	1		2
Greater fork-beard				1	1		2
Blue ling				1	1		2
Tusk				1	1		2
Shagreen ray				1	1		2
Sandy ray				1	1		2
Long-nosed skate				1	1		2
Sail ray				1	1		2
Roundnose grenadier				1	1		2
Barracudinas				1	1		2
European conger eel	1			1			2
Velvet belly				1	1		2
Black-mouth dogfish				1	1		2
Porbeagle shark				1	1		2
Rabbit fish				1	1		2

Table 2.2F. 16 fish species are distributed in 1 ecosystem sub region of the North Sea. Information on the distribution of the fish species is extracted from the species maps on catch distribution in "Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea" (Heessen et al. 2015).

Species	English Ch. - Tidal Front	German Bight-Jutland Current	Tidal Front- Dooley C.	Northern North Sea	Norwegian T.- Skagerrak	Kattegat	SUM Sub Regions
Grey Triggerfish	1						1
Sand sole	1						1
Ekstrøm's topknot	1						1
Boarfish				1			1
Pandora	1						1
Red sea-bream	1						1
Ray's bream			1				1
Norway bullhead		1					1
Seahorses	1						1
Grey mullets	1						1
Hollowsnout grenadier					1		1
Round skate					1		1
Undulate ray	1						1
Norwegian skate					1		1
Lanternfish					1		1
Smooth-head				1			1

Table 2.2G. Sum of fish species found in each of the six defined ecosystem sub regions in the North Sea Information on the distribution of the fish species is extracted from the species maps on catch distribution in "Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea" (Heessen et al. 2015).

Species	Southern Sub Region	German Bight- Jutland	Central Sub Region	Northern Sub Region	Norwegian Tr. Sub Region	Kattegat Sub Region	SUM Sub Regions
SUM Species	92	64	84	96	71	82	141

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3. Changes in ecosystem structure and species over the recent 50 years

Climate change and climate variability in the North Atlantic

All ecosystems in the Northeast Atlantic, including the North Sea ecosystem, have experienced a substantial temperature increase since the cool period in the 1960s and 1970s. The temperature increase can be ascribed the combined influence of multidecadal climate variability by the Atlantic Multidecadal Oscillation (AMO) (Sutton and Hodson 2005) and the global anthropogenic climate change (Rhein et al. 2013; Hoegh-Guldberg et al. 2014). The development of the AMO in the North Atlantic through the 20th century started with a cool phase from 1900 to 1920s, thereafter a warming to the 1940s and 1950s. From 1950s to the 1970s nearly all North Atlantic and North Pacific marine ecosystems experienced a cooling, while from 1982 to 2006 the Baltic Sea and the North Sea were the two ecosystems of the world's oceans with the highest sea surface temperature (SST) increases of 1.35 and 1.31 °C respectively (Belkin 2009). Although there are many similarities in how the warming during 1920s-1940s (Rollefsen and Vedel Tåning 1949; Drinkwater 2006) and during 1980s-present influenced North Atlantic ecosystems (Sundby and Nakken 2008; Drinkwater et al. 2014), the recent warming has been the strongest, assumedly because if the increased contribution from the anthropogenic global climate change. The record-high recent increases in SST in the North Sea and in the Baltic Sea were also associated with the strong influence of fresh water runoff from land (Belkin 2009) that stratifies the water column and amplifies the increase of SST. Hence, the three eastern ecosystem sub-regions defined in Chapter 2 (i.e. the German Bight - Jutland Current, Kattegat, and Norwegian Trench) are the regions in the North Sea with the strongest increase in temperature.

General responses from North Atlantic species to changes in climate

Along with the recent (1980s-present) increasing temperature of the North Atlantic the distribution of marine species from zooplankton to piscivorous fish have generally shifted northward (Cheung et al 2011; Poloczanska et al. 2013). However, when zooming in on individual ecosystems of the North Atlantic there are more nuances in the shifts of species distributions than just a simple northward displacement. For example, in the Barents Sea the shift in distributions are more oriented eastward than northward (Stenevik and Sundby 2007; Landa et al. 2014). This is because the inflow of warm Atlantic water to the Barents Sea has a more eastward than northward component expanding the warm water masses towards the Siberian shelf rather than towards the Polar Ocean. In addition, the shelf break in north towards the large ocean depth of the Polar Ocean forms a barrier for shelf seas species such as gadoids to advance further northward. Similarly, in the North Sea movement of species has not taken place as a simple northward displacement during the recent warming, although the development has been interpreted in such a simple way (e.g. Perry et al. 2005).

Migration pattern of temperate invasive species to the North Sea

Some species have, indeed, spread northwards from the English Channel area and into the North Sea from south: However, the fact that the major inflow of Atlantic water into the North Sea takes place from the northern entrance have major influence on how temperate species from south are spreading into the North Sea. It seems that there are two major factor that determines whether temperate species are spreading into the North Sea from south through the English Channel or from the northern entrance into the North Sea: 1) For mesopelagic and deeper distributed demersal fish species the bottom depth in the English Channel, Strait of Dover, and in the South North Sea Sub regions are simply too shallow for such species to invade the North Sea along this pathway. Pelagic species on the other hand, like anchovy and sardine, seem to have invaded the North Sea from the shallow southern entrance (Beare et al. 2004; Dickey-Collas et al. 2015). 2) The other factor that seems to influence the invading pathway is where the core of species distribution is found prior to the recent warming. Species with their centers of gravity to the west and southwest of Ireland (prior to the recent warming) seem to spread north- and eastwards along the European shelf break and onward into the North Sea from the northern entrance. On the other hand, species with their core distribution south of the British Isles and in the English Channel seems to spread into the North Sea from the southern entrance. The two factors above are, of course, interlinked as the region to the south of the British Isles is generally a shallow region where pelagic fish species and shallow-water demersal species are dominating, while the mesopelagic and deeper distributed demersal species are dominating the shelf region west of the British Isles. The rather rapid and dramatic increase in the hake in the North Sea is an example of invading species that has spread from the west-side of the British Isles, eastward along the shelf break north of Shetland and southward into the North Sea with the Atlantic inflowing water from the northern entrance. These patterns are evident from catch distributions displayed by Heessen and Murua (2015).

Also, shifts in distributions of various zooplankton species have followed similar diversity of patterns of spreading as for the fish species described above. Based on the time series from the Sir Alister Hardy Foundation (SAHFOS) for the period 1958-2002, Beaugrand (2005) showed that so-called warm-temperate pseudo-oceanic zooplankton species have spread northward west of the British Isles and into the Northern Sub-Region of the North Sea from the northern entrance, the temperate pseudo-oceanic zooplankton species seem to have spread into the North Sea from the southern as well as from the northern entrances.

Figure 3.1 shows the various patterns of invasion from the selected temperate fish species described above.

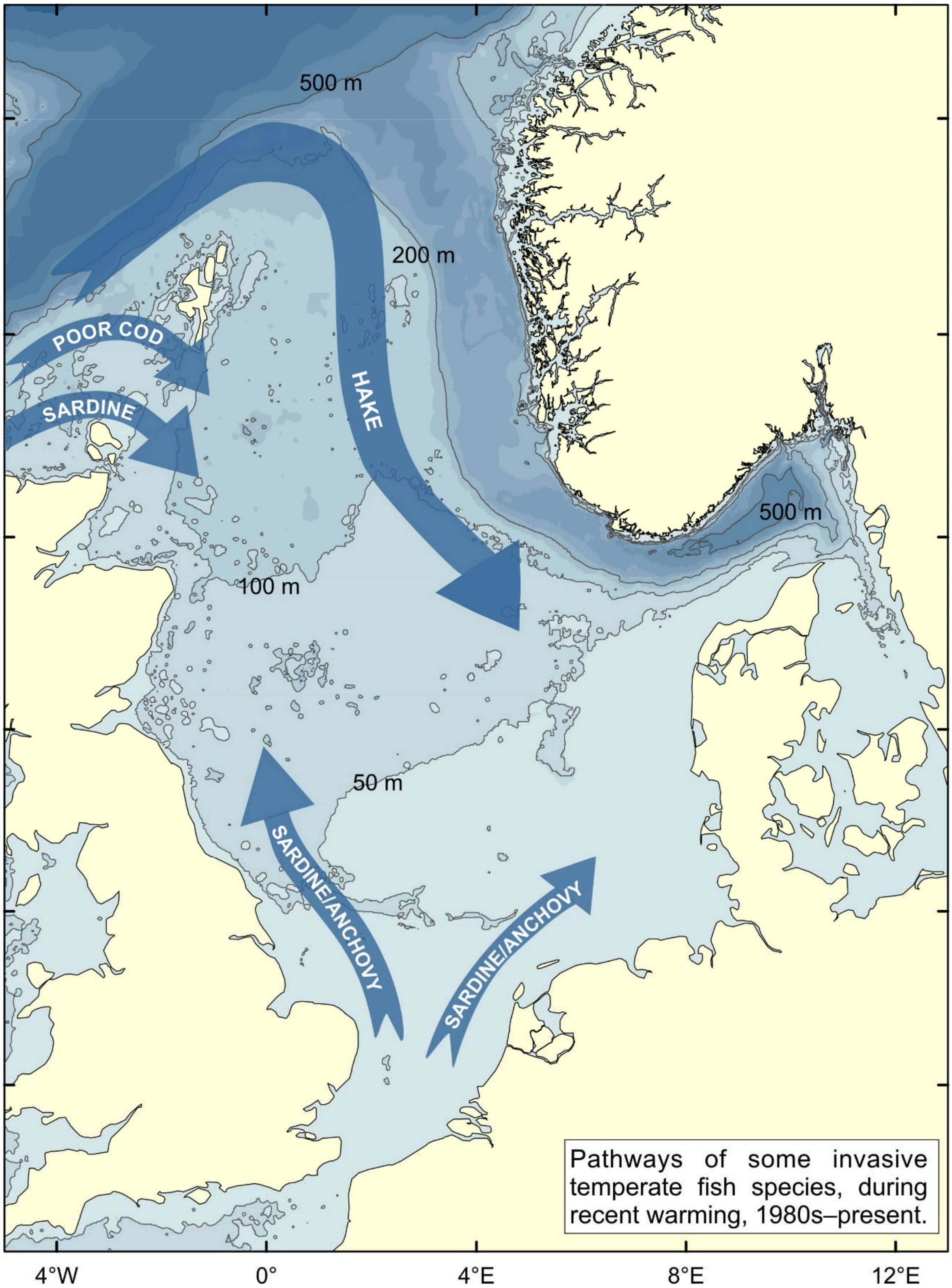

Figure 3.1. Invasive pattern of some temperate fish species into the North Sea during the recent warming 1980s-present. 1) The small pelagic fish species sardine and anchovy, 2) Poor cod, and 3) the demersal/mesopelagic hake.

Change in distribution and abundance of boreal (endemic) species within the North Sea

The major gadoid fish species in the North Sea such as cod, haddock, whiting, saithe, and Norway pout were all found in high abundances during the cool period in the 1960s and 1970s, described by Cushing (1984) as “the gadoid outburst”. These species were found spread out over the entire North Sea during this period. According the Brander (1994) cod was also found spawning all around the British Isles, including in the English Channel. As the sustained warming commenced in the 1970s North Sea biomass of gadoids have steadily declined (Hislop 1996), and continued to do so until around 2005 (Hislop et al. 2015). In response to the decline in biomass, the areas of distribution with the North Sea also seem to have changed. The distribution maps displayed in Hislop et al. (2015) show that the gadoids cod and whiting have shifted more towards northeast. Also, the spawning areas of cod that during the cool period was abundant near the English coast and in the English Channel (Brander 1994) seems to have declined. The recent ichthyoplankton surveys (ICES 2010; ICES 2011) confirms that also cod spawning areas seem to have moved towards northeast. Figure 3.2 indicate shifts in distribution of North Sea gadoid species during the recent warming, 1980s-present.

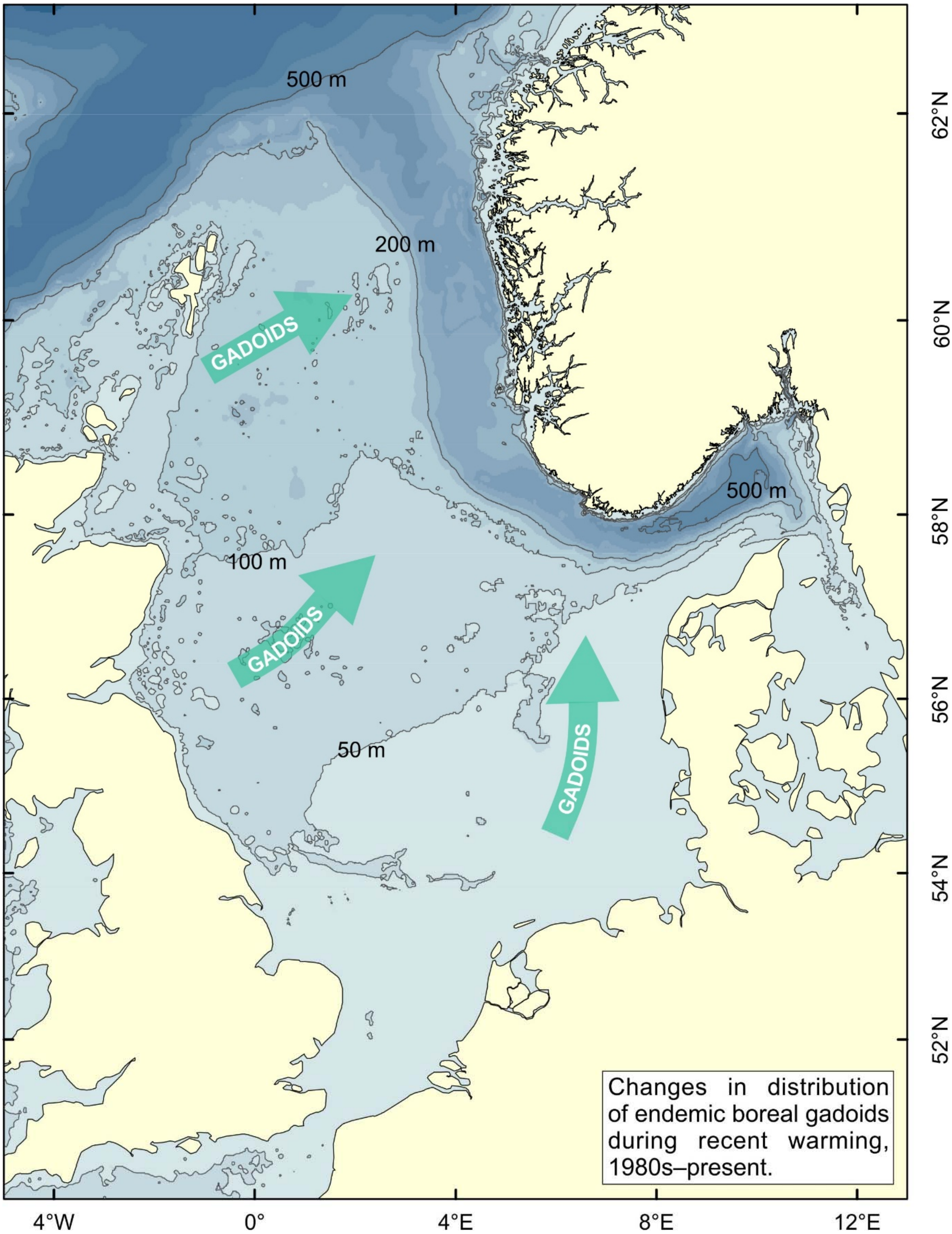

Figure 3.2. Shifts in distribution of North Sea gadoid fish species during the recent warming, 1980s-present.

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4. Key species surveyed and modelled (Materials and Methods)

Introduction

This chapter describes the material and the methods applied in the KINO project. It comprises data on ripe and running fish (4.1), ichthyoplankton surveys (4.2), biophysical modelling (4.3), and a general discussion on our material and methods (4.4). This work, together with our study of the published literature, formed the platform for construction of the new spawning maps which are given by altogether 34 species in Chapter 5.

4.1. Distribution of ripe and running fish

Data were extracted from the IMR 'fish' database which holds the records of individual fish sampled by IMR and related personnel. The fish were sampled from both research surveys and the commercial catches. The data are comprehensive covering many different measurements of an individual fish. Of interest to this project is the date and location of capture and the maturity scale (see Mjanger et al. 2016). The maturity scale varies depending on the species and consists of five to nine classes. For the purposes of determining the spawning time and location only fish in the category classified as spawning (Running gonads. Light pressure on the abdomen will release eggs or milt) were extracted. This consisted for stage 6 for herring, mackerel, and greater argentine, stage 4 for anglerfish and stage 3 for all other species studied. The study also concentrated on the recent time period and thus only extracted data between 1989 and 2013. It is known that global climate change is occurring and that historical distributions and timing of spawning may not be indicative of the present, thus the restriction in the time period.

Summary distribution maps were compiled for 17 species (Table 4.1.1). These maps are available on request.

In some instances the data were compiled by month to indicate the spatial and temporal (month) of spawning. This was not done with many species as there was insufficient data for any detailed analyses.

Table 4.1.1: Species extracted from the IMR fish database with a maturity stage of 3 during the period 1989 to 2013. Data consisted of date and location.

Norwegian common name	English Common name	Scientific name
Brieflabb	Anglerfish	*Lophius piscatorius*
Brisling	Sprat	*Sprattus sprattus*
Hvitting	Whiting	*Melangius merlangus*
Hyse	Haddock	*Melanogrammus aeglefinus*
Lange	Ling	*Molva molva*
Lomre	Lemon sole	*Microstomus kitt*
Lyr	Pollack	*Pollachius pollachius*
Lysing	Hake	*Merluccius merluccius*
Mackerel	Mackerel	*Scomber scombrus*
Rognkjeks	Lumpsucker	*Cyclopterus lumpus*
Rødspette	Plaice	*Pleuronectes platessa*

Sei	Saithe	*Pollachius virens*
Sild	Herring	*Clupea harengus*
Smørflyndre	Witch	*Glyptocephalus cynoglossus*
Torsk	Cod	*Gadus morhua*
Vassild	Greater Argentine	*Argentina silus*
Øyepål	Norway pout	*Trisopterus esmarkii*

4.2. Egg and larvae surveys

The Institute of Marine Research (IMR) has been undertaking a variety of surveys within the North Sea where fish eggs and larvae have been taken along with standard oceanographic and plankton sampling. The relevant sampling periods are in January to March (during the ICES International Bottom Trawl Survey (IBTS) survey), April/May (North Sea Ecosystem survey), July/August (standard transect(s) across the northern North Sea during the ICES 3rd Quarter IBTS), and October/December (again standard transects across the northern North Sea). The details of those surveys where the fish eggs and larvae have been analysed and utilised for this report are detailed in Table 4.2.1.

Table 4.2.1: Details of cruises in the Northern North Sea where fish eggs and larvae were sorted from samples and identified to the lowest taxonomic level possible.

Vessel	Cruise number	Start date	End date	Sampling equipment	Eggs/larvae	Comments
Johan Hjort	2011210	02.07.2011	14.07.2011	MIK (1.6mm mesh)	Larvae	Transects: Utsira, Aberdeen-Hanstholm
G.O. Sars	2012102	23.02.2012	08.03.2012	MIKeyM (335 micron mesh)	Eggs + Larvae	Northern North Sea, Norway 1st Quarter IBTS coverage
Håkon Mosby	2012608	24.04.2012	10.05.2012	Gulf VII (280 micron mesh), MIK, MIKeyM, MOCNESS (180 micron mesh)	Larvae	North Sea Ecosystem survey plus 2 process stations
Johan Hjort	2013203	08.04.2013	22.04.2013	Gulf VII, MIK, Multinet (MAXI) (390 micron mesh)	Larvae	North Sea Ecosystem survey plus 2 process stations
Håkon Mosby	2014610	28.04.2014	14.05.2014	Gulf VII, Multinet (MIDI), Bongo (1.6 mm and 335 micron)	Larvae	North Sea Ecosystem survey plus 2 process stations.

Sampling locations for each of the surveys analysed

The spatial coverage for each of the ichthyoplankton surveys analysed are shown in Figures 4.2.1-4.2.5. The distribution of larvae from fish which tend to spawn later in the year or which spend greater times in the plankton were samples in the summer. The 2011 survey had limited coverage (Figure 4.2.1) and was at the start of the time series in present day, summer, ichthyoplankton sampling in the northern North Sea. The example of the winter survey coverage which was worked up is shown in Figure 4.2.2 and is for February/March 2012. The stations shown here are only for the Norwegian samplings, thus the area coverage is restricted to the north and eastern part of the North Sea. The other parts of the North Sea are sampled by other nations participating in the North Sea 1st Quarter IBTS.

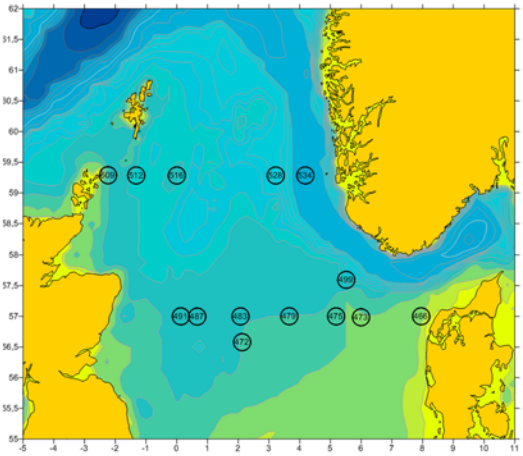

Fig. 4.2.1: Stations sampled by the RV Johan Hjort (2011210) in July 2011. See Table 4.2.1 for details.

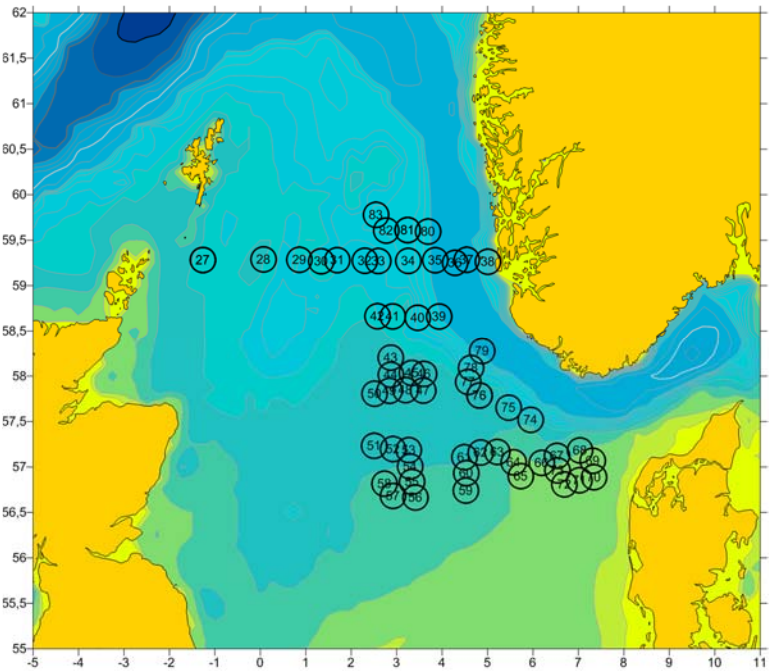

Fig. 4.2.2: Stations sampled by the RV G.O. Sars (2012102) in February-March 2012. See Table 4.2.1 for details. Numbers = station numbers.

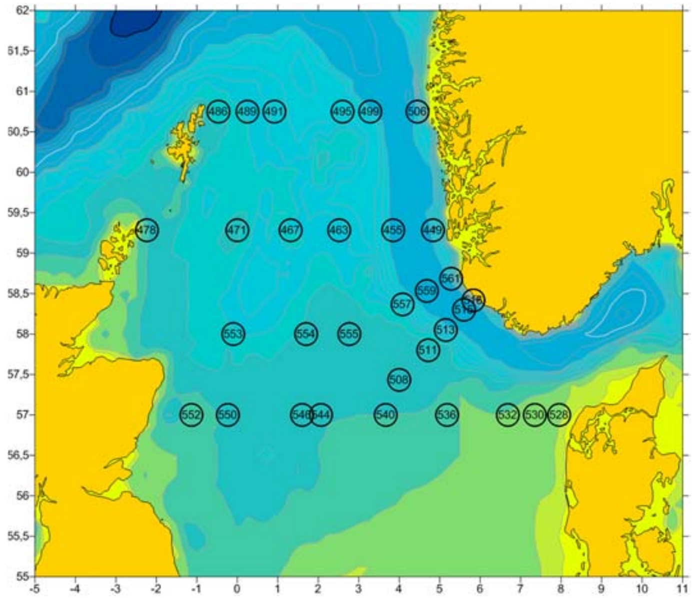

Fig. 4.2.3: Stations sampled by the RV Håkon Mosby (2012608) in April-May 2012. See Table 4.2.1 for details. Numbers = station numbers.

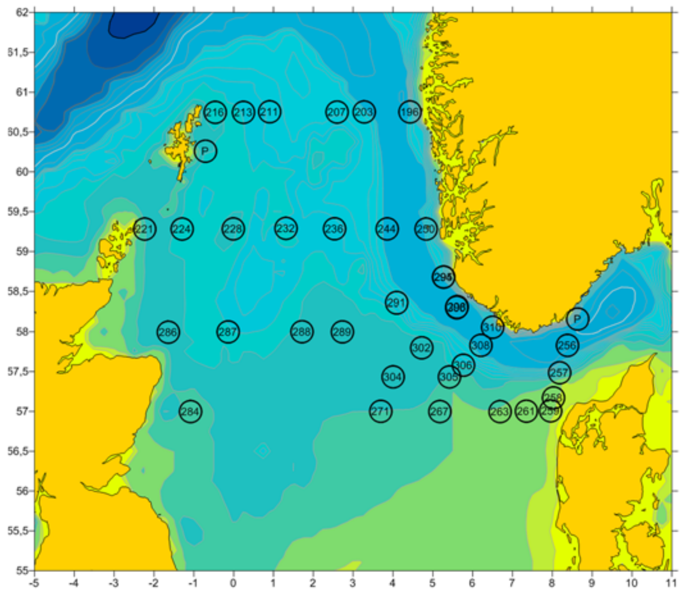

Fig. 4.2.4: Stations sampled by the RV Johan Hjort (2013203) in April 2013. See Table 4.2.1 for details. Numbers = station numbers, P = process stations.

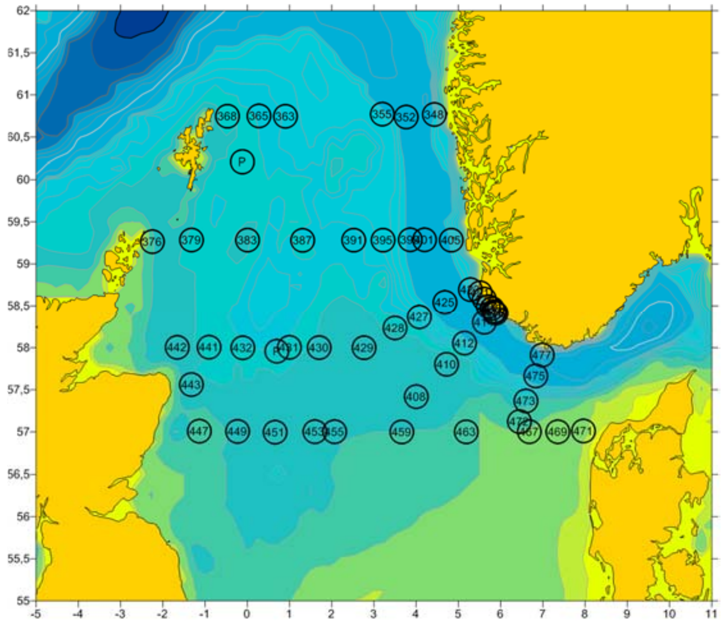

Fig. 4.2.5: Stations sampled by the RV Håkon Mosby (2014610) in April-May 2014. See Table 4.2.1 for details. Numbers = station numbers, P = process stations.

The spatial coverage for the spring surveys is much more complete for the northern North Sea and is shown in Figures 4.2.3-4.2.5. The survey essentially incorporates standard transect lines from north to south of Fedje-Shetland, Utsira-Start Point, Jærens-SSW, and Hanstholm-Aberdeen along with a series of short transects in SW Norway emanating from the coast out across the Norwegian trench.

Sampling equipment

The MIK is a Midwater Ring Net that is 2m diameter (see ICES 2016, SISP 2-MIK2). The body mesh is 1.6mm with the last 1 m of the net plus the cod end with 500 µm mesh netting. The equipment is generally towed in a double oblique haul, at 3 knots, to either 100m depth or to 3-5m above the bottom when bottom depth is shallower than 100 m. A flowmeter is located in the centre of the ring (calibrated, either Hydrobios or General Oceanics) for estimating the volume of water filtered.

The MIKeyM nets are 20cm diameter rings that are attached to the side of the MIK ring (the configuration varies between countries but in the case of IMR there are two, one each side of the mid line of the ring (see ICES 2016, SISP 2-MIK2). The tow characteristics are exactly the same as for the standard MIK i.e. double oblique tows. The mesh in the net and the cod ends is 335 µm. A calibrated General Oceanic flow meter is situated in the centre of each ring to estimate the volume of water filtered.

The MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System) has an opening of 1m^2 when towed and 9 nets (Wiebe et al. 1976, Sameoto et al. 2000). The system has onboard electronic which covey the depth, temperature, salinity and flow to the surface (and electronically saved). This system is equipped with 180 µm mesh nets. The system is towed at 1.5 knots in an oblique tow, from depth to the surface with nets being opened and closed at pre-determined depths.

The Gulf VII high-speed sampler (Nash et al. 1998) (76cm frame) was fitted with a 40 cm diameter nose cone. A calibrated General Oceanics flow meter was fitted slightly off centre in the nose cone to estimate the column of water filtered. The main net mesh and the codends were 280 µm. The sampler was towed at 5 knots in a double oblique haul to 100m depth or to within 10m of the bottom.

Two types of Multinet (Hydrobios) were used. This system is development by Hydrobios from the Bé Multiple Plankton Sampler (see Sameoto et al. 2000, also Munk & Nielsen 2005). The MIDI with a mouth opening of 0.25 m^2 was generally used in a vertical tow mode, whilst the ship was stationary, opening and closing nets at pre-selected depths. There was the option of 5 nets with this system. The net and cod-ends on this system were 180 µm. In addition, the MAXI was also used with a mouth opening of $0.5m^2$ and this was towed in an oblique tow from depth to the surface, opening and closing nets at preselected depths. There was the option of 9 nets with this system. The nets and cod-ends were 390 µm mesh. Both Multinet systems were fitted with internal and external flow meters, depth and temperature and salinity probes. Data were relayed to the ship real-time and opening and closing of the nets were controlled from the ship in real time.

A 90 cm diameter Bongo net system (constructed by SPARTEL (UK)) (see Garcia et al. 2003, Munk and Nielsen 2005) was also used. One of the nets had a 1.6mm mesh and the other 335 µm mesh. Calibrated General Oceanic Flow meters were mounted in the centre of each mouth opening to estimate the volume of water filtered. The system was towed at 3 knots in a double oblique tow to either 100m depth or 8m off the bottom.

A Scanmar depth sensor was attached to the MIK (and by default the MIKeyM), Gulf VII and Bongo and gave real-time depth profiles for the sampling equipment.

Sample processing

With the exception of the MIKeyM samples, all fish eggs (when targeted) and fish larvae were sorted from the samples immediately on retrieval of the sampling equipment. Sorting was undertaken while holding the samples on ice to prevent undue shrinkage and degradation. Eggs and larvae were then preserved in seawater, borax buffered 4% formalin. In the case of the MIKeyM samples, some were immediately sorted at sea and the eggs and larvae reserved as above. In other cases the whole sample was preserved as above and sorted at a later date back ashore in a laboratory.

All larvae were identified under binocular microscopes using either Russell (1976) or Munk and Nielsen (2005) to the lowest taxonomic level possible. In addition, larvae were measured using ocular micrometers on the microscopes and their stage of development recorded using the scales given in each of the two identification keys.

Eggs in the MIKeyM samples were photographed under a binocular microscope using a custom designed programme in Image J. This programme allowed the eggs to be identified to species or category (e.g. gadoid type), the diameter measure and the development stage (see Geffen and Nash 2012) determined plus gave a count of the number of eggs in the samples.

Estimation of abundances and spatial mapping

The densities of eggs or larvae at a station were simply estimated from the number in the sample (N) and the volume (V) of water filtered by the sampler:

$$Density \ = \frac{N}{V} \text{ m}^{-3}$$

In some instances, the densities were converted to numbers of eggs or larvae under a square metre (Abundance) as this gives an indication of abundance in an area by compensating for the variable water depth by multiplying by the maximum depth sampled (D):

$$Abundance \ = Density \times D \text{ m}^{-2}$$

The spatial distribution of eggs or larvae (either by groups or species) were visualised either by creating density or abundance bubble plots or contouring using the kriging option in SURFER (ver. 13: Golden Software, USA).

Results

A vast amount of data were generated from the identification and measurement of ichthyoplankton from the samples. The data consists of species abundances (or densities) by development stage (eggs) and size (larvae) over spatial scales. A total of 13050 larvae were identified to 37 species or 7 families where specific identification was not possible (larvae too damaged or identification was difficult). From all the samples that were analysed the two most abundant species were the gadoid species, Norway pout (*Trisopterus esmarkii*) and the flatfish species, Sand dab (*Limanda limanda*) (see Table 4.2.2).

Table 4.2.2: Proportion of fish larvae identified from surveys in the northern North Sea, total number of larvae identified = 13050. The majority of the larvae were in the April/May surveys.

Rank	Scientific name	Common name	Percent
1	*Trisopterus esmarkii*	Norway pout	22,6 %
2	*Limanda limanda*	Sand Dab	20,0 %
3	*Merlangius merlangus*	Whiting	9,6 %
4	*Ammodytes marinus*	Sandeel	7,8 %
5	*Hippoglossoides platessoides*	Long rough dab	6,6 %
6	*Gadidae*	Gadoid	4,8 %
7	*Melanogrammus aeglefinus*	Haddock	6,2 %
8	*Unidentified*	Unidentified	3,2 %
9	*Clupea harengus*	Herring	3,1 %
10	*Pollachius virens*	Saithe	2,3 %
11	*Pollachius pollachius*	Pollack	1,5 %
12	*Scomber scombrus*	Mackerel	1,4 %

13	*Callionymus lyra*	Dragonet	1,3 %
14	*Gadus morhua*	Cod	1,1 %
15	*Microstomus kitt*	Lemon sole	1,0 %

April/May distributions of larvae

Gadoids

The distribution of larvae in April/May for five of the main codfishes (Gadoids) (*G. morhua*, *M. aeglefinus*, *T. esmarkii*, *M. merlangus* and *P. virens*) are shown here in Figures 4.2.6-4.2.10. In all cases there are substantial differences in the distribution patterns and abundance of larvae between 2012 and 2013. For *G. morhua*, *T. esmarkii,* and *M. merlangius* the abundance and distribution was greater in 2012 than in 2013 whereas for *M. aeglefinus* and *P. virens* the reverse was the case. This illustrates the spatial variability in distributions, much of which is a consequence of the spatial spawning patterns, and the interannual variability.

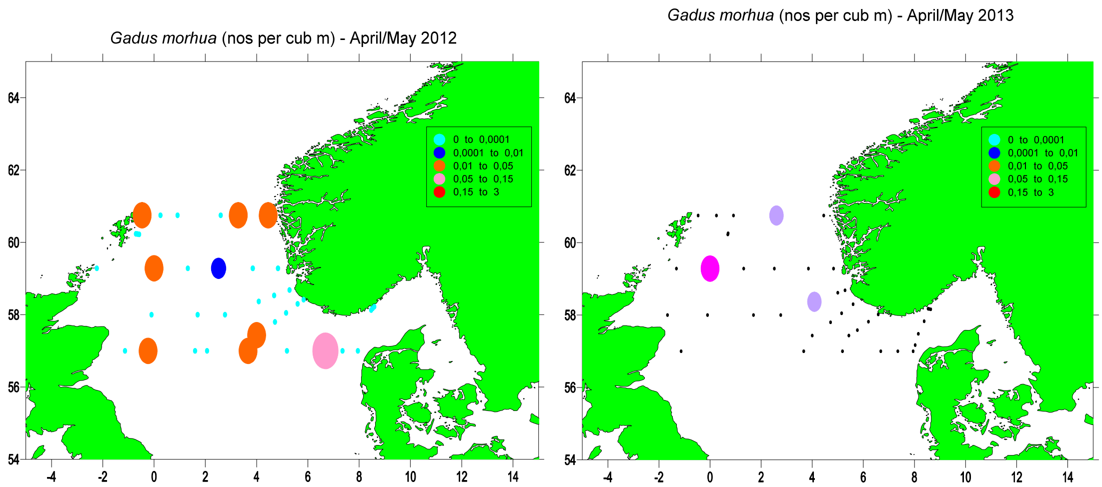

Fig 4.2.6: Distribution of *Gadus morhua* larvae in April/May 2012 and 2013.

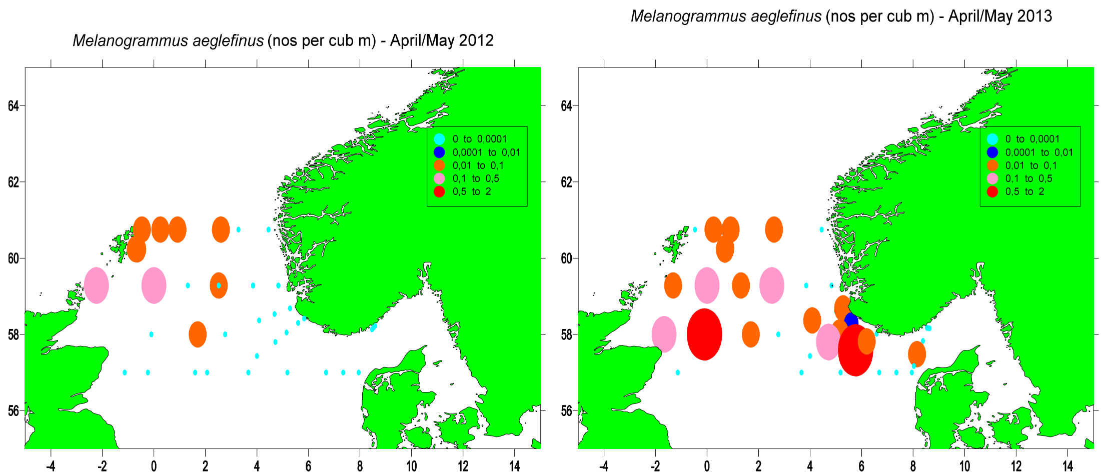

Fig 4.2.7: Distribution of *Melanogrammus aeglefinus* larvae in April/May 2012 and 2013.

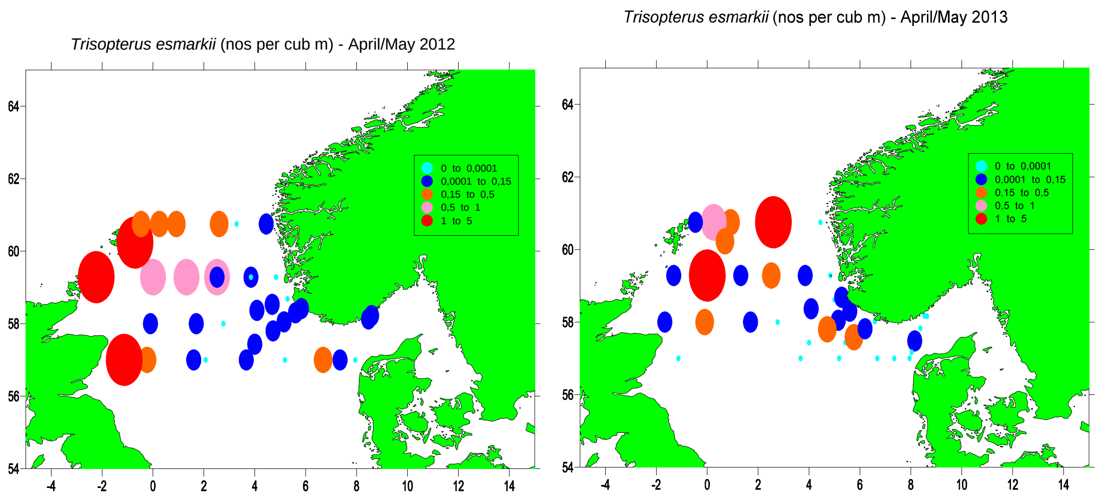

Fig 4.2.8: Distribution of *Trisopterus esmarkii* larvae in April/May 2012 and 2013.

