

# WORKSHOP ON STOCK IDENTIFICATION OF NORTH SEA COD (WKNSCodID)

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## WORKSHOP ON STOCK IDENTIFICATION OF NORTH SEA COD (WKNSCodID)

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# Contents

i	Executive summary .....	II
ii	Expert group information .....	IV
iii	Resolution.....	V
1	Introduction.....	1
	1.1 Historical background .....	1
	1.1.1 Previous Cod Benchmark Stock Assessment .....	2
	1.2 Workshop process .....	6
2	Review information on stock identification of North Sea cod (ToR 1) .....	9
	2.1 Tagging (ToR 1 a.i).....	9
	2.1.1 Review of previous studies .....	9
	2.1.2 Re-analysis of historic mark-recapture data .....	11
	2.1.3 Summary .....	12
	2.2 Scientific surveys (ToR 1 a.ii).....	16
	2.2.1 Review of Previous Studies .....	16
	2.2.2 Summary .....	19
	2.3 Fisheries (ToR 1 a.iii) .....	23
	2.3.1 Recent Spatial Analyses .....	23
	2.3.2 Summary .....	24
	2.4 Dispersal of cod eggs and larva/juveniles (ToR 1 a.iv) .....	28
	2.4.1 Ichthyoplankton and Spawning Ground Surveys .....	28
	2.4.2 Mechanistic models .....	30
	2.4.3 Summary .....	30
	2.5 Genetic analyses (ToR 1 b.).....	30
	2.5.1 Genetic Structure within the Current North Sea Advisory Area .....	31
	2.5.2 Reproductive Connectivity with Spawning Populations in Neighbour Areas .....	31
	2.5.3 Reanalysis of Available Data .....	33
	2.5.4 Summary .....	33
	2.6 Otolith microchemistry (ToR 1 c.) .....	36
	2.6.1 Summary .....	38
	2.7 Morphometrics and meristics (ToR 1 d.) .....	38
	2.8 Life-history and parasites (ToR 1 e.) .....	39
	2.8.1 Life-history .....	39
	2.8.2 Parasites.....	41
3	Plausible scenarios for cod stocks in the North Sea and adjacent areas (ToR 2) .....	43
4	Practical implications of cod stock scenarios (ToR 3) .....	46
5	Recommendations for North Sea cod benchmark (ToR 4).....	53
6	References .....	54
Annex 1:	List of participants.....	62
Annex 2:	Recommendations .....	63
Annex 3:	Working document 01 .....	64
Annex 4:	Working document 02 .....	79

## i Executive summary

**“It seems that cod may be as local as salmon”** (Michael Graham, 1934, *The North Sea Cod*)

The Workshop on Stock Identification of North Sea Cod (WKNSCodID) reviewed information on population structure of Atlantic cod (*Gadus morhua*) in the North Sea and adjacent waters to recommend the most plausible scenario of population structure for stock assessment and fishery management advice. The review considered geographic variation and movements of cod life stages inferred from genetic analyses, scientific surveys, fishery data, tagging, life-history, distribution of eggs and larvae, otolith microchemistry and shape, and parasites. Based on the review, several population structure scenarios were hypothesized (including the scenario assumed in the current advisory unit), and plausibility of each scenario was evaluated. Practical implications of each scenario, including the derivation of a catch time-series, were considered to form recommendations for benchmark stock assessment workshops.

Since 1996, cod were assessed as a single stock in the North Sea (Subarea 4), Skagerrak (Subdivision 20), and the Eastern English Channel (Division 7.d). Adjacent advisory units are Kattegat cod (Subdivision 21), Norwegian coastal cod (subareas 1–2), Faroe Plateau cod (Subdivision 5.b.1), cod West of Scotland (Subdivision 6.a), and cod in the Western English Channel and southern Celtic Sea (subdivisions 7.e–k).

A large body of scientific information is available for identification of cod population structure in the North Sea and adjacent areas, and a diverse group of experts participated in the workshop to help meet WKNSCodID’s objectives. WKNSCodID concluded that North Sea cod appear to be isolated from the cod population on the Faroe Plateau (Subdivision 5.b.1) and Norwegian Coastal Cod (subareas 1–2). Significant and persistent patterns of genetic variation indicate reproductively-isolated populations of *Viking* cod and *Dogger* cod that have some spatial overlap and mixing after spawning. The Skagerrak and northern Kattegat appear to be a nursing ground for Viking and Dogger cod, with most cod in the Skagerrak being Viking cod. These genetically different groups have different rates of maturity and growth. Trends in biomass and recruitment are strongly correlated among subareas of the North Sea, but subarea trends diverged in the last decade, with no apparent rebuilding in the southern North Sea. The common trends in biomass and recruitment among subareas suggest that there is some mixing of populations after spawning in some areas of the North Sea, and common environmental factors throughout the region.

Viking cod inhabit the northeast North Sea (on and around Viking Bank, 4.a). The spatial distribution of Viking cod extends westward to the Shetlands (western part of 4.a) and southward to the Fischer and Jutland Banks (northern part of 4.b), with and a nursery area in the Skagerrak (20). Some Viking cod some juveniles also inhabit the Kattegat (21). This definition is based primarily on genetics and is supported by information from tagging, larval dispersal, size and age at maturity, otolith chemistry, otolith shape and different recent trends in biomass than the southern North Sea.

The Dogger cod population inhabits the south-central North Sea (on and around Dogger Bank, 4.b), along the Scottish coast to the north of Scotland (northern part of 6.a), and in the eastern English Channel (7.d), with some adults seasonally migrating to the western English Channel (7.e–k). The available information does not provide clear evidence of genetic heterogeneity within the Dogger cod population. However, the Dogger cod population appears to have some phenotypic spatial structure, approximately delineated by the 50 m bathycline in the central North Sea (4.b). Cod north of this boundary (4.a and parts of 4.b) exhibit differing rates of growth and maturity, as well as recent biomass trends, compared to those to the south (4.c). There is relatively little mixing of cod between 4.a and 4.b and sedentary behaviour along the British

coast. Geographic shifts in the distribution of North Sea cod and the low abundance of cod in the southern North Sea appear to result from the interacting effects of fishing effort and warming habitats.

WKNSCodID recommends that ICES stock assessments recognize and account for Viking and Dogger cod populations and consider accounting for phenotypic stocks within the Dogger population. A range of spatial approaches to stock assessment methods and advice should be considered, including a single-area assessment of the current advisory unit, fleets-as-areas, spatially structured assessments, fully separated subarea assessments, and survey-based assessments; ideally with simulation testing to evaluate the relative performance of these alternatives. A practical consideration for representing stock structure is that the 2020–2021 North Sea cod benchmark is not prepared to include data for cod north and west of Scotland (northern part of 6.a), so that topic should be addressed at a future benchmark workshop.

Routine stock composition sampling and analysis is needed to fully account for mixing of Viking and Dogger cod in some areas, but most of the populations and phenotypic stocks can be delineated by geographic boundaries. The spatial resolution of stock boundaries depends on the data used for stock assessment. Surveys and recent fishery data can be disaggregated by latitude-longitude rectangles, but further disaggregation of historical fishery data is difficult, and relatively simple groupings of latitude-longitude rectangles would be more practical for deriving a time-series of landings, discards, size composition, and age composition. Therefore, to support alternative spatial approaches for the 2020–2021 North Sea cod benchmark assessment, WKNSCodID recommends a minimum spatial resolution for fishery data (i.e. catch by major fleets) and survey data, over as long a time-series as possible, by ICES divisions (e.g. 4.a, 4.b, 4.c, 7.d) and subdivisions (e.g. 20), and a relatively simple division of the northern North Sea (4.a.West and 4.a.East, divided at the prime meridian, 0° longitude) to approximately represent the most plausible delineation between the Viking and Dogger cod populations.

## ii Expert group information

<b>Expert group name</b>	Workshop on Stock Identification of North Sea Cod (WKNSCodID)
<b>Expert group cycle</b>	Annual
<b>Year cycle started</b>	2019
<b>Reporting year in cycle</b>	1/1
<b>Chair</b>	Steven Cadrin, USA
<b>Meeting venue and dates</b>	14 July 2020 and 3–6 August 2020 by correspondence (Webex) (25 participants)

### iii Resolution

*This resolution was approved on the Resolution Forum February 2020*

2020/2/FRSG43                    **A Workshop on Stock Identification of North Sea Cod (WKNSCodID)**  
chaired by Steve Cadrin, will meet from 3–6 August by correspondence (Webex) to:

- a) Review information on stock identification of North Sea cod and comparative review of Atlantic cod population structure, including critical evaluation of inferences from each source of information, to build up a picture of cod substock structure in the North Sea and adjacent areas, based on the following:
  - i. Distribution and movements of different life-stages of cod, including changes over time, inferred from:
    - 1) WKNSCodID tagging
    - 2) Scientific surveys
    - 3) Commercial landings
    - 4) Dispersal models (e.g. of cod eggs and larva/juveniles)
  - ii. Genetic analyses
  - iii. Otolith microchemistry
  - iv. Morphometrics and meristics
  - v. Life-history and parasites
  - vi. Other approaches not listed above
- b) Based on the evidence from ToR 1, formulate scenarios for cod stocks in the North Sea and adjacent areas, and assess the evidence-based plausibility of each of these scenarios (including current definitions).
- c) Consider the practical implications, for data, particularly historical time-series of catch data, of each of the scenarios in ToR 2, and how any difficulties might be dealt with. For example, considering spatial components with mixing in a single model has different implications for data compared to split stock units. Considerations should include how to deal with changes over time.
- d) Make recommendations for which cod stock scenario(s) to take forward in the forthcoming cod benchmark, including in what format data should be requested and prepared.

The Workshop will report by 20 August for the attention of ACOM and FRSG.



# 1 Introduction

## 1.1 Historical background

Atlantic cod (*Gadus morhua*) are distributed across the continental shelves of the North Atlantic, from the Middle Atlantic Bight off the northeast coast of the United States to the Barents Sea off the coast of Russia—and throughout the North Sea and adjacent waters. Within this broad area, cod are relatively population-rich, with distinct self-sustaining populations inhabiting coastal areas and offshore banks (Sinclair, 1988; ICES, 1994, 2005).

ICES has a long record of research on the population structure of cod in the North Sea and adjacent areas. Spatial structure of cod in the North Sea was recognized by Graham (1934), who reported that cod in the shallower south-eastern North Sea (<40 m depth) grew faster than those in the deeper central North Sea (>80 m). The North Sea Cod Working Group (ICES, 1970) and the North Sea Roundfish Working Group (ICES, 1971) studied the relationships between cod among areas of the North Sea in response to spatial shifts in fisheries, in which catch of cod in the central North Sea (4.b) doubled from 1963 to 1966, and was almost an order of magnitude greater than cod caught in the southern North Sea (Daan, 1969). The Larval Fish Ecology Working Group compiled spawning and larval characteristics for cod stocks throughout the North Atlantic (ICES, 1987), which led to comparative analyses among cod stocks by the ICES Study Group on Cod Stock Fluctuations (ICES, 1990) and the ICES/GLOBEC Working Group on Cod and Climate Change (ICES, 1994, 2005). The most recent benchmark stock assessment of North Sea cod reviewed information on stock identity (ICES, 2015), which has been included in recent ICES advice (e.g. ICES, 2019a).

The North Sea Cod Working Group (ICES, 1970) and the North Sea Roundfish Working Group (ICES, 1971) reviewed information on spawning grounds, nursery grounds areas, age structure, and extensive tagging data—concluding that cod do not disperse uniformly throughout the North Sea. Age compositions of the fishery demonstrated geographic variation in recruitment. For example, the 1963 year-class was abundant in the south and central North Sea (4.b and 4.c) but not in the northern North Sea (4.a) (ICES, 1971). Tagged cod exhibited seasonal movements with limited mixing among the following areas:

1. Norwegian side of the Skagerrak (20),
2. Danish side of the Skagerrak (20),
3. one to several areas along the English coast from Flamborough to the Scottish east and north coasts (4.a and 4.b),
4. central North Sea (4.b),
5. Southern Bight from the Strait of Dover to 54°N (4.c and 7.d)
6. the Western English Channel (7.e)

Historical tagging suggested movements of cod from the Skagerrak to the eastern portion of the North Sea (4.a and 4.b), and seasonal mixing between the central North Sea (4.b) and the Southern Bight (4.c). Some North Sea cod groups were relatively resident, but individual movements varied within spawning groups, and some exhibited long-distance spawning-feeding migrations usually 30–200 km but up to 300 km (ICES, 1994, 2005). Therefore, North Sea cod has not been assumed to be one distinct population (ICES, 1994, 1996, 2005, 2015).

Before 1996, cod were assessed as three separate stocks in the southern and northern North Sea (4.a–c), the Skagerrak (20), and the Eastern English Channel (7.d). In 1995, the stock structure of cod in the North Sea and adjacent areas was reconsidered (ICES, 1996). A continuous distribution of cod larvae from the north-eastern North Sea to the Skagerrak/Kattegat border, the lack of

spawning cod in the Skagerrak, and movement of tagged juveniles from the Skagerrak to the North Sea suggested that cod in the Skagerrak and northern Kattegat were spawned in the North Sea. Egg surveys indicated that cod spawn in the eastern English Channel, suggesting local recruitment, but tagging documented movement of juveniles and adults to the Southern Bight, and fishery catch rates of cod in the eastern Channel were most strongly correlated with catch rates in the southern North Sea (4.c). Working group experts (ICES, 1996) concluded that cod in the North Sea, Skagerrak, and the eastern Channel are not a single, homogeneous stock, but cod in the combined areas could be considered as a single stock for assessments, and as separate stock from cod spawning in the southern Kattegat (21) and Norwegian fjords of the Skagerrak (20).

In 1996, the assessment that combined cod in the North Sea, eastern English Channel, and Skagerrak (Subarea 4, Division 7.d, and Subdivision 20) showed that catches of cod in the North Sea dominated the combined catch, with an annual average of 10% from the Skagerrak and 3% from the eastern Channel (ICES, 1997). ICES (2005) explained that the three areas formed one management unit which was justified based on conventional tagging data that demonstrated mixing of cod between the three areas but little intermingling of cod between the North Sea and other areas. Adjacent advisory units are Kattegat cod (subdivision 21), Norwegian Coastal cod (1–2), Faroe Plateau cod (5.b.1), cod West of Scotland (6.a), and cod in the western English Channel and southern Celtic Sea (7.e–k).

There is evidence of spatial structure within the current advisory unit. Substocks with clear boundaries could not be defined by initial analyses of haemoglobin allozymes (Jamieson and Birley 1989; ICES, 1994), but Hutchinson *et al.* (2001) used more sensitive genetic characters to identify several genetically distinct populations within the southern and northern North Sea (at Bergen Bank, Moray Firth, Flamborough Head and the Southern Bight) that appear to be reproductively isolated and spatially distinct during the spawning season. Trends in cod abundance have also varied among areas of the North Sea. For example, ICES (2005) reported a decrease in age 1–2 cod in the German Bight and a concentration in the north-eastern North Sea (north of the 50 m bathycline from Flamborough Head to the Jutland Bank).