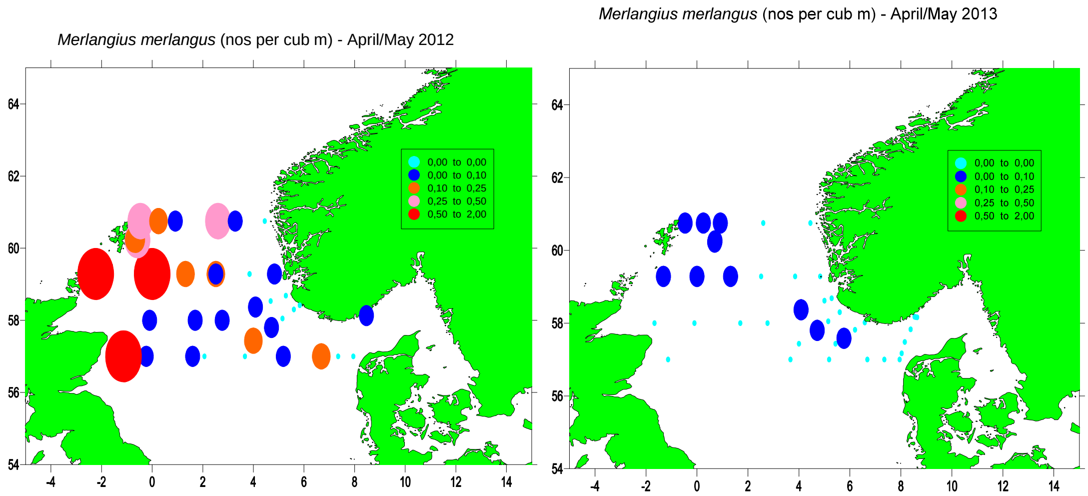

Fig 4.2.9: Distribution of *Merlangius merlangus* larvae in April/May 2012 and 2013.

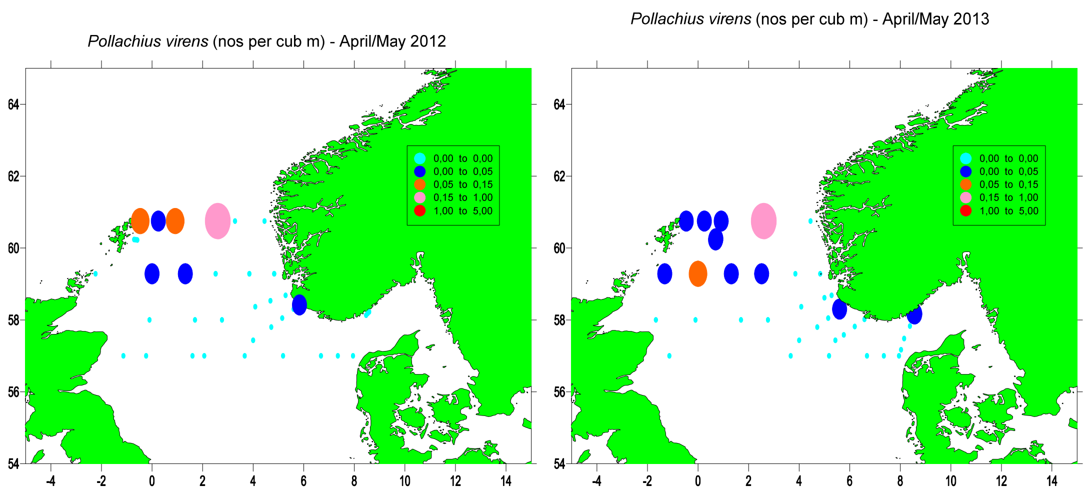

Fig 4.2.10: Distribution of *Pollachius virens* larvae in April/May 2012 and 2013.

Flatfishes

A similar spatial and interannual variability is seen in the flatfishes. *L. limanda* is shown here for illustrative purposes, especially since it is abundant in the northern North Sea.

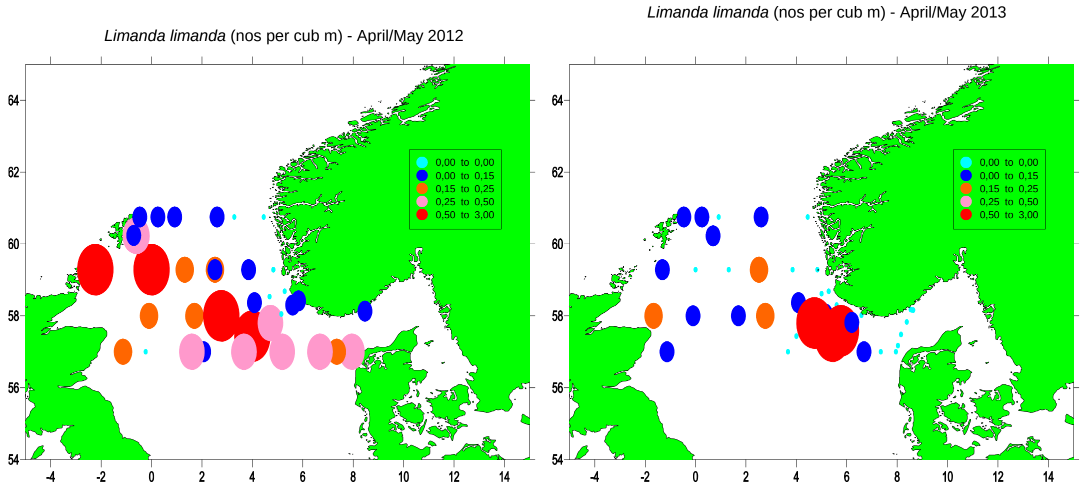

Fig 4.2.11: Distribution of *Limanda limanda* larvae in April/May 2012 and 2013.

Patterns in egg and larvae distributions between February and May

The ability to track the egg stages i.e. spawning through the distribution of newly spawned eggs (stage 1) through to the larvae distributions in April/May provides data for verifying the modelling work. The examples given here are for a flatfish, *H. platessoides* and a gadoid, *P. virens*. Sampling was not undertaken north of 59°N or south and west of 2°E in the February/March 2012 survey. Therefore, distributions outside the sampling area at this time are unknown.

In the case of *H. platessoides*, there is a clear spawning area between 56.5 and 58°N and 2 to 4°E (Figure 4.2.12). The larvae are generally in the vicinity of the spawning ground suggesting relatively limited transport at this time. By April/May the larvae are well dispersed, the presence of larvae in the west illustrating a potential bias in perceptions of spawning grounds when the full spawning area is not sampled.

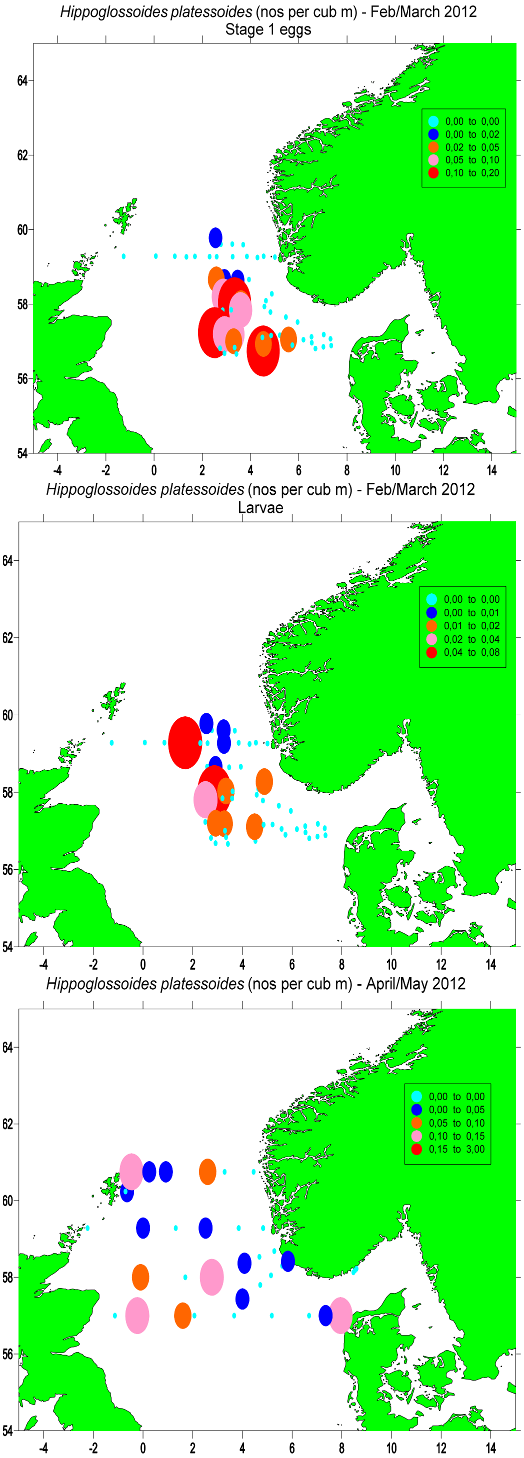

Fig 4.2.12: Distribution of stage 1 eggs and larvae of Long rough dab (*H. platessoides*) in February/March and larvae in April/May 2012 in the northern North Sea.

A further example of tracking the eggs through the larval stages is illustrated with a gadoid, *P. virens*. (Figure 4.2.13). All newly spawned gadoid eggs (Stage 1) are visually identical with the exception of having species specific ranges in egg size. Unfortunately, there is overlap in diameters between species such that, based on size, it is only possible to exclude some of the species. *P. virens* is one of the gadoids with a relatively small egg size and as such gadoid type eggs with a diameter of less than 1.35mm will likely include the eggs of this species (Munk and Nielsen 2005). The highest concentrations of small eggs were to the north and west which is consistent with the known saithe spawning grounds. The larvae had a similar distribution but were much more sparsely distributed. By April/May the majority of the *P. virens* larvae in the survey area were to the north and west, an area not surveyed in the earlier survey. The lack of larvae across the central North Sea is consistent with *P. virens* nursery grounds being close inshore, including the coastline of the Skagerrak.

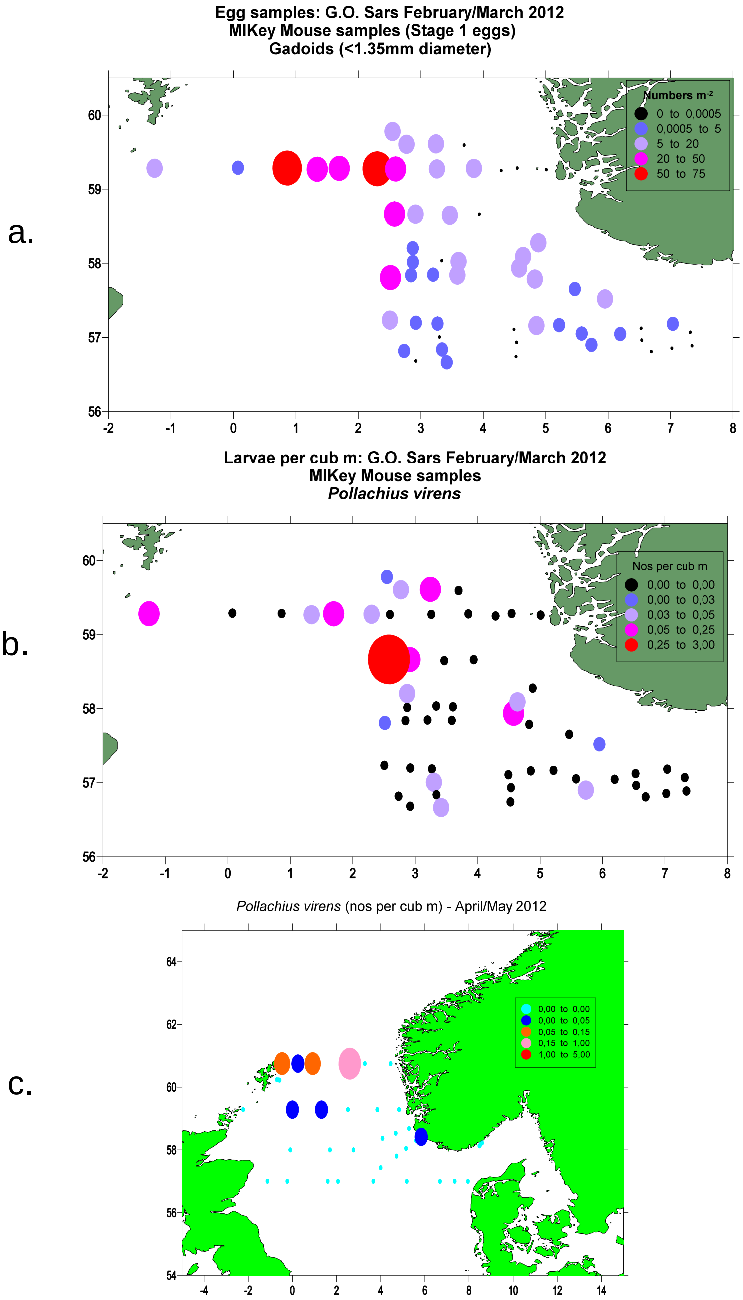

Fig. 4.2.13: Distribution of stage 1 eggs (<1.35mm in diameter) and saithe (*P. virens*) larvae in February/March and saithe larvae in April/May 2012 in the northern North Sea.

Habitat dependent distribution patterns

Species which spawn on the substratum i.e. benthic spawners provide a special case whereby the potential spawning grounds and spatial location of larvae are restricted and if the habitat requirements are known then the locations can be predicted. Whilst the spawning habitats are fixed in location the timing and relative usage of a spawning area may vary. Two examples of such species that occur in the North Sea are sandeels (*Ammodytes* spp) and herring (*Clupea harengus*). This behaviour is illustrated with sandeels (Figure 4.2.14). The larvae are generally closely spatially located to the spawning or hatching grounds as shown in the February/March survey. A more diffuse distribution pattern is seen later in the year, however, in general there is still a tendency for the distributions of larvae to reflect the distributions of the suitable habitat. Often the various sandeel species are not identified to species, and this includes for fishery catch statistics and this can lead to incorrect information on distributions, spawning times etc. In the case of the data for Figure 4.2.14, due to the time of sampling (February to May) the majority are *A. marinus* (lesser sandeel) and not a different species or a mixture of species.

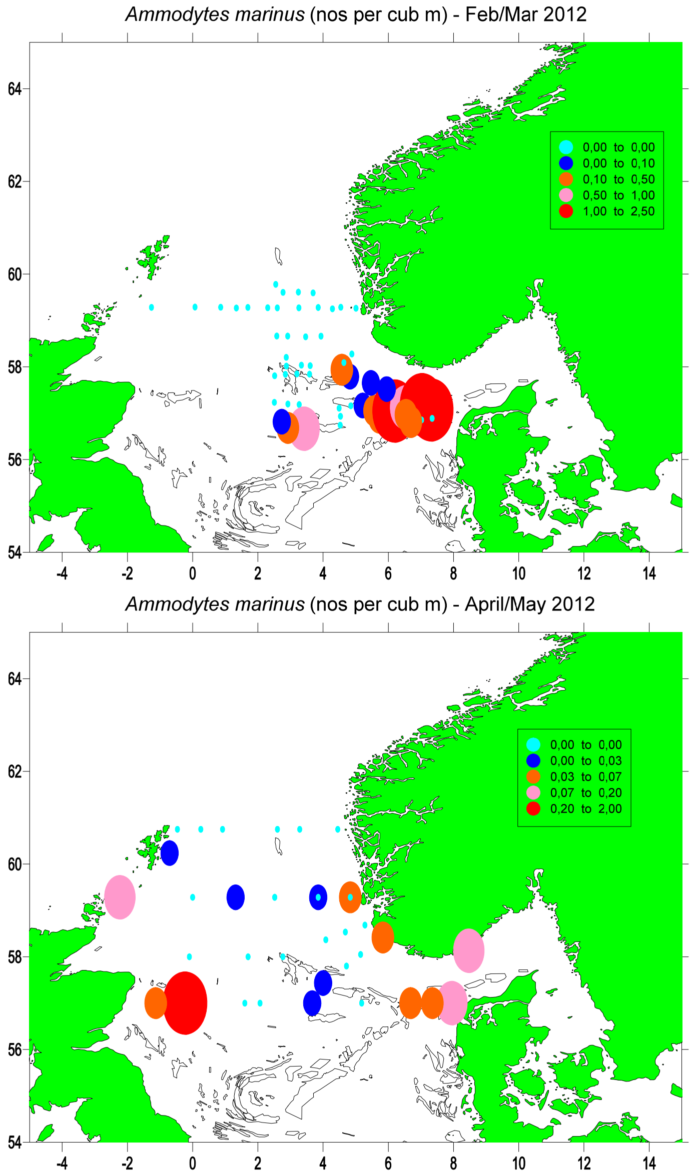

Figure 4.2.14: Distribution of sandeel (*Ammodytes* spp) larvae in February/March and April/May 2012 in the northern North Sea. Much of the suitable sandeel habitat is indicated with polygons.

4.3 Modelling drift pattern

Background

The ocean model system used for the KINO analyses was the Regional Ocean Modelling System (ROMS, Shchepetkin and McWilliams (2005)) - KINO-ROMS. ROMS is a free-surface, terrain-following, primitive equations ocean model widely used by the scientific community on a global scale for a diverse range of applications (https://www.myroms.org).

The KINO model domain covers the Northwest Shelf (NWS) of the eastern Atlantic using an orthogonal curvilinear coordinate system where the model state variables are staggered on an Arakawa C-grid (See Figure 4.3.1). The free-surface, density, and active/passive tracers (salinity, temperature) are located at the centre of the cell whereas the horizontal velocity components (u and v) were located at the west/east and south/north edges of the cell, respectively. The ROMS governing equations are discretized over variable topography using a stretched, terrain-following, vertical coordinate at 40 depth levels. As a result, each grid cell may have different level thickness and volume. The model bathymetry was interpolated from the ETOPO1 Global Relief at 1-minute resolution (http://www.ngdc.noaa.gov/mgg/global/global.html).

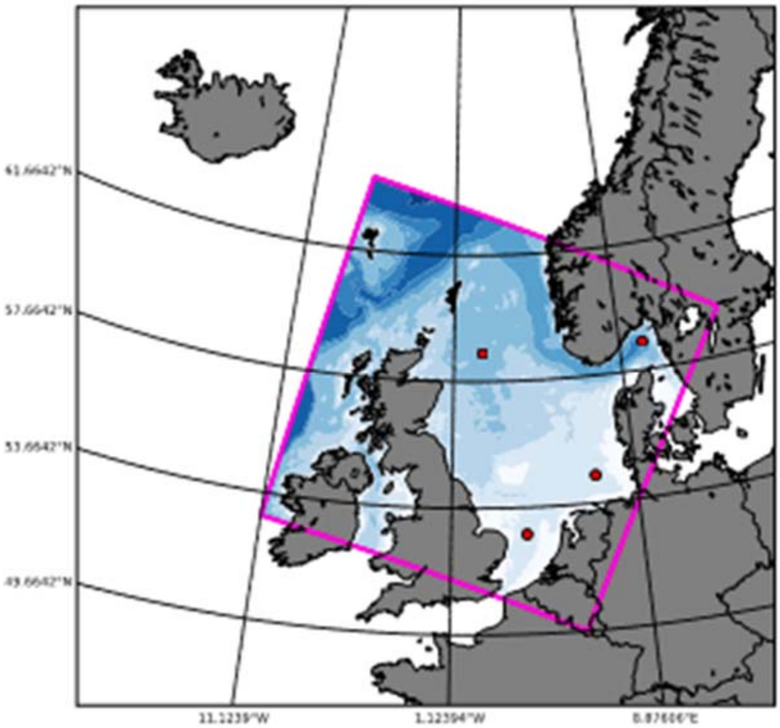

Figure 4.3.1. Modelling domain for KINO project. The modelling domain is characterized by strong tides that creates steep gradients in ocean currents forcing us to simulate using a low time-step to prevent unstable solutions. The area is always characterized by warm, nutrient rich Atlantic water flowing into the area. Along the coastlines of this domain, annual variability in river fluxes creates fresh condition in the surface layer of the water column.

The KINO model was initialized on January 15th 2009 using monthly average values from the GLORYS2V3 simulations as lateral boundary forcing (http://marine.copernicus.eu/). The model was spun-up by repeating the years 2009-2010 three times, before the interior of the model domain reached stable solutions. The GLORYS2V3 global ocean model is available as monthly means for the period 1993-2015 and was also applied as lateral boundary forcing for the final ocean reanalysis products for the years 2011,2012, and 2013. The GLORYS2V3 reanalysis system consists of a global, 1/4° Mercator grid, 75 vertical z-levels, 1m top level, 200m bottom level (ORCA025).

For the experiment presented here, the ocean surface was forced with fluxes derived from 6-hourly atmospheric fluxes from ERA- interim (Dee et al., 2011) that has a resolution of 0.25º. The atmospheric fields from ERA-interim include: precipitation, dew point temperature, total cloud cover, air temperature at 2 m, sea level pressure, wind speed at 10 m, shortwave and longwave radiation at the sea surface. The wind stress is derived from 10 m winds, estimated as in Large and Pond (1981). Ocean-atmosphere heat and momentum fluxes such as surface net heat fluxes (outgoing long-wave radiation) and wind stress were calculated using bulk formula parameterization (Fairall et al., 1996). The input to the bulk calculations included modelled sea surface temperature, the air temperature at 2m height, the sea level pressure, the relative humidity at 2m, the precipitations, the total cloud cover, and the winds at 10m.

The value of river discharge was obtained from the E-HYPE model, which calculates hydrological variables on a daily time-step at a high sub-basin resolution (120 km^2, median) simultaneously for the entire continent. The E-HYPE model calculates water balance, dynamics of hydrological variables and daily discharge for the continental Europe (Strömqvist et al., 2009) for the period 1980-2008, and we repeated the year of 2008 as representative for the years 2009-2013.

During testing of the model system we discovered slight drift in the surface salinity. To avoid this problem, relaxation of sea surface salinity (SSS) of 120 days was activated. Monthly SSS values were obtained from the global GLORYS2V3 model.

The bathymetry of the North Sea is complex and shallow, and early tests of model simulations revealed that the model required using very small time steps (40 seconds) to run stable. We also had to smooth the bathymetry to avoid extremely steep topography that would cause very strong gradients and problem with the simulations. The TPXO 7.1 tidal solutions from Oregon State University with the regional solution for the Atlantic Ocean at 1/12-degree resolution (http://volkov.oce.orst.edu/tides/AO.html) were used containing the following tidal constituents: M2, S2, N2, K2, K1, O1, P1, and Q1. In ROMS, the tidal forcing is super-imposed on the sea surface height (SSH) and vertically integrated momentum and used in the Flather open boundary conditions.

At the open boundaries (north, west, south, east), the Flather conditions were used for the barotropic velocity (Flather, 1976) with the corresponding Chapman conditions (Chapman,

1985) for the sea surface elevation. The baroclinic velocities and the tracers are imposed with radiation-nudging boundary conditions as described in Marchesiello et al. (2001). At the coastal wall, the normal velocity was zero assuming no-slip conditions for the tangential velocity. At the bottom, momentum is dissipated by a quadratic bottom drag coefficient. In addition, a domain wide nudging relaxation with a folding time of 120 days was used to relax the sea surface salinity structure toward the fields provided by the forcing files (GLORYS2V3) to prevent drift in the model. The turbulent kinetic energy was calculated using the closure scheme of Mellor and Yamada (1982).

The physical ocean simulations

The simulation was conducted by running the FORWARD component of the ROMS modelling system (version 3.5), as described above, for the time interval 1 January 2011 – 31 December 2013. The FORWARD run was started using the restart file created from the spin-up simulations (hot start) enabling a stable ocean. The reanalysis was conducted using the following model setup:

- Vertical levels 40 (theta_b=0.1, theta_s=7.0, Tcline=250)
- Horizontal grid resolution 1.6 x 1.6 km (grid points 790 x 798)
- Output stored every 3-hours (24 hours = 5.8 GB)
- The model was run at 40 seconds time-step
- Details and necessary files required to rerun the reanalysis are available on: https://github.com/trondkr/KINO-ROMS.

Particle tracking

After completion of the simulations of the ocean physics for the years 2011-2013, we used the year 2012 to perform particle tracking analysis to observe how the distribution of eggs and larval fish of different species and from different spawning grounds distributed in the North Sea during the typical spawning months. To do this, we used the updated spawning grounds prepared for the KINO project for the selected number of major North Sea fish species:

- Hake (*Merluccius merluccius*)
- Cod (*Gadus morhua*)
- Haddock (*Melanogrammus aeglefinus*)
- Saithe (*Pollachius virens*)
- Norway Pout (*Trisopterus esmarkii*)
- Whiting (*Merlangius merlangus*)

Spawning grounds

The updated spawning grounds for each species contained information as to where the peak spawning takes place as well as the total area of where spawning takes place. Each region where spawning occurs was represented as a polygon. Eggs were released randomly within each polygon over the general or averaged spawning period for gadoids in the northern North Sea. We defined this spawning period as the time period from mid-February to mid-April during spring, where the number of eggs released per day followed a bell shaped curve that peaked in late March. This spawning pattern was identical for each of the six species used in this study (see above).

Individual-based modeling

To connect the physical dynamics to the drift of pelagic eggs and larvae in the North Sea, we used the open source framework openDrift which is freely available at:

https://github.com/knutfrode/opendrift. This framework is developed by met.no and is used in operational oceanography and many institutions including at met.no. The framework currently only contains modules for estimating drift of pelagic eggs and not fish larvae, so we developed an individual-based model (IBM) for larval fish for the KINO project that was integrated into the OpenDrift framework Fig. 4.3.2). This allowed us to simulate the drift and development of fish eggs in the North Sea and to estimate how after a certain time eggs hatched into larval fish and started to exhibit their own vertical behaviour in interaction with the environmental conditions. The pelagic egg module was parameterized for cod by letting egg development time (D) depend on ambient temperature (T) according to $\ln D=3.65-0.145T$ (i.e. similar to (Langangen et al. 2014) based on (Ellertsen et al. 1987)). The IBM model was developed following previously published results of IBM modelling of larval cod (Kristiansen et al. 2009a, 2009b, 2014). The IBM model contains modules for development and growth, predation, and vertical behaviour. Larval mortality was modelled using a size dependent function as outlined in McGurk (1986).

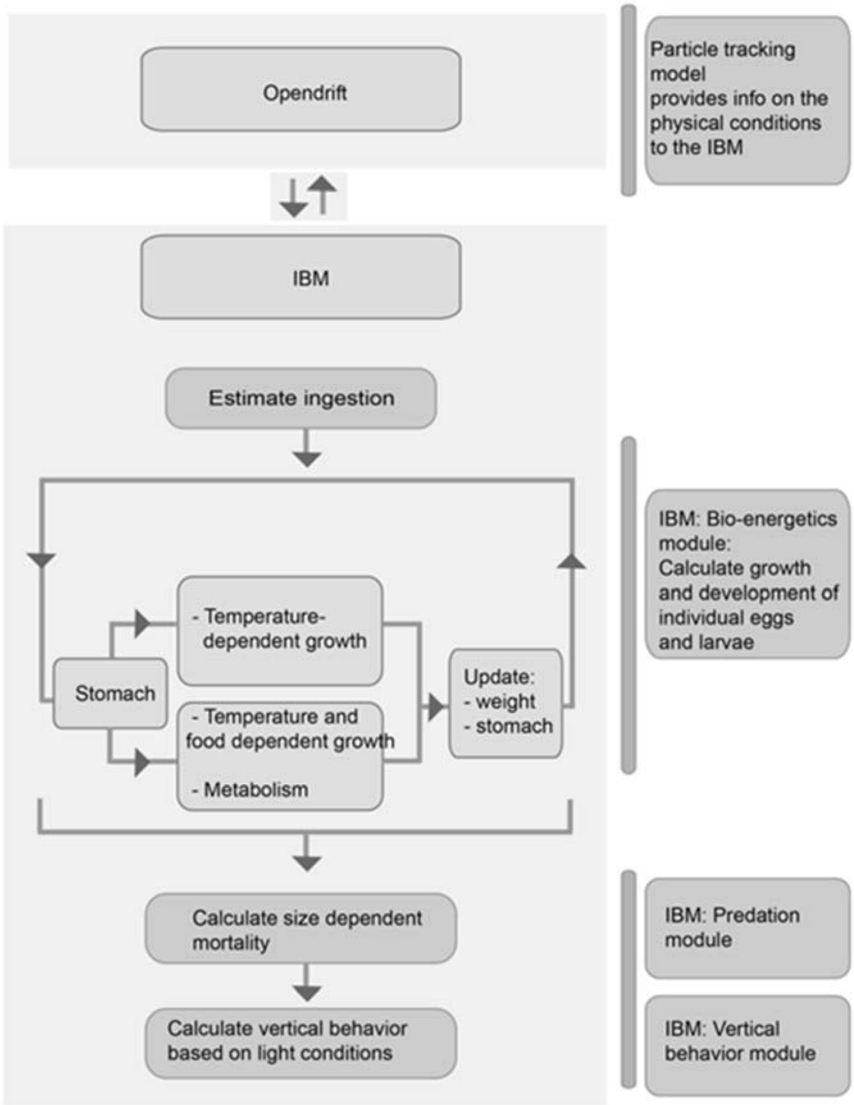

Figure 4.3.2: Schematic overview of the components of the Individual-based model for eggs and larval fish (Kristiansen et al. 2009a, Kristiansen et al. 2009b, Kristiansen et al. 2014) and the connection to OpenDrift.

Analyses of results

The particle tracks from the different spawning grounds provided thousands of streamlines following individual particles through time and space (see Fig. 4.3.3 as an example). To analyse the myriads of particle tracking results we decided to create a new 10 x 10km binned model domain. For each of the bins we summed the number of eggs and larvae contained within that bin for each month between mid-February and mid-May. This process was repeated for each spawning ground for each species.

For each species, the distributions for all of the spawning grounds were then added on top of each other as layers and the new total cumulative distribution per month was calculated. This provided an effective approach to identify the regions within the North Sea that, for each month, has a high or low abundance of eggs and larvae per species.

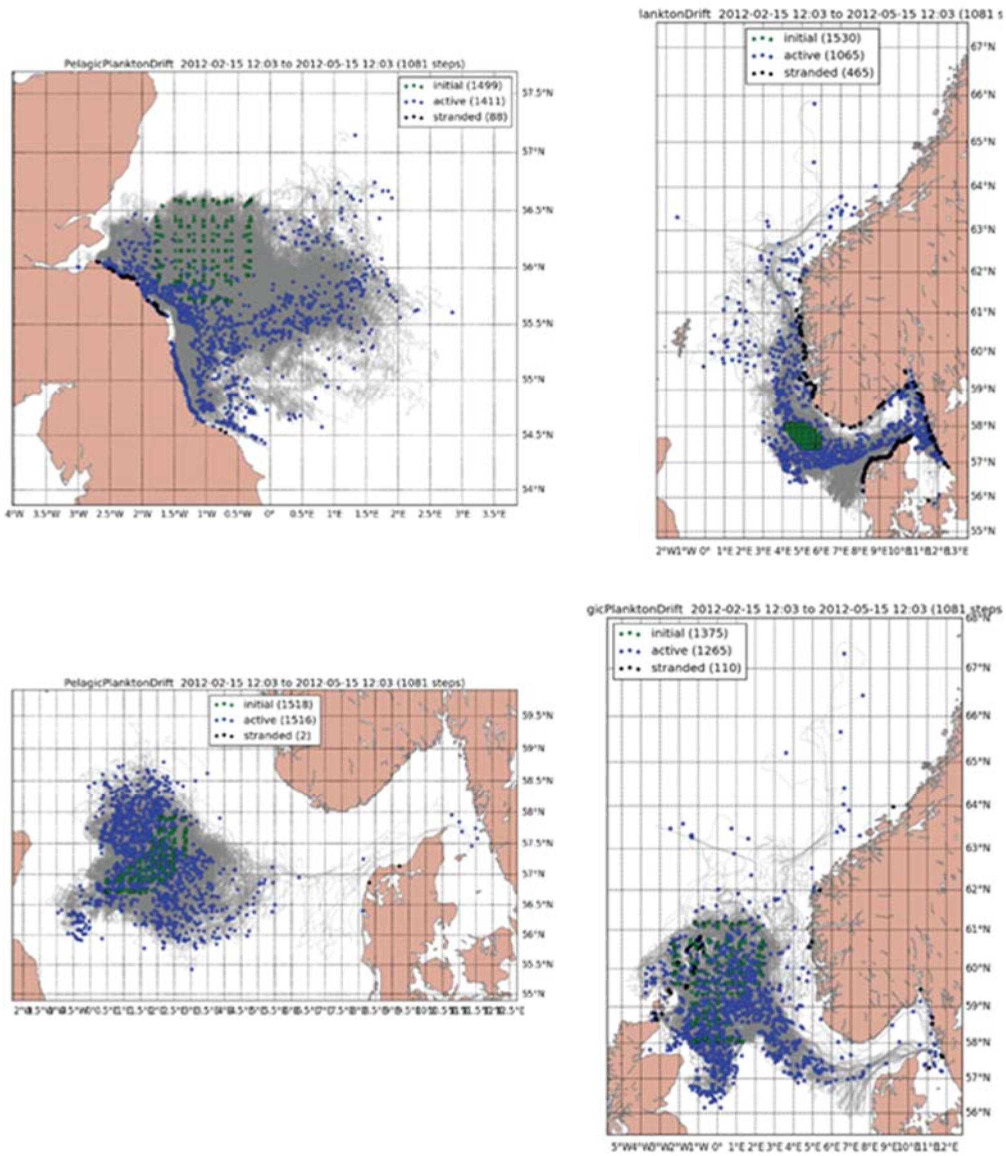

Figure 4.3.3: Sample of particle tracking from various Norway Pout (*Trisopterus esmarkii*) spawning grounds. Blue circles indicate final position at 15.5.2012 while green circles indicate starting positions where eggs are released between 15.2-15.4.2012. Grey lines indicate all positions in between start and finish.

Results

Of the six Gadoid species that were subject to the particle tracking modelling, three are presented here, cod, Norway pout and saithe. The cod is an important commercially exploited species in the North Sea, which has a degree of sub-stock dynamics and has been subject to a steady decrease in biomass from the 1980s due to a combination of changes in climate and too high fishing pressure. Norway pout is commercially exploited in the industrial fishery and the population in the northern North Sea is relatively large. The last species, saithe, is an economically important species of which there is less information on the dynamics of the population. These three provide contrast in their dynamics and our understanding of their early-life history. There is information on the spatial and temporal distributions of eggs and larvae from the field studies which are given in 4.2.

Cod (*Gadus morhua*)

The model outputs indicate that the eggs and larvae are generally still in the vicinity of the spawning grounds in mid February (Fig. 4.3.4). In the most north-eastern spawning area (Viking Bank) there is dispersion both north and southward. There is a very clear south-eastern movement of early life history stages from the north-eastern spawning area (Viking Bank) and eastern spawning area, from Ling Bank to Eigersund Bank, along with the Atlantic inflow into Skagerrak. Also, from the spawning area in the German Bight transport occurs with the Jutland Current toward the Skagerrak region. Finally, the spawning concentrations southeast of the Greater and Little Fisher Banks seem to be transported, as well, towards the Skagerrak region. The distribution of larvae found in April/May 2012 (4.2.6), whilst at low densities, is consistent with the model outputs for April and May. Hence, the high concentrations of cod larvae observed during the ichthyoplankton surveys and from Munk et al. (2009) in the Skagerrak region is consistent with the present modelling, and the larvae here seems to be a mix of all the major eastern spawning areas. The survey observations of cod larvae in the western part of the North Sea seem to be consistent with drift locally from the two western spawning concentrations off the Scottish coast (Smith Bank- Little Halibut Bank and Long Forties), and hence these larvae seem to be separated from the eastern spawning areas. However, it should be emphasized that the spawning aggregation on the Viking Bank also seems to have a transport component westward towards the Shetland region. One particular remarkable feature is the lack of cod larvae transported into the western part of the Central Sub Region, more specifically the area to the north of the Dogger Bank towards the Devil's Hole. It is an interesting observation that this model result is coinciding with the cod larval observations by the time series from the Sir Alister Hardy Foundation for the period 1986-2006 (Edwards et al. 2011) that show very concentrations of cod larvae in this specific region, while during the previous period 1948-1985, coinciding with the gadoid outburst (Cushing 1984), larvae were abundant in this region. It confirms the results in Chapter 3 that spawning areas for cod have been displaced towards northeast in the North Sea.

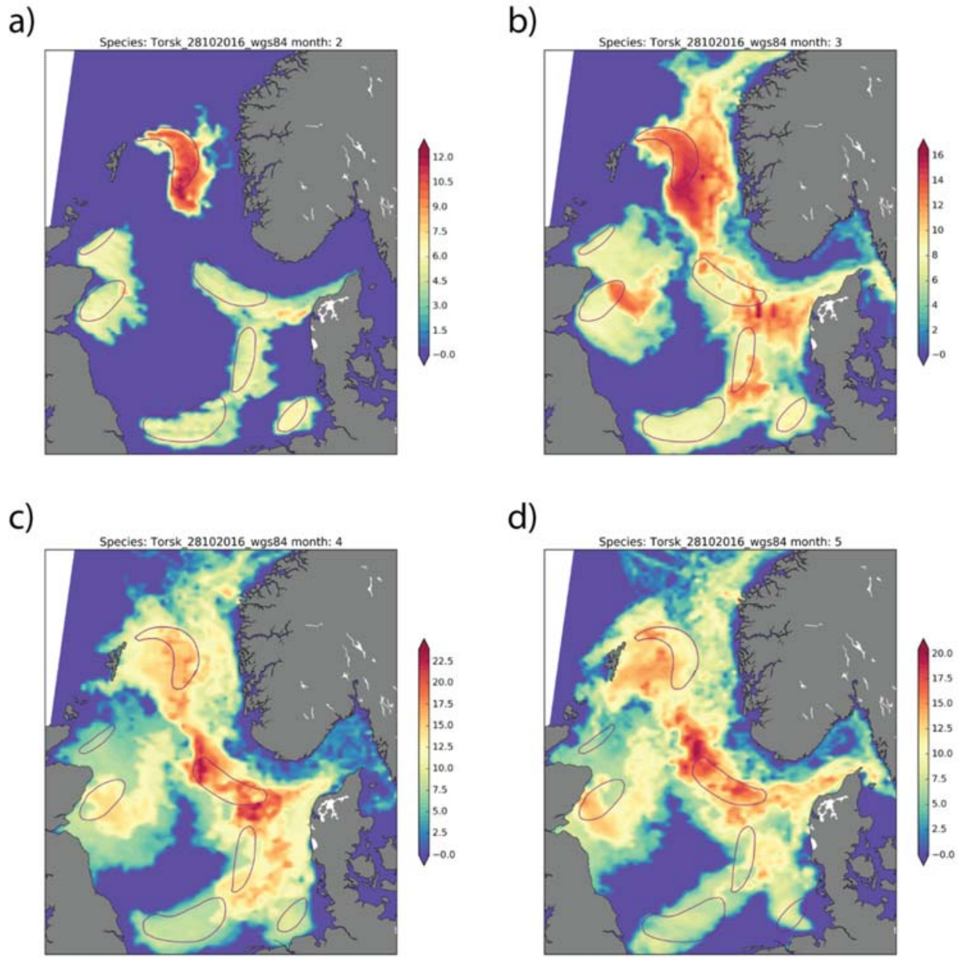

Figure 4.3.4: Horizontal cumulative distribution of cod eggs and larvae during spring 2012 for a) February, b) March, c) April, and d) May. The spawning grounds are shown as outlined polygons. High abundance are shown as red colours while lower abundance is shown as blue and green. The cumulative distributions are calculated based on drift of larval eggs and larvae between the 15.2.2012 and 15.5.2012.

Norway pout (*Trisopterus esmarkii*)

Overall the dispersal of eggs and larvae from the spawning grounds is to the south and east resulting in larvae over much of the northern North Sea (Figure 4.3.5). As with other species, some individuals are advected northward along the Norwegian coast and others are advected into the Skagerrak. The wide spatial coverage in April and May in the model output reflects the field sampling for the same year (see Figure 4.2.8). There are differences in the perception of abundance between the model and the field samples. The main difference is the field sampling suggesting higher densities in the north-western North Sea. This may be because spawning to the west of 4°W resulted in larvae being transported in to the area, spawning to the west of the North Sea was not considered in the model.

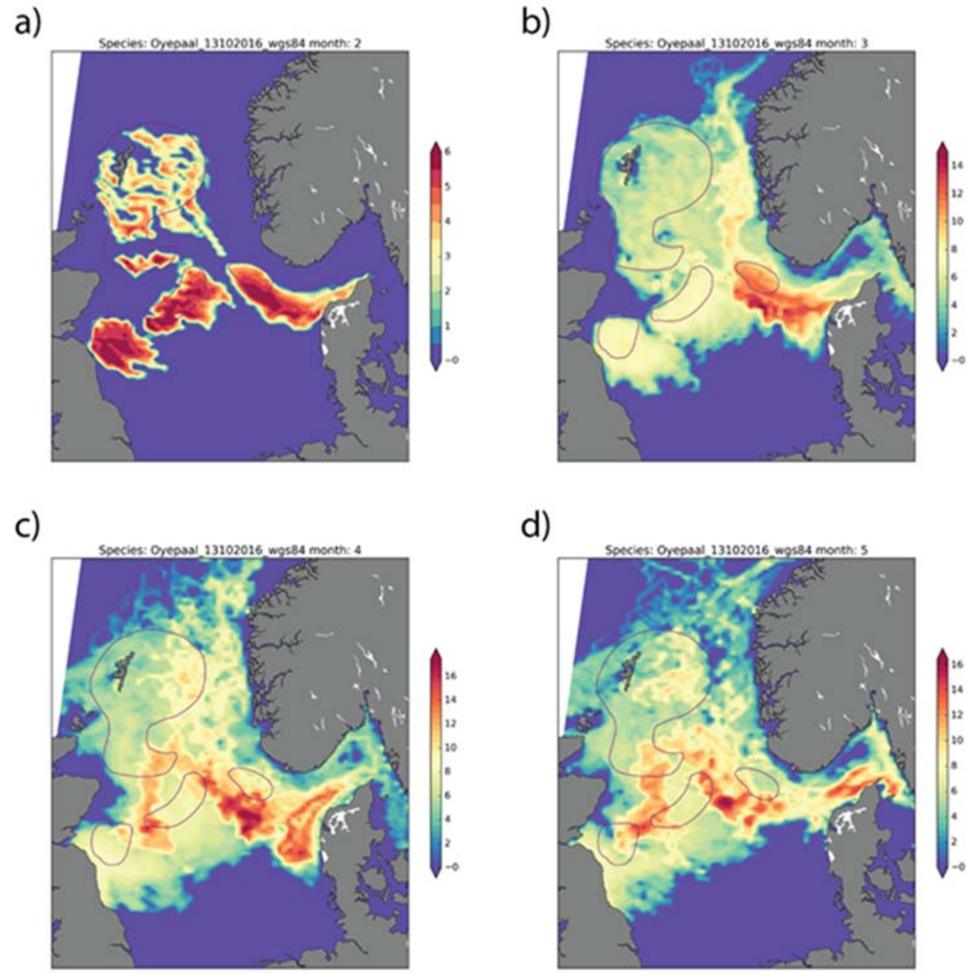

Figure 4.3.5: Horizontal cumulative distribution of Norway Pout eggs and larvae during spring 2012 for a) February, b) March, c) April, and d) May. The spawning grounds are shown as outlined polygons. High abundances are shown as red colours while lower abundance is shown as blue and green. The cumulative distributions are calculated based on drift of larval eggs and larvae between the 15.2.2012 and 15.5.2012.

Saithe (*Pollachius virens*)

This the gadoid species with the most north-easterly modelled distribution of offspring, also consistent with observations on 0-group gadoid fish species (Hislop et al. 2015). Spawning areas on the northern portion of the North Sea shelf generally give model outputs indicating a substantial movement of eggs and larvae northward along the Norwegian coast (Figure 4.3.6). The model output indicates a fairly rapid movement of larvae to the east toward the Norwegian coastline (March) which would be consistent with the inshore, coastal and fjordic nurseries for this species. In addition, there is movement of larvae to the south and east in toward the Skagerrak, again consistent with the known ecology of this species. To the west, there is retention of larvae in the vicinity of the Shetland Islands. These results are also consistent with the data presented from the field sampling (Figure 4.2.13). Of note is the elevated abundance of larvae in the April/May field sampling in the vicinity of the Shetland Islands which reflects the model output for that time period.

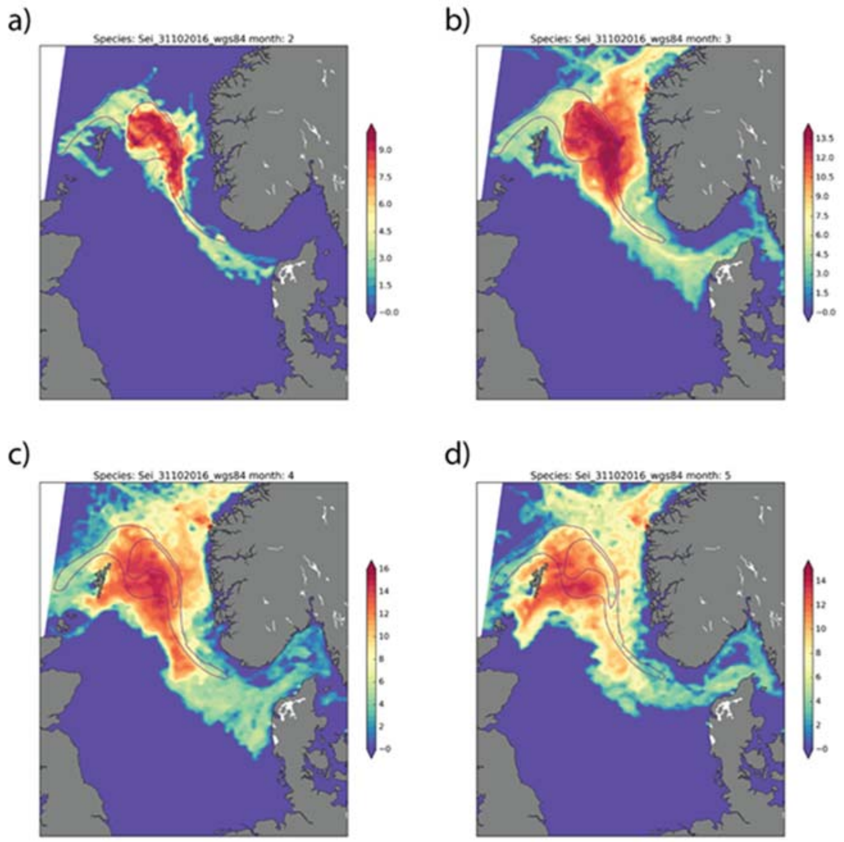

Figure 4.3.6: Horizontal cumulative distribution of saithe eggs and larvae during spring 2012 for a) February, b) March, c) April, and d) May. The spawning grounds are shown as outlined polygons. High abundances are shown as red colours while lower abundance is shown as blue and green. The cumulative distributions are calculated based on drift of larval eggs and larvae between the 15.2.2012 and 15.5.2012.

4.4 General discussion

The overall objective of the project was to use existing data and currently available models to determine the spawning time and location of fishes in the North Sea. In this chapter we reported on how the data on spawning fish times and locations were extracted from the IMR database as input to the production of the spawning maps in Chapter 5. There is also a description of the ichthyoplankton field data and some of the results which were obtained. Lastly a section detailing the particle tracking model and the similarity of the distributions modelled to the field data from the same year.

There are a number of points and caveats with each of these topics which need to be borne in mind when reviewing the results, some of which are discussed below.

Data on spawning fish. Most of the survey data was collected on surveys which are generally fixed in the calendar year. Therefore, fishes with peak spawning periods outside the survey periods will not be well represented in regard to their principal spawning locations. In addition, whilst only fish in spawning condition were analysed it is possible for fish to move considerable distances to their actual spawning location. González-Irusta & Wright (2016), working with the ICES 1st Quarter IBTS data, suggested that cod was probably the only species that was spawning at the time of the survey and thus its distribution did reflect the principal spawning locations. The survey data, especially the standard IBTS data series, does not sample hard substrata so fish which spawn in these areas will not be sampled. Likewise, there are constraints on the sampling depth so shallow and depths greater than 200m are also under-sampled. This has implications for the Norwegian Trench Sub Region. There are also samples from commercial catches in the database which does broaden the annual temporal scope of the available data. However, this is generally for Norwegian vessels or landings in to Norway. This provides a bias toward the Norwegian EEZ. The Norwegian sector bias is also within the survey database as Norway is generally allocated surveys in the northern and eastern part of the North Sea with much less coverage in to UK or Danish territorial waters.

Ichthyoplankton surveys. The surveys are generally fixed in time and thus vary slightly in their timing relative to the annual seasonal cycle. This variability means that it is uncertain whether differences in distribution patterns and abundance between years is caused by variations in production or simply differences due to sampling different parts of the annual production cycle. Information such as the larvae lengths can help to determine the likely causes of variation, however, interannual variations in thermal regime of prey production cycle can influence growth rates for example. The survey data are also taken as an instantaneous ‘view’ of the distributions and sizes, however, the sampling occurs over approximately 21 days. In that time period larvae will have changed location, grown and some will have died. Whilst it is possible to make some correction for the temporal aspects, this has not been done for these surveys.

There is a survey which is conducted between mid January and early March which primarily samples large larvae all over the North Sea. Recently this survey has included sampling eggs and small larvae as well. This is an ICES co-ordinated international survey that has the capability of monitoring the distribution spawning locations for those species spawning in the winter. By examining stage 1 eggs it is possible to verify the match between spawning condition fish caught during the IBTS survey and the actual location of the spawning grounds. With a time-series of these surveys it will be possible to determine the variability in both timing and location of spawning.

Currently IMR undertakes or is involved in a number of surveys through each year. These surveys vary in spatial coverage, however, as a minimum they generally encompass the northern North Sea from 56.5 to 59ºN. The combination of survey data covering fish species distributions, abundance and size provides insight in to spawning locations and timing for a range of species which spawn at different times of the year (winter, spring, summer or autumn) and in different locations. These data, along with the particle tracking modelling, provide information on the large scale patterns in spawning behaviour of fishes in the northern North Sea.

Particle tracking and biophysical modelling. The data on spawning fish and egg and larvae distributions provide temporally restricted views of the spawning and early life history dynamics of fishes in the northern North Sea. The particle tracking and biophysical models provide a mechanism of tying these data together to determine the most plausible spawning locations and timings. However, the output will never be very accurate due to the lack of detailed information on egg and larvae vital parameters and the necessity to make assumptions within the modelling framework.

The oceanographic model used here has high resolution and encompasses very well physical forcing necessary for a realistic annually specific circulation pattern of the North Sea in three dimensions. The model has a spatial resolution exceeding any kind of observation in the field. However, computing power capacity still sets some limits to how many years we were able to simulate the present project. Also, the lack of biological knowledge on the vertical distribution of the larvae and pelagic juvenile set some constraints to the precision of the simulation in horizontal transport pattern.

The egg and larvae stages in the particle tracking model were based on an IBM compiled for cod. This ‘generic’ model was applied to a number of different gadoid species. Whilst this is a reasonable approximation, given a lack of data or models for the other species, there is a probability that subtle differences in e.g. egg buoyancy, development rates or behaviour may alter the perceived drift trajectories of each species. Growth rate of the larvae is generally a function of both the ambient temperature and the available suitable prey. Variability in prey was not included in this model so any variations in growth were a consequence of the temperature fields. The model also did not consider species interactions in the context of predation and so a standard uniform size dependent predation field was applied. Some additional variation between the field and modelled data may therefore occur due to localised predation events which are not captured in the modelling.

Continued uncertainties. The database on spawning fish distributions is a large and valuable resource providing an overview of the spatial dimensions of spawning in the North Sea. The absence of good seasonal coverage restricts the value of this database, with respect to the range of species, to be able to give a full annual perception of spawning. Also, there is uncertainty in the location of spring and early summer spawning due to a lack of comprehensive sampling. The annual ichthyoplankton surveys give an indication of both spatial and temporal variability in spawning, especially when all of the surveys in a year are linked to indicate the temporal aspects. To provide meaningful information on spawning locations, these data need to be used in conjunction with the biophysical models. The combination of these two can provide information on the spatial dynamics of spawning in the North Sea.

Whilst undertaking this research it was obvious that many aspects of the biology, ecology and behaviour of the fishes in the northern North Sea are not adequately known or understood. In regard to the spawning habits specifically, there is still inadequate knowledge of the annual location of spawning grounds of all the fish species, especially the important commercially exploited species. Similarly, there is insufficient data on the timing of spawning for many species and how this varies interannually. Both the locations and timing of spawning and how they vary within and between years is essential for advice when protecting spawning fish.

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5. Synthesis on spawning areas and spawning periods of key species

5.0 Introduction

The present report on spawning areas in the North Sea focuses on 34 fish species distributed in 13 orders. Although more than 140 fish species are identified in the North Sea (Heessen et al. 2015) these 34 species comprise about 80 % of the total North Sea fish catches. Therefore, most of these species are selected because of their economic importance for fisheries, others due to their role as forage fish in the ecosystem. One criterion of selection is also because the species have core area of distribution in the Northern and Central regions of the North Sea (see definitions of regions in Chapter 2 Ecosystem sub regions of the North Sea) where the seismic exploration of interest is taking place. Also some species typically distributed in the Southern region are selected, because of their northward displacement over the recent 40 years induced by the warming climate, and their potential future abundance farther north.

Sandeels (*Ammodytidae*) (section 5.3.1) is a particularly important species because it is the target for the largest fishery in the North Sea. Moreover, it is a key forage fish in the ecosystem. It comprises 20.4 % of the mean fish catches of the North Sea for the period 1970-2010 (Table 1.1). Some of the spawning areas have potential overlap with seismic surveys. The three pelagic species mackerel (*Scomber scombrus*) (section 5.6.1), herring (*Clupea harengus*) (section 5.4.1), and sprat (*Sprattus sprattus*) (section 5.4.3) are important species because they comprise about 27.6 % of the North Sea fish catches (Table 1.1). Herring and sprat, however, have spawning areas outside the potential areas of seismic exploration, but mackerel do have spawning areas that overlap with potential seismic surveys. The major five gadoid species cod (*Gadus morhua*) (section 5.1.1), haddock (*Melanogrammus aeglefinus*) (section 5.1.2), whiting (*Merlangius merlangus*) (section 5.1.3), saithe (*Pollachius virens*) (section 5.1.4), and Norway pout (*Trisopterus esmarkii*) (section 5.1.4) are “the big five” of the North Sea. They are all highly economically valuable in the fisheries and comprises 23.1 % of biomass in North Sea fish catches (Table 1.1). All these five species have core spawning areas in regions of potential seismic studies. Plaice (*Pleuronectes platessa*) (section 5.9.6) is a widely distributed fish species in the North Sea, also in the Northern region, and it comprises 6.1 % of the total North Sea fish catches.

The other flatfishes such as the soles, i.e. sole (*Solea solea*) and solenette (*Buglossidium luteum*) (sections 5.8.1-5.8.2), and the flounders, i.e witch (*Glyptocephalus cynoglossus*), long rough dab (*Hippoglossoides platessoides*), dab (*Limanda limanda*), lemon sole (*Microstomus kitt*), and flounder (*Platichthys flesus*) (sections 5.9.1-5.9.5) have varying degree overlapping spawning areas with potential seismic study areas. Here, the most northerly distributed species are of particular interest; that is witch, long rough dab, lemon sole, and dab.

Hake (*Merluccius merluccius*) (section 5.2.1) is one of the rapidly increasing fish species in the North Sea due to climate change, and it has spawning areas in the regions of potential seismic exploration. Sardine (*Sardina pilchardus*) (section 5.4.2) and anchovy (*Engraulis encrasicolus*) (section 5.5.1) are two species that have been advancing northward during the recent warming, but they still have not established spawning areas in potential conflicting area for the present study.

Finally, there is a group of deep-water fishes that might have spawning areas adjacent to, or into, potential areas of seismic exploration. These are tusk (*Brosme brosme*) (section 5.1.12), ling (*Molva molva*) (section 5.1.13), blue ling (*Molva dypterygia*) (section 5.1.14), greater argentine (*Argentina silus*) (section 5.10.1), roundnose grenadier (*Coryphaenoides rupestris*) (section 5.11.1), and pearlside (*Maurolicus muelleri*) (section 5.13.1).

A comprehensive study of data on egg distributions, data series on catches of ripe and running fish, the scientific literature, and the study of circulation features and water mass characteristics are the basis for the synthesis enabling the construction of the new spawning maps in this chapter. Moreover, modelling of egg and larval drift for the five major gadoids cod, haddock, whiting, saithe and Norway pout, compared to observed distributions of larvae and juveniles, is additionally applied to validate the core spawning areas of these gadoids.

The result on spawning periods, including the spawning tables, are based on published literature alone. There are considerable uncertainties in these results, partly because the literature is based on data from different time periods through 20th and 21st centuries. Periods of changing climate during this time span might have influenced the results. In addition, the literature has most often not distinguished among the various spawning areas that may have distinct spawning periods.

Interpretation of the spawning maps and spawning tables:

In the spawning maps for each species below, the two colors indicate high and low spawning intensities. *In those maps where no high spawning intensity is shown no information is available at a level that allows for indicating the most intensive spawning areas. It does not mean that there are no areas of high spawning intensity*. The general distribution features of biotic variables in the sea are typically exponentially decreasing from the core distributions. Here, the average differences in concentrations of the high and low intensities indicate about 2 orders of magnitude (i.e. 100 times).

In the spawning tables, green color indicates periods of high spawning activity, while yellow color indicates the entire period of spawning. *Similarly, lack of green periods in the spawning tables does not imply non-existing period of high spawning intensity. It simply implies such information is lacking.*

For some of the species the information about the spawning areas are less certain, either because the information is limited, as for bib, tusk, ling, blue ling and pearlside, or because newer information to confirm older is lacking, as for anglerfish.

Reference

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5.1.1 Cod – *Gadus morhua* L. - torsk

General stock features

Cod is one of the five major, commercially exploited, gadoid stocks in the North Sea. In abundance, it ranks number five after haddock, whiting, saithe and Norway pout. The spawning stock biomass has ranged between 270 000 tonnes in the prosperous times in the 1970s to around 40 000t in the mid 2000s (ICES WGNSSK 2016). Currently (2015/16) the stock is perceived to have a spawning stock biomass of around 150 000t. The other four major gadoids displayed similar trends and parallels the climate change. The prosperous gadoid period coincided with the cool period of the North Atlantic, described as the negative phase of the Atlantic Multidecadal Oscillation (AMO) (Sutton and Hodson 2005; Alexander et al. 2014). This had major impacts on distribution, abundance, growth and spawning of North Atlantic fish stocks (Sundby and Nakken 2008; Drinkwater et al. 2014). The overall outcome was a reduction in the abundance of boreal fish species in the northernmost areas of the North Atlantic (e.g. like in the Barents Sea) with an increase in the southernmost areas of distribution (e.g. The North Sea and Irish Sea). In the North Sea the cool AMO period from 1960 to 1980s resulted in the so-called "gadoid outburst" (Cushing 1984; Beaugrand et al. 2003) that created a record-high abundance of the four major gadoid fish stocks in the North Sea around 1970 (Hislop 1996; Myers et al. 1996). After the "gadoid outburst", when cod was distributed across the entire North Sea, the stock size decreased substantially along with a substantial decrease in spatial extent. After 2000 the highest abundances are found in the northern and eastern parts of the North Sea as shown by Hislop et al. (2015) and ICES WGNSSK (2016).

Spawning areas

Based on earlier ichthyoplankton surveys during 1953-1990 Brander (1994) synthesized the location and timing of cod spawning around the British Isles and in the southern and central North Sea. The surveys indicated that cod spawning occurred extensively in the entire southern survey area. However, more recent egg surveys also covering the northern North Sea shows that this region comprises important cod spawning areas. Moreover, the development in spatial distribution in the adult stock (Hislop et al. 2015) seems to have influence the spawning areas, because the recent distributions of cod eggs from 2004 to 2009 display relatively high concentrations in the eastern parts of the North Sea from the Viking Bank to Greater Fisher Bank and southwards to the German Bight (Fox et al. 2008; Munk et al. 2009; ICES 2010, 2011). Ellis et al. (2012) suggest that the area around Viking Bank is an important spawning area supported by the data on distribution on ripe and running cod from the fish data base at Institute of Marine Research. Rogers and Stocks (2001) who have not included the most recent years observations arrived at more even distribution between the eastern and western spawning areas. This is more in line with the observations in ICES WGNSSK (2016) and González-Irusta and Wright (2016). This possibly reflects a change from the 1930s to 1960s where cod eggs were more confined to the western spawning areas, closer to the British east coast (Wright et al. 2003; Fox et al. 2008; Gibb et al. 2008) compared with the more recent observations. Figure 5.1.1-1 represents average distributions of North Sea cod spawning areas in the period after

2000. Whilst spawning does still occur in the southern North Sea the intensity is not as high as in the northern North Sea (González-Irusta and Wright 2016). Core spawning areas are indicated by dark colors, and comprise 1) Viking Bank, eastern Shetland banks, and the coastal northeastern Scotland in the Northern region, 2) Ling Bank - Eigersunds Bank in the eastern part of the Central regions, 3) south of Fisher Banks and 4) Norfolk Bank-Oyster Ground in the Southern region, and 5) the German Bight.

Spawning period

Differences in peak spawning in various regions indicates different components of the North Sea cod (González-Irusta and Wright 2016). There are some indications of earlier start of spawning in the southern region compared to the northern region (Hislop et al. 2015). Spawning in the northwestern North Sea (Viking Bank-Fladen) occurs from January through May (Hislop et al. 2015). At Viking Bank peak spawning occurs in March (González-Irusta and Wright 2016), while in the Northwestern region peak spawning occurs in February-March. In the Southern North Sea peak spawning occurs even earlier; during January-February. Earlier investigations have indicated spawning from January to April (Brander 1994). Morgan et al. (2013) found that younger fish spawns later than the older ones.

Spawning Table North Sea Cod

Viking Bank

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Northwestern North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Southern North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

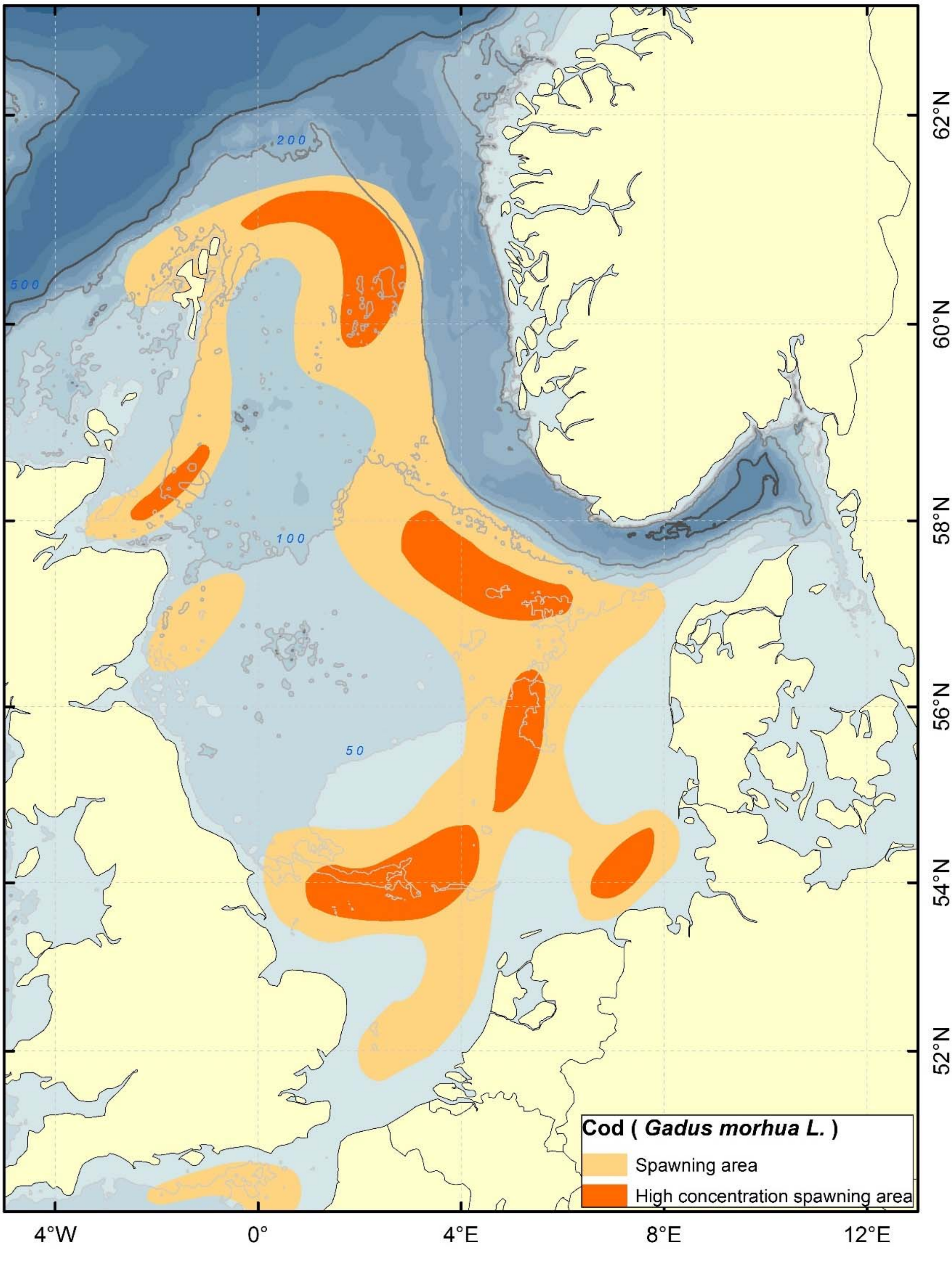

Figure 5.1.1-1. Cod spawning areas in the North Sea mainly based on observations after 2000.

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5.1.2 Haddock – *Melanogrammus aeglefinus* L. - hyse

General stock features

Haddock, in relation to biomass, is a very important gadoid species in the North Sea. In recent years the difference between the stock found to the west of Scotland and the one found in the North Sea has been questioned. Since 2014, ICES assess both stocks as one (ICES WGNSSK 2016) and are now termed the Northern Shelf haddock stock. The spawning-stock biomass has varied considerably over the years ranging from 50 000 to 500 000 during the period since 1972 (ICES WGNSSK 2015). Haddock populations characteristically vary considerably in biomass with the underlying reason being occasional very large recruitments with periods of very poor early life history survival (Dickey-Collas et al. 2003). Similar to the cod, the North Sea haddock was influenced by the "gadoid outburst" (Cushing 1984) showing a peak in spawning-stock biomass in 1970 (Hislop 1996). The subsequent decline was, however, more rapid than for cod. While adult cod are found in all the six sub regions of the North Sea the haddock has a more northerly distribution (Daan et al. 1990). Although haddock are found in the entire North Sea the major catches are confined to the Northern and Central sub region, and also along the southern slope of the Norwegian Trench in the Skagerrak and along the western slope of the Norwegian Trench off western Norway (Hislop et al. 2015). A description of the changes in biomass of the stock is reported by Cook and Armstrong (1986) and Hislop (1996), however, there is little information linking any distributional changes as a response to climate change.

Spawning areas

Little is known about possible changes over time in spawning areas in the North Sea. A cursory overview of haddock spawning sites by Rogers and Stocks (2001) indicates that haddock spawning is confined to the northernmost part of the North Sea, particularly from Viking Bank to Shetland. Wright et al. (2011) also highlight a separate western sub-population spawning along the east coast of Scotland from the Orkney islands southward. The more detailed and recent egg surveys (Munk et al. 2009; ICES et al. 2010) also show that extensive spawning occuring east of the Orkneys and east of the Scottish east coast, in addition to a lesser spawning area near the western slope of the Norwegian Trench from Ling Bank to Eigersund Bank. Albert (1994) did not find spawning further east into the Norwegian Trench proper and concluded that the distributions of adult and maturing haddock moved out of the trench to spawn. This is in agreement with the eggs distributions found by Munk et al. (2009). However, distributions of eggs, larvae and pelagic juveniles (Munk et al. 1999) indicate that the offspring haddock drift southeastward back into the Norwegian Trench and Skagerrak. Figure 5.1.2-1 shows the synthesis of spawning areas from the above literature.

Spawning period

Spawning extends from February through May and the first-time spawners (two-year-old) spawn much later than the older age classes (Wright and Gibb 2005; Morgan et al. 2013). González-Irusta & Wright (2016) indicated peak spawning in March, while Morgan et al. (2013) reported that 50% of the total spawning had occurred by early April.

Spawning Table North Sea Haddock

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

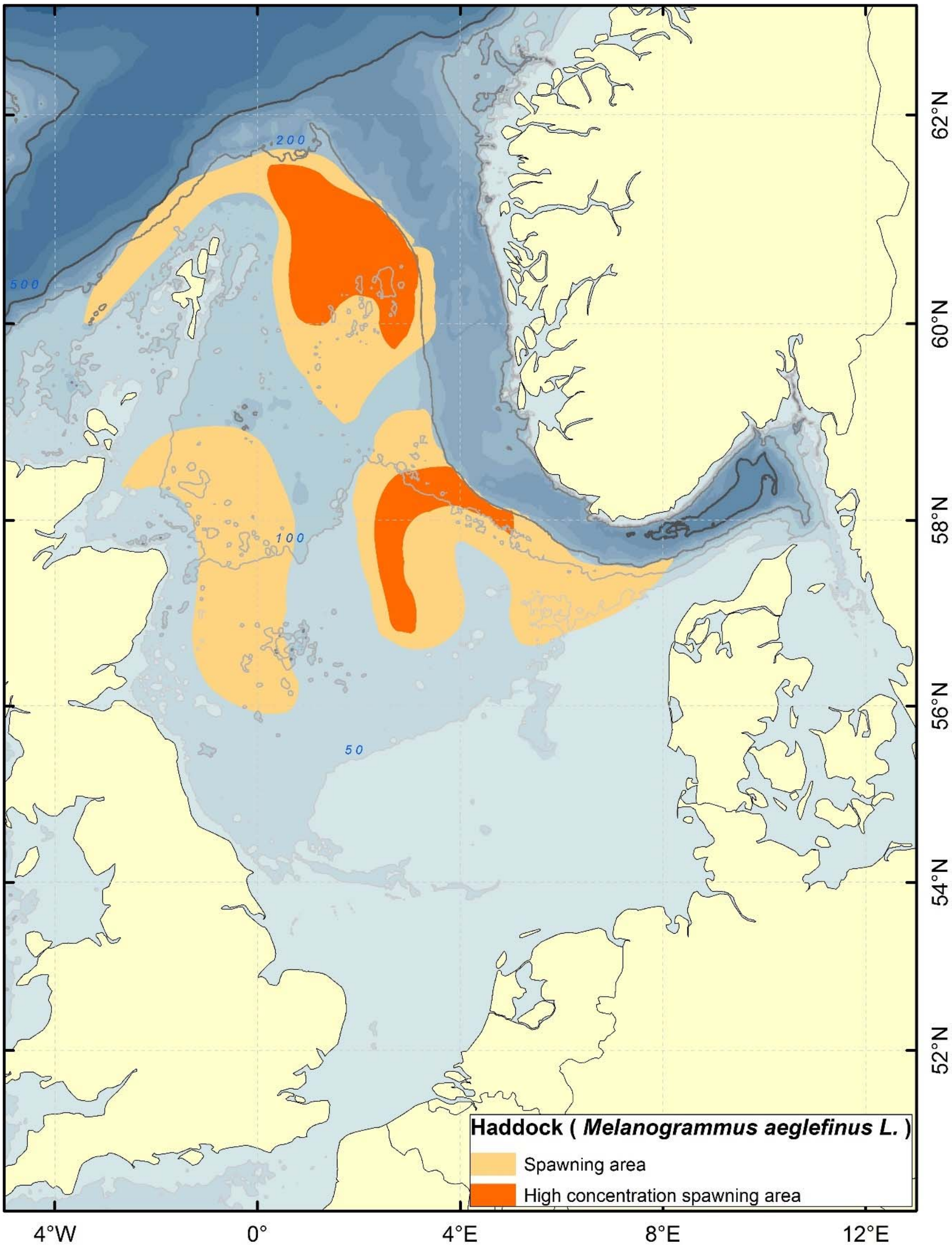

Figure 5.1.2-1. Haddock spawning areas in the North Sea.

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5.1.3 Whiting – *Merlangius merlangus* L. - hvitting

General stock features

Whiting biomass is a significant part of the total gadoid biomass in the North Sea and is subject to commercial exploitation. Spawning-stock biomass has ranged between 170 000 and 600 000 tonnes during the period after 1960 (Hislop 1996; ICES WGNSSK 2016). Whiting, like cod and haddock, was influenced by the "gadoid outburst" (Cushing 1984). However, the peak biomass came later, in 1976, and the decline thereafter was slower and less dramatic. Whiting is widely distributed in all sub regions of the North Sea. In contrast to cod, the changes in spatial distribution from the late 1970s (Hislop et al. 2015), shows the opposite longitudinal shift from the cool period in the in the 1960s-1970s till the present warm phase: As stated in paragraph on cod, distribution has changed eastward onto the western slope of the Norwegian Trench, while the whiting has been displaced eastward with the highest concentrations near the British coast. The cause of these opposite trends is not clear. One possible explanation might be higher predation pressure from cod and haddock in the eastern areas. Although cannibalism is extensive in whiting (Pope and Macer 1996) predation from cod and haddock is also significant. Bromley et al. (1997) who studied diet of 0-group gadoids found that even these young stages of cod and haddock consumed significant amounts of other gadoids, particularly whiting.

Spawning areas

The extensive distribution of the whiting is reflected in the wide ranging spawning areas distributed over much of the North Sea from Viking Bank-Shetland in north to the English Channel in the south (Rogers and Stocks 2001; Ellis et al. 2012). However, spawning of whiting does not seem to have been recorded in the sub regions German Bight – Jutland Current and in the Norwegian Trench. The recent egg surveys (ICES 2010) indicate a more westerly distribution of whiting spawning areas than displayed by Rogers and Stock (2001) and Ellis et al. (2012). This observation should be treated with a bit of caution since the survey was in one year and only partially covered the spawning season. In addition, spawning activity in the English Channel was very high. The spawning areas appear as distinct patches within the relatively wide ranging general habitat. What determines the spawning locations or how fixed in space they are is unknown. Figure 5.1.3-1 shows a synthesis of the whiting spawning areas.

Spawning period

The spawning season starts in January in the English Channel and continues until June or early July in the northern North Sea (Hislop et al. 2015). Generally, there seems to be a delay in spawning time from the English Channel to the northern North Sea (Loots et al. 2011). There have been reported peak spawning in February-March in the English Channel, and in April-June in the northern North Sea (Daan et al. 1990). However, concentration of whiting eggs in the North Sea indicate a quite protracted spawning with the given period.

Spawning Table North Sea Whiting

Northern North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

English Channel

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

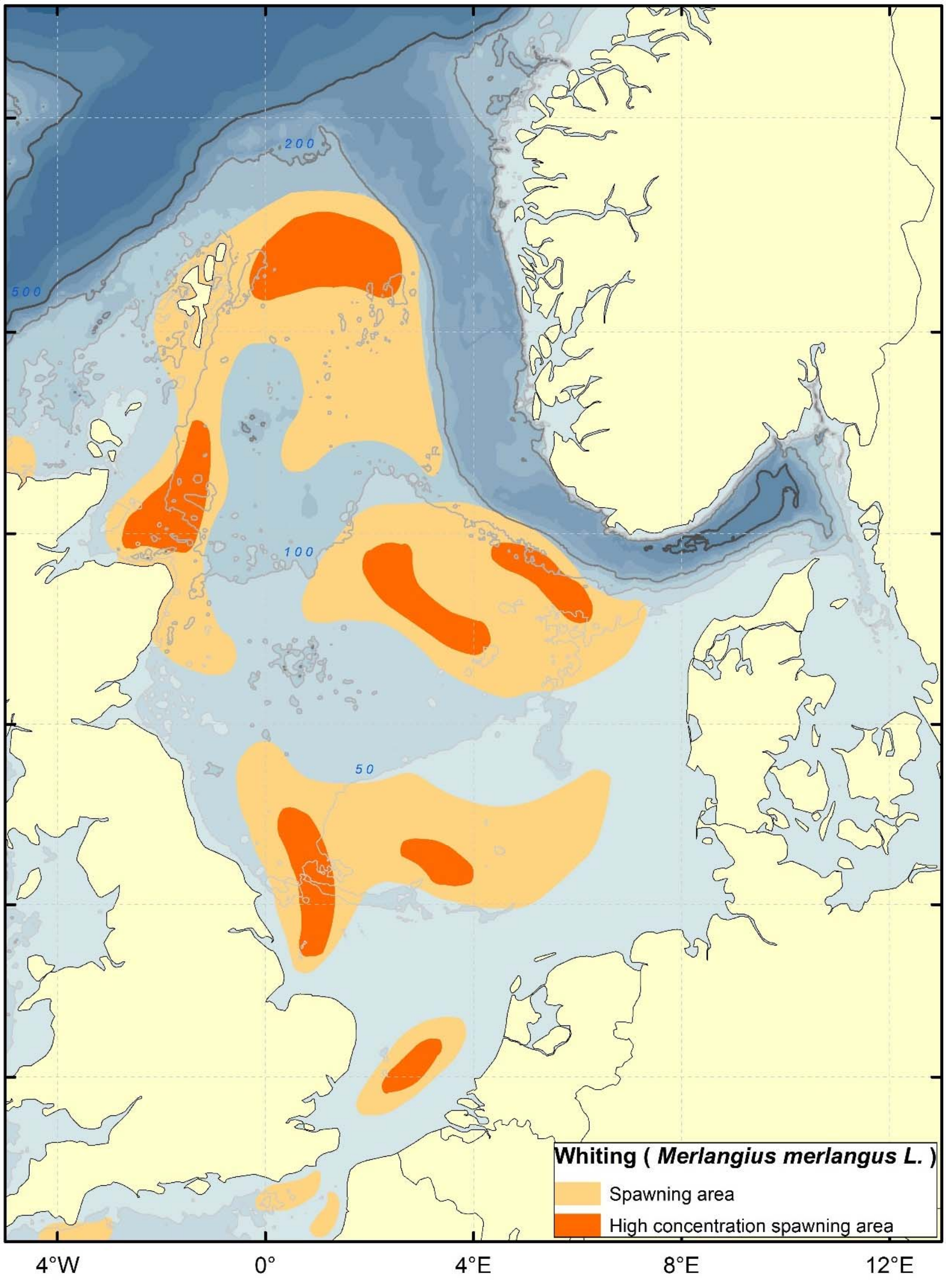

Figure 5.1.3-1. Whiting spawning areas in the North Sea.

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5.1.4 Saithe – *Pollachius virens* L. - sei

General stock features

The saithe stock in the North Sea is relatively large and commercially important. ICES considers the stock residing in the Skagerrak, North Sea and to the northwest of Scotland as one and assess it as such (ICES WGNSSK 2016). The only indication of the stock size in the North Sea and Skagerrak comes from the catches which have ranged between 70 000 and 120 000 tonnes in the period 2004 to 2015. The spawning stock biomass was larger than present during the gadoid outburst (Hislop 1996). Adult saithe in the North Sea are largely confined to the two sub regions Northern and Norwegian Trench. They are also found in the Central and Kattegat sub regions, but to a much lesser extent. In the Southern and German Bight – Jutland Current sub regions they are scarce (Hislop et al. 2015). Along with the other major North Sea gadoids, i.e. cod, haddock, whiting, Norway pout, and cod, the saithe stock was part of the "gadoid outburst" (Cushing 1984) that caused an extensive increase in abundance between the 1960s and 1980s, peaking around 1970 (Hislop 1996). The principal nursery grounds for saithe are inshore, coastal waters with the majority of young fish occurring along the south and southwestern Norwegian, and Shetland coastlines (ICES WGNSSK 2016, Stock annex). In contrast to haddock, whiting and cod, the saithe 0-group feed to a much lesser extent on other fish in the Northern sub region. Instead they feed to a much larger extent on invertebrate plankton (Bromley et al. 1997). Moreover, the 0-group cod, haddock and whiting have all very low predation on small pelagic juvenile saithe. Both of these facts indicate low spatial overlap between offspring saithe and the other three major gadoids. This indicates differential drift patterns of saithe offspring from cod, haddock and whiting offspring.

Spawning areas

Similarly to the northerly stock distribution compared to the other three major gadoids the centre of gravity for saithe spawning areas has also the northernmost location. Core spawning area is located from Viking Bank to Shetland and with a tail extending southwards along the western slope of the Norwegian Trench (Rogers and Stocks 2001). Munk (1999) who mapped the distribution of gadoid offspring above the shelf to the south of the southern part of the Norwegian Trench and south of Skagerrak during the years 1991-1994 found very low concentrations of saithe offspring here, while cod, whiting, haddock and Norway pout were found at very high concentrations. This confirms the conclusion above on prey between between 0-group gadoid (Bromley et al 1997) that saithe has low overlap with the other gadoid offspring. Figure 5.1.4-1 displays the distribution of saithe spawning areas.