### 1.1.1 Previous Cod Benchmark Stock Assessment

Stock identification was not the primary objective of the 2015 benchmark stock assessment for North Sea cod (ICES, 2015), but the benchmark workshop reported evidence of two cod populations in the North Sea:

1. one in the northeast North Sea (eastern portion of 4.a, termed 'Viking' cod) and
2. one in shallower waters of the northwest North Sea (western portion of 4.a) and the southern North Sea (4.b–c; termed 'Dogger' cod, Heath *et al.*, 2014). See Figure 1.1.

Microsatellites and Single Nucleotide Polymorphisms (SNPs) indicated that Viking cod are reproductively isolated from other spawning aggregations in the North Sea (Nielsen *et al.*, 2009b, Poulsen *et al.*, 2011; Heath *et al.*, 2014). Information from genetics also suggested that cod in the North Sea are isolated from Norwegian coastal cod (areas 1–2; ICES, 2015), which is supported by tagging studies that document high site fidelity of cod in Norwegian fjords (Nedreaas *et al.*, 2008), and different trends in juvenile abundance among fjords (Rogers *et al.*, 2014).

Other mechanisms of reproductive isolation among cod groups in the North Sea include limited life-stage connectivity and oceanographic barriers to early life-stage transport (Heath *et al.*, 2008; Munk *et al.*, 2009) as well as limited mixing and natal homing of adults, with residence in >100 m depths and little mixing of Viking fish with neighbouring groups (Wright *et al.*, 2006a; Neat *et al.*, 2014). Genetics and otolith microchemistry indicated that many Viking juveniles settle in the Skagerrak and subsequently make a return migration prior to spawning (ICES, 2015). This return

migration of Viking juveniles could explain observations of relatively high age-0-1 cod abundance in the Skagerrak that did not correspond with a high abundance of those year-classes at age 2+ in the Skagerrak (Svedäng and Svenson, 2006), and the relatively strong year class of cod in 2001 in the Skagerrak that was genetically assigned to originate from the North Sea (Knutsen *et al.*, 2004).

In addition to evidence for population structure of cod within the North Sea, there also appears to be fine-scale population structuring within the North Sea as suggested by patterns of larval transport (Heath *et al.*, 2008), juvenile dispersal (Wright *et al.*, 2006a), and adult movements (Wright *et al.*, 2006b; Righton *et al.*, 2007; Svedäng *et al.*, 2007; Neat *et al.*, 2014). Larval transport models and otolith microchemistry do not suggest mixing of eggs and larvae across the North Sea. In the Skagerrak, there appears to be extensive mixing of juveniles between local, Viking cod and possibly Dogger cod from the southern North Sea. Seasonal adult movements are generally <200 km along the British coast, and adult Viking cod appear to remain in depths >100 m. Although home ranges of cod are relatively compact during the spawning season, spatial distributions increase after spawning with some overlap between Viking cod and Dogger cod east of Shetland (Wright *et al.*, 2006b; Neat *et al.*, 2014). Home ranges of cod aggregations overlap for some life stages outside the spawning period. For example, cod from the shallow population may overlap with the western distribution of Viking cod after spawning

The 2015 benchmark assessment of North Sea cod defined subarea boundaries to investigate spatiotemporal patterns in the cod resource and fisheries (ICES, 2015). Subarea boundaries (Figure 1.1) reflect areas of low mixing but do not necessarily represent distinct population boundaries:

1. Viking
2. Skagerrak (nursery area for Viking).
3. Northwest, and
4. South.

Survey trends were similar for cod in the Northwest, Viking and Skagerrak areas in recent years, but biomass trends have been different in the South since 2010 (ICES, 2015, 2019a). The biomass of adult cod in the Northwest area more than tripled from 2006 to 2013, adult biomass in the Viking and Skagerrak subareas approximately doubled during the same period, but biomass remained low in the South (Figure 1.2; Eero *et al.*, 2015). An exploratory assessment of cod in the Northwest and South subareas produced stock trends that were similar to an assessment of Viking and Skagerrak cod but lower estimates of fishing mortality in the Northwest and South subareas than in the Viking and Skagerrak subareas. Survey information did not indicate major differences in recruitment (Figure 1.2) or recruitment per unit of spawning biomass among any of the subareas. European fishing effort was greatest in the low cod abundance area in the South. European cod landings were greatest in the Viking subarea in recent years where the cod biomass is estimated to be highest, but there was a declining trend in the South subarea where the stock size was lowest. Survey data and analytical assessments suggest that total mortality is greatest in the South, lowest in the Northwest, with intermediate level in the Viking and Skagerrak subarea (Figure 1.1; ICES, 2015).

The 2015 North Sea cod benchmark assessment concluded that different recent trends among subareas are consistent with evidence of population structure. Regional variation in environmental conditions, predation and fishing mortality are expected to lead to some differences in subarea trends. Differences in life-history traits were also found among the subareas consistent with population differences (Harrald *et al.*, 2010; Wright *et al.*, 2011; Yoneda and Wright, 2004).

ICES (2019a) advice for 2020 included a summary of information on stock identity of North Sea cod<sup>1</sup>:

“Cod is widely distributed throughout the North Sea, but there are indications of subpopulations inhabiting different regions of the North Sea (e.g. from genetic studies). The inferred limited degree of mixing suggests slow recolonization in areas where subpopulations are depleted. Figure 1.2 plots a cod biomass index by subregion (with subregions given in Figure 1.1), and highlights differing rates of change in this index. The figure shows a general decline in all areas prior to the mid-2000s and a general increase peaking in 2016–2017 in all areas thereafter, with the exception of the southern area where cod has further declined. There has been a subsequent decrease in all areas, and it is unclear what the reasons are for this; further work is required to investigate climate change, biological, and fisheries effects. Recruitment has declined and remains low in all areas (Figure 1.3).”

There is a long history of recognising the biological stock structure of cod throughout the North Atlantic, including in the North Sea area. Considering information from both traditional and newly developed disciplines adds a richness to the understanding of cod population structure. In parallel to stock structure research, the spatial units of ICES advice for cod fisheries in the North Sea have evolved from multiple advisory units in the North Sea, eastern English Channel and Skagerrak, to a single advisory unit in those areas, to the consideration of subarea trends within the North Sea cod advisory unit. ICES recognized the need to reconsider the population structure of cod in the North Sea and adjacent recommendations for benchmark stock assessments.

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<sup>1</sup> Figure numbering revised to reflect numbering in this report.

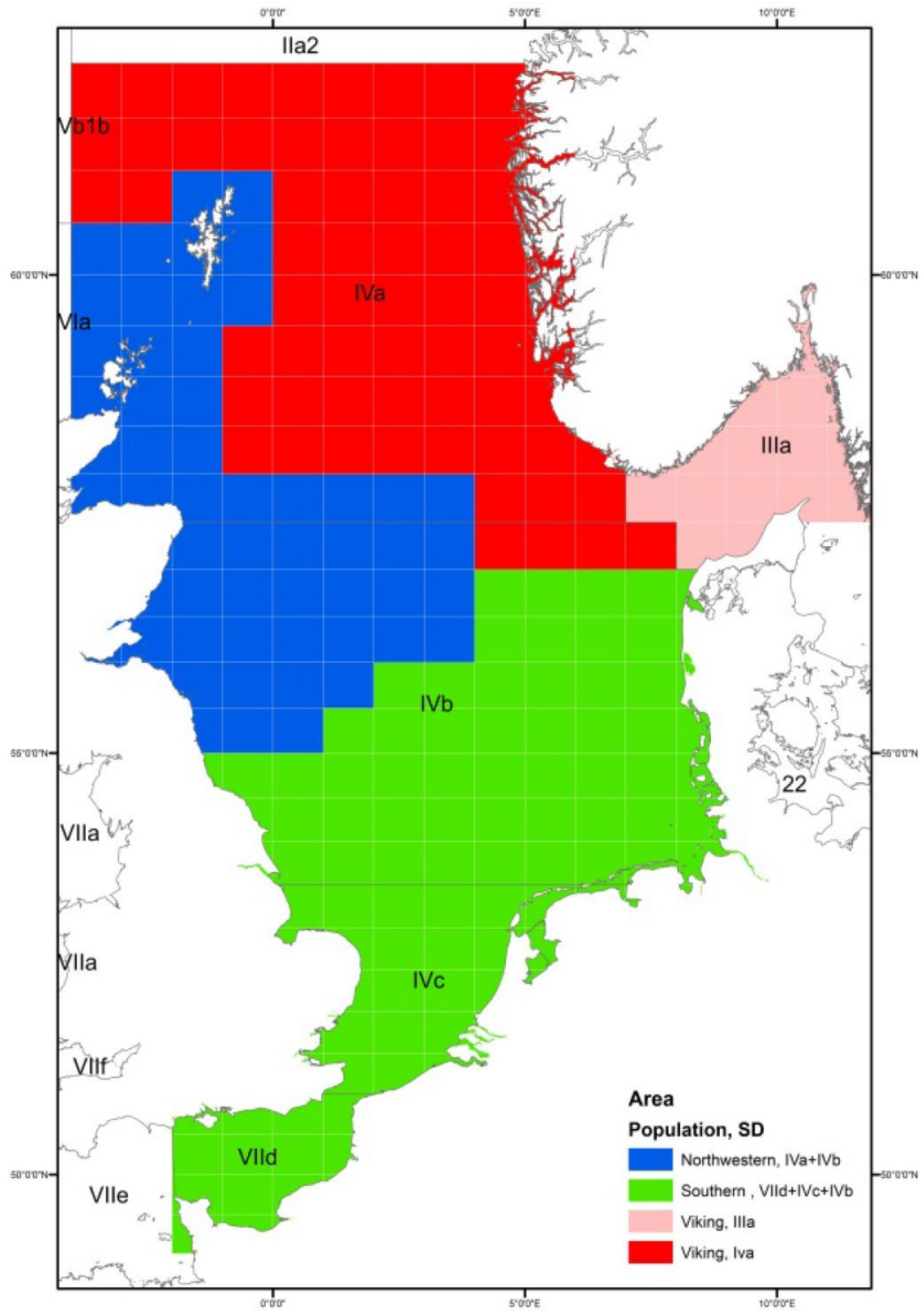
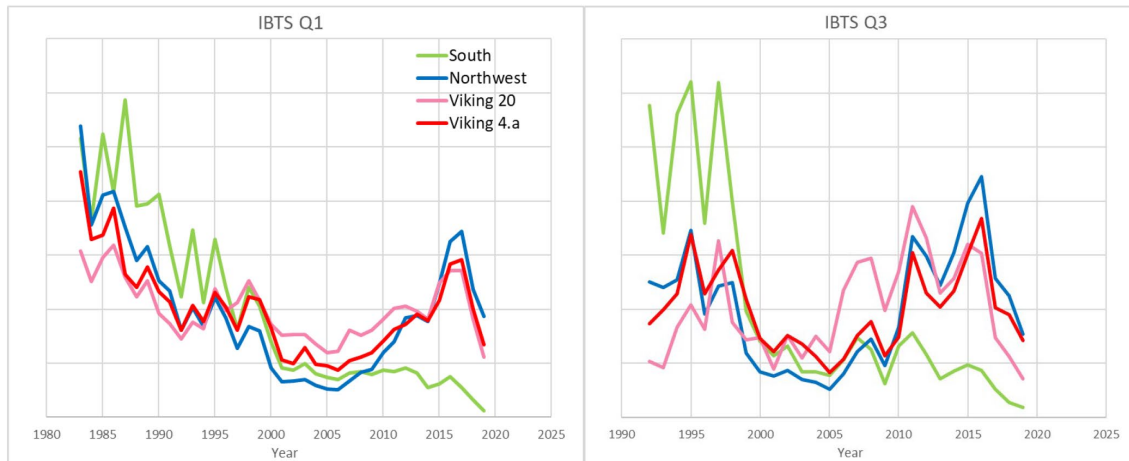
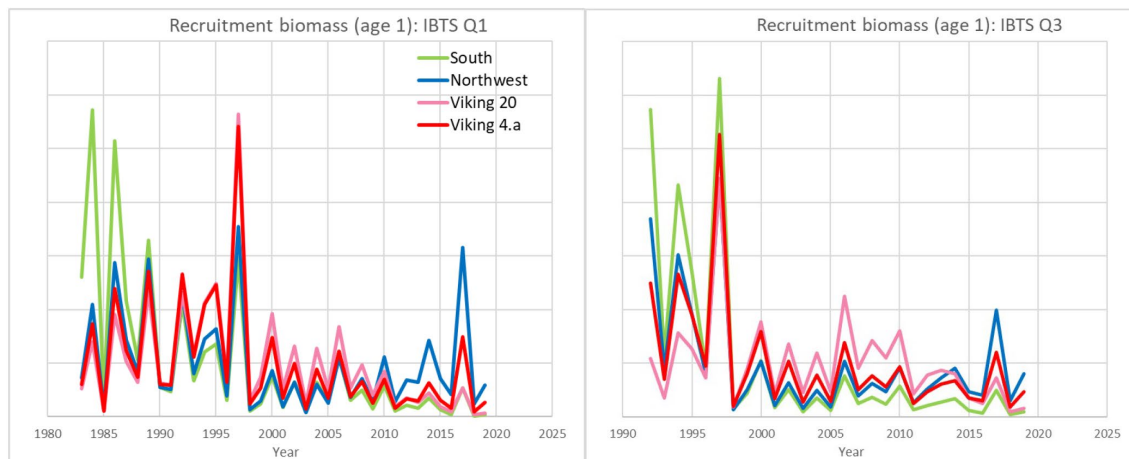


Figure 1.1. Putative subareas used for spatial analyses of North Sea cod by ICES (2015).



**Figure 1.2.** Cod in Subarea 4, Division 7.d, and Subdivision 20. Biomass indices by subregion (see Figure 1.1), based on the NS IBTS quarter 1 and quarter 3 survey data (ICES, 2019a).



**Figure 1.3.** Cod in Subarea 4, Division 7.d, and Subdivision 20. Recruitment indices by subregion (see Figure 1.1), based on NS IBTS quarter 1 and quarter 3 survey data (from ICES, 2019a).

## 1.2 Workshop process

The Workshop on Stock Identification of North Sea Cod (WKNSCodID) met by Webex on 14 July 2020 and 3-6 August 2020 and by correspondence to address its Terms of Reference:

1. Review information on stock identification of North Sea cod and adjacent areas in the context of Atlantic cod population structure information from throughout its range, including critical evaluation of inferences from each source of information, to build up a picture of cod substock structure in the North Sea and adjacent areas, based on the following Terms of Reference:
  - a) Distribution and movements of different life-stages of cod, including changes over time, inferred from:
    - i. Tagging
    - ii. Scientific Surveys
    - iii. Commercial landings
    - iv. Dispersal (e.g. of cod eggs and larva/juveniles)
  - b) Genetic analyses
  - c) Otolith microchemistry
  - d) Morphometrics and meristics

- e) Life-history and parasites
  - f) Other approaches not listed above
2. Based on the evidence from ToR 1, formulate scenarios for cod stocks in the North Sea and adjacent areas, and assess the evidence-based plausibility of each of these scenarios (including current definitions).
  3. Consider the practical implications, for data, particularly historical time-series of catch data, of each of the scenarios in ToR 2, and how any difficulties might be dealt with. For example, considering spatial components with mixing in a single model has different implications for data compared to split stock units. Considerations should include how to deal with changes over time.
  4. Make recommendations for which cod stock scenario(s) to take forward in the forthcoming cod benchmark, including in what format data should be requested and prepared.