Spawning period

Spawning occurs from January in the southern areas of spawning to May in the northern spawning areas (Hislop et al. 2015). Peak spawning is not described.

Spawning Table North Sea Saithe

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

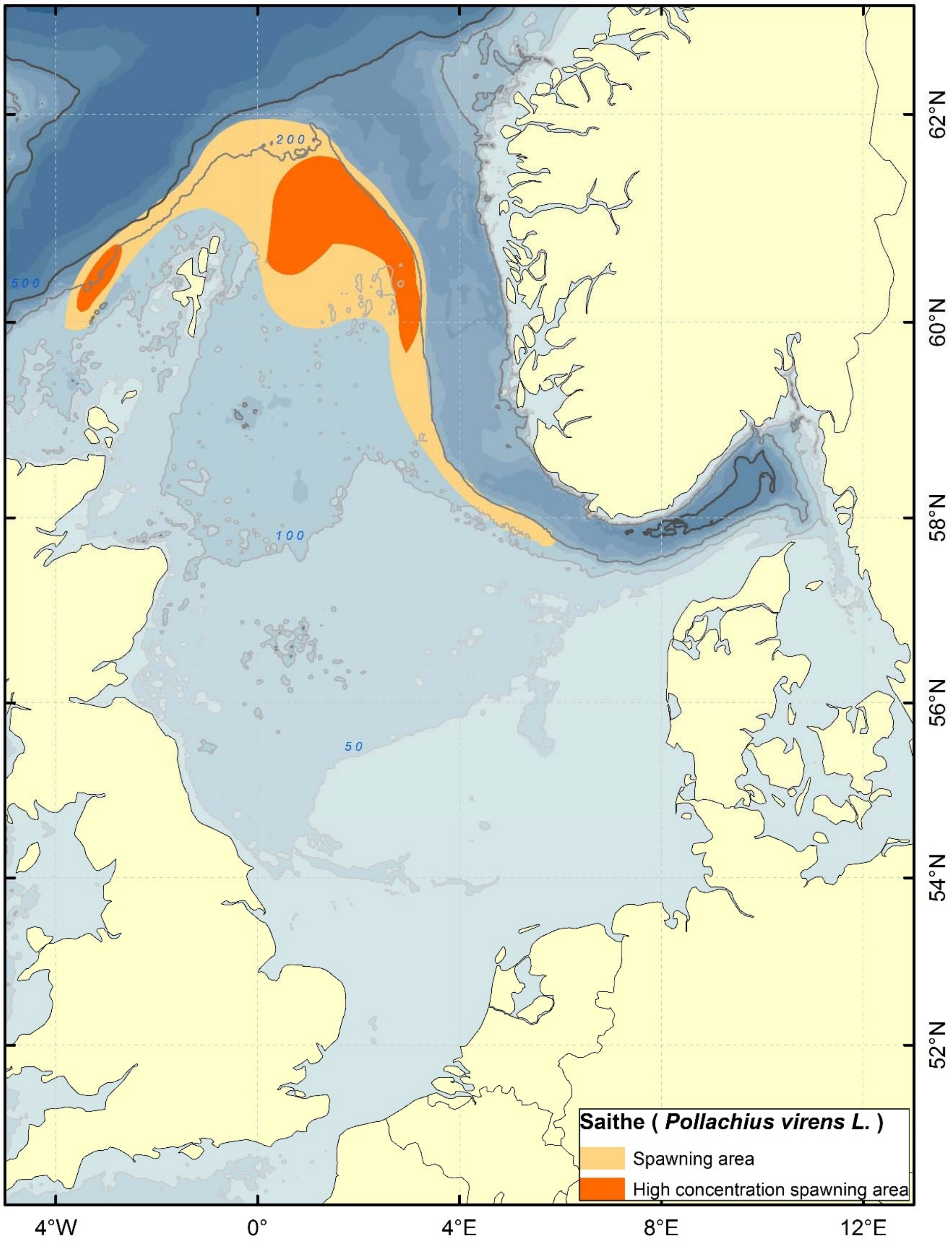

Figure 5.1.4-1. Saithe spawning areas in the North Sea.

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5.1.5 Norway pout – *Trisopterus esmarkii* N. - øyepål

General stock features

Norway pout constitutes a significant portion of the gadoid biomass in the North Sea. Spawning stock biomass since 1983 has ranged between 380 000 and 50 000 tonnes (ICES WGNSSK 2016) and is subject to an industrial fishery. The Norway pout stock has varied considerably in size over the recent 30-40 years due to a combination of variable recruitment and sustained fishing mortality through the industrial fishery. Landings after 1945 indicate that Norway pout also was influenced by the "gadoid outburst" (Cushing 1984) with increasing catches onto around 1975 and thereafter decreasing (Hislop 1996). Norway pout is distributed mainly in the Northern, Central, Norwegian Trench – Skagerrak, and the Kattegat sub regions. Abundance is low in the Southern and German Bight-Jutland sub regions (Hislop et al. 2015). The highest concentrations are found in the Northern sub region. In the past (Albert 1994), as now (Hislop et al. 2015), high concentrations were found along the western slope of the Norwegian Trench, and mainly above shallower depths than 200 m.

Spawning areas

The spawning areas of Norway pout are confined to the Northern and Central sub regions with the most intensive spawning in the Northern sub region (Rogers and Stocks 2001; Lambert et al. 2009). The relative comprehensive egg surveys (ICES 2010; Nash et al. 2012) confirmed the general patterns given by the studies utilizing the distributions of spawning fish. Spawning areas are shown in Figure 5.1.5-1.

Spawning period

Munk and Nielsen (2005) give the spawning period of Norway pout as January to April. This time period is consistent with the eggs and larvae found in the northern North Sea in 2009 and 2010 (Nash et al. 2012). Peak spawning time is not described.

Spawning Table Norway pout in the North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

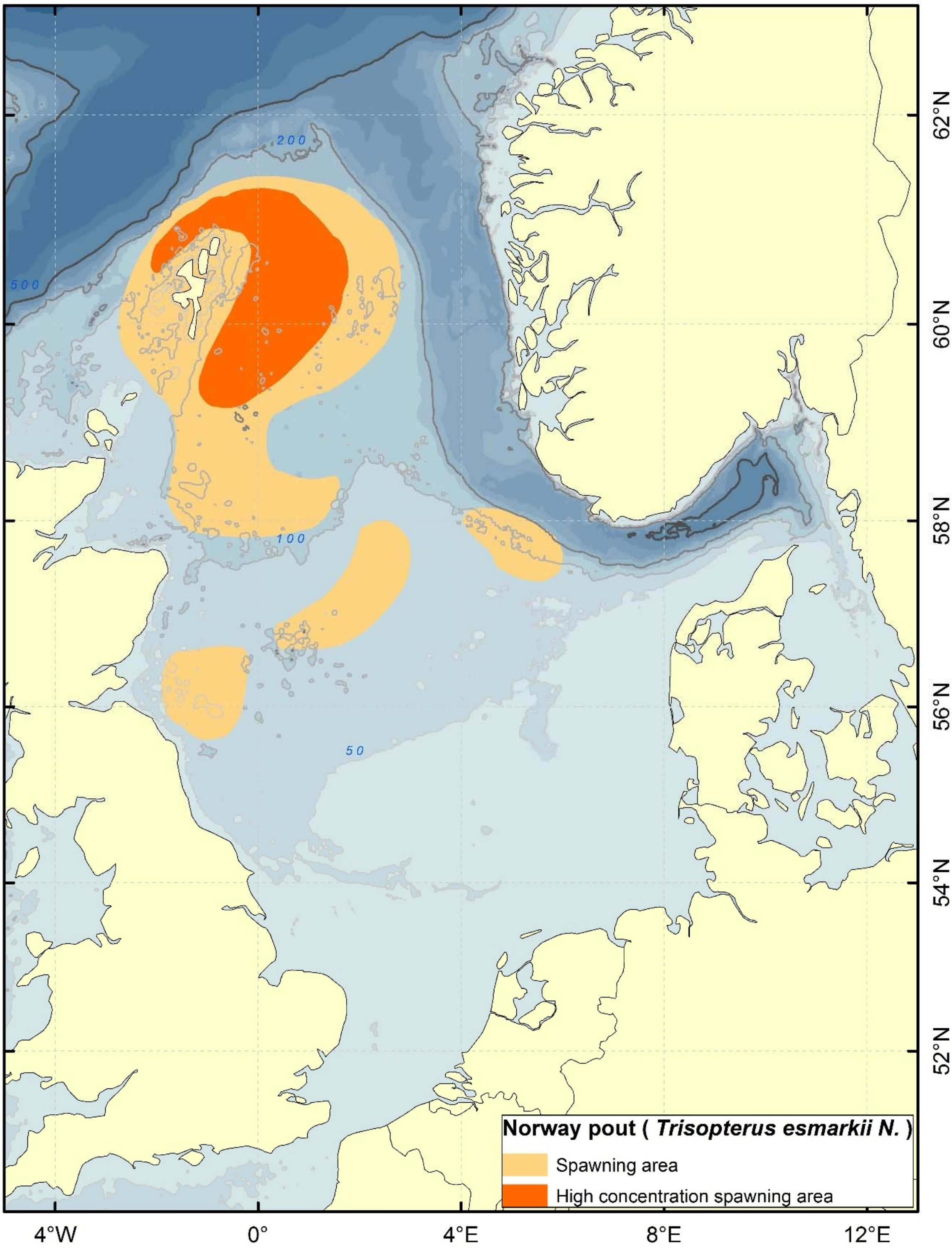

Figure 5.1.5-1. Norway pout spawning areas in the North Sea.

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5.1.6 Pollack – *Pollachius pollachius* L. - lyr

General stock features

Remarkably little is known about North Sea pollack, however, it is in low abundance compared to the other gadoids. As an indication of its relative scarcity, landings of pollack from the North Sea have ranged from 1 000 to 4 600 tonnes over the period 1977 to 2015 (ICES WGNSSK 2016). Pollack is benthopelagic, and generally occurs inshore over hard ground or in association with structures on the bottom (ICES WGNSSK 2016 stock annex). Adult pollack are mainly limited to the northern part of the North Sea with juveniles generally found inshore in coastal nursery areas. The major concentrations occurred in the Northern sub region and along the western and southern fringe of the Norwegian Trench and Skagerrak, generally at less than 200m (Bergstad 1991; Hislop et al. 2015; ICES WGNSSK 2016) (Figure 5.1.6-1).

Spawning areas

The only available information about pollack spawning areas is from the Institute of Marine Research Data Base on ripe and running fish. From these data minor spawning areas are found at two limited locations, one at Viking Bank and the other further south along the western slope of Norwegian Trench at Jærens Rev. The perception of spawning being limited to the eastern part of the northern North Sea may reflect the limitations of the spatial coverage of the available data i.e. concentrating on the Norwegian EEZ. However, the easterly distributed spawning areas is reflected in the general easterly distribution of the adult stock (Hislop et al. 2015). Figure 5.1.6-1 indicates the spawning areas.

Spawning period

According to Fishbase spawning takes place from January to May, depending on the area, and mostly at 100 m depth. Reinsch (1976) gives main spawning in March–April, taking place in the open waters of Skagerrak and the North Sea as well as in coastal waters.

Spawning Table North Sea Pollack

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

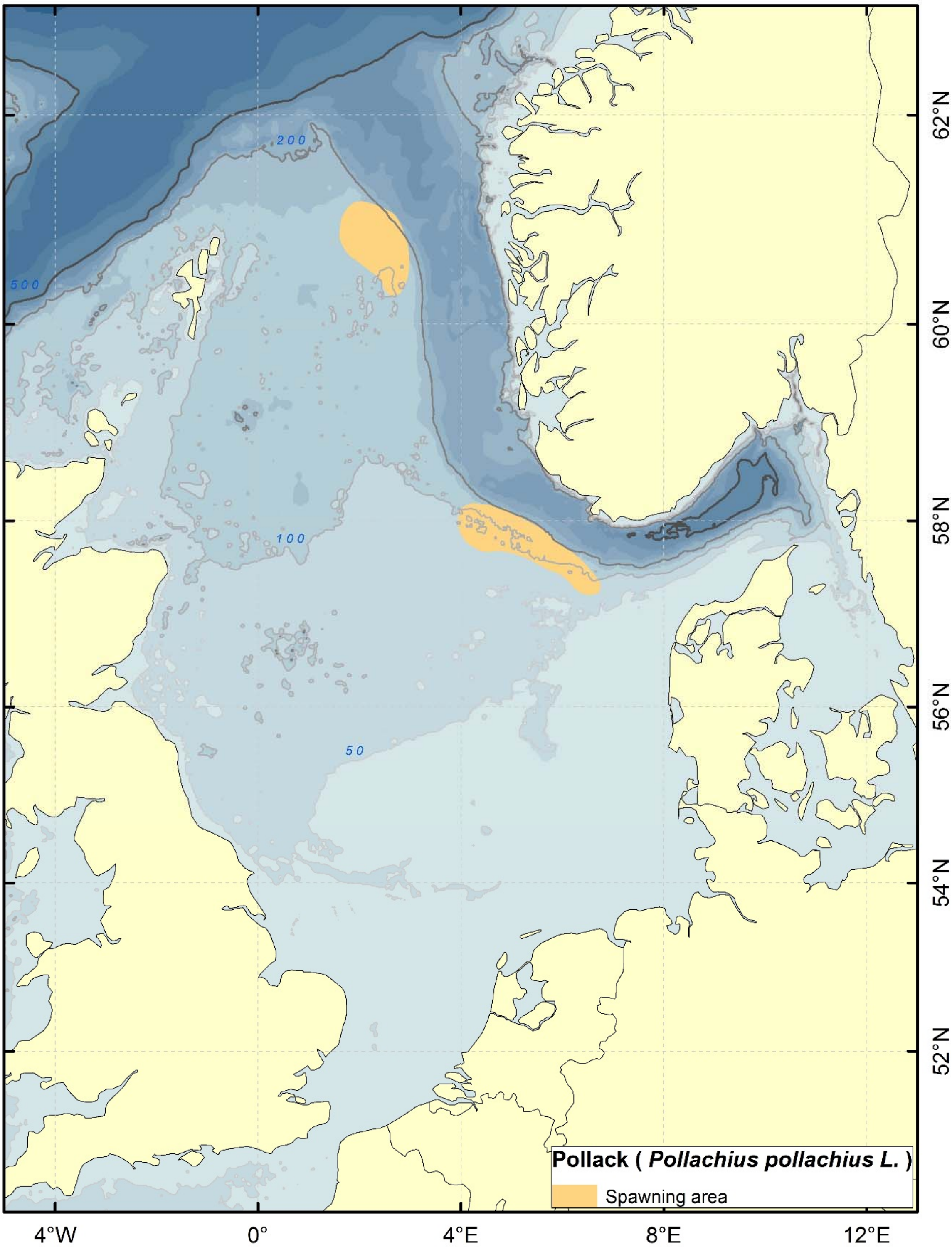

Figure 5.1.6-1. Pollack spawning areas in the North Sea.

References

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ICES WGNSSK 2016.

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5.1.7 Blue whiting – *Micromesistius poutassou* R. - kolmule

General stock features

Unlike the other gadoids considered here, blue whiting is not a shelf species but distributed over deep water west of the British Isles and into the Norwegian Trench (Hislop et al. 2015). During the summer feeding period it also migrates northwards into the Norwegian Sea (Huse et al. 2012). Due to the offshore habitat the environmental (rather than anthropomorphic of fishery) effects on the variability in stock abundance from the 1960s to the present was very different from that affecting gadoids in the North Sea proper, and as such was not influenced by the "gadoid outburst" (Cushing 1984). The principal blue whiting fisheries in the vicinity of the North Sea, prosecuted by Norwegian vessels, are in the Norwegian Deeps and the Tampen area to the east of 4ºW (ICES WGWIDE 2015). Whilst this constitutes a small part of the total catches from offshore areas it constitutes a substantial quantity of fish for the North Sea area and thus indicates a relatively large biomass of blue whiting in the area.

Spawning areas

As a result of its distribution over deep-water, spawning areas are generally located above deep water. Moreover, the spawning occurs at depths down to 500 m (Coombs et al. 1981) off the coast of Ireland. The larvae rise through the water column into the surface layers after the eggs have hatched (Ådlandsvik et al. 2001). The major spawning areas occur along the shelf break off the Irish coast (Ellis et al. 2012) and also to the north and south of this region (Pawson 1979). Spawning has not been observed into the Norwegian Trench, however, spawning does occur in shallower waters e.g. on the Møre shelf off mid Norway (Bjørke 1983). Figure 5.1.7.-1 show a synthesis of spawning area in the vicinity of the North Sea. In conclusion, spawning is only found near the northwestern fringe of the relevant area for this report.

Spawning period

In the entire area of distribution spawning starts in January in the southernmost distribution area in the Iberian waters and progresses northwards to the latitudes of the Faroes. March and April is the spawning season in the regions adjacent to the North Sea (Hislop et al. 2015).

Spawning Table Blue whiting adjacent to the North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

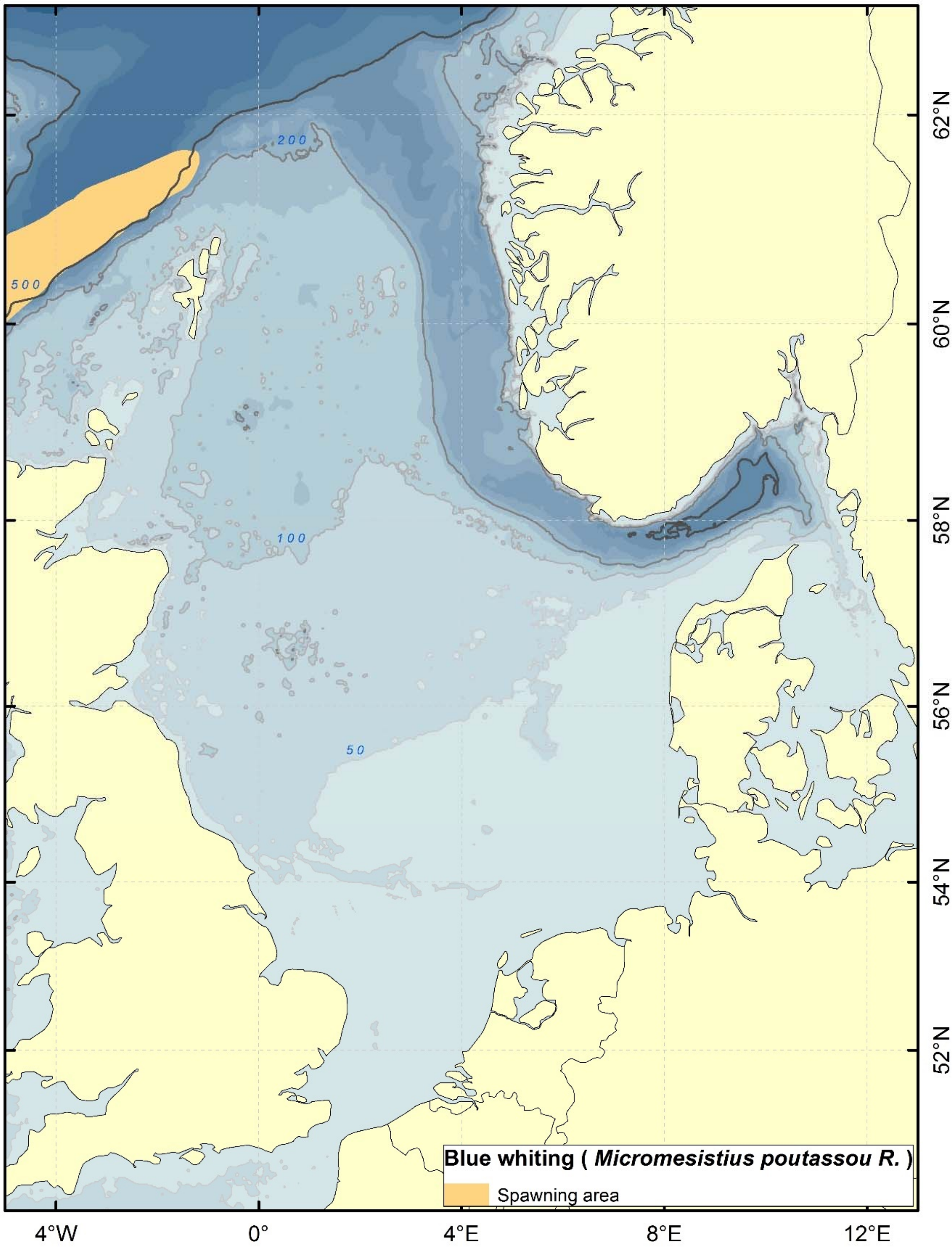

Figure 5.1.7-1. Fraction of the blue whiting spawning in the North Sea area.

References

Bjørke, H. 1983. Spawning of blue whiting (*Micromesistius poutassou*) in Norwegian waters. ICES CM 1983/H:35, 8p.

Coombs, S.H., Pipe, R.K., Mitchell, C.E. 1981. The vertical distribution of eggs and larvae of Blue whiting (*Micromesistius poutassou*) and Mackerel (*Scomber scombrus* in the eastern North Atlantic and North Sea. *Rapp. et Proc.-Verb. Cons. Int. Explor. Mer 178*: 188-195

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Pawson, M.G. 1979. Blue whiting. Laboratory Leaflet No. 45. Ministry of Agriculture Fisheries and Food. Directorate of Fisheries Research, Lowestoft. 18 p. ISSN 0072-6699.

Pointin, F., and Payne, M.R. 2014. A Resolution to the Blue Whiting (*Micromesistius poutassou*) Population Paradox? PLoS ONE 9(9): e106237. doi:10.1371/ journal.pone.0106237.

Ådlandsvik, B, Coombs, S, Sundby, S, and Temple, G. 2001. Buoyancy and vertical distribution of eggs and larvae of blue whiting (*Micromesistius poutassou*): observations and modeling. Fisheries Research 50: 59-72.

5.1.8 Bib – *Trisopterus luscus* L. - skjeggtorsk

General stock features

Bib is a small gadoid with a southerly distribution. It is mainly confined to the Southern sub regions and the German Bight. This species has a varied habitat with smaller individuals occurring inshore over sandy areas and larger individual s further offshore associated with bottom features such as wrecks etc (Hislop et al. 2015; Munk and Nielsen 2005). Some of the larger specimens (> 16 cm) extend their distribution northwards close to the English and Scottish coast (Hislop et al. 2015) The highest abundances are generally to the south of the North Sea, however, within the area considered here they are predominantly found in the English Channel and close to the English, Belgian, and Netherlands coasts.

Spawning areas

Information about spawning areas are very limited. However, spawning areas have been indicated to co-occurs with the regions of highest abundances (Hamerlynck and Hostens 1993). Figure 5.1.8-1 indicates approximate spawning areas of bib. At present it is unlikely that there are any significant spawning areas in the northern North Sea.

Spawning period

Munk and Nielsen (2005) suggest that spawning differs between the western and eastern southern North Sea, January to April in the SW and June to August in the southeast. Peak spawning varies with latitude. The spawning period in the southern North Sea is quite protracted (February-August) (Korf 1971).

Spawning Table North Sea Bib

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

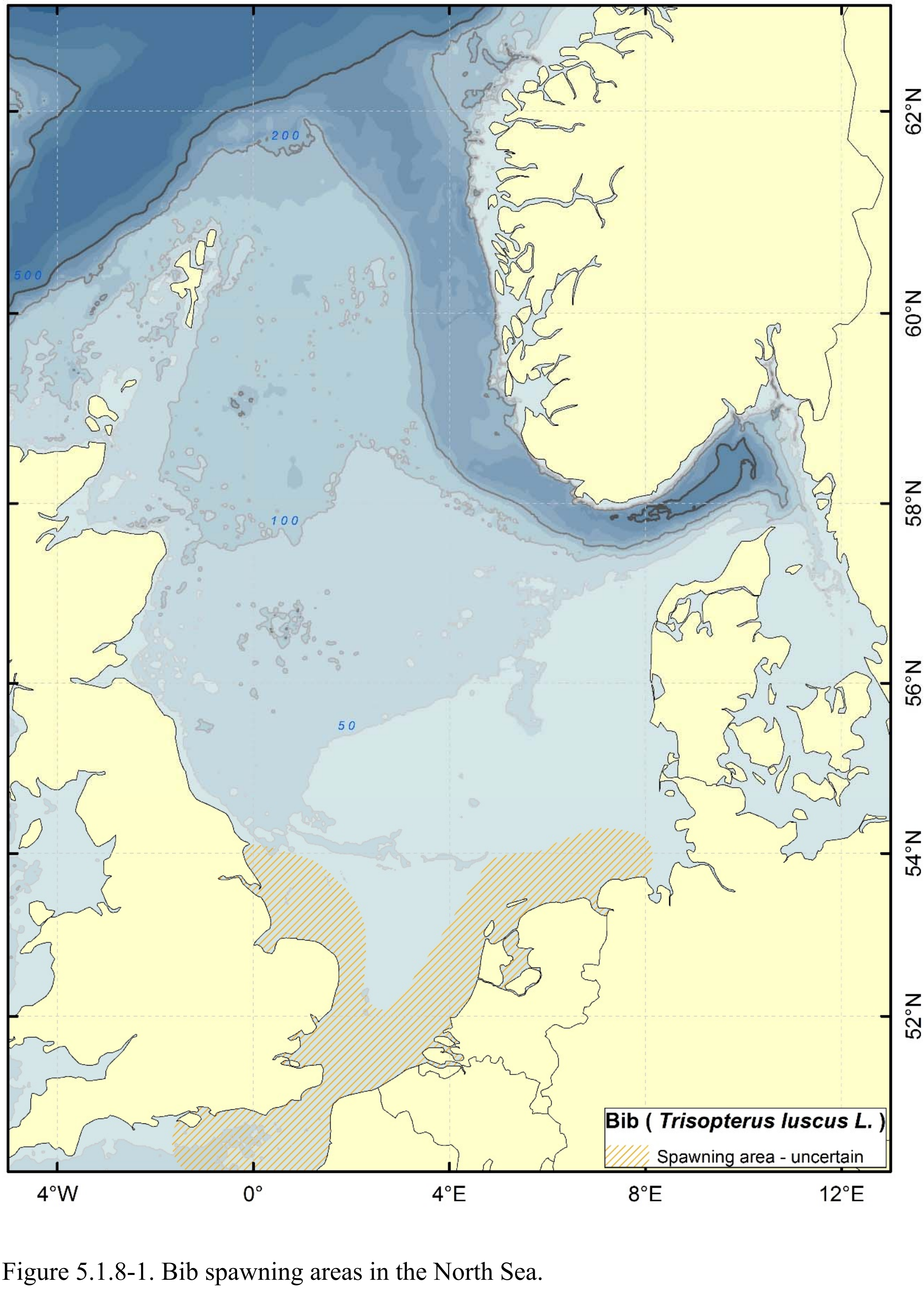

Figure 5.1.8-1. Bib spawning areas in the North Sea.

References

Hamerlynck, O., and Hostens, K. 1993. Growth, feeding, production, and consumption in 0-group bib (*Trisopterus luscus* L.) and whiting (*Merlangius merlangus* L.) in a shallow water coastal area of the south-west Netherlands. ICES Journal of Marine Science, 50: 81-91.

Hislop, J. Bergstad, O.A., Jakobsen, T., Sparholt, H., Blasdale, Wright, P., Kloppmann, M., Hillgruber, N., and Heessen, H. 2015. Bib – *Trisopterus luscus* Linnaeus, 1758. *In*: H.J.L. Heessen, N. Daan, and J.R. Ellis, editors. Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea. Pp. 213-215. Wageningen Academic Publishers and KNNV Publishing, Wageningen, Netherlands (572 pp). ISBN: 978-90-8686-266-5.

Korf, B. 1971. Steenbolk en dwergbolk, een oriënterend onderzoek naar twee mogeelijke voedselconcurrenten van de kabeljauw. RIVO Ijmuiden de Nederlands. Internal report. 56 pages.

Munk P., and Nielsen J.G. 2005. Eggs and larvae of North Sea fishes. Biofolia, Frederiksberg, Denmark. 215pp.

5.1.9 Silvery pout – *Gadiculus argenteus* G. - sølvtorsk

The silvery pout generally found off or along the edge of the continental shelf and of interest here, does occur along the northern margins of the North Sea and in to the Skagerrak (Cohen et al. 1990; Hislop et al. 2015). This species is not subject to a targeted commercially fishery but when in very dense aggregations will occur in the Norway pout and blue whiting industrial fisheries as a bycatch as well as in the northern shrimp fisheries in the North Sea and Skagerrak (Hislop et al. 2015). There is relatively little information on this species.

Spawning areas

This species is thought to spawn over much of its distribution range (Hislop et al. 2015). Given that the majority of the population is off the continental shelf and outside the North Sea (see Cohen et al. 1990; Hislop et al. 2015), any spawning within the confines of the North Sea will only be a minor portion of the reproductive effort of this species. The inclusion of larvae in Munk and Nielsen (2005) suggests that larvae at least occur in the North Sea, however, these may simply be advected in to the area from off shelf spawning grounds. There is not enough information to picture a spawning map for silvery pout.

Spawning period

According to Cohen et al. (1990) occurs in mid winter and spring. However, the early spawning is probably confined to southwestern distribution area, i.e. west and south of Ireland. In the North Sea spawning is thought to occur between March and May (Munk and Nielsen 2005). Information about peak spawning time is not available.

Spawning Table North Sea Silvery pout

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

References

Cohen, D.M., T. Inada, T. Iwamoto and N. Scialabba, 1990. FAO species catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Fish. Synop. 125(10). Rome: FAO. 442 p.

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Baltic Sea. Pp. 187-188. Wageningen Academic Publishers and KNNV Publishing, Wageningen, Netherlands (572 pp). ISBN: 978-90-8686-266-5.

Munk P., and Nielsen J.G. 2005. Eggs and larvae of North Sea fishes. Biofolia, Frederiksberg, Denmark. 215pp.

5.1.10 Poor cod – *Trisopterus minutus* L. - sypike

Poor cod is a widely distributed species ranging from the Mediterranean in the south to mid Norway in the north (Hislop et al. 2015). In general, the distribution tends to be around the margins of the North Sea with a low abundance in the central North Sea. This species is not targeted in a fishery but does appear as bycatch in the industrial fisheries.

Spawning areas

There is no detailed information on the spawning locations of this species, however, since there is no evidence of substantial annual migrations it is suspected that this species spawns over much of the deeper area that it occurs.

Spawning period

Munk and Nielsen (2005) suggest the spawning period in the North Sea is between March and June. In the English Channel and the west coast of Scotland although spawning is protracted the principal period off Scotland appears to be April and to the north (Faroese) spawning occurs toward the end of April (Magnussen and Magnussen 2009). Therefore, the most likely peak spawning time in the North Sea is most probably also in April. In the more southern area peak spawning occurs in March-April (Korf 1971).

Spawning Table North Sea Poor cod

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

References

Hislop, J. Bergstad, O.A., Jakobsen, T., Sparholt, H., Blasdale, Wright, P., Kloppmann, M., Hillgruber, N., and Heessen, H. 2015. Poor cod – *Trisopterus minutus* Linnaeus, 1758. *In*: H.J.L. Heessen, N. Daan, and J.R. Ellis, editors. Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea. Pp. 216-218. Wageningen Academic Publishers and KNNV Publishing, Wageningen, Netherlands (572 pp). ISBN: 978-90-8686-266-5.

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Magnussen, E. and Magnussen, M.D. 2009. Ecology of poor-cod (*Trisopterus minutus*) on the Faroe Bank. Marine Biology Research 5: 133-142.

Munk P., and Nielsen J.G. 2005. Eggs and larvae of North Sea fishes. Biofolia, Frederiksberg, Denmark. 215pp

5.1.11 Fourbeared rockling – *Enchelyopus cimbrius* L. – firetrådet tangbrosme

Four-bearded rockling are patchily distributed, mainly associated with soft sediments (Hislop et al. 2015). This species is known to burrow in shallow water in the western Atlantic (Keats and Steele 1990) which could explain the association with soft sediments. The adults are described as being 'sedentary bottom dwellers' (Cohen and Russo 1979). However, there is the suggestion in the western Atlantic at least, of a seasonal offshore onshore movement probably related to spawning (Bigelow and Schroeder 1953; Tyler 1971).

Spawning areas

The location of the spawning areas is unclear since there is a possibility this species may undertake spawning 'migrations'. The movements are likely to be somewhat limited since this species does have a fossorial mode of life.

Spawning period

Munk and Nielsen (2005) give the spawning period as February to August with Hislop et al. (2015) suggesting spawning is in late spring and later (summer) in deeper water. A study in the Oslofjord indicated a high Gonadosomatic Index (GSI) in August which suggests spawning occurring around that time but definitely completed by November (Nash and Geffen (*unpublished manuscript*).

Spawning Table North Sea Four-bearded rockling

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

References

Bigelow HB, Schroeder WC. 1953. Fishes of the Gulf of Maine. Fishery Bulletin, Fish and Wildlife Service 53, 1 577.

Cohen DM, and Russo JL. 1978. Variation in the fourbearded rockling, *Enchelyopus cimbrius*, a north Atlantic gadiid fish, with comments on the genera of rocklings. Fishery Bulletin 77, 91-104.

Hislop, J. Bergstad, O.A., Jakobsen, T., Sparholt, H., Blasdale, Wright, P., Kloppmann, M., Hillgruber, N., and Heessen, H. 2015. Fourbearded rocking – *Enchelyopus cimbrius* Linnaeus, 1766. In: H.J.L. Heessen, N. Daan, and J.R. Ellis, editors. Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea. Pp. 226-228. Wageningen Academic Publishers and KNNV Publishing, Wageningen, Netherlands (572 pp). ISBN: 978-90-8686-266-5.

Munk P., and Nielsen J.G. 2005. Eggs and larvae of North Sea fishes. Biofolia, Frederiksberg, Denmark. 215pp

Nash, R.D.M. and Geffen, A.J. Unpublished manuscript. The growth and reproduction of the four bearded rockling (*Enchelyopus cimbrius* (L.)) in the Oslofjord, Norway.

Tyler AV. 1971. Periodic and resident components in communities of Atlantic fishes. Journal of the Fisheries Research Board of Canada 28, 935 946.

5.1.12 Tusk – *Brosme brosme* A. - brosme

General stock features

Tusk is one of the deep-water gadoids with distribution in the Norwegian Trench and Skagerrak in addition to the northernmost and deepest part the Northern sub region (Bergstad 1991; Hislop et al. 2015). In the Northeast Atlantic, tusk has a more northerly distribution than the two other deep-water gadoids, ling and blue ling (Bergstad and Hareide 1996). This is also reflected in the North Sea region.

Spawning areas

Spawning of tusk appears to occur over most of it geographical range, mainly from the shelf edge down to around 400m depth (Hislop et al. 2015). Evidence for spawning in the North Sea region is sparse, however, Bergstad (1991) reports female tusk in an advanced stage of maturing and ripening in the Norwegian Trench and Skagerrak, leading to the conclusion that they spawn in this area. Early plankton observations reported tusk eggs in Skagerrak also on the shelf as far south as the Greater Fisher Bank (Ehrenbaum 1909). This southerly observation does not appear in the modern literature. This may be because the beginning of the 20th century was a very cool period, and the southerly spawning at the Great Fisher Bank may have been due to the cool climate at that time. Other plankton observations observed tusk eggs in Skagerrak (Dannevig 1940) and in the northern part of the Norwegian Trench (Bjørke 1981). Two early stage larvae were found in the 2013 ichthyoplankton samples, one at 60 ^{o}N close to the deep water to the north and the other in the Skagerrak, again close to the deep water. Both are consistent with the perceived spawning locations for this species. Figure 5.1.12-1 indicate the tusk spawning areas based on the above cited literature.

Spawning period

Munk & Nielsen (1995) give March to May, Hislop et al. (2015) give April to July (these are the dates given in Russell (1976) based on the Schmidt (1909) publication. Time of peak spawning is not given.

Spawning Table Tusk in the North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period Green: Peak spawning

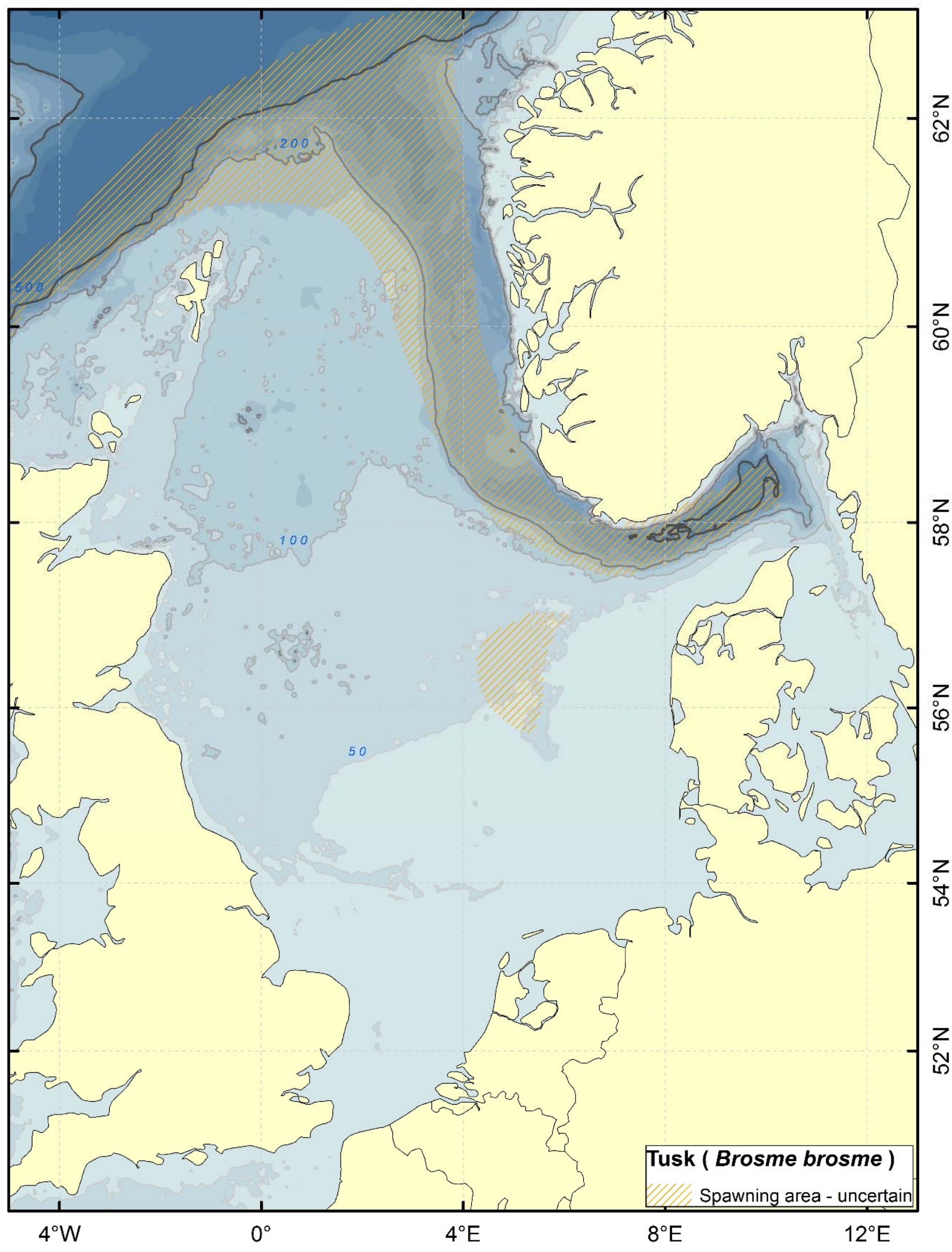

Figure 5.1.12-1. Tusk spawning areas in the North Sea.

References

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Hislop, J., Bergstad, O.A., Jakobsen, T., Sparholt, H., Blasdale, Wright, P., Kloppmann, M., Hillgruber, N., and Heessen, H. 2015. Tusk – *Bromse brosme* Ascanius, 1772. *In*: H.J.L. Heessen, N. Daan, and J.R. Ellis, editors. Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea. Pp. 220-222. Wageningen Academic Publishers and KNNV Publishing, Wageningen, Netherlands (572 pp). ISBN: 978-90-8686-266-5.

Munk P., and Nielsen J.G. 2005. Eggs and larvae of North Sea fishes. Biofolia, Frederiksberg, Denmark. 215pp.

5.1.13 Ling – *Molva molva* L. - lange

General stock features

Ling is more widespread within the North Sea compared to the two other deep-water gadoids, tusk and blue ling (Hislop et al. 2015). The ling is generally distributed over the Northern sub region and in the Norwegian Trench and Skagerrak.

Spawning areas

The information on spawning areas for ling in the North Sea region is sparse and what is present is to a certain extent contradictory. During the cool period at the beginning of the 20th century ling eggs occurred as far south as Greater Fisher Bank and toward the German Bight (Bergstad and Hareide 1996). As for the similar observation of tusk eggs in this region (Ehrenbaum 1909) one may question whether this far southerly spawning may be linked to the particular cool climate at that time resulting in southerly displacement of boreal fish stock. During the warm period of the 1940s, ling eggs were observed in the Oslo Fjord (Dannevig 1945). Ling larvae have been observed in various locations in Skagerrak and in the Norwegian Trench (Myrberget 1965; Lindquist 1968; Bergstad and Gordon 1994), indicating that spawning might also take place in these deep regions. A small number of relatively small ling larvae occurred in the May 2012 survey to the west of Shetland and north of 60ºN and around 58ºN close to the Norwegian Trench. Munk and Nielsen (2005) indicate that the eggs are spawned close to the bottom. Figure 5.1.13-1 represents an indication of possible ling spawning areas based on the sparse number of records in the available literature.

Spawning period

Munk and Nielsen (2005) suggest March to July, however, this spans the full latitudinal range of this species. The same information is given in Russell (1976) with the caveat that the main spawning is April to June.

Spawning Table Ling in the North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

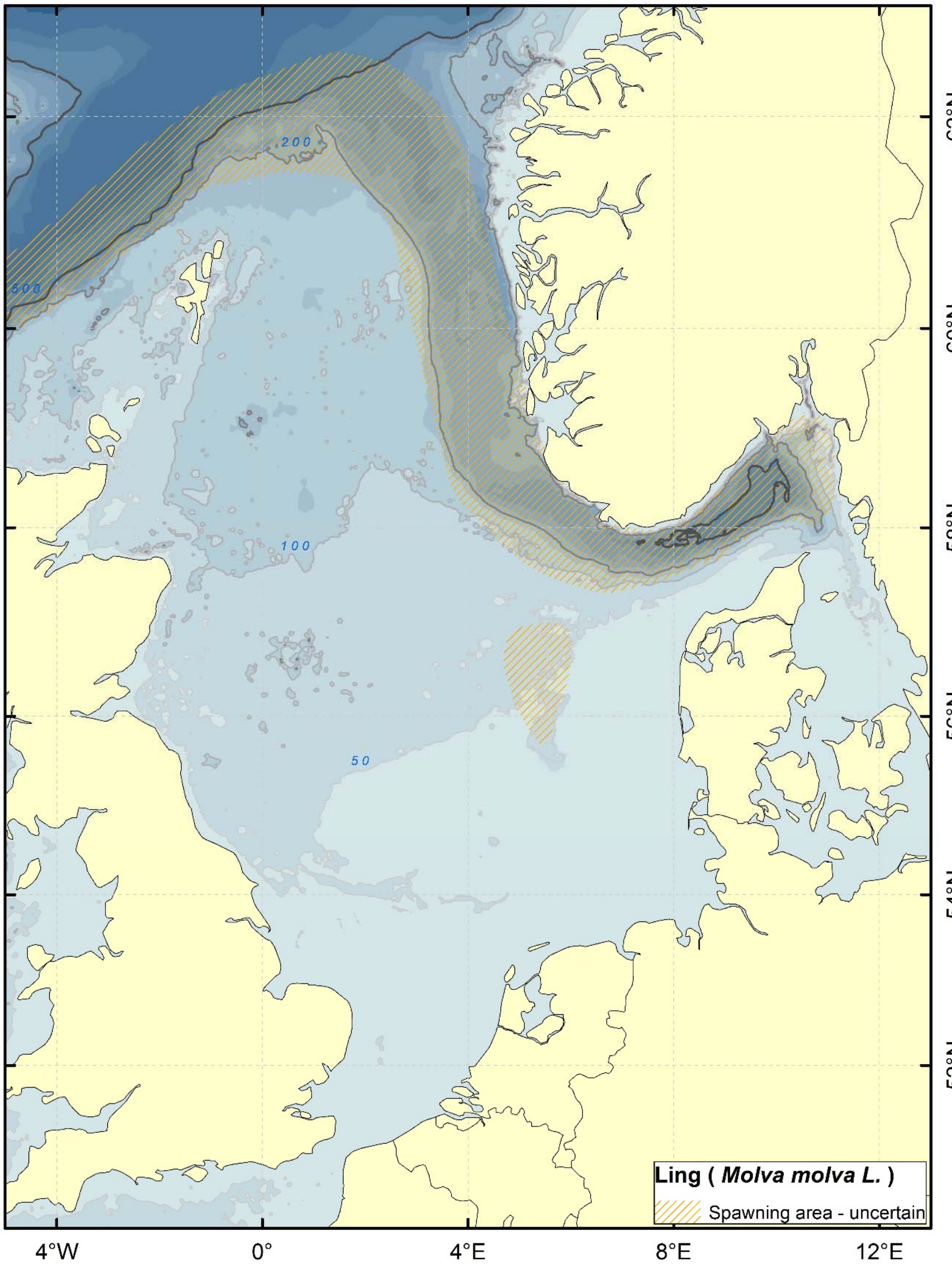

Figure 5.1.13-1. Ling spawning areas in the North Sea.

References

Bergstad, O.A., and Hareide, N.R. (eds.) 1996. Ling, blue ling and tusk of the Northeast Atlantic. Fisken og Havet Nr. 15-1996. 126pp.

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Dannevig, A. 1945. Undersøkelser i Oslofjorden 1936-1 940. *Fiskeridirektoratets Skrifter Serie Havundersøkelser, VIII(4):* 1-9 1.

Hislop, J., Bergstad, O.A., Jakobsen, T., Sparholt, H., Blasdale, Wright, P., Kloppmann, M., Hillgruber, N., and Heessen, H. 2015. Ling – *Molva molva* Linnaeus, 1758. *In*: H.J.L. Heessen, N. Daan, and J.R.Ellis, editors. Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea. Pp. 232-234. Wageningen Academic Publishers and KNNV Publishing, Wageningen, Netherlands (572 pp). ISBN: 978-90-8686-266-5.

Lindquist, A. 1968. Ichthyoplankton of the Skagerrak: maps and tables concerning May and June. Meddelande Havsfiskelaboratoriet, Lysekil, 42: 13 p. 180 maps.

Munk P., and Nielsen J.G. 2005. Eggs and larvae of North Sea fishes. Biofolia, Frederiksberg, Denmark. 215pp.

Myrberget, S. 1965. Distributions of mackerel eggs and larvae in the Skagerrak, 1957-1959. Fauna, *18:* 120-13 1.

5.1.14 Blue ling – *Molva dypterygia* s.l. - blålange

General stock features

Blue ling in the North Sea is mainly limited to the Skagerrak and the southern part of the Norwegian Trench (Hislop et al. 2015). The distribution maps in Hislop et al. (2015) indicate that the distribution is not continuous distribution toward the shelf break west of the British Isles, however, this is based on survey data in the northern North Sea which is shallower than 200m depth. Other publications e.g. Wheeler (1978) indicate that the distribution is continuous, however, at depths greater than 200m which is contiguous with the occurrences primarily in the Norwegian Trench where the surveys do occur at depths >200m. The western components of the blue ling are found along the entire European shelf edge from the northern Bay of Biscay to north of Scotland, around the Rockall Channel and around the Faroe Islands (Large et al. 2010). For the component in the Norwegian Trench and Skagerrak catch depths ranges from 200 to more than 600 m depth, generally deeper in winter than summer and autumn (Bergstad 1991).

Spawning areas

The western component of blue ling spawn along the shelf break off the Hebrides and in addition some separates spawning sites around several banks further west and southwest of the Faroe Islands (Large et al. 2010). Based on the distribution of maturing fish, Bergstad (1991) concluded that blue ling also uses the Norwegian Trench "to some extent" as spawning area. In contrast to the widely distributed tusk eggs along the European shelf break, blue ling eggs are much more sporadically distributed (Bergstad and Hareide 1996). Whether this is a consequence of insufficient sampling is unknown. However, small juvenile blue ling have been sampled in demersal trawl along the western slope of the Norwegian Trench and into Skagerrak in 2015 and in 2016 (Kristin Helle, personal comm). This is consistent with transport by the inflowing Atlantic Current from spawning areas at the entrance of the Norwegian Trench in the Norwegian Sea. Hislop et al. (2015) report that blue ling migrate toward spawning grounds (650-1100m depth), starting in January, and congregate in large schools. Figure 5.1.14-1 indicates the assumed regions of spawning blue ling.

Spawning period

Munk and Nielsen (2005) give April to May for the distributional area (Iceland to Scotland).

Spawning Table North Sea Blue ling

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

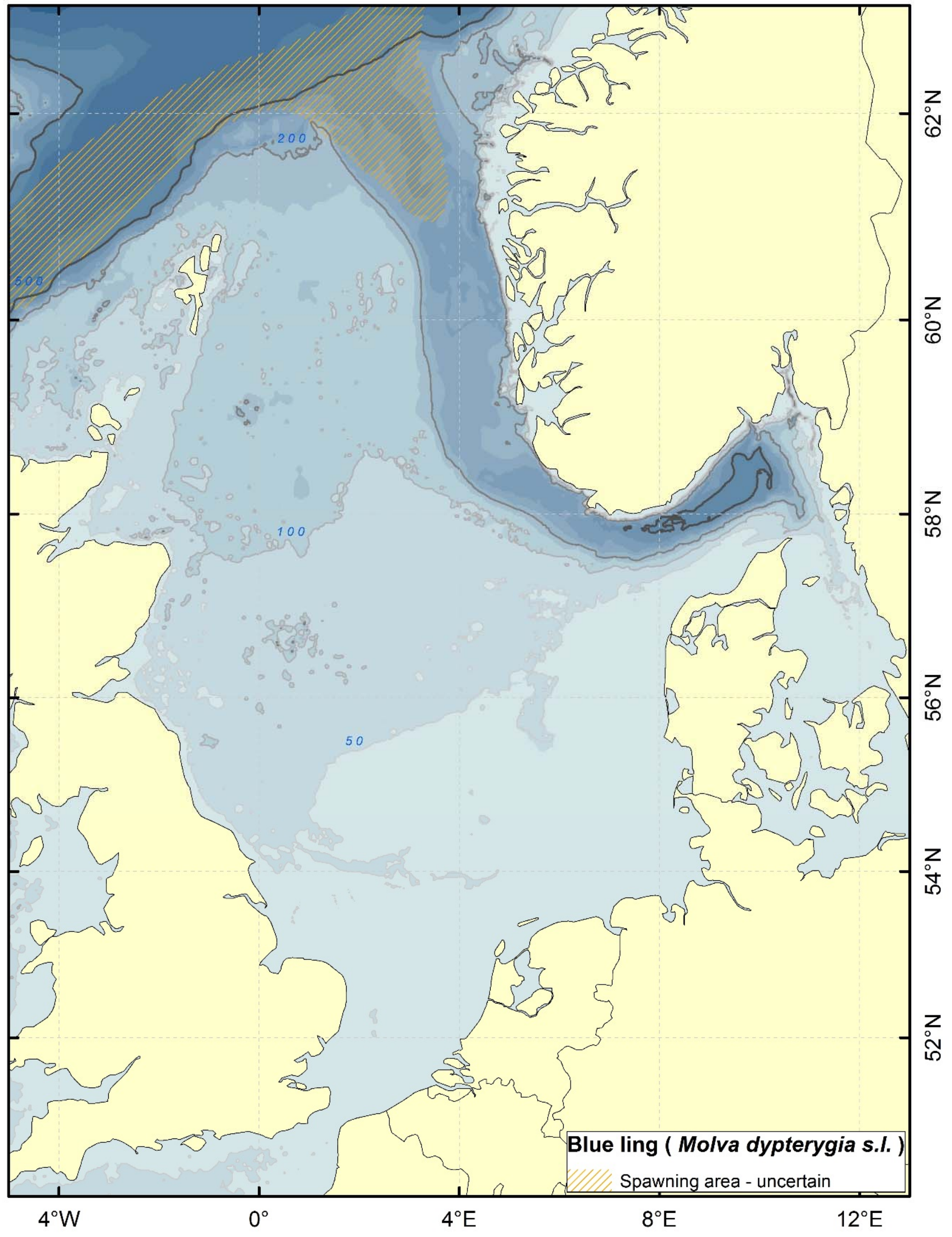

Figure 5.1.14-1. Blue ling spawning areas in the North Sea.

References

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Large, P. A., Diez, G., Drewery, J., Laurans, M., Pilling, G. M., Reid, D. G., Reinert, J., South, A. B., and Vinnichenko, V. I. 2010. Spatial and temporal distribution of spawning aggregations of blue ling (Molva dypterygia) west and northwest of the British Isles. ICES Journal of Marine Science, 67: 494–501.

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Wheeler, A. 1978. Key to the fishes of northern Europe. Warne, London. 380pp.

5.2.1 Hake – *Merluccius merluccius* - lysing

General stock features

The European hake is widely distributed from the Mediterranean, along the Iberian and French coast, west of the British Isles and Irish Sea to the North Sea and further northwards to the Norwegian Møre coast. It is uncertain how the European hake is divided in sub/metapopulations. However, from ICES it is managed as one southern and one northern stock unit, divided at the Cap Breton canyon in the Bay of Biscay (ICES 2012). The major catches of the northern stock have been west of Ireland and Scotland (Baudron and Fernandes 2014; Heessen and Murua 2015). In the North Sea the catches have undergone multidecadal variations from the beginning of the 20th century (Baudron and Fernandes 2014). There were low catches at the beginning of the 20th century which increased from the 1920s to reach a peak around 1950 (with exception of the 2nd World War when catches were understandably low). Post 1950, catches declined dramatically. From the 1980s when spawning stock biomass (SSB) estimates became available, SSB remained very low until the beginning of 2000s, most probably due to over exploitation. Thereafter, SSB has increased and around 2010 North Sea catches reached the same level as during the record-high period in the 1950s. The multidecadal pattern in catches of the North Sea hake seems to be inverse of the boreal (cold-temperate) gadoids (cod, haddock, whiting, Norway pout and saithe) which is generally referred to as the "gadoid outburst" (Cushing 1984). From figures of Heessen and Murua (2015) showing catch rates by periods it is apparent that during the recent years of increasing stock the centre of gravity for the northern component of hake has been displaced towards northeast and subsequently from the northern entrance of the North Sea and southwards with the Atlantic inflowing water masses. Hence, there are indications that the Atlantic Multidecadal Oscillation (AMO) resulting in a multidecadal temperature pattern of the North Atlantic (Sutton and Hodson 2005) might be an explanatory forcing of the displacement of the northern component and of the increase of the component in the North Sea.

Spawning areas

Historically, there are limited data and information concerning hake spawning with the North Sea. This is because hake has been found at very low concentrations until the very recent years. The centre of spawning activity for the northern stock unit has been near the shelf edge south of Ireland and west of Cornwall, England (Coombs and Mitchell 1982; Alvarez et al 2004). With the northeastwards displacement of the stock unit over the recent years, as described by Baudron and Fernandes (2014) it is reason to believe that also spawning areas have also been displaced northeastwards. Ellis et al. (2012) reported spawning areas all along the shelf break to the west of the British Isles as far north as 60 ºN, i.e. to the north of Scotland. However, the extent of hake spawning at these latitudes is unclear (Ellis et al. 2012). Eggs and newly hatched larvae have been observed north of 58 ºN (Howell 1921). Bergstad (1991) found that hake was abundant in the Norwegian Trench both as feeding adults and as 0-group fish. However, at that time there was no documentation of spawning in these areas. Werner et al. (2016) suggest that hake are abundant in the Norwegian Trench during winter and spring and migrate westward onto the shelf to spawn in summer and autumn. Samples from IMR's fish data base show ripe and running hake occurring on the North Sea shelf west and south of the Norwegian Trenchin limited amounts. However, more recent data from the International Bottom Trawl Surveys (IBTS) for the years 2011-2015 studied by Werner et al. (2016) show substantial larger amounts of mature fish over larger parts of the shelf west of the Norwegian Trench. This clearly shows a dramatic increase in abundance of hake in the eastern part of the Northern Sub Region and in the northern part of the Central Sub Region of the North Sea, apparently in response to the recent large-scale warming of the Northeast Atlantic. Spawning appear to occur over rough ground and often associated with canyons subsea cliffs (Heessen and Murua 2015). Figure 5.2.1-1 shows our current understanding of hake spawning grounds based on Ellis et al. (2012), and IMR's Fish Data Base and the recent data from IBTS (Werner et al. 2016).

Spawning period

According the Heessen and Murua (2015) hake spawn large parts of the year with main season between December and July with later spawning in the northern parts. Munk and Nielsen (2015) give June to August for the North Sea, Russell (1976) reports July and August based on Ehrenbaum's (1905-09) works. Werner et al. (2016) who compiled spawning data and literature thoughout the European shelf show large diversity in spawning periods. However, for the recent years Werner et al. (2016) suggest the peak spawning in the central and northern North Sea occurs in July and August, with lower levels of spawning in June and September, and some spawning in January and February.

Spawning Table Hake

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

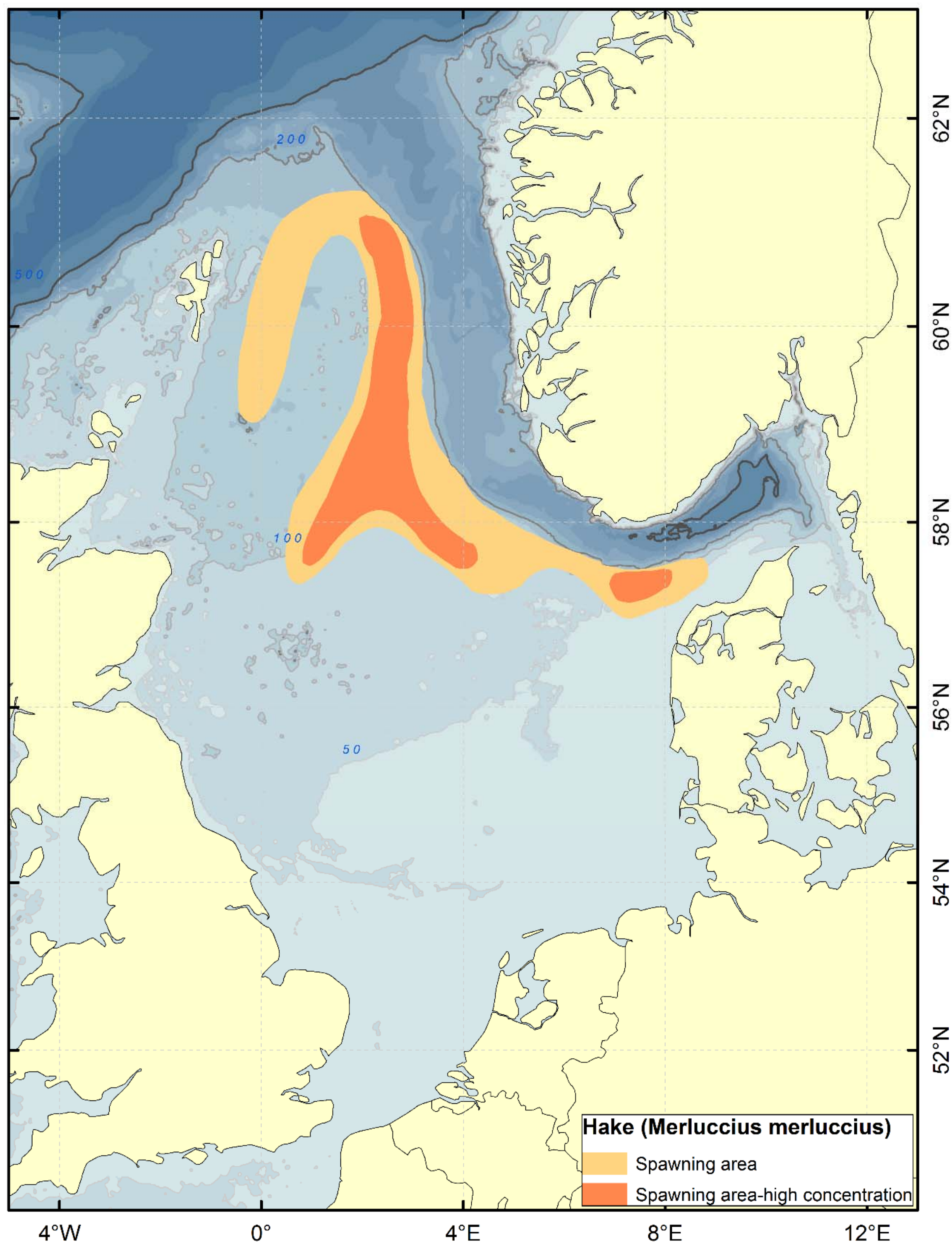

Figure 5.2.1-1. Hake spawning areas in the North Sea.

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5.3.1 Sandeels – *Ammodytidae* - tobis

There are five species of sandeel in the North Sea (Wheeler 1969), lesser sandeel (*Ammodytes marinus*), small sandeel (*Ammodytes tobianus*), two species of greater sandeel (*Hyperoplus lanceolatus* and *Hyperoplus immaculatus*), and smooth sandeel (*Gymnammodytes semisquamatus*). However, only the two *Ammodytes* species are abundant. The small sandeel is found mainly in shallow waters along the shore (Reay 1970). In offshore waters where the main commercial sandeel fishery takes place, lesser sandeel dominate. In Norwegian landings, greater sandeel (*H. lanceolatus*) and the small sandeel occur in very low numbers (IMR unpublished date), and there has been only one observation of *H. immaculatus* (http://www.imr.no/nyhetsarkiv/2011/mai/blant_uflekket_storsil_og_andre_tobis/nb-no). As there is very limited knowledge about the smooth sandeel and the two greater sandeel species, and this report deals with spawning areas in offshore waters, only lesser sandeel is described here. In addition, a more detailed description of lesser sandeel in the Norwegian sector of the North Sea is given in the above chapter (Chapter 4).

General stock features

Lesser sandeel (hereafter referred to as sandeel) is a small, highly abundant fish in the North Sea. Sandeel feed on plankton and thus form an important mid-trophic link between plankton production and a variety of top predators such as larger fish, sea mammals and sea birds (Harwood and Croxall 1988; Greenstreet *et al.*; Wanless *et al.* 2005). Sandeel burry most of the time in the seabed in sandy areas where the proportion of fine silt and clay particles is low (Macer 1966; Wright *et al.* 2000). Due to the dependency on suitable habitat, sandeel fishing grounds appear as a patchwork in the North Sea (Wright 1996; Jensen *et al.* 2011; Johannessen and Johnsen submitted). During winter, sandeel hibernate in the sand. In spring sandeel, which are then very lean, commence feeding again. They emerge from the seabed at dawn in dense pelagic schools to feed on zooplankton. The schools are targeted by predators and trawlers. At dusk, sandeel return to their sandy habitat where they are protected from both predation and trawling. Around mid-summer ≥1-year old sandeel has normally built up sufficient energy reserves to hibernate again (Winslade 1974). Hence, the main fishing season is from April – June/July (ICES 2009a). Larvae are pelagic until around June (Lynam et al. 2013). In contrast to older sandeel, young-of-the-year (YOY) continue to feed until October-November in order to obtain sufficient energy to hibernate through the winter (Deurs *et al.* 2011). Figure 5.3.1-1 shows the North Sea spawning areas of sandeel and the Norwegian fishing grounds.

Spawning areas

Sandeel spawn where they live. The eggs are laid on the seabed where they remain until hatching (Wright and Baily 1996). The larvae are pelagic (Lynam *et al.* 2013). Hence, spawning grounds correspond to fishing grounds. In the Norwegian sector of the North Sea, sandeel grounds have been identified by use of three sources of information (Johannessen and

Johnsen submitted): 1. Vessel monitoring system (VMS) providing vessel speed and location every 15 minute (since 2001), 2. trawl trajectory data for the period 1996-2007 from the trawler F/F Traal, and 3, ecosounder data from an annual acoustic sandeel survey (2005-2015). Sandeel grounds in Scottish waters are modified from Wright (1996), and sandeel grounds from the rest of the EU zone from Jensen *et al.* (2011).

In the Norwegian sector of the North Sea, fishing grounds, which represent the main spawning areas, are indicated in the map (marked with black lines).

Spawning period

The majority of ≥II-group sandeel (Boulcott *et al.* 2007) emerge for a short period from the sand to spawn around December-January (Macer 1966; Bergstad *et al.* 2001). The eggs are laid on the seabed where they remain until hatching around February-March (Wright and Baily 1996). At hatch, the larvae can be at very high densities which then diffuse and are dispersed by the local currents. Larvae are pelagic until around June (Lynam *et al.* 2013).

Spawning Table Sandeel

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period Green: Peak spawning

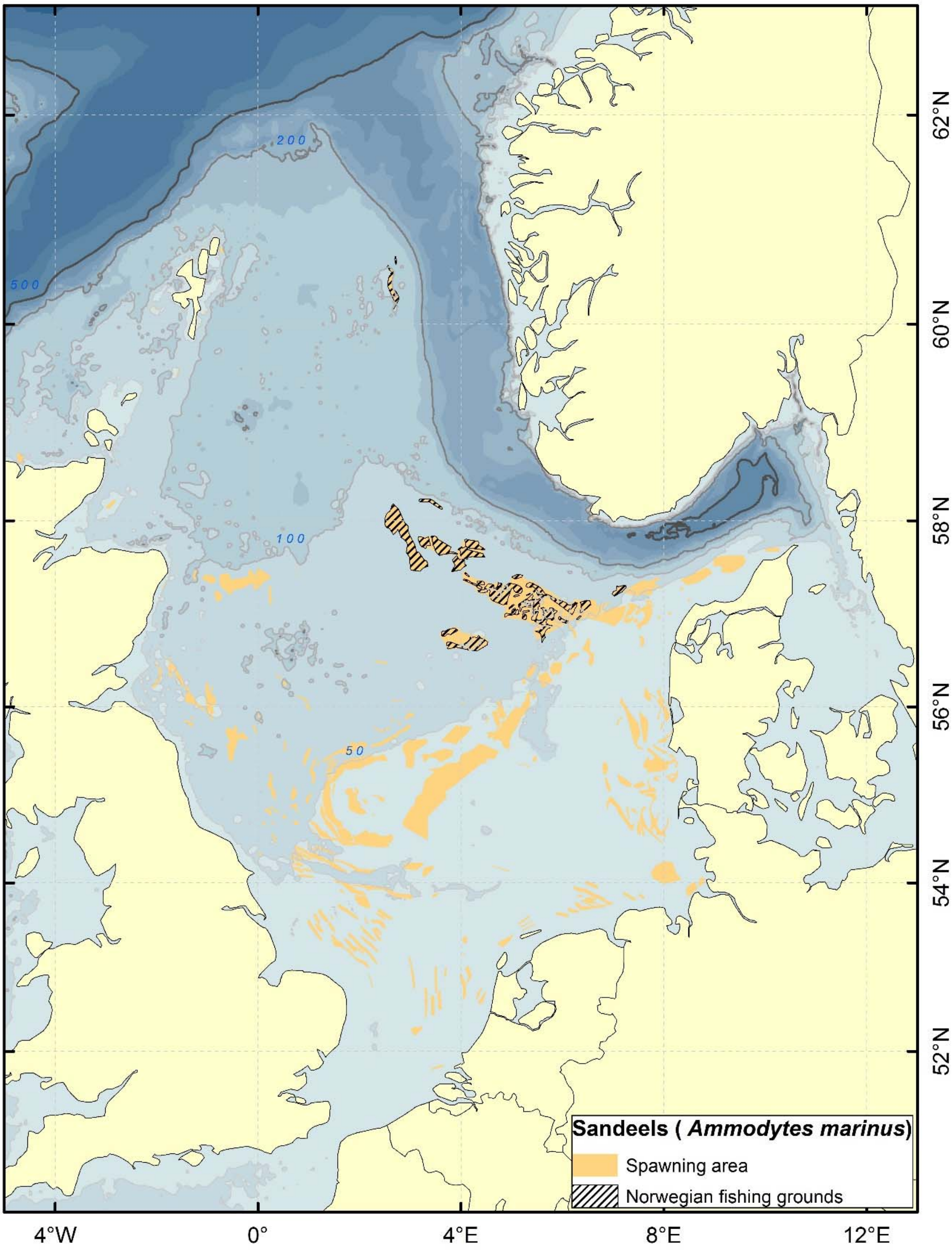

Figure 5.3.1-1. Sandeel spawning areas in the North Sea. Norwegian fishing grounds, which correspond to the main spawning areas in the Norwegian zone, are marked with black lines.

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5.4.1 Herring – *Clupea harengus* - sild

General stock features

Herring is a demersal spawner which deposits its eggs on gravel beds or rocks, general in areas with reasonably fast flowing currents (see Geffen 2009). In the North Sea the principal stock which is assessed and the subject of a commercial fishery is the Autumn Spawning component, however, spring and winter spawners do also occur in the North Sea (see Dickey Collas et al. 2010). The spring spawning components which occur offshore in the northern North Sea are from the western Baltic stock, general in the vicinity of the western entrance to the Skagerrak, and Norwegian Spring spawners which occur along the west coast of Norway and also in the vicinity of the Shetland Islands. Herring are distributed over the entire North Sea, although at small numbers in the Norwegian Trench (Dickey-Collas et al. 2015). Herring has a wide salinity as well a temperature tolerance; salinity from 4 to 35, and temperature from 4 to 15 ºC (Pörtner and Peck 2010).

Movements of herring (adults, larvae and juveniles) within the North Sea

The historical distribution of herring in the northeast Atlantic, on a monthly basis, is illustrated in ICES (1951). Much of this information is still applicable over 60years later, however, there are changes due to the disappearance of e.g. the Dogger Bank component of the stock and changes in the relative proportions of the stock components. Adult herring, mainly from the North Sea autumn spawning stock, but probably some from the west of Scotland, southern extension of Norwegian Spring spawners and some Western Baltic Spring spawners are aggregated in the northern North Sea on their feeding grounds, at least in June and July (Figure showing distribution of herring in June/July 2015 from the ICES coordinated acoustic survey (HERAS) in ICES HAWG (2016)). During the period July to spawning aggregations of herring migrate westward to the west of Scotland spawning grounds, west toward the Orkney-Shetland grounds and south and east toward Buchan, Banks and also the winter (December-February) spawning grounds in the Buchan (English Channel) area.

After spawning the North Sea adults migrate east or north-eastward back to their over-wintering or summer feeding grounds in the northern North Sea (see Corten 2013). Whether this fish migrate in large concentrated schools or in a scattered, diffuse manner is unknown.

After hatching (often starting in mid September) larvae drift south and eastward toward the nursery areas in the Skagerrak to southern Bight (see Corten 2013). The start of the drift progresses from north to south with Downs larvae drifting north and east in to the southern Bight area starting in late December. The distribution of the larvae is documented in January-February each year during the MIK (herring larvae) survey which is undertaken in conjunction with the ICES coordinated International Bottom Trawl Survey (IBTS) (ICES IBTS 2016). This survey has shown considerable variation in the distribution and abundance of larvae over the area since the late 1970s (ICES HAWG 2016 and references therein).

Spawning areas

North Sea autumn spawning herring spawning areas are located on suitable substrata along the east coast of Great Britain, around the Orkney and Shetland islands and in to the eastern English Channel (Dickey Collas et al. 2009, 2010, Ellis et al. 2012, Corten 2013, Hufnagl et al. 2014) (see Figure 5.4.1-1).

Spawning period

Each of the spawning areas, from Shetland in north to English Channel in south, has its specific spawning period (Dickey-Collas et al. 2015). However, there also seem to be different spawning groups on the various spawning areas having their specific time of spawning (Dickey-Collas et al. 2010).

Spawning Table North Sea Herring

Orkney-Shetland

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Buchan

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Banks

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Downs

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

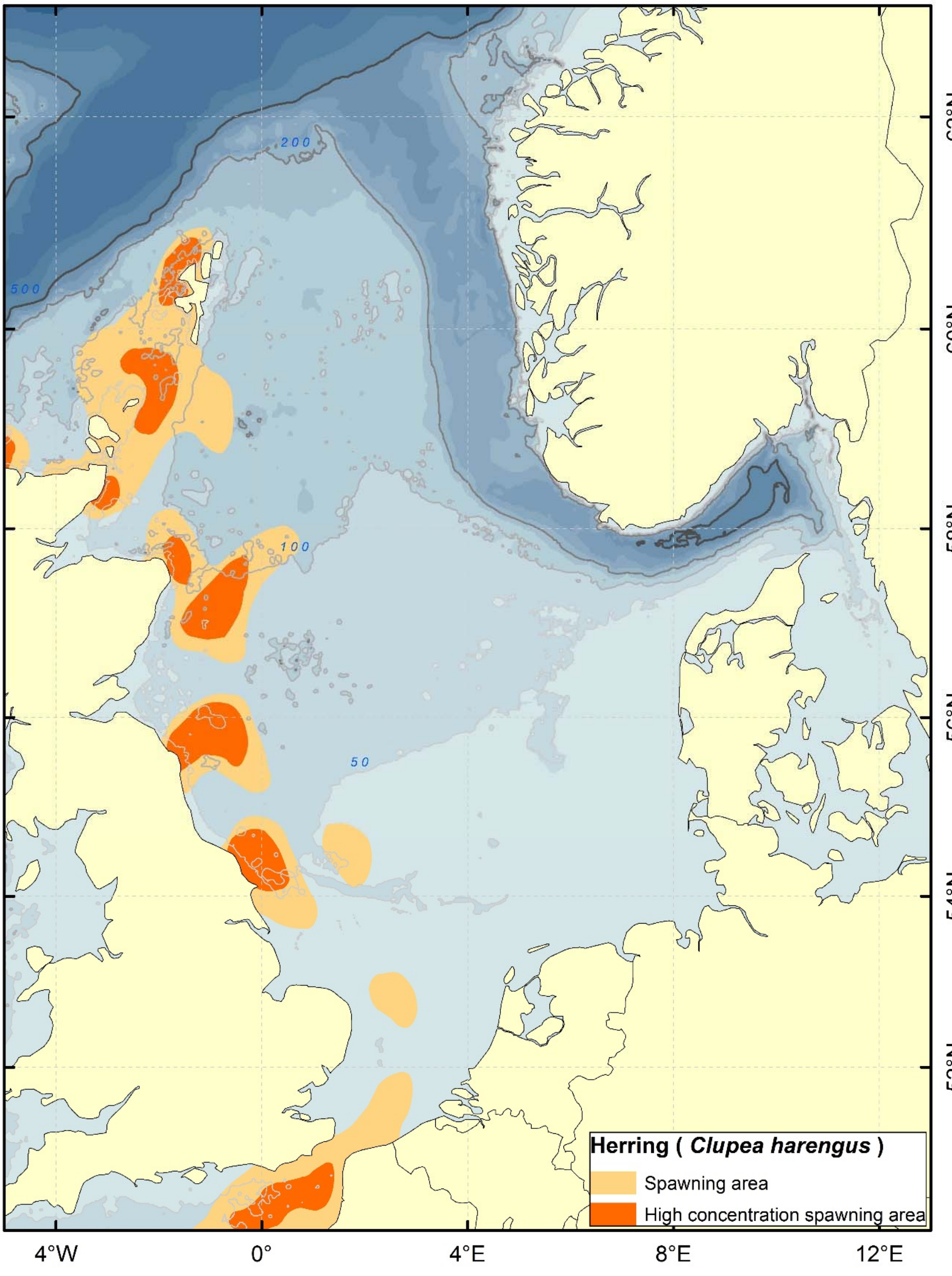

Figure 5.4.1-1. Spawning areas of herring in the North Sea.

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5.4.2 Sardine/pilchard – *Sardina pilchardus* - sardin

General stock features

The sardine or pilchard is a southern species which is common and commercially exploited from the southwest of the British Isles, southward into the Mediterranean. The abundance of sardine (pilchards) in the western part of the English Channel and the Celtic Sea has fluctuated over time with changes in the environmental conditions (Alheit and Hagen 1997) and has often been associated with the 'Russell Cycle' which involves changes in the planktonic community (McManus et al. 2016). However, since about 1995 there has been a steady increase in the incidence of sardines through the English Channel and in to the southern North Sea along with increases in the north-western North Sea (Beare et al. 2004, Dickey Collas et al. 2015). The recent 20 years of warmer conditions it has spread northwards along the entire British coast of the North Sea, though at moderate concentrations. However, the numbers in Scottish groundfish surveys during 1995-2003 are unprecedented in a historical context (Beare et al. 2004). In the German Bight sardine abundance has increased substantially (Voss et al. 2009; Alheit et al. 2012). The northern distribution originates from along the west coast of the British Isles. The catch rates for the two periods 1977-1994 and 1995-2013 as shown in the figure by Dickey-Collas et al. (2015).

Spawning areas

Although the stock has spread substantially northwards during the recent 40 years spawning of sardine seems still confined to the southernmost part of the North Sea. In addition to the tradition spawning area in the English Channel, spawning occurs in the eastern part of the Southern sub region, and over recent years had occurred in the German Bight (Kanstinger and Peck 2009). Although the pattern of distribution of sardine and anchovy is similar in many ways, a distinct difference in spawning areas is that sardine spawning areas are more offshore while anchovy spawning areas are more inshore and confined to brackish water regions. These distinctions also seem to be mirrored in the Bay of Biscay distributions of the two species (Planque et al. 2007). Figure 5.4.2-1 is a synthesis of our current knowledge of sardine spawning and shows our present perception of the distribution of sardine spawning areas.

Spawning period

Spawning for this species, to the south of the North Sea, is known to occur between May and November with peaks occurring in May-June and again in October-November (Dickey Collas et al. 2015). The one year study (April 2010-March 2011) in the southern North Sea (south of 56^{o}N) indicated stage 1 eggs i.e. spawning between April and July (peak abundances in May/June) and mainly inshore along the Dutch coastal zone (van Damme et al. 2011). The later spawning was not evident in this study. In contrast, Munk and Nielsen (2005) suggest that spawning in the southern North Sea occurs between June and August. It is unclear whether spawning populations have been established in the northern North Sea.

Spawning Table Sardine in the North Sea

Southern North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

English Channel

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

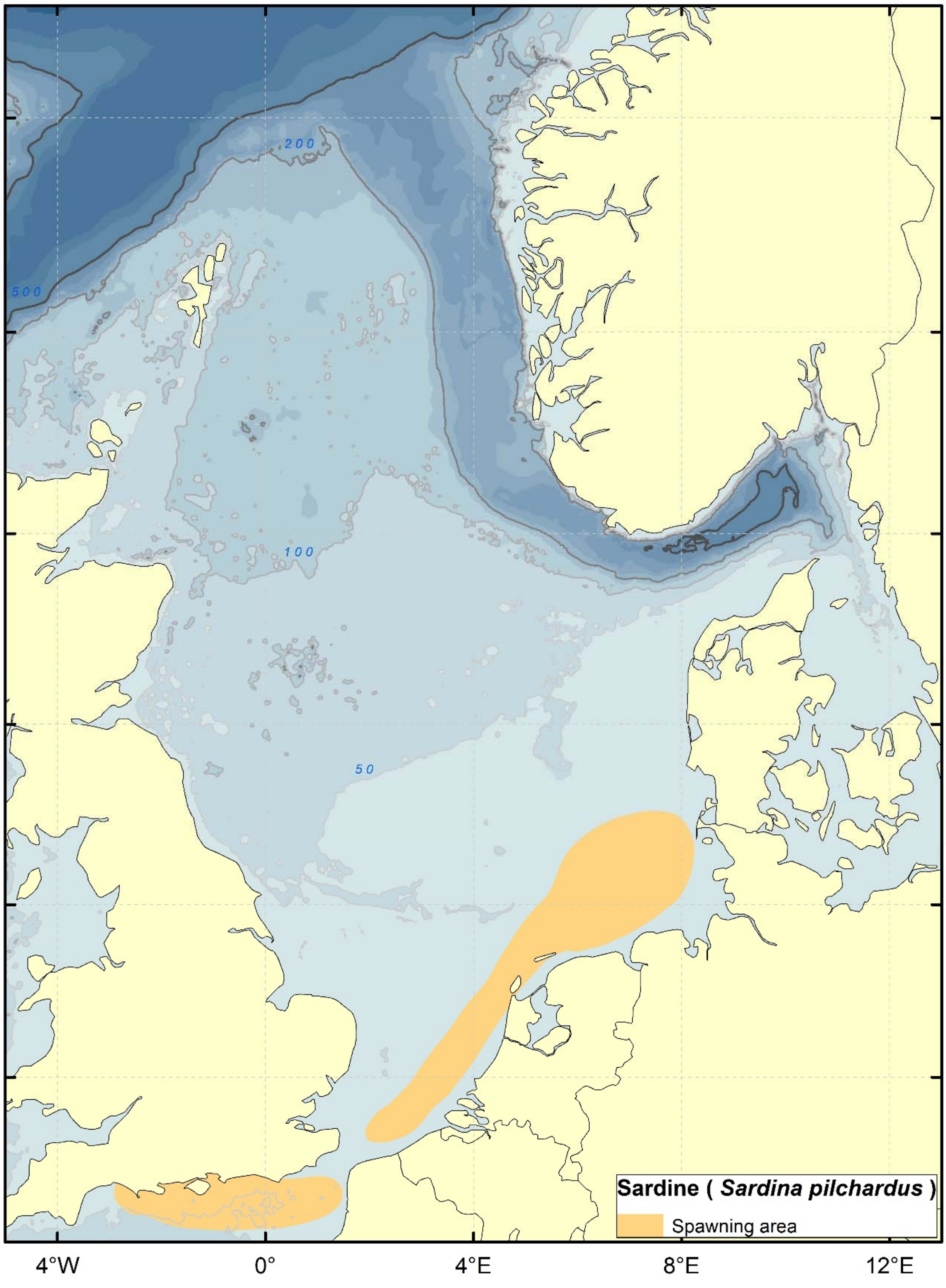

Figure 5.4.2-1. Spawning areas of sardine in the North Sea.