Workshop participants met on 14 July 2020 for introductions, a quick review of previous ICES science and advice for North Sea cod, a decision to refine conclusions about stock identity from the 2015 benchmark, identification of initial population structure scenarios, and to agree on the general approach. Participants agreed to build on conclusions and recommendations from the 2015 Benchmark (ICES, 2015) with some refinements. For example, information supporting boundaries with West of Scotland (northern portion of 6.a), the Western English Channel (7.e) and the Kattegat (21) were reviewed. Some tagging information was available to consider mixing with 6.a, 7.e, and 21. Information on otolith chemistry and genetics was also available to consider mixing with the Kattegat (21). The delineation of subareas also needed to be revised to account for new information on stock identity north and west of the Shetland Islands (Figure 2.4).

The 2020 benchmark stock assessment of cod west of Scotland (ICES, 2020) was not primarily focused on stock identification but reported: “Stock structure remains an issue for cod in Division 6.a. The latest evidence (WD 4.1) suggests that there are at least three substocks which remain largely geographically isolated throughout the year with the northern offshore component (currently responsible for the majority of the landings) more closely linked to cod in the northern North Sea than the rest of Division 6.a.”

Workshop participants agreed to address the terms of reference by adopting the general approach developed for the Workshop on Redfish Stock Structure (ICES, 2009) which involved sequential stages of consensus summary statements from all participants:

1. Define current spatial management units and their justification.
2. Identify all plausible hypotheses of population structure (including current management units).
3. Review available information on stock identity, grouped into broad disciplines
4. Form consensus conclusions about stock inferences within each discipline
5. Evaluate each stock structure hypothesis based on interdisciplinary synthesis

Initial stock identification hypotheses and putative advisory units for the 2020–2021 benchmark assessment were formed:

Hypothesis 1. The current advisory unit of North Sea cod (4, 7.d and 20) is a closed, homogeneous population.

Hypothesis 2. The cod resource in the current advisory unit of North Sea cod (4, 7.d and 20) is a metapopulation (i.e. a system of interacting biological populations, termed subpopulations, that exhibit a degree of independence in local population dynamics as well as connectivity between subpopulations, Cadrin *et al.*, 2014) with three interacting subpopulations (Viking-Skagerrak, Northwest, South; Figure 2.4).

Hypothesis 3. The substocks of cod in the North Sea (Figure 2.4) are demographically independent.

Hypothesis 4. There is considerable connectivity of cod between the northwest North Sea (4.a) and north of Scotland (northern part of 6.a).

Hypothesis 5. There is considerable connectivity of cod between the eastern English Channel (7.d) and the western English Channel (7.e–k).

Hypothesis 6. There is considerable connectivity of cod between the Skagerrak (20) and the Kattegat (21).

Workshop participants contributed to topical groups according to Term of Reference #1 to identify and review the available literature on stock identity of cod in the North Sea and adjacent areas. Technical reviews of each publication and some unpublished documents considered the objective of the study, representativeness of samples for the hypothetical stocks, power of sampling and analytical design for detecting meaningful differences between groups. Group leaders assigned group members to draft a brief review of specific source documents, group members reviewed drafts to form group consensus on each source document, and group leaders drafted a summary of information on their assigned topic for Workshop consensus on inferences related to population structure of cod in the North Sea and adjacent areas as well as relative support for alternative hypotheses. The chair drafted an interdisciplinary summary of inferences related to population structure of cod in the North Sea and adjacent areas, with relative support for alternative hypotheses, for Workshop discussion and iterative refinement to develop consensus conclusions and recommendations. Christoph Stransky and Manuel Hidalgo, members of the Stock Identification Methods Working Group (SIMWG), who did not participate in the workshop reviewed the draft report in advance of the 2020–2021 North Sea cod benchmark workshop.

At the suggestion of Workshop participants, the Workshop Chair contacted the ICES Advisory Committee Chair in advance of the draft report to communicate two aspects of Workshop recommendations: 1) spatial data compilation to support a range of spatial approaches to stock assessment methods, and 2) connectivity between cod in the northern part of 6.a and the North Sea, which is expected to be beyond the scope of the 2020–2021 North Sea cod benchmark.



## 2 Review information on stock identification of North Sea cod (ToR 1)

### 2.1 Tagging (ToR 1 a.i)

Tagging studies document movement patterns, the degrees of residence or dispersal, and relative movement rates among areas (Harden Jones, 1968). Many tagging studies have been conducted in the North Sea area to investigate the movement and spatial distribution of cod (e.g. Robichaud and Rose 2004, Righton *et al.*, 2007; Neat *et al.*, 2014). These studies involve the tagging, release, and recapture of individuals, with the aim of shedding light on individual behaviours such as foraging and migration, as well as population-level characteristics that are informative to management. For example, tagging studies can reveal the level of mixing that occurs between populations (e.g. Espeland *et al.*, 2008), spatial distribution relative to management units (e.g. Neat *et al.*, 2014), and can help disentangle the complex issue of stock structure and stock identification. Evidence for stock structure and stock identification provided by tagging data for North Sea cod includes studies completed throughout most of the last century and span the management units: Subarea 4 (divisions 4.a–c), Divisions 7.d–e, Division 6.a, Division 7.a, divisions 7.f–h and subdivisions 3.a.20 and 3.a.21, and two general approaches: mark-recovery and electronic telemetry (predominantly Data Storage Tags; DSTs). Historic mark-recapture data were also re-analysed for the workshop.

#### 2.1.1 Review of previous studies

In the southern North Sea (4.c) and eastern Channel (7.d), Righton *et al.* (2007) used historical mark-recovery data (dating back to the 1960s) as well as electronic tags ( $n = 30$ ) to investigate the movement patterns of cod. The authors show that the spatial distribution of tag returns depends on both season and age. Fish recaptured during the spawning season (quarter 1 and quarter 4) were typically caught within their release area, whereas recapture outside of their release area was much more common during the summer foraging season (quarter 2 and quarter 3). Adults were found to disperse further than juveniles (body length  $< 50$  cm), moving northwards into 4.b and in a south-easterly direction into 7.d and 7.e. The connectivity of cod between 4.c and 4.b, and from 4.c into 7.d and 7.e, is documented further in the work of Bedford (1966), Le Franc (1969), Daan (1969), De Clerck, (1973), Hobson *et al.* (2009), Neat *et al.* (2014) and Griffiths *et al.* (2018), as well as in the re-analysis of historic mark-recovery data presented below. For instance, 40% of cod tagged in 7.d were recaptured in 4.c (Bedford, 1966), whereas 20-30% of all individuals tagged in 4.c were recaptured in 4.b (Figure 2.2).

Righton *et al.* (2007) reported that cod tagged in 4.c moved an average distance of 135 km ( $\pm 135$  km) between their release and recapture locations but their northern range rarely extended into 4.a. This finding is consistent with the work of Neat and Righton (2007) who reported that 129 large juvenile ( $>30$  cm) and adult cod tagged with electronic tags in 4.c showed no evidence of northward expansion. This result is discussed in a thermodynamic perspective, with the authors highlighting that cod within the southern North Sea currently inhabited thermal environments that were super-optimal for growth (Neat and Righton, 2007; Righton *et al.*, 2010). These cod showed no evidence of a northward dispersal to cooler waters even though they appeared to be more than capable of such redistribution (Neat and Righton, 2007; Neat *et al.*, 2014). These findings could indicate a local preference for environmental conditions (e.g. temperature, salinity, depth, bottom type; González-Irusta and Wright, 2016) or reliance on patchily distributed

prey (e.g. the lesser sandeel, *Ammodytes tobianus*; Magnussen, 2011), both of which could influence the spatial distribution of cod in the North Sea. Further, as temperature effects are often expressed on individual-level traits (Gillooly *et al.*, 2001; Neuheimer and GrønkJær, 2012), differences in temperature regime will be relevant to the way weight-at-age and maturity-at-age are considered in the assessment process. However, there is currently a limited amount of electronic tagging data available in the northern and central parts of 4.b which adds uncertainty to conclusions of a southern-northern divide in North Sea cod.

Behaviour may also play a key role in the stock structure of cod (Metcalf, 2006). In a large meta-analysis that included cod tagged in the North Sea and adjacent areas, Robichaud and Rose (2004) illustrated that, throughout much of its spatial range, cod exhibit four migratory behaviours: sedentary resident, accurate homers, inaccurate homers, and dispersers. Sedentary behaviour is found to be most common (42%), occurring mainly in coastal environments, followed by inaccurate homers and dispersers (both 20%). This difference in migratory behaviour could have large effects on stock structure and the spatial scale at which management decisions are relevant. In the North Sea and adjacent waters, some cod are thought to remain as sedentary residents (Norwegian coastal cod; Espeland *et al.*, 2008) while others migrate seasonally between foraging and spawning grounds (cod in the southern North Sea; Righton *et al.*, 2007). A similar argument is made by Wright *et al.* (2020) who conclude that cod in 6.a can be split into four populations based on behaviour. Three are sedentary and remain in shallow coastal waters (< 100 m) with some exchange between southern components and cod in 7.a. In comparison, the fourth population west of Scotland is highly migratory, occupying a spatial range that extends from the deeper, more offshore waters of 6.a, east into 4.a and west into 6.b (Wright *et al.*, 2020). Further evidence for the extended spatial range of this offshore component is provided by the work of Easey (1987). Cod tagged west of the Hebrides dispersed widely along the west coast of Scotland with recaptures in 6.a and on the western boundary of 4.a (around Papa Bank). Individuals also moved into 4.a, with 8% of recaptures occurring in Moray Firth and central North Sea, but no recaptures were made around the Shetland Isles. In comparison, 82% of cod tagged around Papa Bank were recaptured near the 4°W stock boundary and in 6.a to the west of Orkney. Further, in Wright *et al.* (2006a) cod released off the North coast of Scotland showed a similar range of movement, with recaptures occurring in 6.a and 4.a. These studies demonstrate that mixing of cod between 6.a and 4.a may occur and can be attributed to the presence of an offshore migratory population. The tagging data used in Easey (1987) and Wright *et al.* (2006a, 2020) span the period 1960–1984, so further work is needed to confirm the temporal consistency of such observations.

A second key finding by Robichaud and Rose (2004) is that cod biomass exhibits a strong relationship with spatial range, with large migratory populations having the largest biomass. Such a trend could influence our interpretation of stock structure and stock identification, as reductions in biomass may result in range contractions. This topic is discussed in the context of Irish Sea cod by Connolly and Officer (2001) who suggest that the movement of cod from 7.a into 7.f–g may have become less frequent through time as the abundance of both stocks has declined.

In the northern North Sea, extensive mark-recovery work has indicated that adult cod located in Norwegian coastal waters (northeast part of 4.a; Viking Bank) display high rates of site fidelity, with little movement south (Nedreaas *et al.*, 2008). This tendency to remain is further supported by electronic tagging results showing that cod from the Viking Bank occupies a unique thermal habitat and exhibit low connectivity with other areas (Righton *et al.*, 2010; Neat *et al.*, 2014). The resident behaviour of cod in Norwegian fjords justifies their exclusion from the North Sea cod advisory unit. However, some tagging data suggests mixing between Viking Bank cod and cod that inhabit the shallower waters to the east of the Shetland Isles during the summer foraging season (Wright *et al.*, 2006b; Neat *et al.*, 2014). In the northwest of 4.a, cod tagged to the west of the Shetland Isles were recaptured locally, with electronic tagging data supporting this pattern of residency and high site fidelity (Wright *et al.*, 2006a, 2006b). This is also true of cod tagged and

released in the Moray Firth and Firth of Forth, with only a few individuals that moved out of the area (Wright *et al.*, 2006a, 2006b). These studies suggest that the cod population in 4.a is made up of several sedentary resident populations with relatively small spatial ranges and little mixing during the spawning season.

Similarly, high site fidelity has also been found within Norwegian coastal waters of the Skagerrak, with up to 98% of tagged individuals remaining within 2 km of their release location (Espeland *et al.*, 2008; Rogers *et al.*, 2014). Some movement from the Skagerrak into the North Sea is observed, however, this is relatively rare (less than 2%). Such findings allow the authors to conclude that cod in Norwegian fjords of the Skagerrak are highly sedentary and exhibit fine-scale stock structuring at relatively small spatial scales. On the Danish side of the Skagerrak, most tagged cod were recaptured locally, but some adults and juveniles were recaptured in 4.c (mostly between January to July) and 4.a (August to October), as well as in 3.a.21 (Kattegat; Danielssen, 1969). A similar trend was observed within Swedish coastal waters of the Skagerrak, with age-1 and age-2 cod moving from 3.a.20 (Skagerrak) to 4.a–b and from 3.a.20 to 3.a.21 (Pihl and Ulmestrand, 1993). These trends along the Swedish coast of the Skagerrak (including the Gullmar fjord) and Kattegat are further supported by the recent electronic tagging work of Svedäng *et al.* (2007). Of cod tagged in the Skagerrak, 38% remained resident in the area, 18% moved into 4.a and were recaptured there, whereas 28% were recaptured in the Skagerrak after moving from 3.a.20 into the North Sea and returning. This apparent spawning site fidelity and spawning migration are similar to the movement patterns of cod in the southern North Sea (e.g. Righton *et al.*, 2007). Contrary to this, 96% of cod tagged in the Gullmar fjord remained resident in the area. These results support the hypothesis that cod in different areas of the Skagerrak exhibiting variable migratory behaviours, and some cod in the Skagerrak have connectivity with the North Sea.

### 2.1.2 Re-analysis of historic mark-recapture data

The available mark-recapture data for tags at liberty at least 90 days ( $n=6202$ ) were analysed by plotting recaptures by ICES division of release (Figure 2.1), maturity, quarter-year and decade (Figure 2.2). Cod were mostly recaptured in the same division where they were released (88% of cod released in 4.a were recaptured in 4.a, 95% of cod released in 4.b were recaptured in 4.b, and 68% of cod released in 4.c were recaptured in 4.c). However, a considerable portion of cod moved from 4.c to 4.b (28% of cod released in 4.c were recaptured in 4.b), and some cod moved from 4.c to 7.d and from 4.a to 6.a. Most (70%) of tagged cod were juveniles ( $< 68.3$  cm), which exhibited high fidelity in 4.a and 4.b, but 28% of juvenile cod released in 4.c were recaptured in 4.b. Adults dispersed more than juveniles (e.g. most recaptures of adults tagged in 4.c recaptured in 4.b, and 10% of adults tagged in 4.a recaptured in 4.b). The high residence in 4.a and 4.b was consistent among seasons, but movement of cod from 4.c to 4.b peaked at 64% in quarter three (i.e. the majority of cod tagged in 4.c and recaptured in quarter 3 moved to 4.b). These general patterns appear to be relatively persistent through time, but sample sizes were much greater in the 1960s. The net direction and displacement of tagged cod from English and Scottish tag experiments generally changed south of the Firth of Forth (in 4.b), and there was little exchange with cod further north (Figure 2.3). North of this area, there are both inshore sedentary groups and offshore migratory cod in both the Viking area (northeast North Sea, depths  $> 100$  m) and around the Northern Isles (Wright *et al.*, 2006a, 2006b; Neat *et al.*, 2014).