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5.4.3 Sprat – *Sprattus sprattus* - brisling

General stock features

Sprat is common all around the British Isles and more specifically in the English Channel, North Sea and the Skagerrak (Dickey-Collas 2015). However, it is abundant in all sub regions of the North Sea, although at quite low numbers in the northern Norwegian Trench and in the northeastern part of the Northern sub region. It is subject to a commercial industrial fishery (ICES HAWG 2016). Sprat occur over much of the North Sea, however, the greatest abundances tend to be in the southern North Sea and the Kattegat (Dickey Collas et al. 2015, ICES HAWG 2016). This species is tolerant of low salinities and as such also occurs in estuarine areas and in the Baltic. Sprat is also highly tolerant to low-oxygen condition and can thrive in oxygen concentration down to 7 – 15 % saturation (Kaartvedt et al. 2009). The Figure in Dickey-Collas 2015 shows the distribution of sprat catch rates from the standard ICES coordinated surveys.

Spawning areas

Sprat spawning areas extend through the Southern sub region, the German Bight and Jutland Current, and in Kattegat. Spawning also occurs northwards along the English and Scottish coast. In essence, spawning occurs in most areas where sprat occur (Dickey Collas et al. 2015). The main spawning areas are found in the German Bight (Baumann et al. 2009; Kanstinger and Peck 2009; Wahl and Alheit 1988), in the Southern Bight (ICES WKSPRAT 2014), and in the English Channel (Milligan 1986). Figure 5.4.3-1 shows our current perception of the location of sprat spawning areas based on the available literature.

Spawning period

Spawning generally occur over a prolonged period (spring to late summer) with the peak between May and August. The prolonged spawning period was illustrated in the southern North Sea ichthyoplankton study (van Damme et al. 2011) were stage 1 eggs occurred over much of the sampled area from March to June. Stage 1 eggs (newly spawned) were also found in January/February and July but at much lower abundances and were patchily distributed. The January to July spawning period is also reported in Munk and Nielsen (2005). In general spawning occurs where the water temperatures are between 8 an 15^{o}C. Individuals are multiple batch spawners so will spawn intermittently over a protracted period.

Spawning Table North Sea Sprat

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

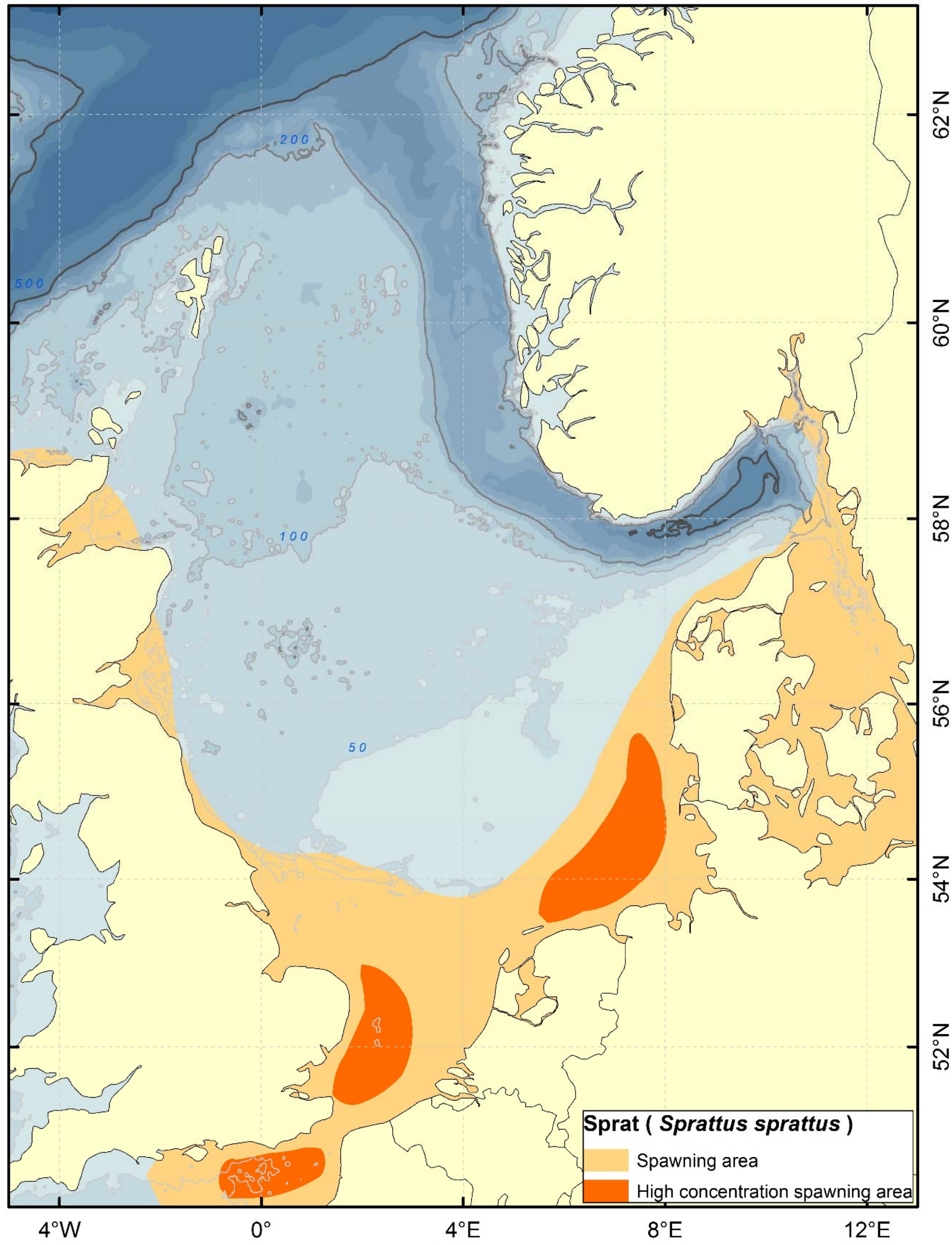

Figure 5.4.3-1. Spawning areas of sprat in the North Sea.

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5.5.1 Anchovy – *Engraulis encrasicolus* - ansjos

General stock features

Anchovy has a southerly distribution in the North Sea and was generally confined to the Southern and Central sub regions in the cool period from the 1970s. However, during the recent warming anchovy has been slowly increasing in abundance in the North Sea (Alheit et al. 2012; Petitgas et al. 2012). A fraction of the anchovy in the northeastern most part of the North Sea might have been supplied from the population west of the British Isles (Beare et al. 2004). However, Petitgas et al. (2012) argue that anchovies are simply increasing in abundance rather than a new colonisation from the south due to increasing water temperatures etc. Dutch catch data show this species occurring in the fisheries periodically since at least the late 1800s and the ICES IBTS also showing pulsed elevations of abundance which have been much larger in more recent years (since 2000) (Petitgas et al. 2012, Heessen et al. 2015). Presently it is found in all sub regions of the North Sea except for the northwestern area where it still is very scarce. Anchovy in the North Sea are not currently commercially exploited. The Figure in Heessen et al. (2015) shows the changes in anchovy catch rates in the standard ICES trawl surveys for the two intervals 1977-1994 and 1995-2013.

Spawning areas

Although the stock now occurs substantially to the north over the recent 40 years, spawning of anchovy is still confined to the southernmost part of the North Sea. Spawning conditions are similar to the Bay of Biscay with spawning inshore and in brackish water (Planque et al. 2007, Heessen et al. 2015). Anchovy spawns in the Wadden Sea (Boddeke and Vingerhoed 1996), and. has also started to spawn in the German Bight again after being absent from that area since the 1950s. Spawning occurs here, inshore (Kanstinger and Peck 2009). Even in the Bay of Biscay the centres of spawning are now occurring further north than previously (Bellier et al. 2007). Figure 5.5.1-1 shows anchovy spawning areas in the North Sea during over recent years.

Spawning period

Munk and Nielsen (2005) indicate that anchovy spawn between June and August in the North Sea and the northern Kattegat. The 2010/2011 ichthyoplankton study in the southern North Sea showed anchovy eggs inshore, along the Dutch coast during June and July (van Damme et al., 2011). Due to the very rapid development time off anchovy eggs (Geffen and Nash 2012) this indicates spawning must occur in the area. The southernmost population spawns from March to August with a maximum in May/June (Cunningham 1890; Planque et al. 2007).

Spawning Table Anchovy in the North Sea

Zuidersee- Kattegat

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Southernmost region

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

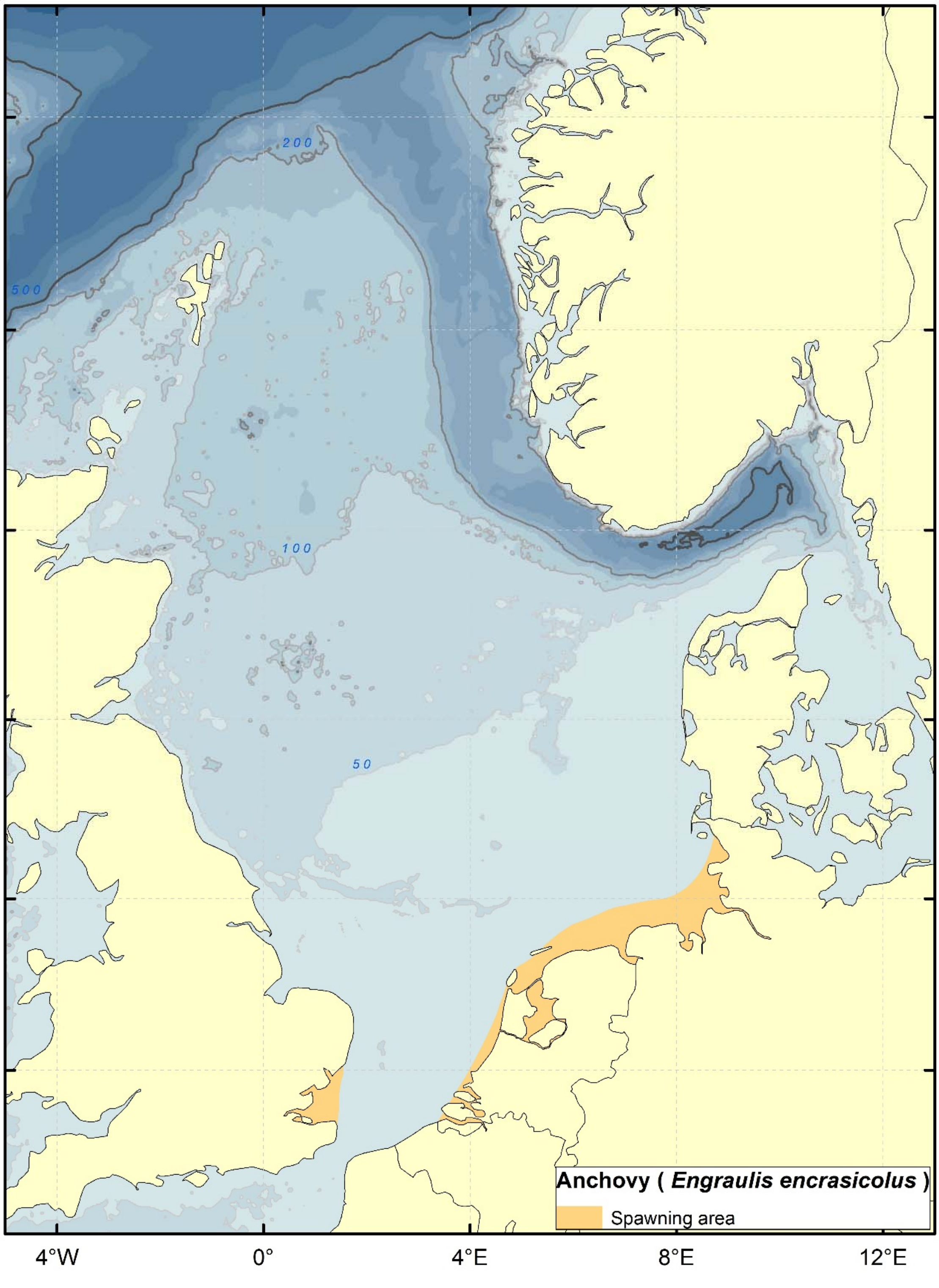

Figure 5.5.1-1. Spawning areas of anchovy in the North Sea.

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5.6.1 Mackerel – *Scomber scombrus* - makrell

General stock features

Mackerel is a wide-ranging species where the largest part of the population is to be found in open ocean to the west of the British Isles (ICES WGWIDE 2015). During recent years of warming it now occurs over a much larger portion of the Nordic Seas during summer feeding (Asthorsson et al. 2012; Langøy et al. 2012). The NE Atlantic mackerel stock can be considered as comprising a southern, western and North Sea component, however, the North Sea component is much smaller than the other two. The various components of mackerel in the Northeast Atlantic seems to mix together during summer feeding (Ellis and Heessen 2015). Mackerel is abundant in all sub regions of the North Sea. During winter and spring it is most abundant in the Northern sub region while it spread southwards during summer and autumn (Ellis and Heessen 2015). The figure in Ellis and Heessen 2015) shows winter/spring and summer/autumn distributions of mackerel in the North Sea.

Spawning areas

Mackerel spawning occurs in the surface layers and it appears that there is a temperature threshold, which seems to be the only constraint for spawning to be initiated (Jansen and Gislason 2011). Rogers and Stocks (2001) indicate spawning in most of the North Sea between 53º 30' N and 59ºN, while Ellis et al. (2012) indicate spawning between 52 ºN and 60 ºN. However, over the whole spawning season there were generally three areas where there was elevated stage I egg productions (see van Damme 2015 ICES WD). These areas were relatively consistent over the years. The ichthyoplankton survey in 2010/2011 (van Damme et al. 2011) found very few mackerel eggs, however, larvae occurred in the southern part of this area and further south in June and July. Based on the information in the literature, Figure 5.6.1-1 shows the main spawning areas.

Spawning period

Munk and Nielsen (2015) state that spawning in the North Sea occurs between May and July.
Surveys of mackerel eggs, co-ordinated by ICES, have been undertaken in the North Sea, between 54º and 59.5ºN (see van Damme 2015 ICES WD, for survey area coverage) since 1980. Between 1980 and 1984 the surveys were annual, 1986 to 1990 were biannual and 1996 to 2011 were triannual (see van Damme 2015 ICES WD). The 2014 survey was undertaken in 2015 by The Netherlands alone. Since 2002 the egg production (spawning) curves have varied (see van Damme 2015 ICES WD). Peak spawning in 2002 to 2011 has generally occurred either around 18-22 June or possibly later, in to early July. The peak in 2011 may have been before the first survey in early June and 2015 was approximately 5th June. This suggests that peak spawning may vary over approximately a month. The majority of the egg production (spawning) over this recent time period (2002-2015) occurs between the mid May and mid July.

The stage I eggs in the North Sea generally had a preference for 13-14ºC, however, these early stage eggs were found in water temperatures ranging from 8-15/16ºC.

Caveats for spawning locations and times in the North Sea

The timing of the survey during the year is fixed and thus may not reflect the temporal dynamics of mackerel spawning in the North Sea. Similarly, the fixed survey area may not reflect the actual spatial structure of spawning over the entire North Sea. The survey is undertaken triennially or after four years in the most recent time period therefore there are uncertainties about fine scale temporal and spatial patterns in spawning and egg productions.

Spawning Table Mackerel in the North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

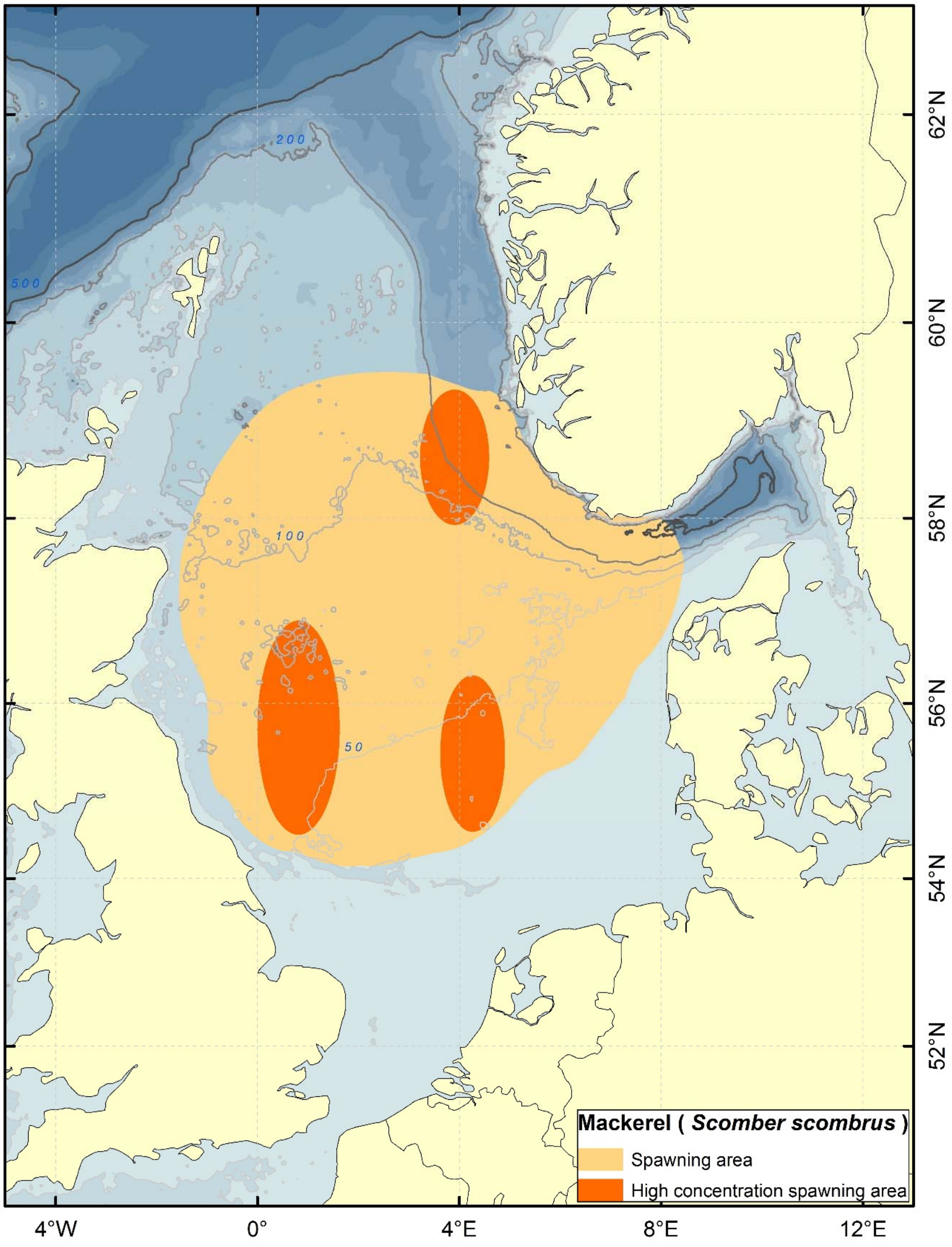

Figure 5.6.1-1. Spawning areas of mackerel in the North Sea.

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5.7.1 Horse mackerel – *Trachurus trachurus* - hestmakrell

General stock features

Horse mackerel is a highly migratory pelagic species which has a seasonal occurrence in the North Sea. It is generally found somewhat deeper in the water column than the Atlantic mackerel, and has a more southern distribution with spawning areas tending to also be further south than for Atlantic mackerel (Fives et al. 2001). ICES currently assesses and provides advice for three horse mackerel stock units in the Northeast Atlantic are managed in three stock units based on their fisheries: 1) the southern stock along the northern Iberian Peninsula, 2) the western stock located in an extended area west of France, the western English Channel, west of the British Isles, in the Norwegian Sea and in the northern part of the North Sea, 3) the stock unit occurring in the Southern sub region of the North Sea and the German Bight plus the eastern English Channel (Abaunza et al. 2003, ICES WGWIDE 2015). The North Sea horse mackerel stock is subject to a commercial fishery. However, the stock is deemed to currently be in a poor condition (ICES WGWIDE 2015).

The Figure in Ellis (2015) shows the summer and winter catch rates of horse mackerel. The figure indicates two summer migration pathways into the North Sea. The southerly summer distribution in the Southern sub region and in the German Bight seems to extend through the English Channel, while the northerly summer distribution along the Atlantic inflowing water in the Northern sub region seem to be supported from the component to the west of the British Isles. For an 11-year period, from 1988 to 1999, when there were high catch rates of horse mackerel in the Northern sub regions, the variability in catch rates was highly correlated with the influx of Atlantic water to the North Sea (Iversen et al. 2002). Reid et al. (2001) suggested that the increased abundance of horse mackerel during this period coincided with a general increase in the Atlantic Current and a change in plankton abundance, possibly linked to the North Atlantic Oscillation (NAO).

Spawning areas

Eggs and larvae from horse mackerel have been found in the Southern Bight of the North Sea (van Damme et al. 2011), in the English Channel, and in the outer part of Bay of Bristol (Macer 1974). In addition, spawning occurs along the shelf edge to the west of the British Isles (Coombs et al. 2001). These observations were synthesized by Ellis et al. (2002). In conclusion, even if horse mackerel has periods of high abundance in the Atlantic part of the northern North Sea during summer the behaviour seems to be limited to summer feeding. IMR's Fish Data Base shows no occurrence of ripe and running fish in this region. Figure 5.7.1-1 shows the perception of spawning distributions in the North Sea based on the available information.

Spawning period

Stage 1 eggs found in the southeastern North Sea in May to August (van Damme et al. 2011). The highest abundances were in June and July, suggesting this as the peak spawning time in this area. Russell (1974), based on Macer (1974) suggests peak spawning in the Southern Bight as being slightly earlier i.e. May and June but as with Munk and Nielsen (2005) spawning may continue in to August and September. Spawning outside the North Sea, from the Bay of Biscay to west of Ireland, occurs from December to August/September (Ellis 2015).

Spawning Table Horse mackerel in the North Sea

Southern North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Bay of Biscay-Ireland

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

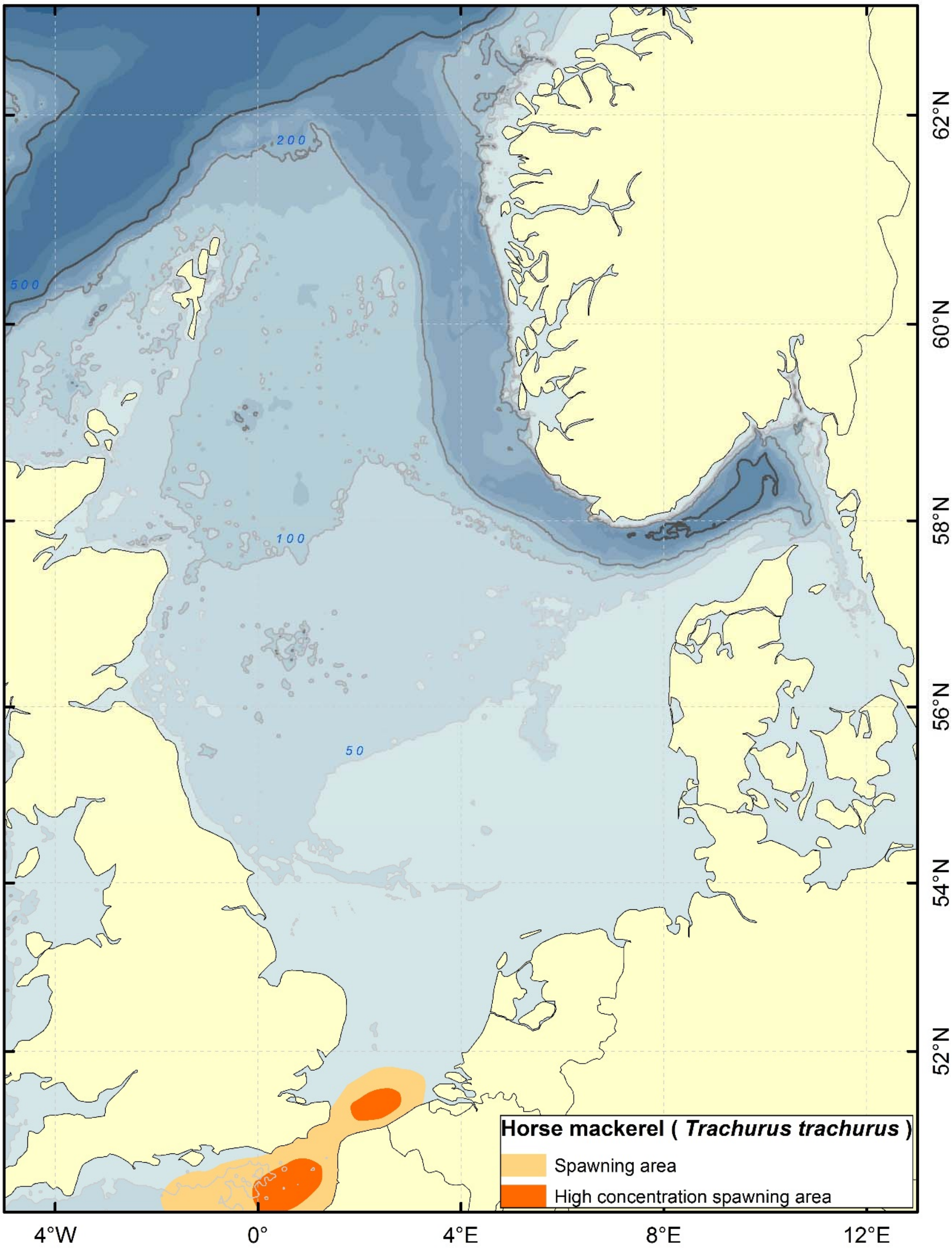

Figure 5.7.1-1. Horse mackerel spawning areas in the North Sea.

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5.8.1 Sole – *Solea solea* - tunge

General stock features

Sole has a high commercial value but is relatively rare in the North Sea (Daan et al. 1990, Rijnsdorp et al. 1992). Catches peaked in 1991 and 1992 (Heessen 1996). The occurrence of sole in the North Sea is limited by the boundary between mixed and stratified water columns, indicated by the 50-m isobath (Rijnsdorp et al. 1992). The population in the Skagerrak and Kattegat is the most northern one and is genetically distinct from the North Sea population (Rijnsdorp et al. 1992, Cuveliers et al. 2012). Highest abundances are found in the Southern sub region and the German Bight. Moreover, it is found in the southern and eastern part of the Central subregion, Jutland Current and Kattegat. It is seldom found in the Northern Sub region and Skagerrak- Norwegian Trench (figure in Rijnsdorp et al. 2015). Normally sole is found in the shallow regions close to the southeastern coast, but during cold winters they migrate in to deeper water to avoid the coldest water, since critical low temperature for sole is 3 ºC. (Rijnsdorp et al. 2015). Their natural habitat is sandy and sandy/muddy substrata with larger individuals occurring in deeper water (Rogers 1992).

Spawning areas

Sole is a nocturnal batch spawner (Houghton et al. 1985), and spawns generally in coastal waters down to 30 m depth (Rogers and Stock 2001; Rijnsdorp et al. 2015). However, some minor offshore spawning areas are also found on the shallow Dogger Bank (Ellis et al. 2012). In addition, Höffle et al. (2015) report ripe and running sole offshore at deeper waters west of Jutland extending northwards to the edge of the Norwegian Trench. The main spawning grounds in the North Sea are in the German Bight, off Texel, off the Belgian coast, on the Norfolk Banks and in the Thames estuary (Rijnsdorp et al. 1992). During a survey in March, stage I eggs were only found along the continental coast, while later surveys found high egg concentrations on both sides of the North Sea and in the Thames estuary (Figure 3; Beek 1989). The latest eggs were found off the Jutland coast. The peak concentrations of eggs normally occur in the English Channel and the German Bight (Lacriox et al. 2013; Savina et al. 2010). Figure 5.8.1-1 shows a summary of the spawning areas based on the above literature.

Spawning period

Russell (1976) and Munk and Nielsen (2005) give the spawning season as April to August. Stage 1 eggs occurred on the southern North Sea in 2010/2011 between March and August with the highest abundances occurring in April to June (van Damme 2011). The spawning peak usually occurs in late May (Rijnsdorp et al. 1992) and the planktonic phase lasts for about four weeks at 10–15°C. The onset is governed by the rise of temperature at the end of winter and is shifted to earlier or later following particularly mild or cold winters, respectively. The end of the spawning season is then equally sooner or later. In the Bay of Biscay spawning occurs somewhat earlier than in the North Sea, around February-March (Rijnsdorp et al. 2015).

Spawning Table Sole

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

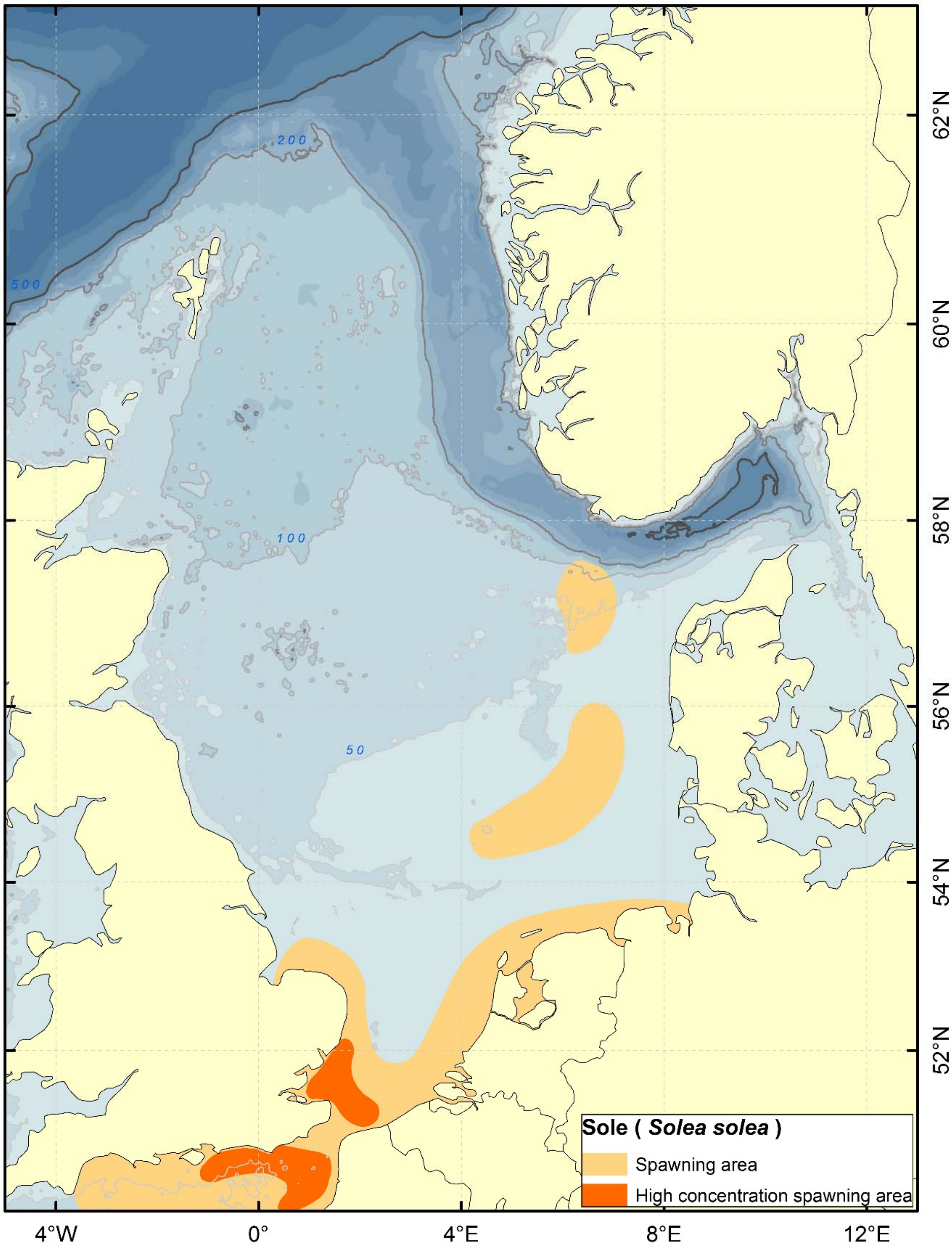

Figure 5.8.1-1. Spawning areas of sole in the North Sea.

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5.8.2 Solenette – *Buglossidium luteum* - glasstunge

General stock features

Solenette inhabits similar areas as the sole, i.e. southeastern North Sea. Similar to sole, abundance in the Northern subregion and Norwegian Trench-Skagerrak are insignificant (Rijnsdorp et al. 2015). The highest concentrations are more offshore, towards the northwest, compared to the sole, as they avoid the near-coast lower salinities (van Hal et al. 2010). The figure in Rijnsdorp et al. (2015) shows the principally southeastern distribution of solenette catch rates in the North Sea.

Spawning areas

Spawning areas is assumed to largely coincide with the distribution of the adults (van der Land 1991; Nottage and Perkins 1982). Therefore, the core spawning areas are found somewhat more offshore than for the sole. The spawning areas are Figure 5.8.2-1 shows the current perception of spawning areas based on information available in the literature.

Spawning period

Russell (1976) gives the spawning season of solenette in the southern North Sea as May to August with a peak in June. This is based on data from the early 1900s. Munk and Nielsen (2005) suggest a slightly earlier start to the spawning season, namely April. This is consistent with the data on stage 1 solenette eggs in the southern North Sea presented by van Damme et al. (2011). In the region from English Channel to Irish waters spawning is somewhat later, from May/June till August (Rijnsdorp et al. 2015).

Spawning Table North Sea Solenette

North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

English Channel-Ireland

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period Green: Peak spawning

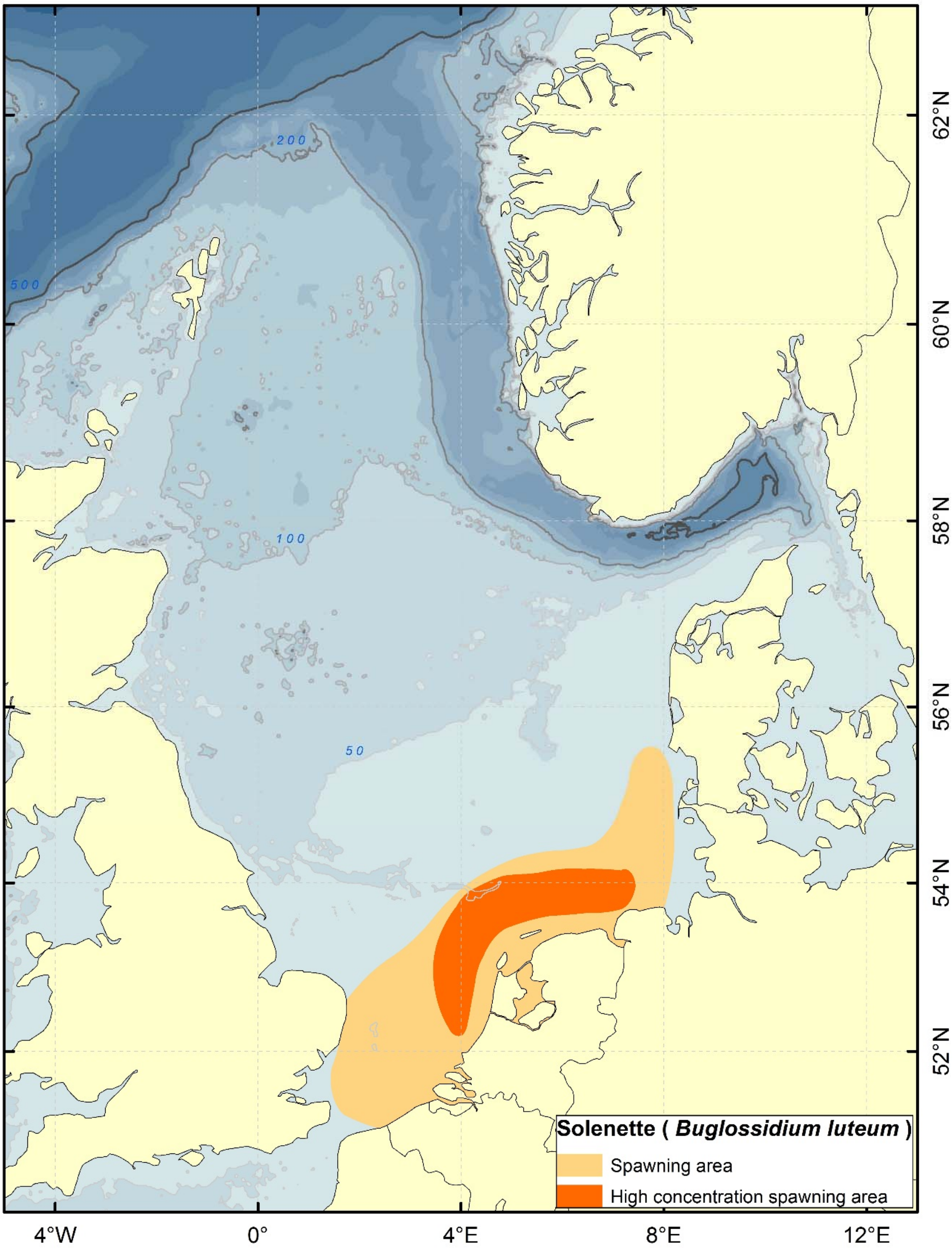

Figure 5.8.2-1. Spawning areas of solenette in the North Sea.

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5.9.1 Witch – *Glyptocephalus cynoglossus* - smørflyndre

General stock features

Witch is not a targetted commercial species and rarely studied, however, catches peaked in the 1970s and then rose again in the 1990 (Heessen 1996). When landed, it is consumed in restaurants (Goldsmith et al. 2015). Witch is one of the northerly distributed flatfishes with the highest abundances in the Skagerrak region and off the Scottish coast in the Northern and partly in the Central sub regions (van der Land 1991; Goldsmith et al. 2015). It rarely occurs in the Southern sub region and in the German Bight-Jutland Current (see figure in Goldsmith et al. 2015). In Skagerrak witch is found along the edges of the Norwegian Trench from 230 m and down to 400 m depth (Bergstad and Tveite 1993).

Spawning areas

Females in spawning condition can be found along the 200-m isobath in Q1 and in the Kattegat and off Britain in Q3 (IBTS survey databases, reported in Höffle et al. (2015)). The lack of spawning in the southern North Sea was illustrated by van Damme et al. (2011) where only late larvae were sampled in the most northern area surveyed in the southern North Sea. Figure 5.9.1-1 summarizes the known information on witch spawning areas based on the ICES DATRAS IBTS database.

Spawning period

As its eggs are inconspicuous, larvae were identified eastwards from the Moray Firth and between Shetland and Norway, with peak abundances in March (Taylor et al. 2007). However, the spawning season goes on until September and Ehrenbaum (1909) identified July as the peak period. It is uncertain whether these reported discrepancy in peak spawning is due to observations from two different time periods or whether it is due to regional differences.