The same tag-recapture data were also analysed using Kernel Density Estimates (KDE) for the Northwest, Viking and South subregions (Figure 2.4). In order to acknowledge the connectivity between the northwest unit and 6.a.North (ICES, 2020), a probability density surface for tag-recapture data from this region was also included. The data was constrained to recaptures occurring after at least 90 days but consisted of a mixture of mature and immature fish released and recaptured at different times of the year. The choice of smoothing parameter used to produce

the probability density surfaces followed the recommendation of Fotheringham et al. (2000) to define  $h_{opt} = (2/3n)^{1/4} sd$ , where  $n$  is the number of tag returns for a specific area (Northwest, Viking, South, 6.a.North) and  $sd$  is the standard distance measuring the dispersion of recaptures around the mean centre of recaptures for a given area. To capture the general pattern of movements of fish released in the considered areas (Figure 2.4), the probability density surfaces for 50% and 95% of recaptures were generated and presented in Figure 2.5.

The pattern of movements suggests that cod released in the southern subarea (Figure 2.4) were generally recaptured in the Eastern Channel, the Southern North Sea, and the Central North Sea but tend not to go further north (Figure 2.5). Cod released in the Viking region were mostly recaptured in the same unit, up to the boundary with Skagerrak, with some recaptures to the south-east of Shetland where overlap with the Northwest unit occurs. However, cod tagged in the Viking area were not recaptured in the Southern North Sea. Northwest cod were mostly recaptured in coastal waters of the northeast coast of Scotland and to the south-east of Shetland. Finally, cod released in the Northern Offshore region of 6.a were recaptured from the Outer Hebrides to the north of Shetland, with likely northern inshore cod entering the Moray Firth. The data presented is informative of the general movement patterns of cod released in the different areas considered, but caution is advised regarding some limitations of the analysis. Further work is needed to address the potential difference in the range of movements of juvenile and adults and to consider seasonal patterns of releases and recaptures for inferences of spawning/feeding migration. Further, spatiotemporal patterns in fishing effort are not accounted for in the analysis, which might result in an overrepresentation of some recapture locations.

### 2.1.3 Summary

Similar to patterns of cod movement observed throughout the North Atlantic (e.g. Robichaud and Rose, 2004), some cod groups in the North Sea are relatively sedentary (e.g. adult Viking cod, cod in Norwegian fjords of the Skagerrak, and Scottish coastal cod), but others migrate seasonally between foraging and spawning grounds (e.g. cod in the southern North Sea, 4.c). Tagged cod that were recaptured during the spawning season (quarter 1 and quarter 4) were typically caught within their release area, whereas recapture outside of their release area was much more common during the summer foraging season (quarter 2 and quarter 3). Adults were found to disperse further than juveniles, moving north into 4.b and southwest into 7.d and 7.e. There is connectivity of cod between 4.c and 4.b, and from 4.c into 7.d–e, but cod tagged in 4.c rarely moved into 4.a. There is also some evidence of exchange between cod in 4.a and 6.a and 6.a and 7.a. Future tagging research should address the lack of recent tagging data spanning the 6.a–4.a boundary, limited tagging data in the central and northern parts of 4.b, and seasonal patterns of movement.

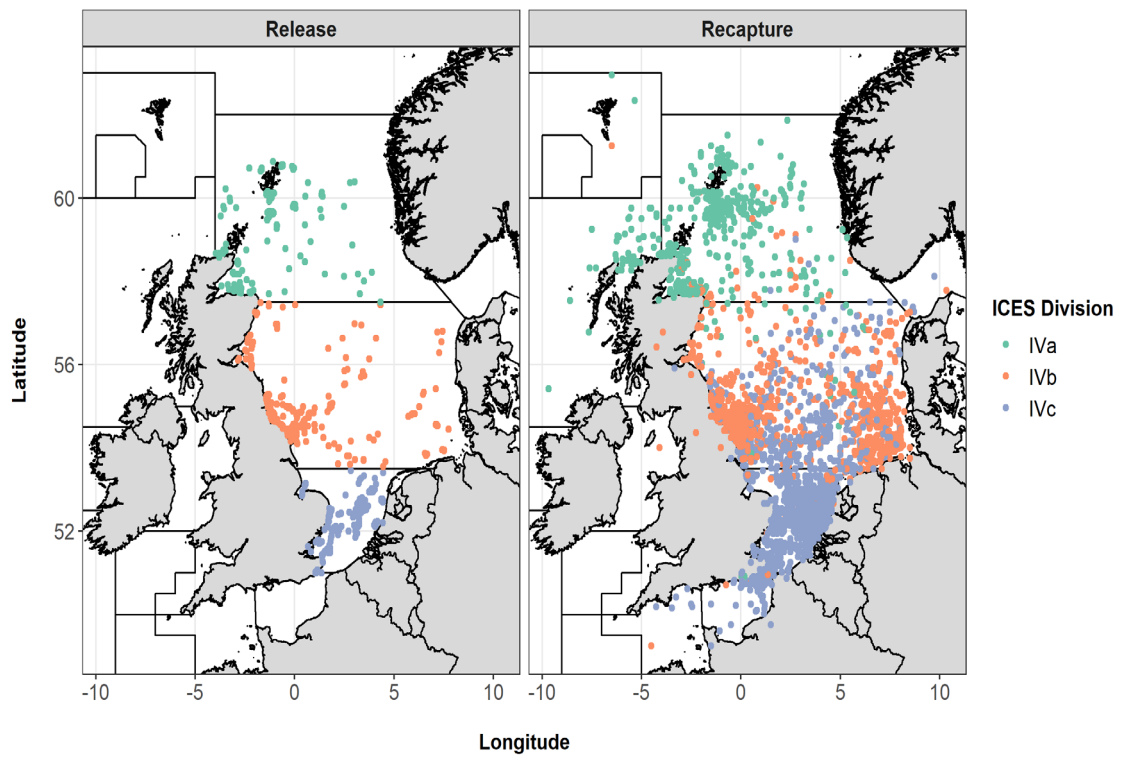


Figure 2.1. Releases and recaptures of cod with conventional tags at large at least 90 days by release areas in the North Sea, including recaptures of 818 releases from 4.a, 1884 releases from 4.b, and 3500 releases from 4.c.

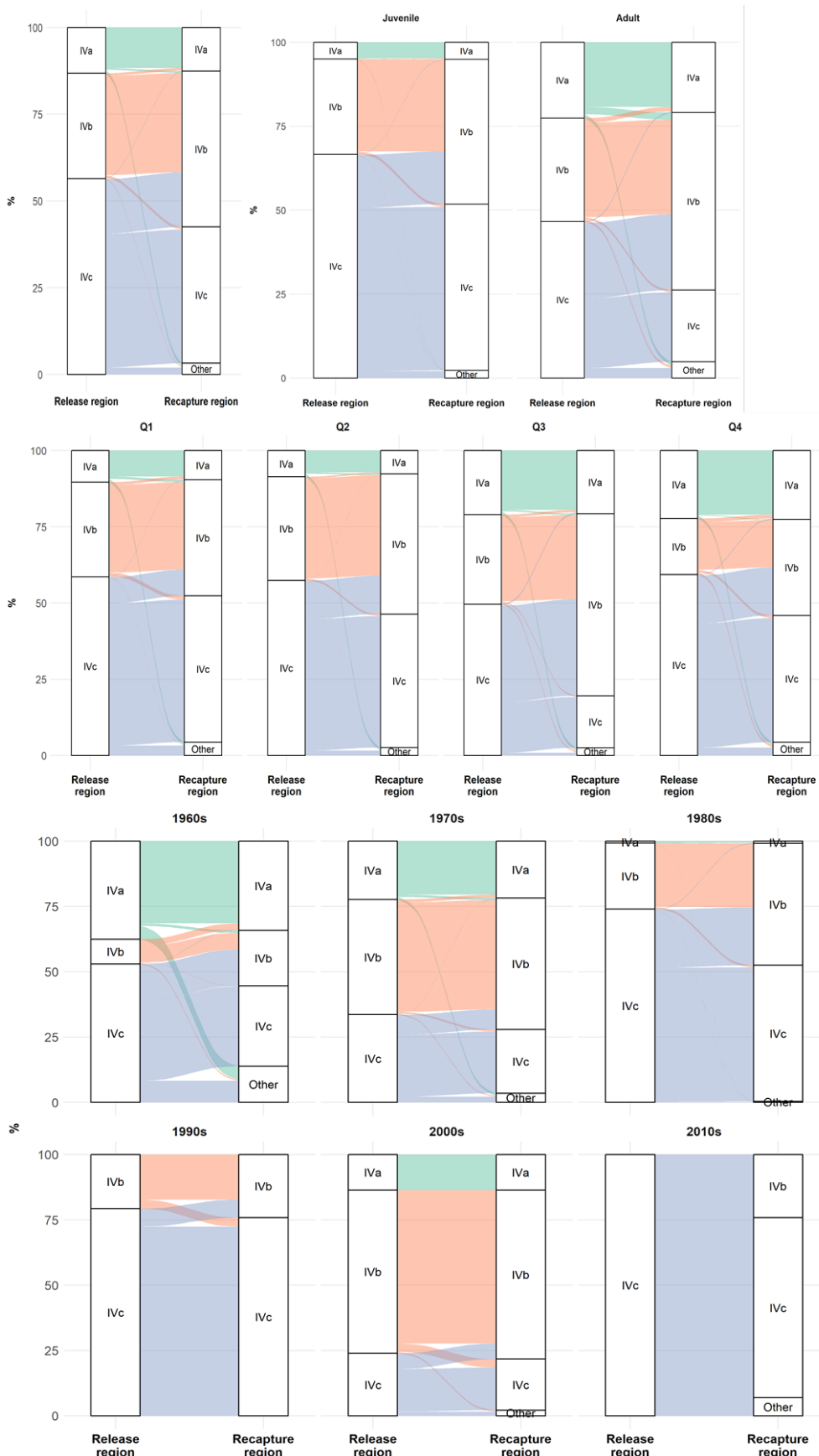


Figure 2.2. Observed residence within and movement among ICES Divisions in the North Sea by tagged cod at large at least 90 days (all: top left; by maturity, top right; by quarter-year, middle panels; and by decade, bottom panels).

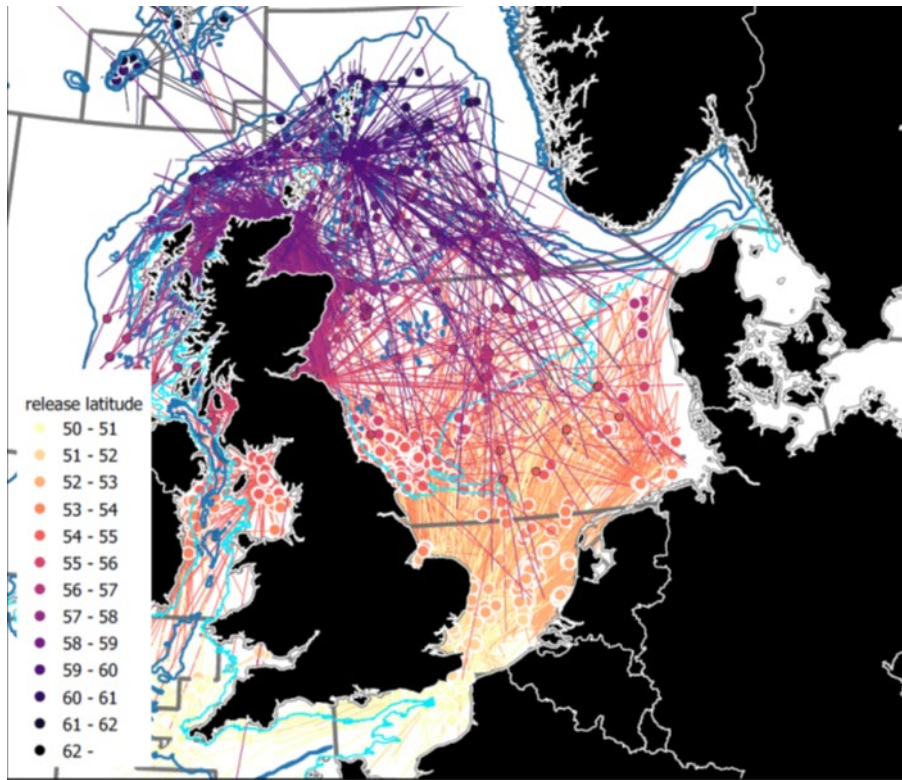


Figure 2.3. Net displacement of tagged cod at liberty for  $\geq 90$ days relative to latitude of release (see colour coding). Dots represent distribution of tag releases and lines show net displacement to recapture. Data from English and Scottish tag-recapture database 1963–2015.

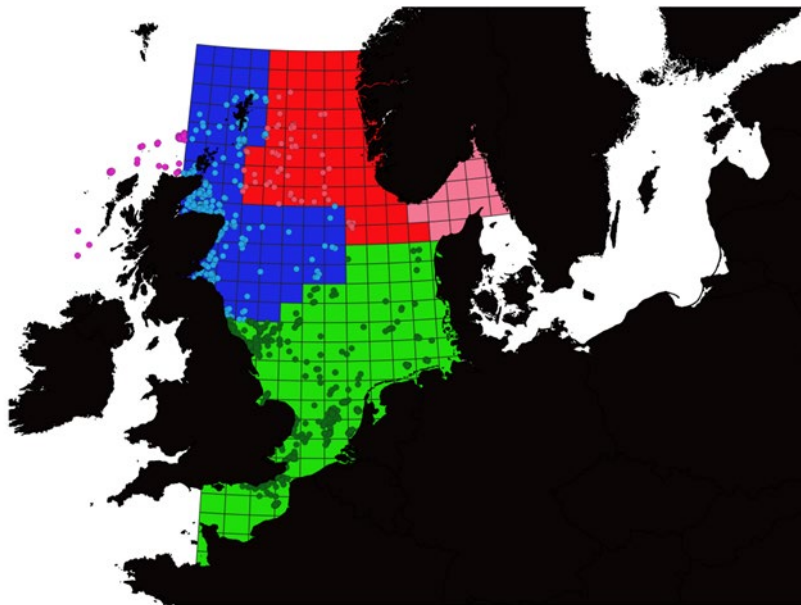


Figure 2.4. Release locations of cod tagged in 6.a.North (purple), the Northwest North Sea (blue), Viking (red), and the Southern North Sea (green).

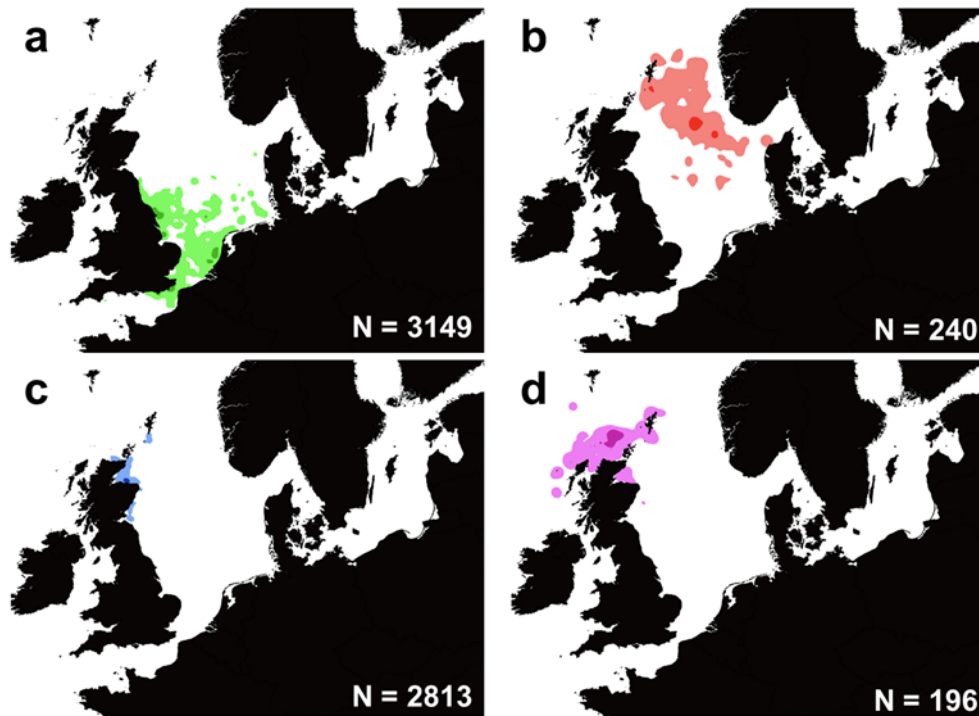


Figure 2.5. Probability density surfaces for 50% (light) and 95% (dark) of the recaptures for (a) the Southern subarea, (b) Viking, (c) Northwest North Sea and (d) 6.a.North. The number of recaptures are indicated.

## 2.2 Scientific surveys (ToR 1 a.ii)

Species distributions and abundance trends offer basic information for investigating stock structure. Fishery-independent data in the North Sea offers high-resolution information on seasonal distributions of juveniles and adults, spawning grounds, nursery grounds, and seasonal movement patterns that are not constrained by fishing patterns (e.g. Pawson and Jennings 1996). Several analyses of survey catches of cod in the North Sea and adjacent areas were available. Most studies documented similar shifts in geographic distribution, and some offered interpretations on the factors and drivers causing shifting distributions.

### 2.2.1 Review of Previous Studies

Blanchard et al. (2005) tested the hypothesis of an ideal free distribution for North Sea cod, determining if young cod contract to optimal or near-optimal habitats as stock size declines. Temperature was used as a proxy for habitat suitability. Young cod followed the assumptions of the ideal free distribution model. During years of low abundance, cod concentrated in areas of highest suitability, but cod were more widely dispersed and occupied areas of less suitable habitats during years of high abundance. The area of high suitability diminished as North Sea temperatures increased over the study period (1977–2002), which did not include the recent divergence in stock dynamics between northern and southern North Sea (Figure 1.1). One implicit assumption of the ideal free distribution is that there is no stock structure or barriers to movement, which does not appear to be valid for North Sea cod.

Lewy and Kristensen (2009) quantified the spatial distribution of cod in the North Sea and Skagerrak. In contrast to the result for young cod reported by Blanchard et al. (2005), the concentration



of the stock did not increase when stock abundance decreased. The centre of gravity of the distribution moved to the northeast, and the concentration of the stock was constant or declined, but the spatial correlation and dispersion of cod catches were relatively constant during winter throughout the period. The study demonstrates the changes in distribution within the North Sea and Skagerrak, which may reflect different trends in abundance among subareas.

Rindorf and Lewy (2006) investigated potential causes of a shift in the distribution of cod, including climate, abundance, distributional history of cohorts, site fidelity and fishing mortality. The centre of gravity of North Sea cod moved north during a series of warm and windy winters that affected the distribution of eggs, larvae, and settlement. The model for spawners included effects for both displacements the previous year and displacement as juveniles, which could be interpreted as homing of adults to where they were spawned. The authors implied that the lack of conclusive genetic evidence for separate spawning populations at the time (Hutchinson *et al.*, 2001) could follow from minor inaccuracies in homing that lead to genetic mixing. Warm temperatures could also have resulted in disproportionately large decreases in the survival of cod larvae in the south-eastern North Sea. The time-series analysis showed a spawning stock consisting of few age groups to be more susceptible to a lasting change in displacement over a greater range of parameter combinations. Fishing mortality at the scale of the North Sea was not directly correlated with displacement of any age groups but decreased the number of older fish and likely increased the sensitivity of the distribution to climatic changes. The models were fit to data on a North Sea scale, but the centre of gravity cannot explicitly represent local populations or stock identity, which were not the aim of the study. The study provides some evidence and mechanisms for the displacement of early life stages shifting the distribution and homing of adults maintaining it. The time-series results suggest that the poor state of the stock has exacerbated this shift, but no potential mechanisms are provided to explain this behaviour.

Svedäng and Svenson (2006) evaluated the abundance and distribution of cod in the Eastern Skagerrak from coastal surveys to understand the degree of connectivity between cod subunits, and to identify structuring elements for cod relating to behaviour (e.g. juvenile dispersal, homing) for explaining reproductive isolation in the absence of hydrographical boundaries. Survey data were analysed for 2000–2005, mostly May–October, from the Swedish Eastern Skagerrak coast, with age-length keys from the International Bottom Trawl Survey (IBTS), which may have biased ageing for local populations with different growth patterns). The cod resource along the eastern Skagerrak coast had a low number of adults despite a large abundance of juveniles. Despite recruitment and reduction of fishing effort, no recovery was observed. The available literature suggests homing behaviour in other cod populations in the Northeast Atlantic. Therefore, the loss of cod in the eastern Skagerrak may not result from a shortage of recruits but rather from a shortage of local recruits. These findings support a view on cod populations as essentially behavioural entities with natal homing, whereas dispersal of early life stages may be less important as a structuring mechanism. Núñez-Riboni *et al.* (2019) concluded that the eastern Skagerrak is a boundary region for changes in thermal suitability of the habitat. Therefore, environmental conditions in the eastern Skagerrak may have changed over time and could have contributed to emigration.

Núñez-Riboni *et al.* (2019) investigated the historical-geographical distribution of cod in the North Sea and the relationship to thermal habitat suitability. Models using climate change projections were evaluated to determine future thermal habitat suitability for cod. Distribution of cod was based on quarter 1 North Sea IBTS data, and bottom temperature data were from quarter 3. Thermal habitat suitability for cod generally improved in the northern areas and decreased in southern areas of the North Sea. These trends are predicted to continue in the coming decades under climate change scenarios. The Skagerrak, the central and northern North Sea, and the edge of the Norwegian trench are expected to remain thermally suitable for cod throughout the 21<sup>st</sup> century. The results indicate that the decadal displacement of North Sea cod can be explained

with temperature changes alone. Stock structure population dynamics (e.g. recruitment and fishing mortality) were not accounted for in the model, but increased temperature could lead to lower survival. Climate projections and the direct causes of geographic shifts are uncertain, but differences among phenotypic stocks of the Dogger cod population may increase if the warming trend continues.

Holmes et al. (2008) tested for asynchrony in the dynamics of putative populations in the North Sea and West of Scotland cod stocks with the aim of providing evidence to support a metapopulation hypothesis. Several spawning areas (Clyde, Southwest, Minch, Shetland, Viking, Moray, Scottish East Coast, Fisher, Flamborough, and Dogger) were based on published studies using a variety of methods including tagging, genetics, and otolith chemistry. Indices were derived using the stratified mean methodology which does not account for differences in survey conditions and may be influenced by anomalies. Statistical testing was rigorous, but the large number of spawning areas limited the significance of pairwise comparisons once corrections were applied. Trends in spawning-stock biomass (SSB) differed between putative spawning areas in both 6.a and the North Sea from 1983 to 2005. There was a general decline in the North Sea, but the extent of decline varied between areas. Areas thought to contain resident inshore populations generally showed more rapid declines than those in adjacent offshore areas. Recruitment indices were more variable with strong within-year correlations and few significant differences in trends across areas. Recruitment in the southern North Sea (i.e. Dogger) declined rapidly before any trend was seen for the North Sea as a whole. Within-year correlations suggest widespread environmental influences on recruitment ( $R$ ). The low  $R$ /SSB in Viking compared to higher  $R$ /SSB in Fisher and Dogger might suggest young cod move north as they become older. This would undermine the subpopulations proposed by ICES (2015) but could be an artefact of survey catchability. Conventional and archival tagging data suggest extensive movement between the southern North Sea (4.c) and the central North Sea (4.b), but little movement of young cod from the southern and central North Sea (4.b–c) to the northern North Sea (4.a). Therefore, the perceived northward shift of cod may represent changes in the relative abundance of local populations. The trends in SSB are indicative of a metapopulation structure although the conclusion is not definitive because of the limited significance of pairwise comparisons and lack of support from recruitment indices.

Holmes et al. (2014) examined trends in local SSB of several species by fitting a smoother to log SSB from 1986–2010 IBTS Quarter 1 survey data in three subareas, representing three putative cod subpopulations, with boundaries defined from available data (Viking, Northwest North Sea, Southern North Sea; an earlier version of the subareas refined by ICES, 2015). Results for cod support the hypothesis of distinct subpopulations. There was a net decline in all but one subpopulation over the study period, with significant differences in the rates of decline. The Viking subpopulation, the most genetically differentiated group, had a different SSB trend from all other subpopulations, while the Northwest North Sea and Southern North Sea subpopulations had only marginally different trends. In general, the magnitude of differences in SSB trends reflected the degree of reproductive isolation. The results suggest two or three stocks in the North Sea. However, population asynchrony after quarter 1 was not considered, and there have been considerable subarea changes since 2010. Differences in SSB dynamics could result from separated stocks or differential environmental conditions, particularly for cod in the Northwest North Sea and Southern North Sea (Figure 1.1).

Nicolas et al. (2014) analysed the spatiotemporal distribution of young cod in the North Sea, using survey data to determine long-term wide-scale patterns and shifts, detect significant drivers of recruitment (e.g. temperature, quantity and quality of zooplankton prey), and develop predictive models of future cod recruitment distribution. Survey data (1983–2005) were analysed by natal areas (Clyde, west coast, Minches and north coast, Shetland, Viking and Bergen Banks, Moray Firth, Firth of Forth, Fisher Banks, Flamborough, and Dogger Bank), using the boundaries

developed by Heath et al. (2008), but the results do not indicate whether or not stock structure is suggested by the data. Years of overexploitation truncated the age structure of cod in the North Sea, particularly in the southern North Sea (4.c). The southern area has been reliant on recruitment, which was in turn impaired by warming temperatures in the south and reduced *Calanus* abundance. The centre of distribution of the stock moved northwards, and the decline in the south is likely to be the result of local depletion, rather than northern movement of fish. Results indicate significantly different recruitment dynamics between the natal areas.

### **Survey Indices and Abundance Maps for North Sea Cod**

Nicola Walker and Casper Berg, WD01 (Annex 3: below)

Updated biomass indices by subregion show continued differences in recent trend between the South and subregions further north (Figure 2.6), but a high level of synchrony in recruitment with significant correlations in both biomass and recruitment between all subregions (Figure 2.7). This was confirmed by similar correlational analyses based on SSB and recruitment estimates from SURBAR models fitted to area-specific survey indices (Figure 4.3). Survey data from the North Sea were combined with adjacent Division 6.a (West of Scotland) and Subdivision 21 (Kattegat) to map the spatiotemporal distribution of cod in the North Sea and surrounding areas, indicating a north-westwards shift of older cod towards the west of Scotland (Figure 2.8). Although combined indices display the same trends associated with the retrospective pattern in the assessment of North Sea cod, they suggest considerable migration of older cod from the North Sea to north and west of Scotland (6.a).

Workshop participants suggested that the strong synchrony in cod recruitment and biomass among subareas of the North Sea may reflect similar spawning and nursery environments which impact recruitment of both Viking and Dogger populations, despite reproductive isolation. For example, the Skagerrak is a nursery ground for both Viking and Dogger cod populations, and recruitment for multiple areas could be affected by the same environmental drivers. If the larval/juvenile pools from different subpopulations overlap in space and time (e.g. Skagerrak), it would also produce synchrony in recruitment. Discrete cod stocks in the Northwest Atlantic Ocean exhibit strongly correlated stock trends that are driven by common environmental causes rather than demographic dependence (Sinclair, 1996; Rothschild, 2007), but the Northwest Atlantic cod stocks are separated by much larger distances than North Sea cod stocks and have no apparent mixing.

### **2.2.2 Summary**

There is strong long-term synchrony in time series of cod biomass and recruitment among subareas of the North Sea, except for a recent divergence in biomass trends, in which biomass increased in the Viking and Northwest areas, but biomass remained low in the South. There was a suggestion that cod may have retreated to favourable habitat in the north when abundance decreased, but archival tagging data do not support this hypothesis (Neat and Righton, 2007). Overfishing led to truncated age structures (particularly in the southern North Sea, 4.c), so the populations have been more dependent on recruitment, which may be limited by the environment (e.g. temperature). Distribution changes are more likely to result from changes in local populations than fish movement. Studies generally support two or three distinct cod stocks in the North Sea that have different stock dynamics, but differences could also be explained by environment. The strong synchrony in cod recruitment and biomass among subareas of the North Sea may reflect similar spawning and nursery environments which impact recruitment of both Viking and Dogger populations, despite reproductive isolation.