Spawning Table North Sea Witch

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

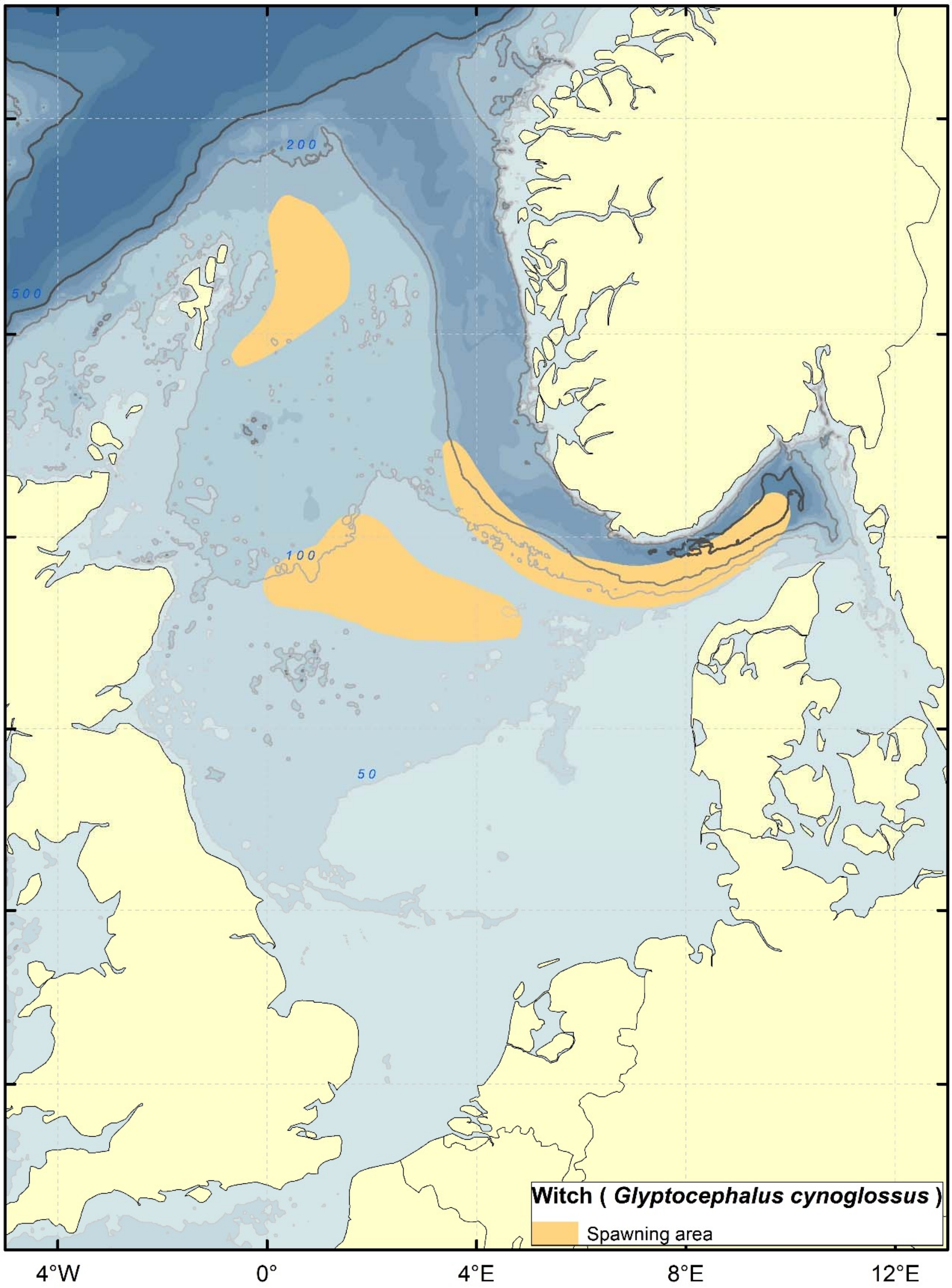

Figure 5.9.1-1. Spawning areas of witch in the North Sea.

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5.9.2 Long rough dab – *Hippoglossoides platessoides* - gapeflyndre

General stock features

The eastern Atlantic long rough dab is commercially unimportant and few papers are dedicated to it alone, unlike the American plaice (a sub-species that attains a larger size and is found in the western Atlantic) (Heessen 1996). However, in the English summer surveys, it was the fourth most abundant flatfish and the only non-commercial species which contributed significantly to the total catches (Daan et al. 1990, Ehrich et al. 2009). Long rough dab is typical for demersal fish assemblages in the northern North Sea (Ehrich et al. 2009) and appears to prefer deeper water, occurring regularly below the 50-m line and becoming the dominant flatfish past 100 m depth (Callaway et al. 2002). Unlike most demersal fish, the gradient of smaller to larger fish in increasing depths seems to be only weakly developed or non-existent (Daan et al. 1990). In summary, the highest concentrations of long rough dab are found in the Northern and Central sub regions and in Kattegat (see figure in Goldsmith et al. 2015).

Spawning areas

Spawning areas are also largely confined to the northern part of the North Sea, and core spawning areas have been identified around Viking Bank in the Northern sub region and in the area from Ling Bank to the Little and Great Fisher Banks (ICES WGEGGS2 2010) but also off the coast of Scotland and southward the northern edge of the German Bight (van der Land 1991; Munk et al. 2009;). The current perceived spawning areas for long rough dab in the North Sea area are shown in Figure 5.9.2-1.

Spawning period

According to Goldsmith et al. (2015) spawning starts in mid February peaking in April. It is assumed that spawning decays in May.

Spawning Table Long rough dab in the North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

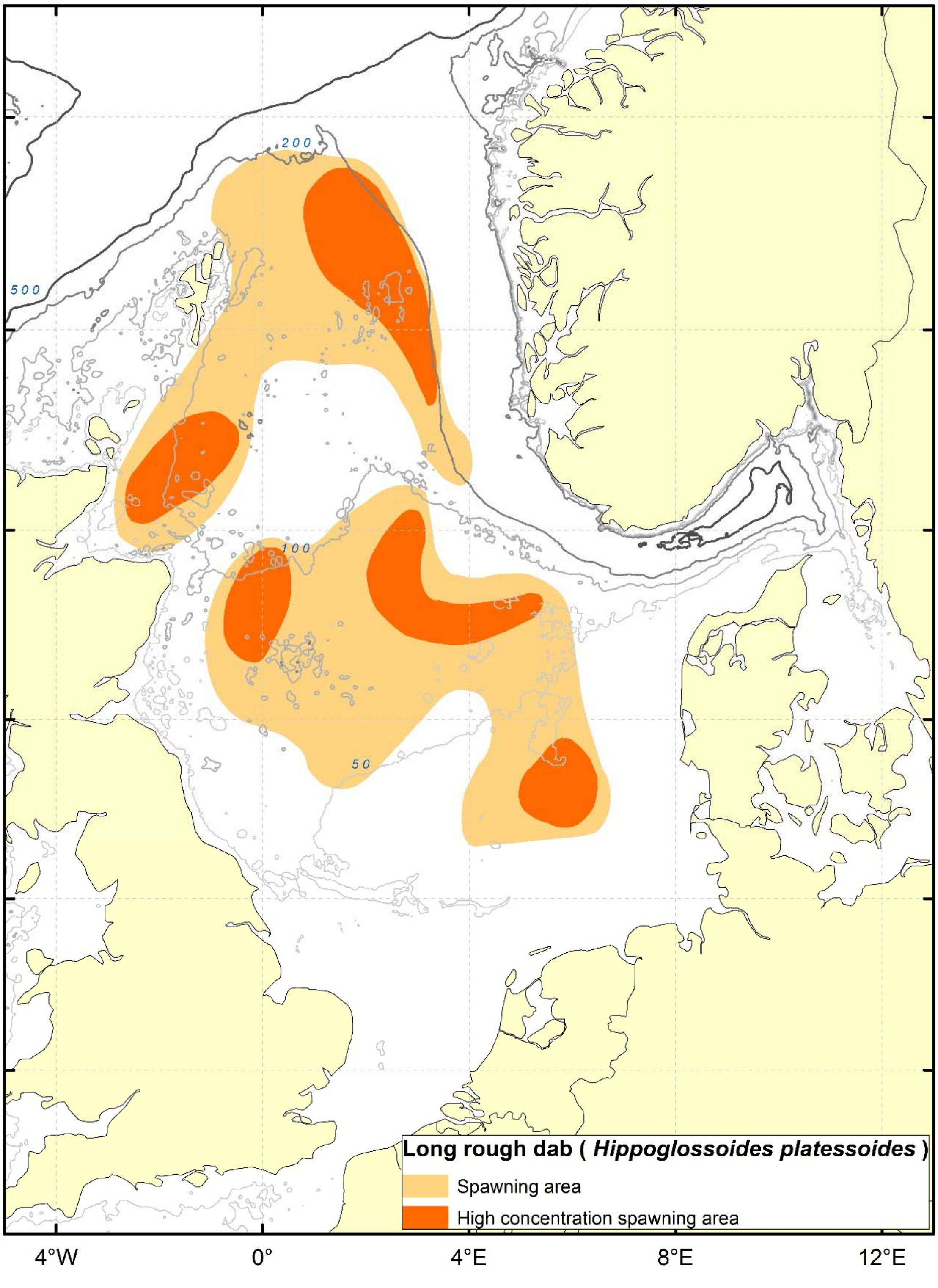

Figure 5.9.2-1. Spawning areas of long rough dab in the North Sea.

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5.9.3 Dab – *Limanda limanda* - sandflyndre

General stock features

Dab was the dominant flatfish species in the English summer surveys (1977-1986), as well as the most common demersal species in the southeastern North Sea (Daan et al. 1990). According to beam-trawl surveys it was the dominant species between the 50 m and 100 m isobaths, while with the larger GOV trawl plaice was the dominant species in that depth range (Callaway et al. 2002). Highest catches, as for most other flatfish species, occurred in the German Bight, and the eastern parts of the Central and Southern sub regions (see figure in Goldsmith et al. 2015).

Spawning areas

While spawning occurs across the entire southeastern North Sea (Rijnsdorp 1992), centres of dab spawning were identified in the German Bight northwest of Helgoland, along the northern Dutch coast, as an isolated patch off Flamborough and along the southern edge of Dogger Bank (Figure 1; van der Land 1990, Lelievre et al. 2012). Peak egg densities were found along the Dutch and German coasts, with a gradual decrease to the North up to the Fisher Banks (Aurich 1941). The peaks occur some distance from the shore and drop off rapidly, often over distances of less than 10 nautical miles (Aurich 1941). General environmental conditions in spawning areas were shallow depths and intermediate levels of temperature and salinity, the latter two factors seem to govern usage of occasionally used spawning grounds which are influenced by river plumes (Lelievre et al. 2014). However, the range of the acceptable range of temperature and salinity is wider (Aurich 1941). Male dab arrives earlier on the spawning grounds and stay throughout the duration of the season, while females appear to return to feeding habitats close by in between batches (Rijnsdorp 1992). Figure 5.9.3-1 shows the spawning areas as compiled by Höffle et al. (2015).

Spawning period

Spawning period is reported to occur from January to August in the southern area, i.e. off Brittany and southern England. Further north it occurs from April to June (Daan et al. 1990; Rijnsdorp 1992).

Spawning Table North Sea Dab

Central North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Brittany-Southern England

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period Green: Peak spawning

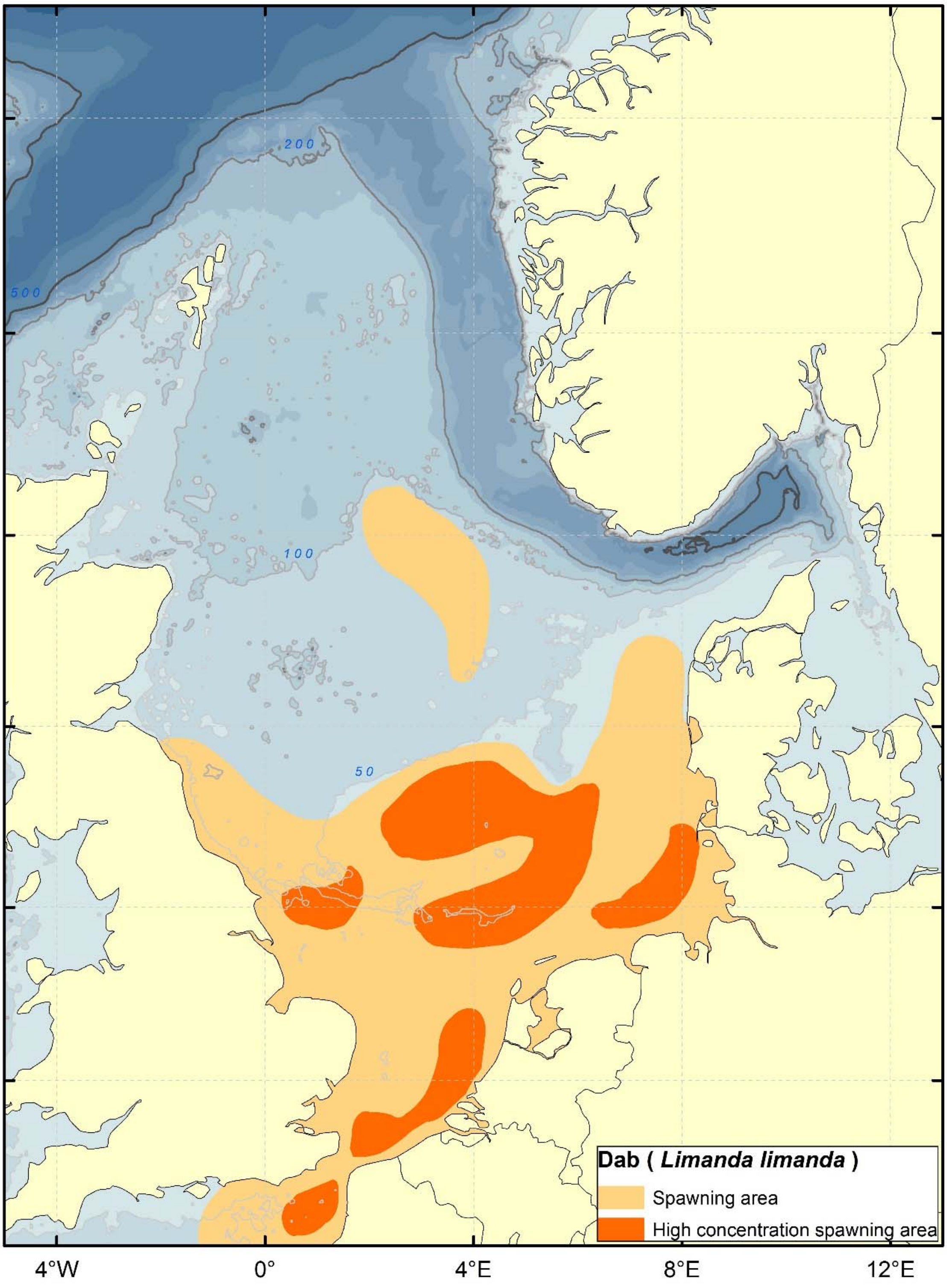

Figure 5.9.3-1. Spawning areas of dab in the North Sea.

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5.9.4 Lemon sole – *Microstomus kitt* - lomre

General stock features

Lemon sole, whilst commanding a high market price, does not occur at high enough densities to be a target species for a directed fishery (Heessen and Daan 1996). Since 1945 and particularly since the 1980s, catches of lemon sole have tended to increase (Heessen and Daan 1996, Rijnsdorp et al. 1996). This species, along with long rough dab and witch, belongs to the northern demersal fish assemblage (Ehrich et al. 2009). In the central and northern North Sea the species is considered abundant (Daan et al. 1990). Like long rough dab, lemon sole does not show a size dependent depth gradient and as such has no clearly defined nursery areas (Daan et al. 1990). In summary, this species is spread out in most of the North Sea, but in low concentration in the Southern sub region (Goldsmith et al. 2015). The species is also less abundant in the northeastern part of the Northern sub region. The highest concentrations are found in the western part of the Central sub region.

Spawning areas

The distribution of ripe and running lemon sole is largely coinciding with the areas of highest concentration in the distribution of the stock, i.e. across the Central sub region from the English coast to the western slope of the Norwegian Trench. Spawning occurs at around 100 m depth with the majority of larvae occurring east of the Moray Firth (Taylor et al. 2007). Figure 5.9.4-1 shows the spawning areas as presented by Höffle et al. (2015).

Spawning period

Russel (1976) reported spawning to occur from January through October.

Spawning Table North Sea Lemon sole

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

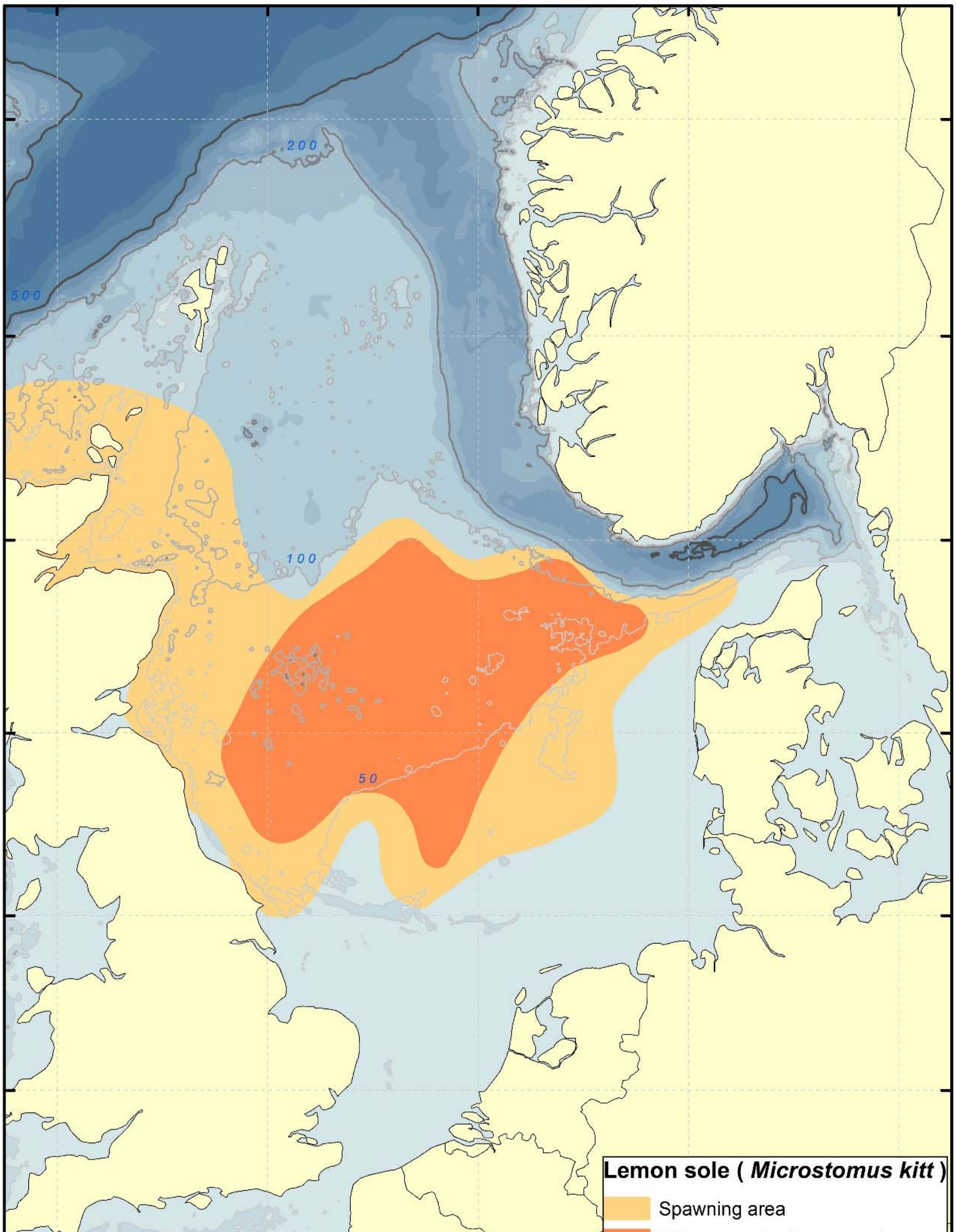

Figure 5.9.4-1. Spawning areas of lemon sole in the North Sea.

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5.9.5 Flounder – *Platichthys flesus* - skrubbe

General stock features

The flounder is a very widely distributed species from throughout the Mediterranean, into the Baltic and northward to the Barents Sea (Wheeler 1978). The tendency is for this species to tolerate less saline water the cooler the environment, hence their significant presence in the Baltic (Wheeler 1978, Goldsmith et al. 2015). Conway et al. (1997) found flounder larvae to be the second most abundant flatfish larvae in the southern North Sea, however, the species appears to be rare in the North Sea (Daan et al. 1990). This is probably due to its catadromous behaviour where by it spends much of its life in brackish water, tending to make annual migrations out to sea for spawning. Therefore, flounder is usually found near the coast or in estuaries and larvae are only found off the Dutch and German coasts (Taylor et al. 2007). It occurs mostly along the continental coast in the southeastern North Sea and the population size was more or less stable between 1970 and 1993 (Heessen 1996, Ehrich et al. 2009). However, on an even longer time scale, between the first and the last decades of the 20th century, stock size has sharply increased (Rijnsdorp et al. 1996). The distribution given in the figure of Goldsmith et al. (2015) accurately reflects the distribution in the winter and summer, however, may not be fully representative of the distribution at other times of the year e.g. spawning time.

Spawning areas

The current literature concerning flounder spawning in the North Sea indicate the principal spawning areas are confined to the eastern part of the Southern sub region and in the German Bight (Höffle et al. 2015). Spawning occurs farther inshore than for dab (Lelievre et al. 2012) and has been observed between 20 m and 40 m depth out to about 60 nautical miles offshore, north and northwest of the Dutch coast, in the Channel and northwest of Helgoland (Figure 4; van der Land 1990). From the Netherlands northwards the egg densities decrease (Lelievre et al. 2012). Munk et al. (2009) observed flounder at a Jutland Current section at 55 ºN. Some lesser concentrated spawning also takes place at Dogger Bank. Preferred hydrographic conditions for spawning appear to be >32 salinity and temperatures of 4 – 6°C at depths of around 20 m (Aurich 1941). Figure 5.9.5-1 shows the spawning areas as compiled from the information given in Höffle et al. (2015) and Munk et al. (2009). There is considerable uncertainty concerning spawning in the northern part of the North Sea due to a lack of suitable survey material.

Spawning period

The spawning season lasts from January to April in the southern part of the North Sea and extends until July in the North (Simpson 1949). Highest concentrations of eggs occur in February in the southern area.

Spawning Table North Sea Flounder

Central North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Southern North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

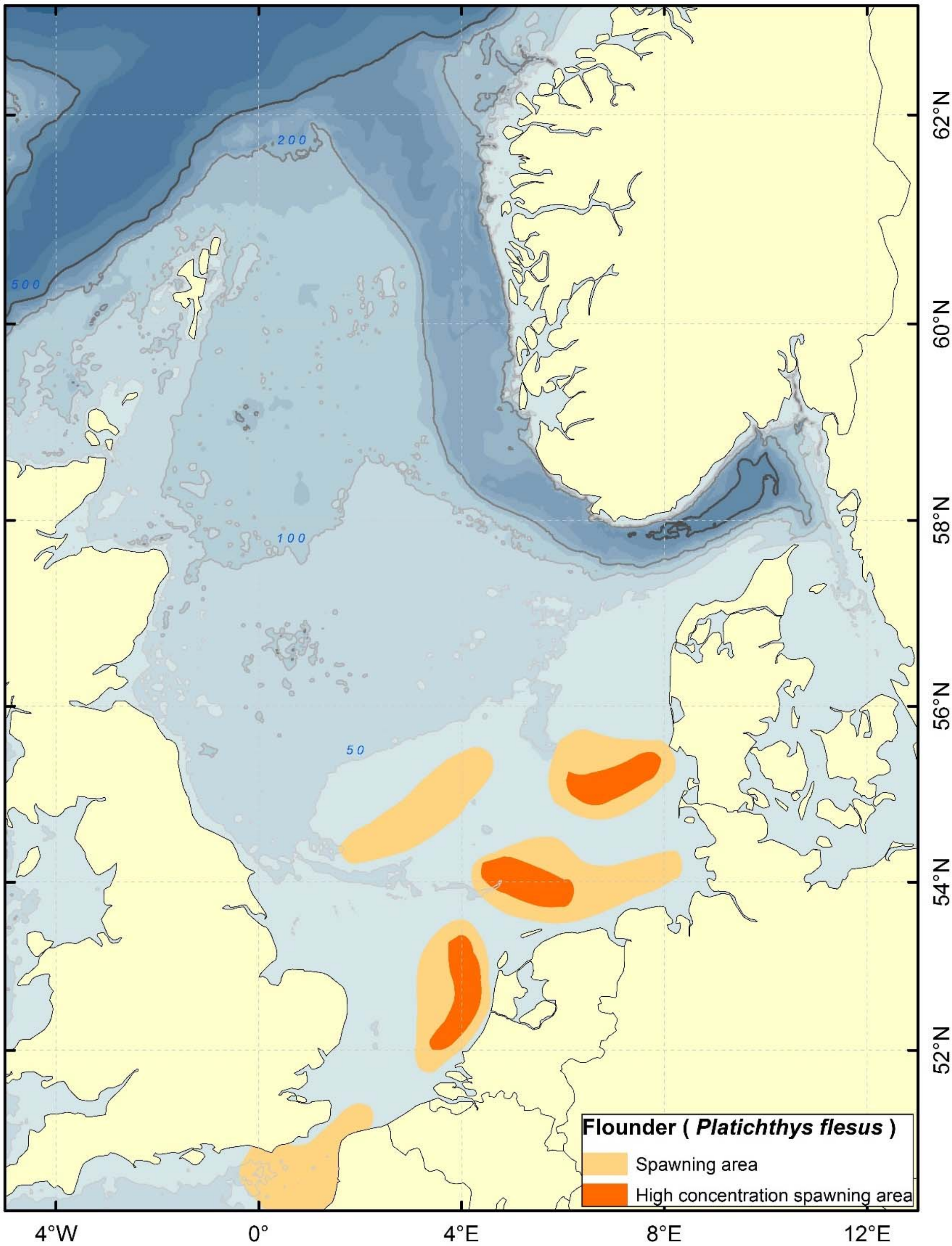

Figure 5.9.5-1. Spawning areas of flounder in the North Sea.

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5.9.6 Plaice – *Pleuronectes platessa* - rødspette

General stock features

Plaice is a commercially exploited species with a long history of exploitation and has been the subject of a considerable amount of research. This species generally inhabits relatively soft substrata and occur between 0 and 200m but are most abundant between 10 and 50m (Wheeler 1978). Plaice distribution is widespread, occurring in the Mediterranean, along the eastern Atlantic up in to the Barents Sea. They also occur around Iceland. As with many species the distribution of the stock has changed over time and since the 1980s the abundance of plaice in the northwestern region of the North Sea, in the vicinity of the Orkney and Shetland Islands has increased (Engelhard et al. 2011). The figure in Goldsmith et al. (2015) shows catch rates of plaice in the North Sea from the standard trawl surveys. Plaice nursery grounds are generally shallow water, sandy, coastal areas which are generally not estuarine. These occur all around the margins of the North Sea with notable nurseries including the Wadden Sea and the inner Skagerrak (e.g. Hufnagl et al. 2013). In this species there is a displacement offshore, into deeper water with age and size.

Spawning areas

Spawning of plaice is patchy and occurs in a variety of specific locations across its whole distribution. In regard to the North Sea specifically, spawning occurs from the English Channel and the Southern Bight in south (Harding et al. 1978; Coombs et al. 1990; van der Land 1991; van Damme et al. 2009), northeastward towards the southern slope of the Skagerrak deeps, and northwestwards to the Orkneys and Shetland (see Höffle et al. 2015). The patchy nature of spawning locations may be more governed by the location of the suitable shallow water nurseries rather than ideal ambient conditions for spawning (Hufnagl et al. 2013).

Much of the research covering plaice eggs has centred on the spawning in the southern North Sea and as such much of the literature on plaice eggs is confined to the Southern sub region of the North Sea giving an impression that this is the principal spawning area (Harding et al. 1978; van der Land 1991; van Damme et al. 2009; van der Veer et al. 1998). However, Munk et al. (2009) found the high egg concentrations in the eastern part of the Central sub region, south of Great and Little Fisher Banks and Höffle et al. (2015) found ripe and running plaice extended all the way to Shetland. Further evidence for these more northerly spawning areas are provided by Rogers and Stock (2001 and Ellis et al. (2012). These increases in the plaice population in the northern North Sea, particularly since 1990s (Engelhard et al. 2011) may partially account for these more recent observations. However, there has been a vibrant plaice population in the Skagerrak for a considerable amount of time. Figure 5.9.6-1 shows the current perception of plaice spawning grounds in the North Sea. At present there is uncertainty as to the location of spawning in the Skagerrak.

Not all North Sea plaice spawn within the North Sea, three spawning centres are in the eastern English Channel from which more than half the fish belong to North Sea populations (Houghton and Harding 1976). Like those spawning in the Southern Bight, these fish appear to come from populations on the western side of the North Sea (Hunter et al. 2003, 2004). It should also be noted that plaice will make substantive migrations, off the bottom in the water column, prior to and during the spawning season (Hunter et al. 2003, 2004).

Spawning period

Spawning is confined to the early part of the year and with a relatively short spawning period of about 4 months (Goldsmith et al. 2015). According to Hufnagl et al. (2013) plaice generally spawn between December and March with reproduction starting earliest in the Eastern English Channel. Peak spawning occurs in the Southern Bight in February and south of the Dogger Bank and in the German Bight mainly during February and March (Harding et al. 1978; van der Land 1991). For southern and central NS (Dutch grounds) Rijndorp et al. (2005) found that spawning season started in late December and ran to beginning of April with peak spawning in January. In the eastern English Channel spawning starts in December and is progressively later north through the North Sea (Bagenal, 1966). Spawning peaks in mid-January in the Southern Bight and in February/March in the more northern regions (Simpson 1949; Harding et al. 1978).

In older males, but not in young males, a secondary peak of running males emerges in March (Bromley 2000). Judging by the proportion of running females, spawning commences in January, peaks in February and ends in March. Spawning activity is most intense on the central-southern ground during January/February, compared with February/March at the central-northern ground. On the Flamborough ground, spawning was progressively delayed moving north eastwards, being concentrated in January in the south and February/March in the north.

Spawning Table North Sea Plaice

Northern North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Southern North Sea

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

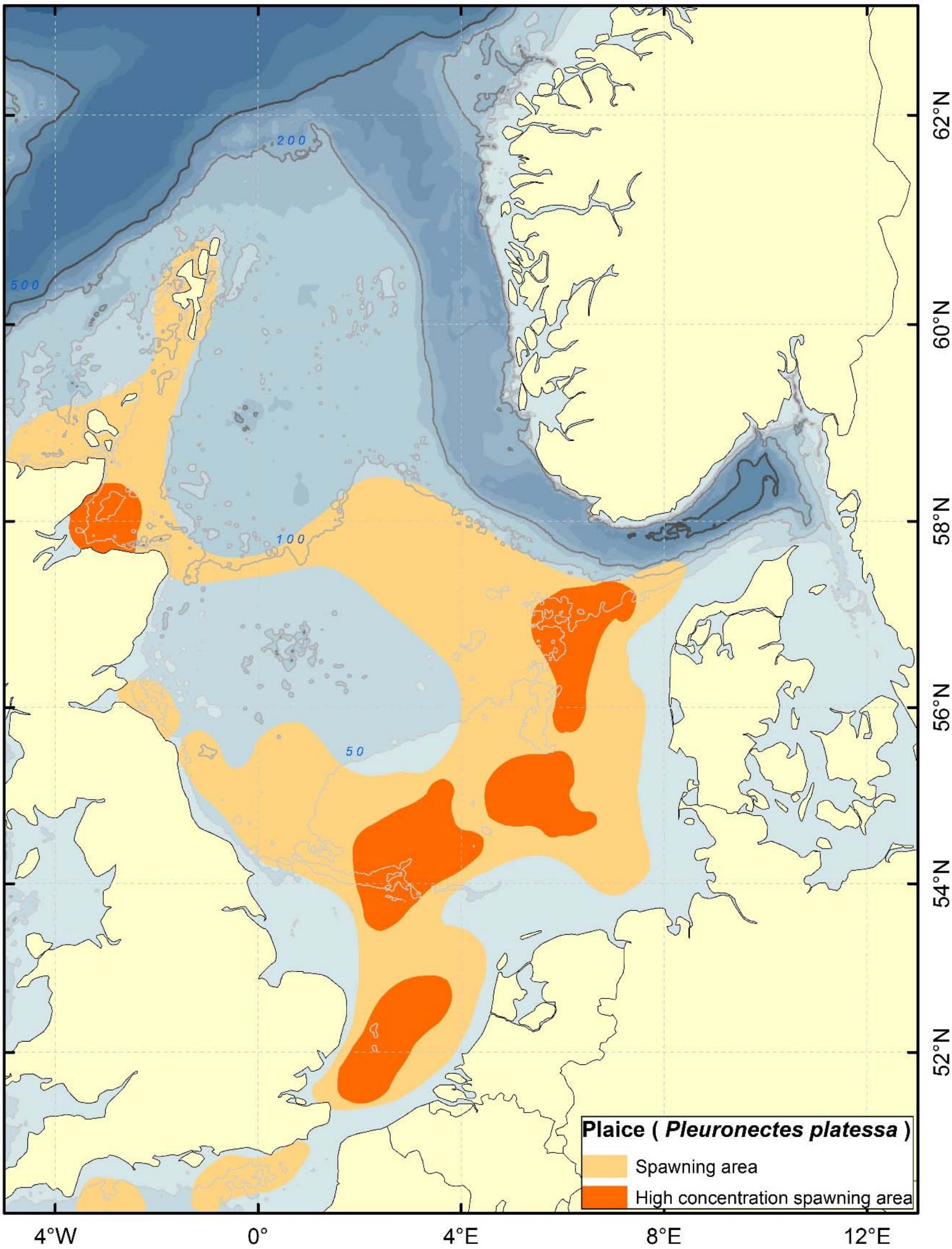

Figure 5.9.6-1. Spawning areas of plaice in the North Sea.

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5.10.1 Greater argentine – *Argentina silus* - vassild

General stock features

Greater argentine is found close to muddy bottoms near the edge of the continental shelves at bottom depths between 150 and 550 m, but can be caught down to 1500 m (Heessen 2015). The preferred temperature range is 5-8 ^{o}C. The lesser argentine (*Argentina sphyraena*) is also found above muddy bottom, but at shallower depths, often on the shelf, typically 50-200 m. The figure in Heessen (2015) shows the combined catch rates of greater and lesser argentines from trawl surveys where the lesser argentine occupies the shallower shelf regions while greater argentine dominates the outer slopes. In the North Sea, greater argentine predominantly occur in the Norwegian Trench and the deeper parts of the Skagerrak (Bergstad and Isaksen 1987).

Spawning areas

There is very little information on the spawning of this species and *A. sphyraena*. Spawning of greater argentine occurs patch-wise along the shelf (Heessen and Kuiter 1991). The eggs are generally found typically between 150 and 350 m depth (Bergstad and Gordon 1994). Figure 5.10.1-1 indicates probable locations where greater argentine spawn.

Spawning period

Eggs and larvae have been found year around in the Rockall region as well as in Skagerrak. Maximum intensity in the Rockall region is during the second half of the year (Ehrich 1983) while in the Skagerrak maximum is during spring (Bergstad and Gordon 1994). In Norwegian waters farther north, i.e. the Møre coast, spawning occurs from March through summer with the maximum spawning intensity in May (Johannessen and Monstad 2003).

Spawning Table Greater argentine

Møre

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Skagerrak

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Rockall

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

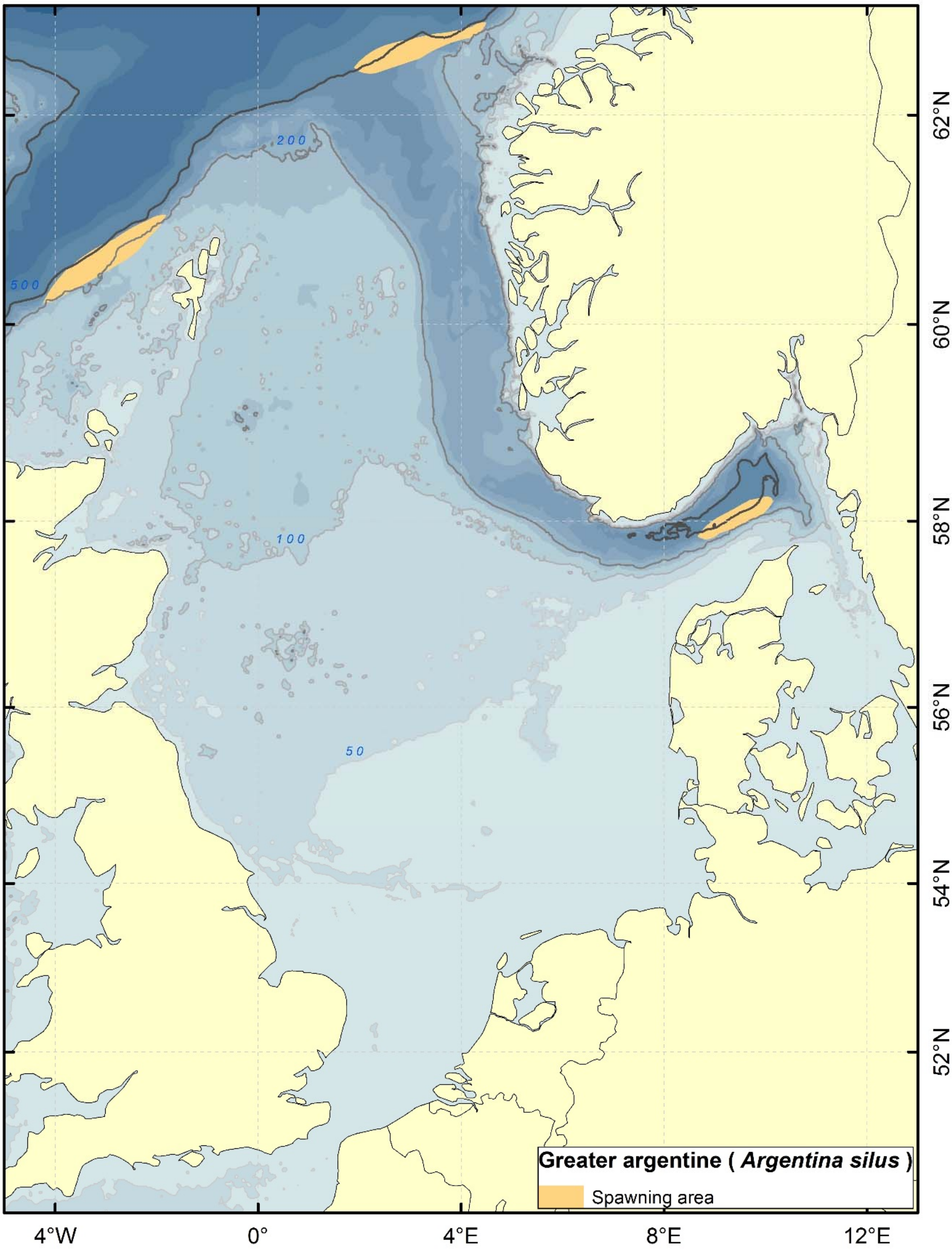

Figure 5.10.1-1. Greater argentine spawning areas in the North Sea.

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5.11.1 Roundnose grenadier – *Coryphaenoides rupestris* - skolest

General stock features

Roundnose grenadier is a deep-water species rarely found shallower than 250 m depth (Bergstad 1990). Therefore, in the North Sea and the adjacent waters, it is confined to the Skagerrak-Norwegian Trench and the surrounding continental slope regions, however, there are occasional records of catches from the Northern sub region of the North Sea (see the figure in Bergstad (2015)). This species has a preference for temperatures above 5 ^{o}C (Bergstad and Isaksen 1987) which implies that it is confined to the Atlantic water masses. The Norwegian Trench-Skagerrak population appears to be isolated from the populations in the deep Norwegian fjords (Bergstad and Gordon 1994) and has recently been confirmed using molecular methods (Knutsen et al. 2012).

Spawning areas

In contrast to many other high-latitude fish, spawning occurs in autumn (October-December) (Bergstad and Gordon 1994). The eggs are large, 2.2 – 2.8 mm and with an extended incubation time of the eggs (Bergstad and Gordon 1994, Bergstad et al. 2014). Eggs are found in the deeper parts of the Skagerrak region (Bergstad and Gordon 1994). It is uncertain whether spawning also occurs farther north in the Norwegian Trench. Figure 5.11.1-1 shows the roundnose grenadier spawning area.

Spawning period

Spawning occurs in later autumn in Skagerrak (Bergstad and Gordon 1994), while west of the British Isles it occurs over a more protracted period (Allain 2001).