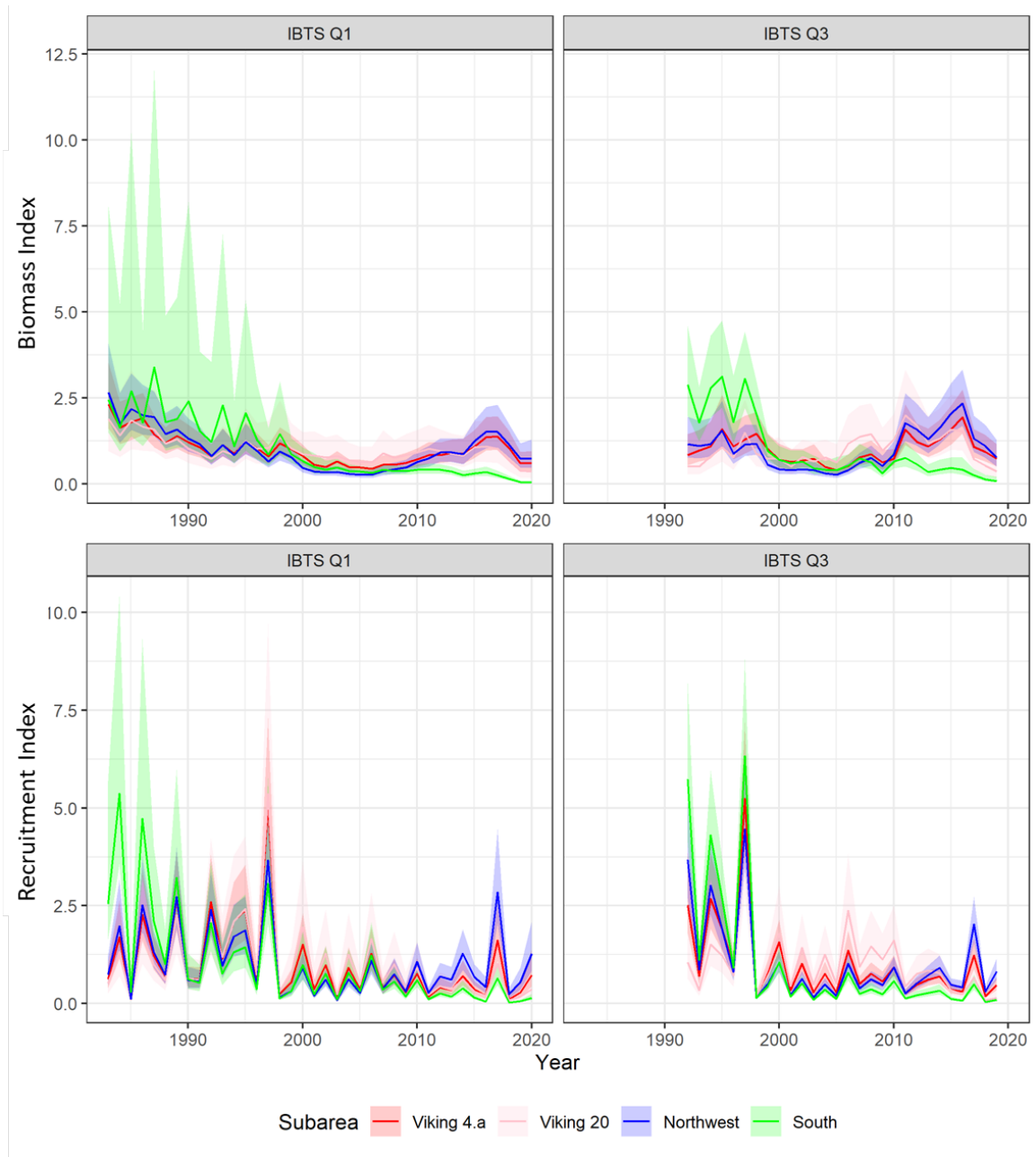
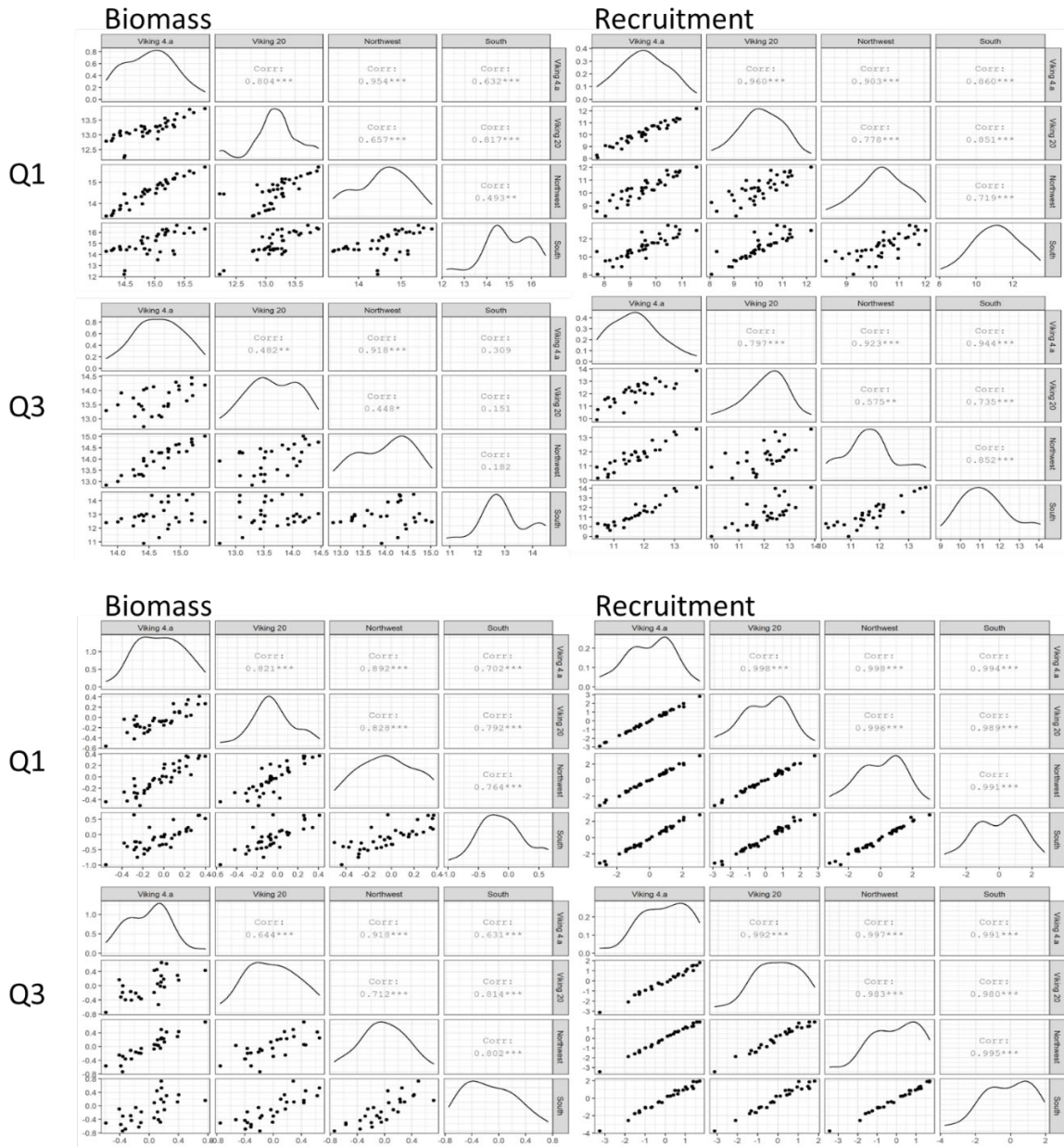


Figure 2.6. Cod survey indices by subregion (see Figure 2.4) with 95% confidence intervals based on NS-IBTS-quarter 1 and quarter 3 data. The indices and confidence intervals are standardised by the mean of the index for each subregion.



**Figure 2.7. Correlations between log survey indices of cod biomass (left) and recruitment (right) for quarter 1 (quarter 1) and quarter 3 (quarter 3) surveys by subregion. The lower triangle of subplots shows scatterplots of differenced log biomass for each pair of subregions, the top triangle the Pearson correlation coefficient and the diagonal the distribution of differenced log index values for each subregion. Top four matrices are correlations among subregion time series, and bottom four matrices are correlations among detrended series (1st order difference of lag 1 year).**

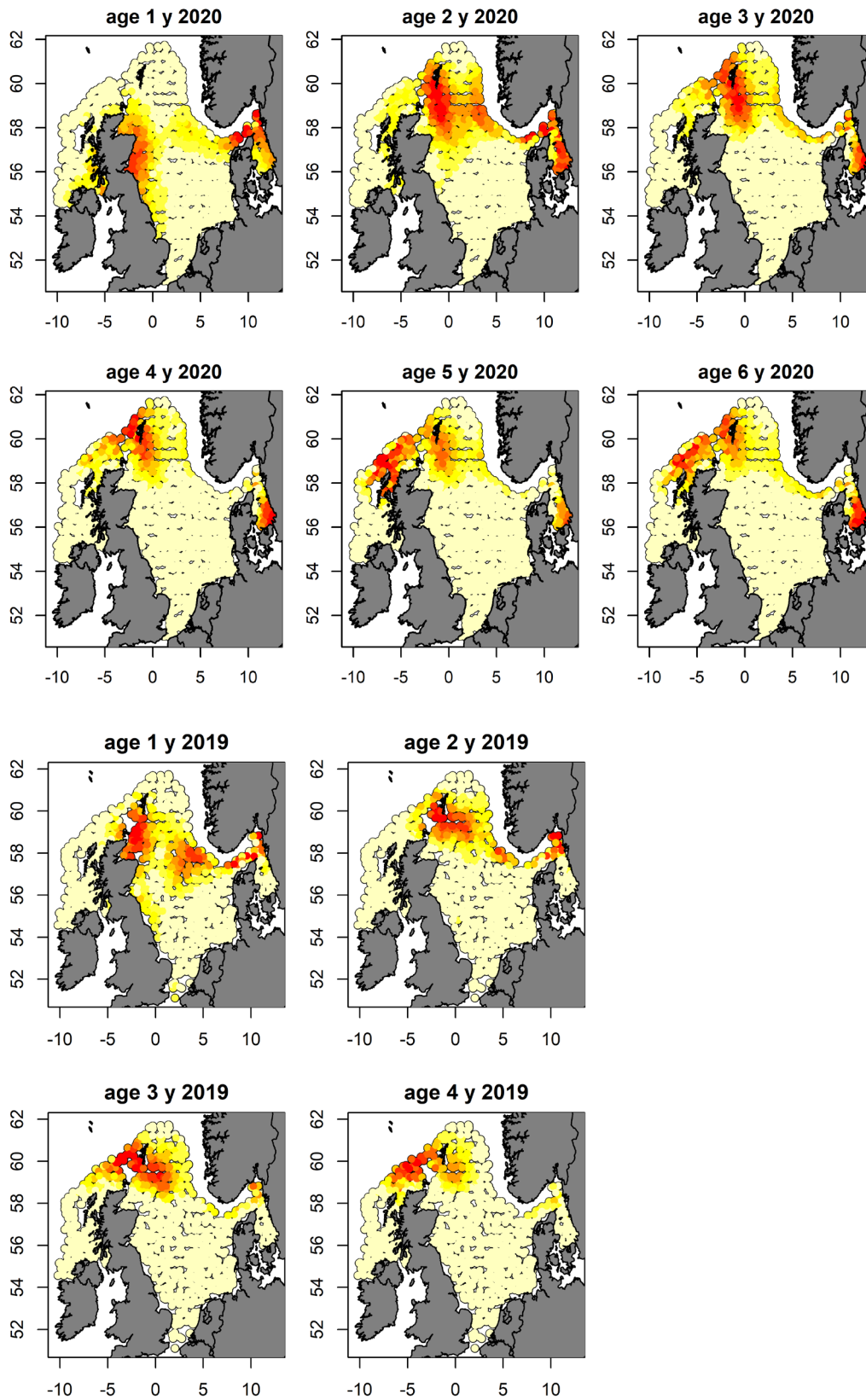


Figure 2.8. Recent spatial distribution of cod caught in the NS-IBTS Quarter 1 (top 6 panels) and Quarter 3 (bottom four panels), ScoWCGFS and BITS. Individual subplots are produced separately hence the colours are indicative of trends only. See Annex 3: below for the entire time-series.

## 2.3 Fisheries (ToR 1 a.iii)

Fishing grounds and spatiotemporal patterns in fishery data can be informative for stock identification (Pawson and Jennings, 1996). Although fishery-independent survey data has high spatial resolution, it has relatively low spatiotemporal density in which most surveys occur only once per year and sample relatively few locations, making it difficult to investigate seasonal patterns, spawning or recruitment aggregations. Therefore, fishery data is a valuable supplement to survey data for understanding distributions of cod in the North Sea and adjacent areas.

Cod are caught in virtually all demersal gears in subarea 4 (divisions 4.a–c), division 7.d and subdivision 3.a.20, including beam trawls, otter trawls, seine nets, gill nets, trammel nets and lines (ICES, 2019b). Most of these fleets take a mixture of species, with some directed mainly towards cod (e.g. large-meshed otter trawls and some fixed gear fisheries) and others with cod as a bycatch (e.g. beam trawls targeting flatfish). The fleets landing the greatest volume of cod in the EU are Bottom Trawl >100 mm mesh ('TR1', mainly operated by Scotland, Denmark and Germany), Gillnet ('GN1', mainly Denmark and Norway), Bottom Trawl 70–100 mm ('TR2'), Beam Trawl >120 mm ('BT1') and Beam Trawl 80–120 mm ('BT2').

Engelhard et al. (2014) described long-term distribution shifts of cod in the North Sea based on commercial landings-per-unit-effort (LPUE) by ICES rectangle (1913–2012) and examined associations of climate change and fishing pressure with shifting distributions. They found similarities in spatial patterns of LPUE and survey CPUE data (1977–2012). LPUE was digitized from historical fisheries 'statistical charts' produced by the UK Ministry of Agriculture, Fisheries and Food (now the UK Department for Environment, Food and Rural Affairs) for British otter trawls landing in England and Wales (1913–1980), and supplemented with data from Marine Scotland (1968–2012) and CEFAS (1982–2012). LPUE was normalized by annual means to adjust for technological changes. Survey CPUE was from the winter IBTS CPUE 1977–2012 for cod >29 cm. Decadal changes in North Sea cod distribution were summarised using the LPUE of British trawlers, identifying an easterly shift beginning in the 1990s and a northerly shift in the 2000s. These results were similar to observations of shifting distribution in the 1990s surveyed catches (e.g. ICES, 2005). LPUE data suggest a more marked distribution shift in the past 20–30 years than the previous 70 years. High LPUE was recently concentrated in the northern and northeastern North Sea (4.a). Centres of gravity in latitude, longitude, and depth were derived for both the LPUE and CPUE data and were found to be positively correlated. Cod fishing mortality and SSB had no correlation with latitude or depth centres of gravity. Both were correlated to longitude centre of gravity, with high fishing mortality and low biomass associated with the eastward shift. Results suggested that the northward shift was due to warming, but the eastward shift was linked to fishing pressure. Despite uncertainties related to fishery LPUE data due to discarding and misreporting and differences in spatiotemporal resolution, spatial patterns in fishery LPUE and survey CPUE were similar. These results demonstrated the local depletion of subpopulations, and the authors suggested that accounting for subpopulations in management may help alleviate the problem of local depletion and shifting fishing effort.

### 2.3.1 Recent Spatial Analyses

The EU-Norway Technical Group Meeting on additional technical measures aimed at the protection of both juvenile and adult cod (WGTM; Graham and Olsen, 2020) summarised logbook and Vessel Monitoring System (VMS) information associated with cod landings from fishing activities in the North-East Atlantic and Baltic Sea. Annual cod landings by ICES rectangle and metier for EU countries fishing in the North Sea were available from prior analysis. Norwegian data was added to the previously analysed data set, and the spatial distribution of cod landings was presented for the main gear types. Recent spatial distributions of North Sea cod landings

were compared to modelled distributions of cod from survey data. Landings were widespread throughout the North Sea (Figure 2.9). Large mesh (>100 mm) trawls and seines (TR1) caught most of the cod landings, followed by gill nets and small mesh (<100 mm) trawls and seines (TR2). Surveys (quarter 1) and the large-mesh trawl fleet (kg/std.trawl >35 cm) mainly caught cod from the Skagerrak and westward along the Norwegian Trench, and around Orkney and Shetland (2016–2018). Gill netters (GN) generally caught cod in similar areas as the large-mesh trawl fishery (but smaller amounts in some areas). Cod landings from the small-mesh trawl fleet (TR2) were concentrated in the Skagerrak.

WGTM also used electronic logbooks (EFLALO) and VMS (TACSAT) data to summarise the core fishing areas for the large mesh trawl TR1 fleet at a higher spatial resolution (Figure 2.10). As part of an informal data request, logbook and VMS data for trips landing cod were linked at a national level and provided to the WG to maintain vessel anonymity. The daily reported cod catch for each vessel was split equally between VMS pings (minimum frequency 2 hrs) each day, and data was compiled to a spatial grid of ~15nm. These aggregated data were available for bottom contacting trawl gears in two gear groupings (mesh size <100 mm, 100 mm +) for 2014–2018, with assumed fishing speeds of 3–5 knots for otter trawls and 0.5–5 for seines. The distribution of TR1 VMS-linked landings is highest to the west and south of the Shetland Isles with the general distribution occurring across the central area of 4.a and following south along the Norwegian trench (Figure 2.10). The spatial distribution of landings contracted in recent years, with relatively sparse landings along the Norwegian trench and in the Viking area, suggesting a westerly shift from Viking to Shetland.

Spatial analyses of Scottish VMS-linked logbook landings by Marine Scotland in 2012 used a similar data preparation and linking approach to the current ICES Data Call. Data were aggregated to 7.5 nm grid cells (vessels > 15 m with assumed fishing speeds of 0.5–5 knots). Results suggest a relatively continuous distribution of catches across the 4.a–6.a boundary, except in windsock closed area adjacent to 4.a (Figure 2.11).

### 2.3.2 Summary

An easterly shift in fishery catches in the 1990s linked to fishing, and a northerly shift in the 2000s due to warming suggest local depletion of subpopulations in the central-southern North Sea and off England and Scotland (Engelhard *et al.*, 2014). These shifts were followed by a shift back from Viking to Shetlands in recent years (2016–2018; Graham and Olsen, 2020). The spatial distribution of cod landings is relatively continuous across the 4.a–6.a advisory unit boundary suggesting that there is not a population boundary between 4.a and 6.a.



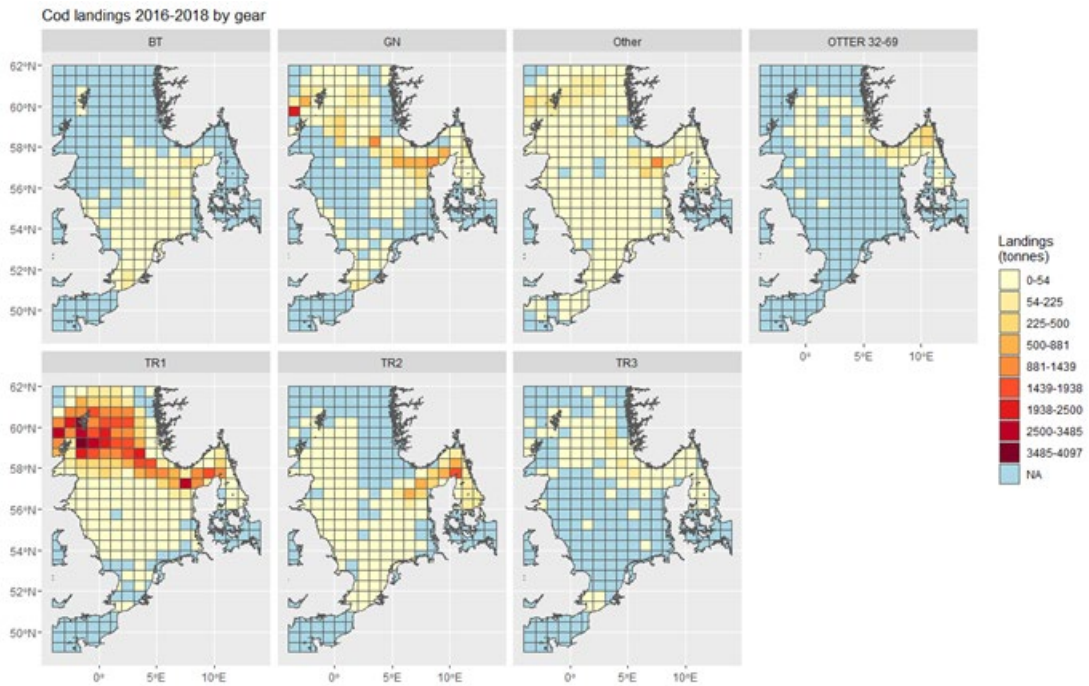


Figure 2.9. Cod landings 2016–2018 by metier. BT: Beam Trawls, GN: Gill nets, Other: longlines and other gear, Otter 32.69: *Pandalus* fishery, TR1: Trawls and seines with mesh size above 100 mm, TR2: Trawls and seines with mesh size between 70 to 99 mm, TR3: Trawls and seines with mesh size between 16 to 32 mm mesh size. NA: areas with no cod landings. From EU-Norway WGTM report (Graham and Olsen, 2020).

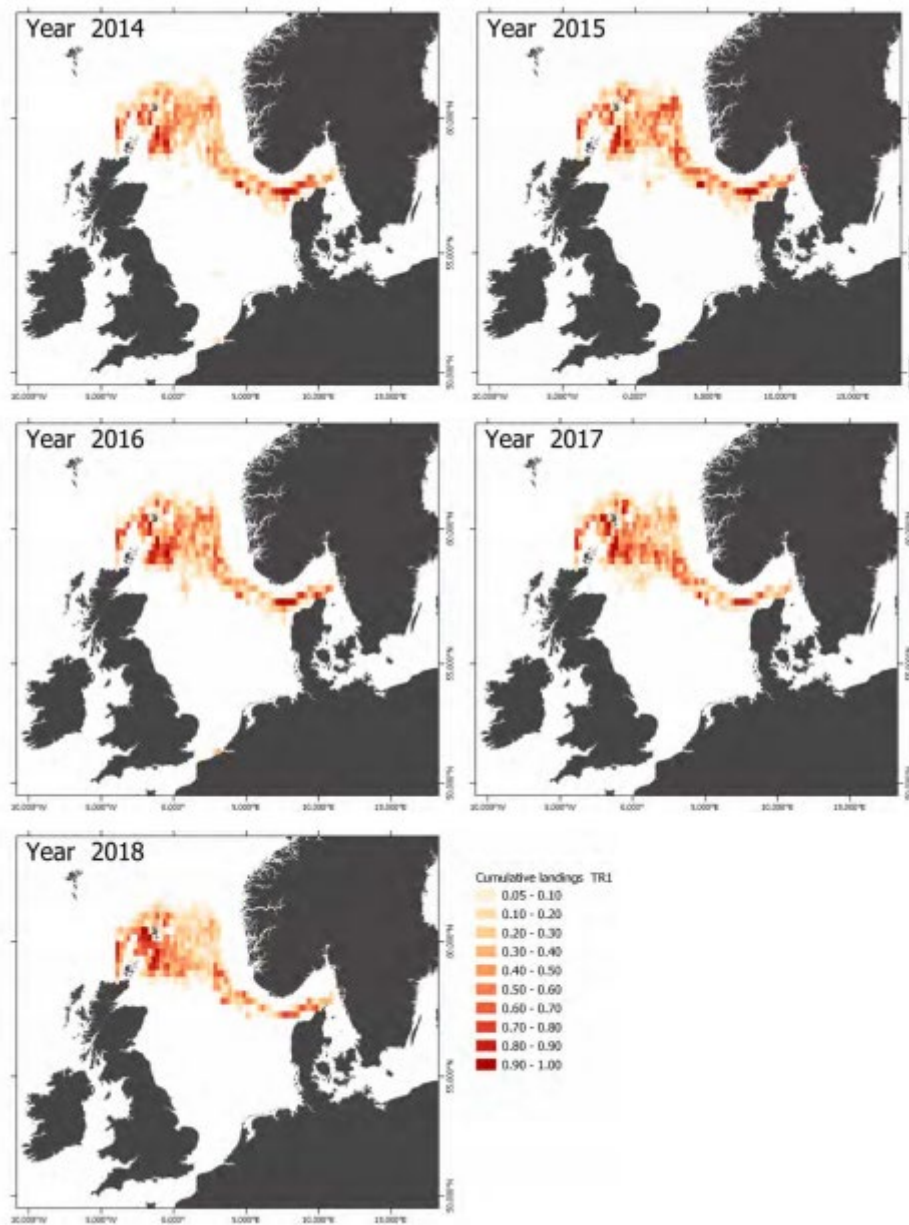


Figure 2.10. Cumulative distribution (%) of annual VMS linked logbook landings for all countries 2014–2018 displayed at 15x15 nm grid cell resolution for all bottom contacting trawling and seine gears using > 100 mm mesh sizes (TR1).

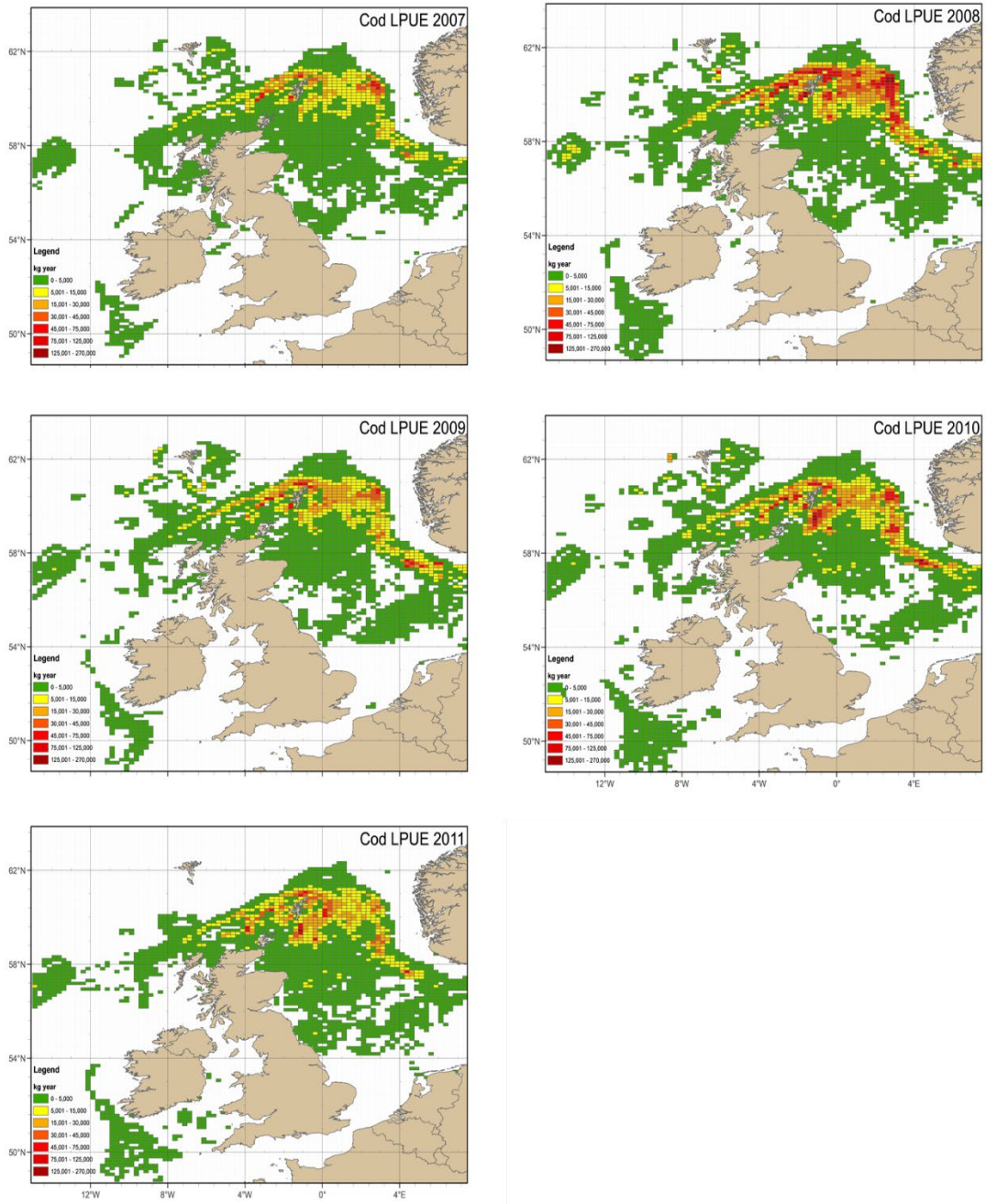


Figure 2.11. Spatial location of VMS-linked logbook for Scottish vessels LPUE in 2007–2011.

## 2.4 Dispersal of cod eggs and larva/juveniles (ToR 1 a.iv)

The distribution and dispersal of early life history stages can help to determine self-sustaining areas or link spawning grounds to distant nursery areas (Harden Jones, 1968). Twelve papers were reviewed that were grouped into three broad categories: (1) studies describing the distribution of spawning and early life stages from survey data; (2) studies examining connectivity to adjacent management areas primarily through the transportation of cod eggs and larvae and (3) mechanistic models.

### 2.4.1 Ichthyoplankton and Spawning Ground Surveys

Three papers focused on cod spawning grounds (Fox *et al.*, 2008; González-Irusta and Wright, 2016; Höffle *et al.*, 2018). Two of these were based on the ICES co-ordinated egg/ichthyoplankton surveys conducted in 2004 and 2009. The surveys were carried out across the North Sea either in conjunction with the North Sea International Bottom Trawl Survey in quarter 1 (NS-IBTS-quarter 1) or in dedicated surveys between 16 February–23 March 2004 and 17 January–6 March 2009, using DNA-based molecular methodology to identify early developmental stage cod eggs. Fox *et al.* (2008) compared findings from the 2004 survey to egg production inferred from the distribution of mature cod caught in contemporaneous trawl surveys and found hotspots of egg production around the southern and eastern edges of the Dogger Bank, in the German Bight, Moray Firth, and to the east of the Shetlands, coinciding with known spawning locations from 1940–1970 (from Daan, 1978). However, the study did not find significant numbers of cod eggs at the historic spawning ground off Flamborough Head, leading the authors to conclude that while most major spawning grounds in the North Sea are still active, some localised populations may have diminished.

Höffle *et al.* (2018) applied Generalized Additive Mixed Models to both 2004 and 2009 ichthyoplankton surveys with the aim of delimiting spawning grounds. Although patterns of egg production were not entirely consistent with predictions based on catches of mature females (potentially due to timing of the survey), they concluded that spawning areas seemed to remain stable with spawning more common in the southeastern North Sea. The study also showed similar distribution patterns of eggs at different stages, indicating that dispersal of eggs may be slow. González-Irusta and Wright (2016) also employed a Generalized Additive Modeling approach to identify spawning grounds by relating abundances of spawning fish from the IBTS Quarter 1 surveys to environmental variables. In addition to predicting widespread but non-uniform spawning in the North Sea, these models showed that cod prefer high salinity waters, temperatures around 5–7°C, select coarse sand habitats, and avoid areas of very high tidal flow.

All three papers agreed that spawning appeared widespread throughout the North Sea and has remained stable over time but with local changes in concentration. However, these results are based on only a few years of sampling (ichthyoplankton surveys in 2004 and 2009 and adult spawning distributions 2009–2014) and may not be representative of the present day. Furthermore, the ichthyoplankton surveys in 2004 and 2009 had limited temporal coverage of the cod spawning season, and some spawning grounds in the northeast were therefore not well sampled. Although these studies do not address stock identification directly, they suggest fine-scale population structuring.

### Connectivity with Adjacent Management Areas

Three papers examined the influence of hydrography on the locations of early life stages of cod by presenting egg and larval densities on interpolated hydrographic maps. ICES (1996) considered the relationship of cod in the northern North Sea (4.a) and cod West of Scotland (6.a). They reported a continuous distribution of gadoid eggs, larvae and pelagic age-0 cod from the North

Sea to the Hebrides. Oceanographic information for the area suggested that a proportion of the cod spawned west of the 6.a–4.a boundary drift into the North Sea, but larval transport in the opposite direction is unlikely. They concluded that there is interchange between cod in 6.a and 4.a, but the extent and implications for stock assessment were uncertain.

Munk et al. (2002) considered data collected by a Danish survey in the central North Sea between 14–23 March 1997, and Munk et al. (2009) used results from the ichthyoplankton survey in 2004. Although neither study addressed stock identification, both associated spawning grounds and larval distributions with hydrographic features such as salinity fronts and regions of freshwater influence, providing some understanding of the mechanisms driving these distributions, which could explain limits to mixing.