Spawning Table Roundnouse grenadier

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

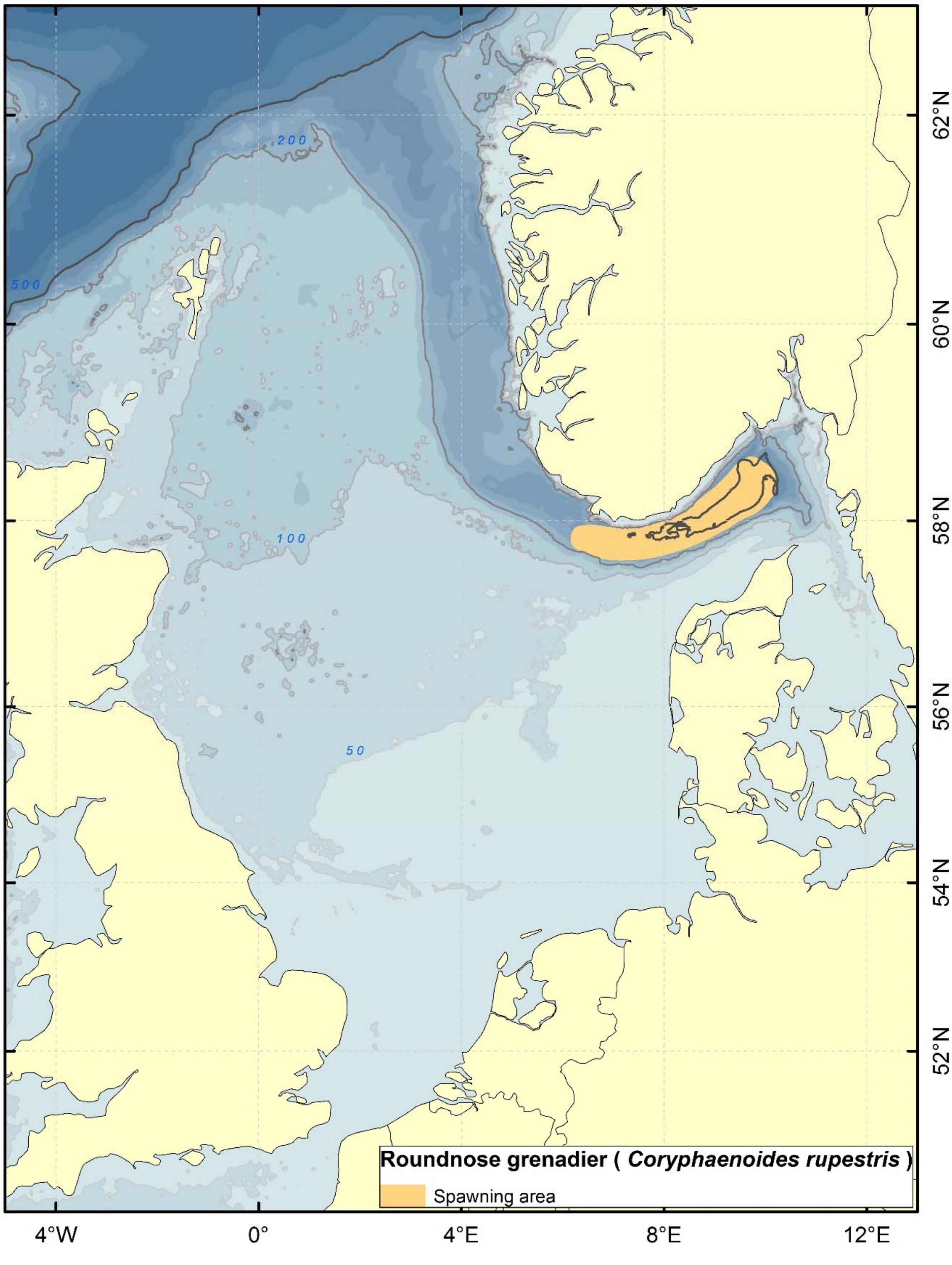

Figure 5.11.1-1. Spawning areas of roundnose grenadier in the North Sea.

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5.12.1 Anglerfish – *Lophius piscatorius* - breiflabb

General stock features

Anglerfish is widely distributed in the northern North Sea, Irish Sea and west of the British Isles (Ellis and Velasco 2015), but it is scarce in the Southern sub region of the North Sea and in the German Bight-Jutland Current. The figure in Ellis and Velasco (2015) shows the catch rates of anglerfish in the North Sea and adjacent waters. Catches in midwater, especially of females, over deep water, have been attributed to spawning migrations (Hislop et al. 2001). Large fish seems to occupy deeper waters while the younger specimens are confined to shallower regions (Laurenson et al. 2008).

Spawning areas

West of Scotland mature fish are typically found at deeper waters (Afonso and Hislop 1996) indicating spawning along the shelf edge. It appears that spawning grounds are in deep water (150-900m) (Hislop et al. 2001) and as such could only occur in the northern extreme of the North Sea or along the Norwegian trench in the eastern northern North Sea. However, early studies by Bowman (1920) showed that angler fish eggs were also abundant in shallower regions in the northwestern North Sea in the region from Shetland to Fladen Ground and westwards to north of Peterhead, Scotland. It is uncertain whether these early spawning areas still exist today. However, these distributions also have some support from "todays" observations (Hislop et al. 2001). It should be noted that the eggs are laid in 'gelatinous ribbons' which may be more than 10x0.25m in size, also newly hatched larvae may also be in very high densities (Hislop et al. 2001), presumably before they disperse. Both the eggs and the larvae are pelagic. Figure 5.12.1-1 shows the anglerfish spawning areas in the vicinity of the North Sea.

The Black-bellied anglerfish (Lophius budegassa)

There as a congener to the Angler, namely the Black-bellied anglerfish. This species was not recognized prior to 1970 and as can be misidentified for the anglerfish. This is a southern species which is generally found to the west of the British Isles and southward (see Ellis and Velasco. 2015). It occurs occasionally in the northern North Sea but generally in deep water. Spawning is along the edge of the continental shelf. Presumably this species has similar spawning characteristic to the related *L. piscatorius*.

Spawning period

There is no clear consensus in the literature on the spawning period of anglerfish. Russell (1976) deducted that spawning occurred from February to August. On the other hand, Laurenson et al. (2008) reports ripe catches of ripe females in Scottish waters from November to March. The question is whether assessment of ripe is identical to ripe and running. We here assume that spawning is during first half of the year.

Spawning Table Anglerfish

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

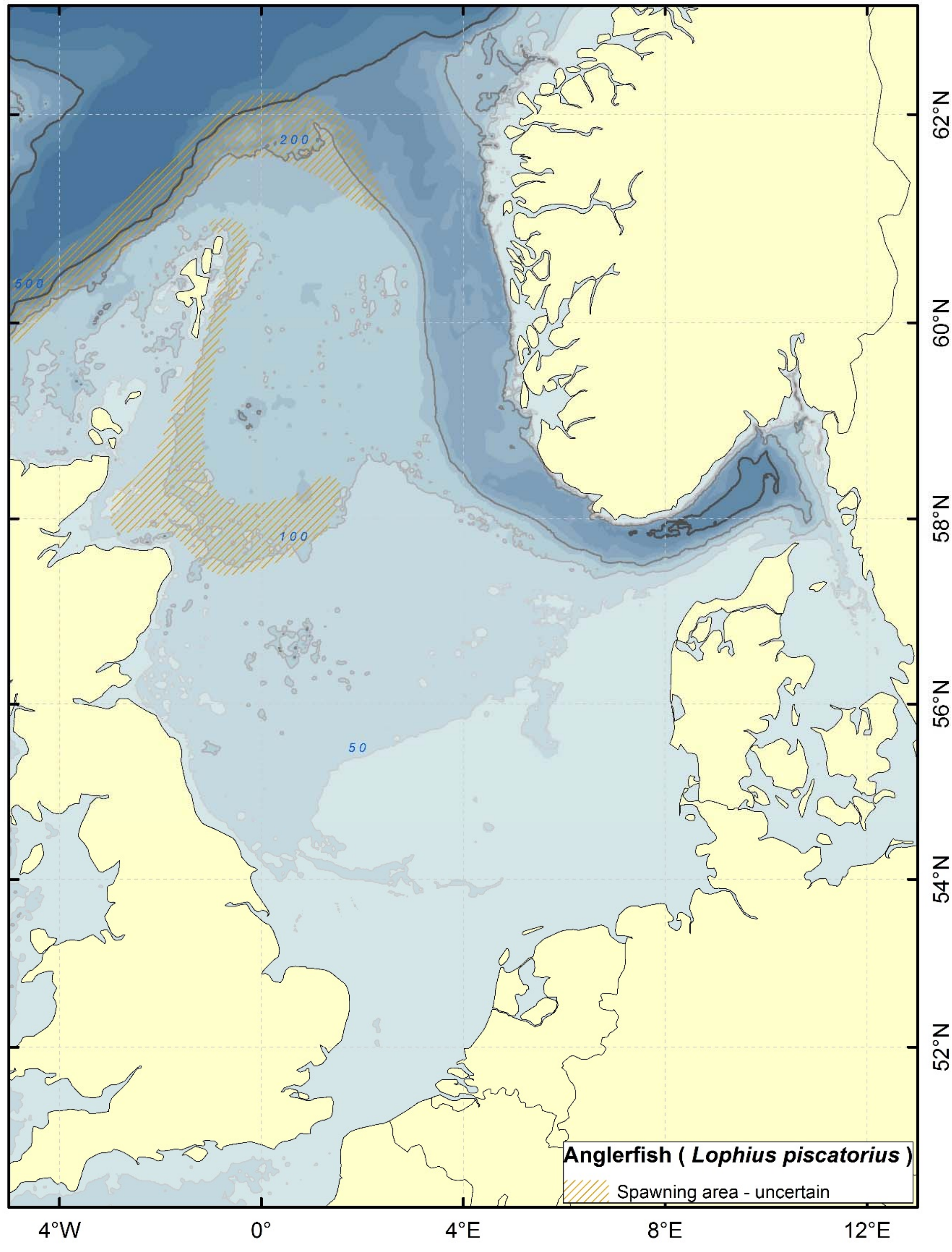

Figure 5.12.1-1. Spawning areas of anglerfish in the North Sea.

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5.13.1 Pearlside – *Maurolicus muelleri* - laksesild

General stock features

Pearlsides are widely distributed over large areas of the North Sea and adjacent waters, but is very scarce in the Southern sub region and the German Bight-Jutland Current (Kloppmann and Ellis 2015). This species is mesopelagic with depth range about 100-500 m. Pearlside is not a commercial species, but it is considered as an important prey species for other fish. Pearlside matures at the age of 1 year (Kristoffersen and Salvanes 1998).

Spawning areas

Pearlside eggs are found in the mesopelagic zone, typically at depths greater than 200 m. In the Norwegian Sea, eggs are found from 200 to 500 m depth (Salvanes 2004). Spawning is known to take place in Norwegian fjords. In addition, Gjøsæter (1981) reported that that eggs were also found off the West Norway coast (unpublished data from Bjørke). Figure 5.13.1-1 indicates presumed location of the spawning areas associated with the North Sea region.

Spawning period

Major part of spawning occurs in late spring to late summer, but eggs can be found throughout the year (Coombs et al. 1979). In Norwegian fjords (West Norway) pearlside eggs have been found in large concentration during late spring

Spawning Table Pearlside

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC

Yellow: Total spawning period   Green: Peak spawning

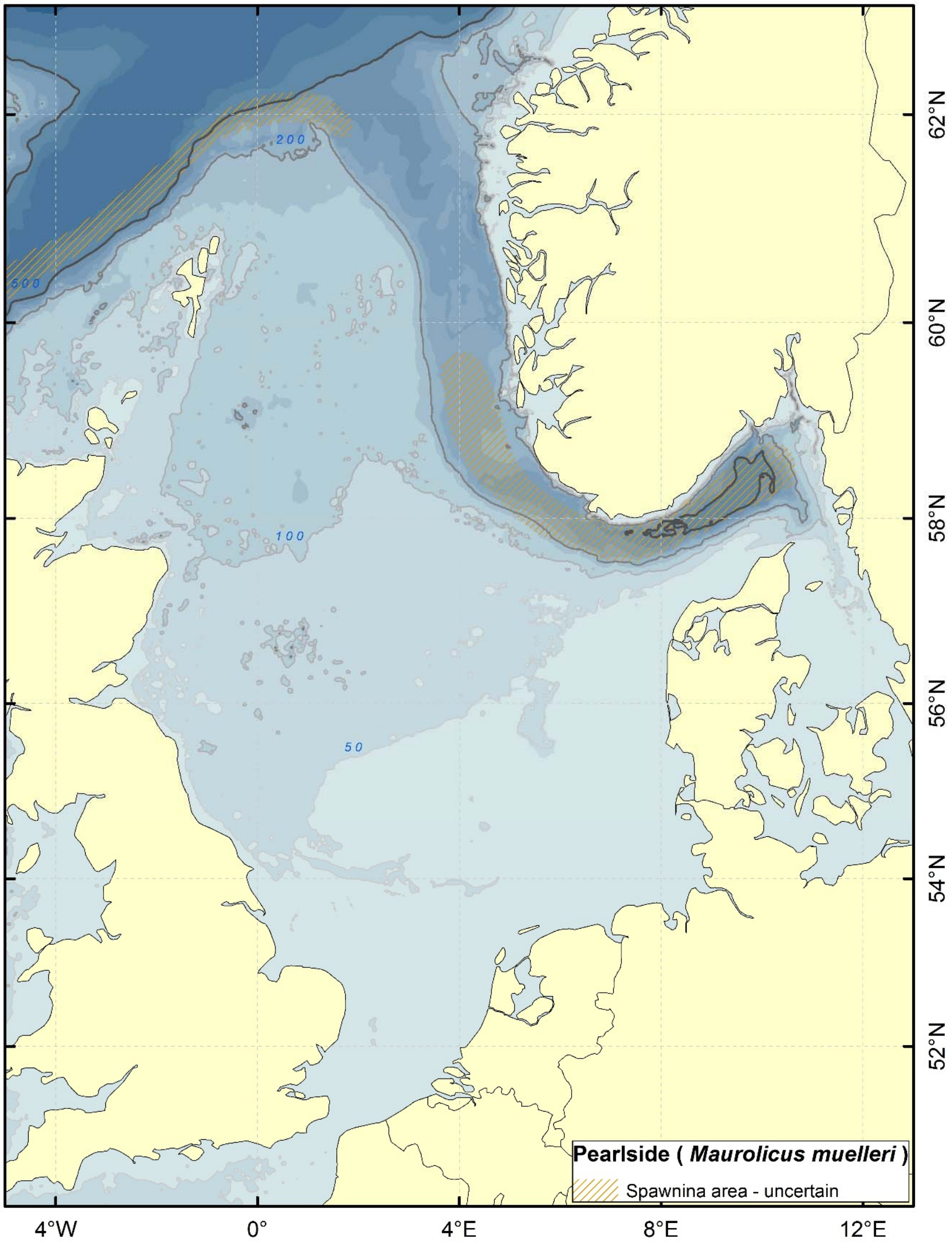

Figure 5.13.1-1. Spawning areas of pearlside in the North Sea.

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6. Knowledge gaps and future research

A behavioural attribute in marine vertebrates is their aggregation within limited parts of their natural habitats to spawn. These spawning areas are most often revisited year after year to a varying degree of precision depending on ambient conditions that vary over a range of spatial and temporal scales. The selection of the spawning areas are long-term adaptations to optimize food conditions and suitable drift pattern for the pelagic offspring. Demersal or benthic spawners, with heavy eggs that either are distributed in the bottom boundary layer or adhere to the bottom generally rely on specific sea bed substrates. Therefore, species such as herring and sandeel, have very precise spawning areas. In the case of sandeel the spawning area, nursery ground and adult habitat are all the same location. Spawners with pelagic eggs may have less fixed spawning areas due to the fluctuating properties of the free water masses. Species such as mackerel for instance, initiate spawning at a specific temperature rather than at a specific geographical location. Such fluctuations in thermal habitats are found over a range of time scales from days to months, interannual and multidecadal. While the short-term fluctuations are most often associated with small spatial space scales, multidecadal fluctuations, such as the warming of the North Sea from the cool 1960s and 1970s to the present warm phase, are associated with very large spatial changes. These changes in habitat result in changes in spawning locations, examples being hake (section 5.2.1), sardine (section 5.4.2), and anchovy (section 5.5.1). This implies that comprehensive and precise observations on spawning locations in the past might be invalid for the present situation. To illustrate this point we highlight the comprehensive investigation on spawning areas for anglerfish by Bowman (1920) (section 5.12.1). Since these detailed studies were conducted very little research has been undertaken on anglerfish. Therefore, there is no supporting information to confirm whether the nearly 100-year old detailed information is still valid for the present ocean climate and hydrography. In the case of more recent investigations, often the sampling is not at a high enough spatial resolution to identify the mosaic of 'patchy' spawning sites. Finally, there are also annual shifts in the spawning areas that makes observations of eggs and mature fish for one single year or combining many years, insufficient for predicting the spawning areas in future years. It should be borne in mind that the spawning maps in the present report are based on "snap shots" from a range of time periods and assumed to be broadly indicative of the average current spawning areas. These maps do not account for inter-annual variability in location or intensity of spawning over geographical scales. Both of these factors are dependent on the ecology and population dynamics of the fishes and interannal and longer-term climate forcing.

One particular challenge for egg surveys, especially in the North Sea, is that a number of species utilise the same spawning areas at about the same time. This problem is probably more acute than in other areas, e.g. north of 62 □N. The early stages of eggs, especially gadoids, are identical in visual appears, only differing in their size ranges that also overlap in varying degree. Therefore, for some species it is impossible to determine species specific distributions due to the overlap in spatial distribution and the inability to visually confirm the species identification. Precise visual species identification is only possible with later egg stages when the embryo within the egg is sufficiently developed and the species-specific morphology and pigment patterns are visible. The consequence is that for species identification of early stage eggs, the most informative development stages for determining species specific spawning distributions and timing, molecular identification techniques will need to be employed. At present, these methods are considerably more laborious and expensive, although it would be possible to develop more cost-efficient methods and protocols.

This work had highlighted our uncertainties with respect to the spawning ecology and dynamics of fishes in the northern North Sea. Whilst we still do not know the location of *spawning areas* with a reasonable level of precision our biggest knowledge gap concerns the *spawning periods*. Collectively the spawning areas for fishes in the North Sea cover a very wide area, therefore to provide realistic advice for non-intrusive seismic exploration by the oil industry considerable more information is needed on spawning periods, in particular. Spawning periods vary between species and annually for a range of reasons: Boreal species, in general, tend to have their spawning periods confined to spring time, while many temperate species have a more extended spawning period throughout the year. Another factor is the latitudinal effects of spawning period, since spawning needs to be synchronized with the plankton production to provide enough food for the planktonic offspring to survive.

In conclusion, future research should focus on reducing the largest knowledge gap which is on the spawning periods of the various fish species. We propose that the main part of the future research programme concentrates on sampling fish eggs in selected areas of the North Sea at a high frequency. The objective is to determine the spawning times of the principal species at these locations. Initially, the sampling sites should cover a latitudinal gradient (north-south) since the onset and duration of spawning is likely to vary across this gradient. Also, the gradient will provide information on potential longer-term changes in spawning period and duration with climate change. In addition to the research on spawning periods there is also a necessity to provide some support for research over broader geographical scales, which will provide information on changes in spawning grounds and how the spawning periods seen in the detailed studies relate to the North Sea in general.

7. Appendices

7.1 Lesser sandeel (*Ammodytes marinus*) – a vulnerable species to overfishing and habitat destruction in the North Sea

Lesser sandeel (hereafter sandeel) is planktivorous fish that can grow to a maximum length of 24 cm. Being highly abundant, it forms an important mid-trophic link between plankton and higher trophic levels, including larger fish, sea mammals and sea birds (Hardwood and Croxall 1988, Greenstreet et al. 1998, Furness and Tasker 2000, Wanless et al. 2005). Hence, sustainable management of this species is important not only for the fishery, but also for the functioning of the ecosystem of the North Sea. Here, historical patterns in landing of sandeel from fishing grounds in the Norwegian sector of the North Sea (NEEZ) are described as a basis for evaluating ‘demographic connectivity between sandeel grounds. This, in turn, is used to evaluate the vulnerability of sandeel to habitat destruction and to overfishing. The results and conclusions are a synopsis of a paper by from Johannessen and Johnsen (submitted), with focus on factors that are important for sustainable management of sandeel in NEEZ.

7.1.1 Biology

Sandeel live manly as infauna, but appear also in large, pelagic schools. As infauna, sandeel bury in the seabed in relatively coarse sand (Macer 1966, Wright et al. 2000). The dependency on suitable sandy habitat is reflected in a patchy distribution with spatially separated sandeel grounds (Fig. 7.1.1). During winter sandeel hibernate in the sand. In spring, sandeel, which are then very lean, emerge from the seabed at dawn to feed on zooplankton in dense, pelagic schools which are targeted by trawlers and predators. At dusk sandeel return to their sandy habitat. Around mid-summer ≥1-year old sandeel have normally built up sufficient energy reserves to hibernate again (Winslade 1974), whereas 0-group sandeel may continue feeding until November in order to build up sufficient energy reserves to hibernate through the winter (van Deurs et al. 2011).

The majority of sandeel become sexually mature at the age of 2. Spawning takes place in December to January in the same area as they live (Bergstad et al. 2001). The eggs are laid on the seabed where they remain until hatching around February-March (Wright and Baily 1996). The larvae are pelagic until around June, when they settle (Lynam et al. 2013). After settlement sandeel have high site fidelity (Jensen et al. 2011). Hence, potential exchange of individuals between sandeel grounds is mainly during the pelagic larval stage (Berntsen et al. 1993, Proctor et al. 1998, Christensen et al. 2008).

7.1.2 Fishery and management

The sandeel fishery is carried out with fine-meshed (≤16 mm) bottom trawls. The trawls are equipped with metal chain footropes, which only allow trawling on smooth, sandy bottom substrate. Fishing is carried out during daytime, and the main fishing season is between April and June/July (ICES 2009). In some years there has been a substantial fishery of young of the year sandeel in the second half of the year.

The sandeel fishery in the North Sea developed gradually from the early 1950s and reached a plateau in the mid-1970s. Between 1977 and 2002 the species sustained the largest fishery in the North Sea with annual landings varying between 569 and 1140 kt (mean 772 kt). In 2003 landings dropped abruptly and have since then fluctuated between 177 and 438 kt. The reduction in landings was particular severe in NEEZ where the fleet in 2003-2005 caught only 5-10% of the long term annual mean (ICES 2014).

Except for some national management regulations such as the closure of the sandeel fishery off the northeastern UK coast in 2000 in order to protect the local sandeel stock close to seabird colonies (Greenstreet at al. 2006), and some unilateral regulations in NEEZ from 2005 onwards (Table 7.1), the sandeel fishery in the North Sea was practically unrestricted until 2011. The only year the total allowable catch advice (TAC) by ICES limited landings was in 2007.

An essential aspect of management of marine resources is to identify the unit stock. If a fish stock consists of several sub-stocks, unbalanced fishing effort may result in the collapse of sub-stocks, even under moderate overall fishing mortality (Frank and Brickman 2001). Violation of the unit stock assumption may thus have severe impact on both fishing yield and biodiversity (Cowen et. al. 2000, Sterner 2007, Reiss et al. 2009). In the North Sea ICES treated sandeel as a unit stock until 2011. However, it had long been recognized that sandeel in the North Sea probably consists of several sub-stock (Pedersen et al. 1999), and based on modelling studies of larval drift and differences in growth rates and age at maturity, seven sub-stocks were identified, and since 2011 this has been the basis for the assessment of sandeel in the North Sea by ICES (ICES 2014).

The modelling studies of larval dispersion (Berntsen et al. 1993, Proctor et al. 1998, Christensen et al. 2008) were all based on the assumption of the sandeel larvae drifting passively. However, there is mounting evidence to suggest that pelagic larvae of many marine demersal fishes have well developed capabilities to cope with moving water masses and settle in favourable habitats (Leis 2006). Hence, modelling studies treating larvae as passive drifters can only provide theoretical patterns of larval dispersal. As all the seven sub-stocks of sandeel in the North Sea consist of fragmented fishing grounds (Jensen et al. 2011), an important question is whether the modelling studies are realistic for identifying unit stocks.

Here, the question of demographic connectivity between sandeel is approached by analysing historical patterns in landings from individual fishing grounds in NEEZ, of which all but one (Vikingbanken) belong to the same stock as defined by ICES (stock no. 3). Demographic connectivity is defined as the exchange of individuals between subpopulations which is sufficient to affect population dynamics.

7.1.3 Sandeel ground in NEEZ

All sandeel grounds in NEEZ are depicted in Fig. 4.X.1. Generally, sandeel habitats are larger coherent sandy areas. However, Vestbanken consists of many smaller sandy patches surrounded by rougher bottom. Over part of these rough bottom areas there are relatively high densities of sandeel which reside in patches of sand that are too small for the commercial sandeel trawlers to operate (Johannessen and Johnsen submitted).

7.1.4 Historical landings

Fig. 7.1.2 shows annual landings per year from the individual sandeel grounds in NEEZ for the period 1994-2008 (2008 was the last year with landings before introduction of a new spatial management system in NEEZ). For Vikingbanken it was possible to reconstruct historical landings back to 1977. It can be noted that all sandeel grounds had periods of consecutive years with landings and consecutive years without landings, except Vestbanken where sandeel have been landed uninterruptedly. All together there were 68 years with landings and 67 years without landings for the period 1994 to 2008 (due to some misreporting of landings with respect to fishing grounds, very low landing are treated as 0). In all years without landings the sandeel grounds were confirmed commercially depleted, i.e. the concentrations of sandeel were too low to sustain a profitable fishery (Johannessen and Johnsen submitted). The problem with commercial depletions have been grater at the northern fishing grounds (ρ=0.809, p=0.008; Spearman rank correlation between number of years without landings and the ranked distance from south to north; e.g. Inner Shoal east was ranked as 1 and Vikingbanken as 9), and commercial depletions have increased over time (ρ=0.739, p=0.002; Spearman rank correlation between number of years without landings and time).

Johannessen and Johnsen (submitted) concluded that the main cause of local depletions was overfishing, but that ecological changes in the North Sea around the turn of the century which resulted in poor recruitment in several fish stocks (Payne et al. 2009, Alvarez-Fernandez et al. 2012), might have contributed to the increasing problem over time.

7.1.5 Recruitment and local spawning stock

The mean age of sandeel in the landings in the first half of the year (the main fishing season) is 1.4 years, when 0-group is excluded (ICES 2002). Hence, continuous landings from the various sandeel grounds depend on regular recruitment. There are no estimates of spawning stock from the various sandeel grounds. Therefore, to study the relationship between local spawning stock and local recruitment, Johannessen and Johnsen (submitted) assumed that: 1 - the local spawning was higher in years with landings than in years without landings, which correspond to commercial depletion; and 2 – years with landing reflected higher recruitment success than years without landings.

Years with landing and years without landings were non-randomly distributed ($p<0.001$; Chi-square analysis), with a pronounced pattern of periods with continuous years with landings and periods of continuous years without landings (Fig. 7.1.2). However, such patterns may either reflect global or local phenomena. Global phenomena could for example be a result of continuous years of with good conditions for recruitment on a larger scale, and conversly, continuous years without landings bad conditions. If global phenomena, the same pattern should occur on all sandeel grounds, or at least on sandeel grounds that belong to the same unit stock as defined by ICES, i.e. all sandeel grounds in NEEZ except Vikingbanken. However, the patterns of periods with and without landings were not the same at the various sandeel ground ($p<0.001$; log-likelihood homogeneity ratio test for contingency tables), also with Vikingbanken exclude ($p=0.001$). Even between closely situated sandeel grounds there are substantial differences. This is particularly evident at Vestbanken and the closely situated Outer Shoal and Inner Shoal east and west. In 2002 to 2006 there were continuous years with recruitment at Vestbanken as reflected in relatively high proportion of I-group in the landings (39-92%), whereas the neighbouring grounds were all commercially depleted and suffered recruitment failure during the same period (Fig. 7.1.2). Interestingly, Vestbanken has natural refuges in for sandeel in the small sandy patches that are spread around the rougher bottom stretches (Fig. 7.1.1, indicate by a lighter red colour). Except for minor area at Inner Shoal west, none of the other sandeel grounds in NEEZ have such natural refuges.

Consequently, sandeel grounds with commercial concentrations of sandeel appear to have both more regular and substantially higher recruitment than sandeel grounds without commercial concentrations. It should be noted though, that none of the commercially depleted sandeel grounds were biologically depleted as an annual acoustic survey in April/May revealed sandeel on all sandeel grounds in NEEZ (Johannessen and Johnsen submitted). However, the sandeel schools at the commercially depleted fishing grounds were too small to be identified directly from the echo-sounder monitor, but were detected during post-processing using specialised software.

Commercial depletions of sandeel grounds may result in long-term recruitment failure. The importance of a local spawning stock and the consequences of depleting sandeel grounds is particularly evident at the isolated Vikingbanken. At this sandeel ground there two periods with continuous landings, around 1980 and in the mid-1990s (Fig. 7.1.2). During both periods there were continuous years of recruitment reflected in high proportions of 0- and I-group sandeel in the landings (Johannessen and Johnsen submitted). Both periods were followed by longer periods with recruitment failure following commercial depletions. In 1995 approximately 150 kt were landed from Vikingbanken, which is the highest landings of sandeel ever recorded from a single statistical square (~30x30 n. miles) in the North Sea (ICES 2010) [15], and thus underline the extraordinary high productivity in this area. It should be noted that although ICES uses a knife-edge maturity ogive of 2 years, studies have shown that larger individual of I-group can also be mature. In the central North Sea Boulcott et al. (2007) found that 50% maturity corresponded to ~13 cm. Strong year-classes of I-group may thus contribute to relatively high spawning stocks. For example, at Vikingbanken the high landing of sandeel in 1995 consisted of I-group sandeel, of which 35% were ≥13 cm at the start of the growing season in April. Hence, the local spawning stock was probably relatively large around the turn of the year 1994/1995, despite low abundance of ≥II-group. In 1996 I-group once again dominated landings (64%), suggesting relative good recruitment in 1995 and that the 1994-year-class was mainly fished at the I-group stage.

Johannessen and Johansen (submitted) suggested that homing of post-larvae and juveniles to natal ground was the most likely mechanism behind the importance of local spawning stocks.

7.1.6 Summary and conclusion

Historical landings of sandeel from fishing grounds in NEEZ have shown that overfishing may result in commercial depletions of sandeel grounds, which in turn may result in local recruitment failure lasting from a few to many years. The fact that sandeel spend most of the time buried in the sand, makes it vulnerable to mortality of other causes as well, for example toxic substance spread over the sandeel grounds. In additions, due to the dependency of suitable habitat sandeel is vulnerable to habitat destruction, both from substrate extraction and dumping.

The sandeel grounds in NEEZ are clearly defined as the areas where the trawling activity takes place. The only exception is the patches of sand spread around rough bottom areas at Vestbanken (Fig. 7.1.1). These patches appear to served as natural refuges for sandeel, and thus contributed to the continuous fishery at Vestbanken during a period when all other fishing grounds in NEEZ were commercially depleted. Most of the rough bottom area at Vestbanken does not contain sandeel. However, future activity that may have negative impact on sandeel, should always investigate the potential presence of sandeel patches.

In conclusion, sandeel is an important species for the North Sea ecosystem. There seems to be low demographic connectivity between sandeel fishing grounds in NEEZ over relatively short distances. Sustainable management of sandeel therefore depends on protection of sandeel habitats and keeping local spawning stocks at sufficiently high levels to ensure regular and high recruitment.

7.1.7 References

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Table 7.1.1. Unilateral regulations of the sandeel fishery in NEEZ.

Period	Regulation
≤2004	Fishing period: 1 March - 31 October, no TAC limit.
2005	Fishing period: 1. April - 23 June, no TAC limit.
2006	Experimental fishery only in order to estimate stock size based on CPUE.
2007	Fishing period: 1 April - 4 May to estimate stock size based on CPUE.
	Closure of fishery: 5 May - 15 May pending TAC advice from ICES.
	Fishing period: 16 May - 23 June, TAC limit and closure of English Klondike, Østbanken, Albjørn-Lingbanken, Nordgyden and Vikingbanken.
2008	Fishing period: 1 April - 3 May to estimate stock size basec on CPUE.
	Closure of fishery: 4 May - 8 May pending TAC advice from ICES.
	Fishing period: 9 May - June 3, closure of Østbanken, Albjørn-Lingbanken, Nordgyden and Vikingbanken.
	3 June: Norwegain authorities closing the fishery prior to reaching TAC limit.
	Fishing period: 2 June - 8 June, 5 vessels fishing on Østbanken, Albjørn-Lingbanken and Nordgyden. No fish were landed.
2009	Fishing moratorium.
2010	Implimentation of a spatial management system.

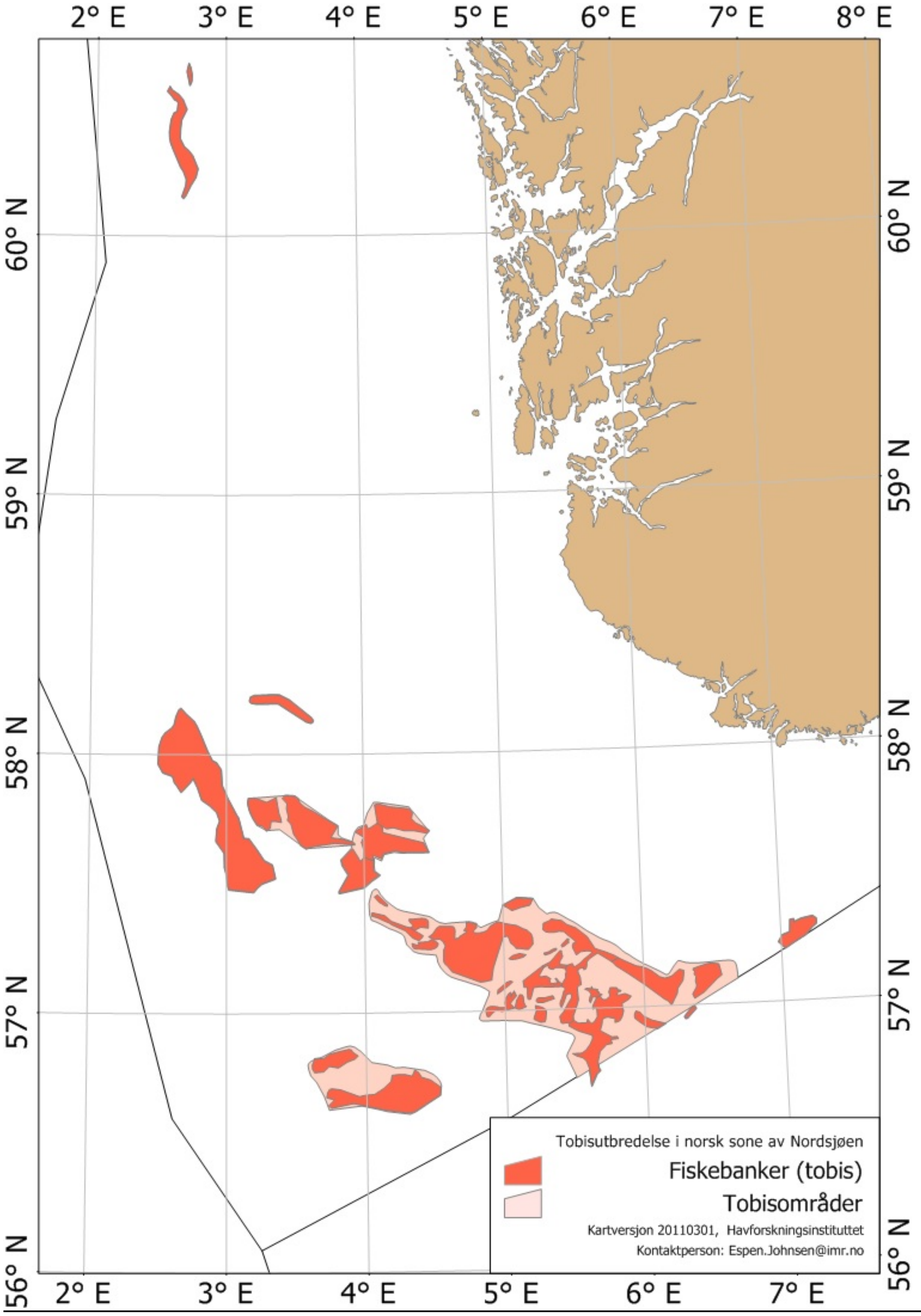

Fig. 7.1.1. Sandeel grounds in NEEZ. Red areas indicate fishing areas and high concentrations of sandeel. Light red indicates areas where there are patches of sandeel that are too small for the sandeel trawlers to operate.

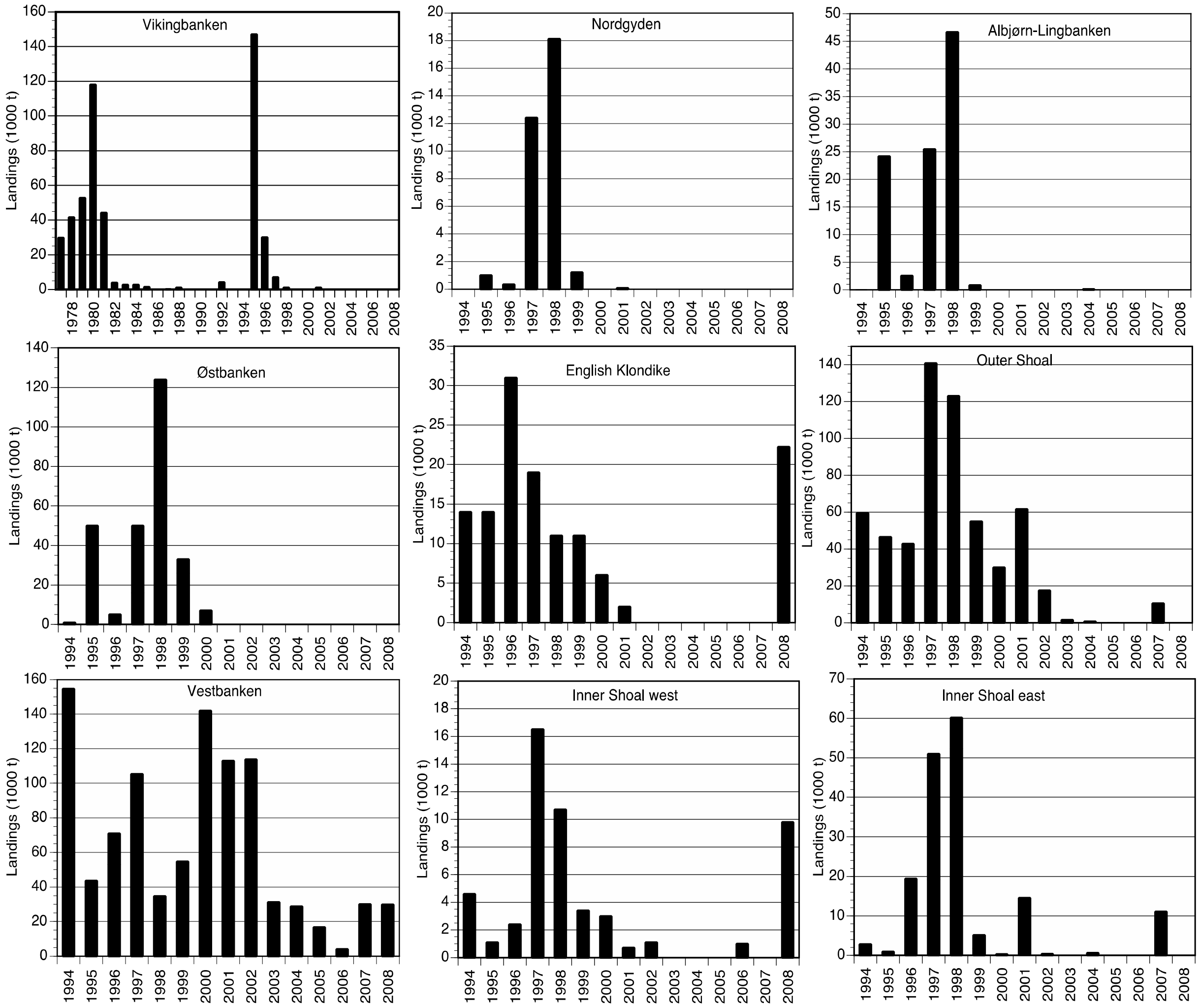

Fig. 7.1.2. Landings of sandeel from sandeel grounds in NEEZ 1994-2008, except Vikingbanken 1977-2008. Notice different scale

7.2 Other works (with electronic links to the papers) developed during, and particularly for, the KINO project

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