Three papers were directly relevant to the question of stock identification and the eastern extent of the current North Sea stock boundary. Knutsen et al. (2004) investigated the origin of coastal juvenile cod in the Skagerrak by means of microsatellite DNA analyses combined with crude predictions of North Sea inflow from a biophysical model, indicating that early staged cod can be transported into the Skagerrak in some years. Despite potential biases in larval influx due to net transport not being explicitly modelled, this study provided genetic evidence that the Skagerrak acts as a nursery area for North Sea cod which mix with the locally spawned cod, supporting the rationale for the Skagerrak being part of the North Sea cod assessment area.

Two later studies employed genetic analyses to investigate connectivity and stock mixing in the Kattegat. André et al. (2016) tested natal homing by combining information from behavioural groups of cod identified by DSTs with individual genetic analyses. They found temporally stable genetic differentiation among cod spawning populations in the eastern North Sea-Skagerrak-Kattegat region and provided evidence of juvenile transport from the North Sea into the coastal Skagerrak and Kattegat, most likely at the egg and larval stages. The study also provided evidence of a return eastward migration consistent with philopatry, although the extent of tag returns and uncertainty about the scale of the North Sea/west Skagerrak population is a constraint to demonstrating natal homing. A recent study by Hemmer-Hansen et al. (2020) provides further evidence that the Kattegat is part of a nursery area for North Sea cod. They found at least two genetically distinct populations of cod in the Kattegat with a north-south gradient in mixing proportions: “North Sea cod” and “Kattegat/transition zone cod”. The North Sea genotype appeared to enter the Kattegat during the pelagic phase and otolith analyses showed 45% of cod from both genotypes to be resident in the Kattegat, but North Sea genotypes did not spawn in the area.

All three papers provide evidence that both the Skagerrak and Kattegat are important nursery grounds for North Sea cod. Together they provide support for the hypothesis that North Sea cod are transported into the Skagerrak and Kattegat as juveniles and mix with resident cod. North Sea cod do not appear spawn in the Skagerrak and Kattegat, but they migrate out of the region to spawn.

Huserbråten et al. (2018) investigated spill-over of North Sea cod into nursery habitat along the Norwegian northwestern coast by means of a coupled hydrodynamic particle trajectory model. This study supports the possibility of leakage of North Sea cod recruits out of the north-eastern North Sea and into the Norwegian Sea, but it is not validated with field observations. In particular, the release points were based on extrapolated potential egg production rather than observations of known spawning locations, and it was unclear how many of the cod larvae survive and move back into the North Sea. Furthermore, evidence of spawning activity on the Trench, which would support the authors’ tentative hypothesis of a Trench dispersal unit in the north-eastern North Sea, is lacking.

### 2.4.2 Mechanistic models

Andrews *et al.* (2006) presented a spatially and physiologically explicit model describing the demography and distribution of cod on the European shelf. Stock identification was not an objective of the paper, which focused on the construction, parameterisation, and calibration of the model as well as testing of basic movement hypotheses. The main conclusions were: (1) aggregated spawning is essential to a qualitatively correct prediction of the spatial distribution of the spawning stock and (2) the long-term advective movement of settled individuals is primarily the result of net transport by local bottom currents.

A similar modelling approach focused on the development of genetic populations (Heath *et al.*, 2008). Although the modelling framework was designed to evaluate the results of molecular genetics studies, this application focused on model construction and the consequences of speculative assumptions about first-spawning migrations and fidelity to natal areas (Clyde, west coast, Minches and north coast, Shetland, Viking and Bergen Banks, Moray Firth, Firth of Forth, Fisher Banks, Flamborough, and Dogger Bank). However, there were some common behaviours across migration scenarios that could be relevant for stock identification. Modelled fish in Dogger Bank and the Southern Bight emerged as being of high natal purity and local native origin regardless of migration scenario while fish in Shetland and the Bergen Banks consistently showed low fidelity. This consistency lends support to a substock in the south, despite first-spawner behaviour being largely unknown. The introduction of a small amount of spawner straying (5% based on tagging data) resulted in significant deviations from natal purity, providing evidence against discreteness of possible subpopulations. It was also shown that increased fishing mortality increased the degree of natal purity. Overall, there was no superior migration scenario, suggesting that cod populations are maintained through a variety of mechanisms. It was proposed that separation of some populations is possible through distance and oceanographic processes affecting the dispersal of eggs and larvae, but homing may be necessary to explain the separation of others.

### 2.4.3 Summary

Spawning distributions have only been studied in a few years (based on ichthyoplankton surveys in 2004 and 2009 and adult spawning distributions 2009–2014) but appear widespread across the North Sea and have remained stable over time, with local concentrations. It is likely that both the Skagerrak and Kattegat are important nursery grounds for North Sea cod. The Skagerrak is part of the current North Sea cod assessment region. However, there is evidence that North Sea cod move into the Kattegat as 0-group juveniles, probably via larval transport, and mix with resident cod until they start to mature and migrate out of the region. There is some modelling support for a single substock in the southern North Sea as well as support for mixing of eggs and larvae among some natal areas. These studies provide a foundation for stock identification but need to be considered with other evidence to build a more complete picture of stock structuring.

## 2.5 Genetic analyses (ToR 1 b.)

Genetic information provides the most definitive inference of reproductive isolation among discrete spawning groups (Waples and Gaggiotti, 2006). Several publications were reviewed that covered a range of spatial sampling designs and used a wide array of genetic characters. The data available from two studies (Heath *et al.*, 2014; Fairweather *et al.*, 2018) were re-analysed to test alternative hypotheses of population structure developed at the workshop.

### 2.5.1 Genetic Structure within the Current North Sea Advisory Area

The genetic population structure of Atlantic cod within the North Sea in the context of ICES advisory units was last reviewed by Wright *et al.* (2015). They concentrated on the North Sea ICES (subarea 4) and found evidence for population structure at finer scales than currently considered in the ICES advisory work. In particular, they found support for the presence of unique genetic units represented by spawning individuals collected in the deeper, offshore parts of the North Sea and more shallow areas, respectively (Figure 2.12). The unique genetic profile of cod in the northern/deeper regions of the North Sea were supported by several studies applying different types of genetic markers (Nielsen *et al.*, 2009b, Poulsen *et al.*, 2011; Heath *et al.*, 2014, Sodeland *et al.*, 2016; Fairweather *et al.*, 2018). No available study has sampled cod in both coastal Norway and offshore deeper areas (i.e. the yellow and red areas in Figure 2.12), so it is unknown if they represent the same biological population. However, given the scale at which population structure is normally observed in marine fishes, it is plausible that sampling in these geographical regions have targeted the same population (Wright *et al.*, 2015).

Hutchinson *et al.* (2001) described even finer scale genetic structure within subarea 4. However, the study was based on a relatively low number of genetic markers (5 microsatellite loci), and the patterns were relatively weak and not significant when correcting for multiple testing. Furthermore, it was not clear if the presented results were temporally stable. Finally, studies applying more genetic markers have not confirmed clear patterns of structuring within the “Dogger unit” (Heath *et al.*, 2014, Barth *et al.*, 2018; Fairweather *et al.*, 2018), but the available studies have varied in the markers used, and no study has been conducted with an exhaustive set of genome-wide markers and a robust spatiotemporally replicated sampling. Consequently, while additional fine-scale genetic structure may exist within Subarea 4, current genetic data suggest the presence of at least two major genetic units. The genetic differences indicate that the Viking cod and Dogger cod populations follow independent evolutionary, and hence also likely demographic, trajectories.

Three recent studies confirmed the genetic isolation of population components in the northern parts of the North Sea (Sodeland *et al.*, 2016; Fairweather *et al.*, 2018; Wright *et al.*, 2020). The increased power with recent technological developments allowed a more comprehensive understanding of the underlying genomic patterns associated with population structure. The studies found differences between the units for genetic markers located in parts of the genome which are believed to harbour inversions (Sodeland *et al.*, 2016; Wright *et al.*, 2020). These were large blocks of the genome with hundreds of genes found to be highly divergent among several cod populations (Hemmer-Hansen *et al.*, 2013; Bradbury *et al.*, 2013; Berg *et al.*, 2015).

Adults in spawning condition collected in offshore regions from the Skagerrak grouped genetically with spawners from the North Sea and were different from the neighbouring Kattegat population (Knutsen *et al.*, 2011; André *et al.*, 2016) and also from inner fjord samples from the Norwegian Skagerrak coast (Knutsen *et al.*, 2011; Sodeland *et al.*, 2016; Barth *et al.*, 2017). These data support the inclusion of offshore Skagerrak with the North Sea, but also a separation of inner fjord and offshore along the Norwegian Skagerrak coasts.

### 2.5.2 Reproductive Connectivity with Spawning Populations in Neighbour Areas

*Skagerrak (20) and Kattegat (21)*: Several studies suggest a high degree of connectivity between the North Sea and neighbouring Skagerrak and Kattegat. This connectivity is likely mediated through transport of North Sea early life stages to both Skagerrak (Knutsen *et al.*, 2017) and the Kattegat (André *et al.*, 2016; Hemmer-Hansen *et al.*, 2020). Genetic and tagging data suggest that

some cod in the Kattegat return to their natal spawning areas in the North Sea when they reach sexual maturity (André *et al.*, 2016; Hemmer-Hansen *et al.*, 2020). Consequently, Skagerrak and Kattegat may be important nursery areas for the North Sea/Skagerrak spawning populations. These dynamics have important consequences for stock assessments in the Kattegat (Hemmer-Hansen *et al.*, 2020), with implications for estimating stock size, management reference points, and associated uncertainties. Consequences for the North Sea stock assessments are unclear at present, but the results demonstrate that assumptions of closed, homogenous units under the current advisory areas for both the North Sea and adjacent areas are violated.

Several studies found that spawning cod in the Kattegat are genetically different from spawning components in the North Sea (Berg *et al.*, 2015; André *et al.*, 2016; Barth *et al.*, 2017). The central spawning area for the Kattegat cod appears to be in the southern parts of the Kattegat (Hemmer-Hansen *et al.*, 2020).

Most genetic analyses of cod sampled from the Skagerrak and Kattegat did not classify North Sea genetic lineages to the Viking or Dogger populations. Wright *et al.* (2015) attempted to identify the two North Sea types with the genetic markers currently used routinely for stock composition analyses in the Kattegat. Results suggest different geographic distributions for Viking and Dogger cod, but the power for identifying Viking and Dogger with these markers is relatively low, and sampling was limited to one time period. Therefore, results cannot provide estimates of relative proportions of Viking or Dogger cod in the Skagerrak and Kattegat.

*Skagerrak/Kattegat fjords:* Cod in the inner parts of the Norwegian Skagerrak fjords were different from both offshore Skagerrak and North Sea spawning components (Knutsen *et al.*, 2011; Barth *et al.*, 2018), supporting the presence of genetically differentiated fjord populations in the region. Unique genetic fjord signatures were not identified in Swedish Skagerrak/Kattegat fjords. However, there is evidence for the presence of adult fish with both North Sea and non-North Sea genetic profiles, and the fjord cod with non-North Sea profiles appear more closely related to the Kattegat/transition zone populations (Svedäng *et al.*, 2019). A mix of local and North Sea cod were also found in Norwegian fjords (Barth *et al.*, 2018; Jorde *et al.*, 2018), and a few cod with transition zone (Kattegat/Western Baltic) genetic profiles were identified (Barth *et al.*, 2018). In Norwegian fjords, genetic and tagging data suggested the presence of stationary adult fish with North Sea genetic signatures (Barth *et al.*, 2018). Consequently, genetic data also indicate a complex scenario of mixing of different populations in Skagerrak/Kattegat fjords (Barth *et al.*, 2018; Jorde *et al.*, 2018; Svedäng *et al.*, 2019).

*West of Scotland (6.a):* Genetic studies found a high degree of similarity between cod in area 6.a and the cod in the shallow parts of subarea 4 (Nielsen *et al.*, 2009b; Heath *et al.*, 2014). Detailed geographic sampling has added to the understanding of the core geographic distribution of the genetic units in the northern North Sea and West of Scotland. Wright *et al.* (2020) suggested that a border at 1°W between 6.a and 4.a would be better aligned with the geographical distributions of populations than the current border at 4°W. However, the study also identified a genetic gradient from west to east and hence that genetic breaks may not be clear-cut over short geographic distances.

*Norway (1–2):* Norwegian cod (Northeast Arctic cod and Norwegian coastal cod) sampled off Lofoten (2.a) were genetically different from cod in the North Sea (Fairweather *et al.*, 2018). Cod in the White Sea (area 1) were also different from those in the North Sea (Fairweather *et al.*, 2018).

*Faroe (5.b.1 and 5.b.2):* Genetic data showed that cod on the Faroe Bank and Faroe Plateau are different from cod in the North Sea (Poulsen *et al.*, 2011).

*Western English Channel & southern Celtic Sea (7e-k):* There is evidence from genetic data for a genetically differentiated unit in 7.e–k (Heath *et al.*, 2014).



### 2.5.3 Reanalysis of Available Data

Genetic data from Heath et al. (2014) and Fairweather et al. (2018) were reanalysed to provide more information about potential fine-scale genetic structure within the North Sea and adjacent areas. From Heath et al. (2014), the full data set was extracted (90 SNP loci; 6 potential outlier loci were removed from the publicly available data set) and used to calculate pairwise overall  $F_{ST}$  among all samples included in the original study. From Fairweather et al. (2018), only the samples of direct relevance for the North Sea and neighbouring areas was extracted. The full data set (1127 SNP loci) was used, which differ from Fairweather et al. (2018) who removed markers through data filtering (e.g. markers that were outliers or could not be reliably calibrated across the aggregated data sets) and hence used a reduced set of loci (796 SNP loci). Pairwise  $F_{ST}$  (Weir and Cockerham, 1984) were calculated in the R (R Core Team, 2019; RStudio Team, 2019) package “hierfstat” (Goudet and Jombart, 2020) and plotted as a heatmap with the “heatmap.2” function from the package “gplots” (Warnes *et al.*, 2020).

The analyses of pairwise  $F_{ST}$  from Heath et al. (2014) confirmed the three major units (“Viking”, “Dogger” and “Celtic”) originally identified, where Viking cod and Dogger cod were distributed within the current North Sea advisory unit. An additional split was evident within the putative Dogger population in the data from Heath et al. (2014; Figure 2.13), but these groups were not as well supported, because samples from the same area (W Shetland) sampled at different times were placed in different groups. Furthermore, the distribution of samples in the two groups did not align well with the geographic origin of sampling. The reanalysis of data from Fairweather et al. (2018) found four main groups, represented by samples from the Faroe Islands, northeast deep North Sea (likely representing Viking cod), shallow North Sea (likely representing Dogger cod) and Irish Sea/Celtic Sea (likely representing the Celtic cod population; Figure 2.14). In conclusion, the reanalysis confirmed the presence of Viking and Dogger genetically distinct units within the current North Sea cod advisory area and did not find strong support for additional genetic heterogeneity within the region.

### 2.5.4 Summary

Relatively low rates of effective migration and gene flow will result in a genetic homogenization of populations (Waples and Gaggiotti, 2006; Nielsen *et al.*, 2009a). Therefore, the genetic differences found between Viking cod and Dogger cod are most likely of biological significance, and these populations may maintain demographic independence at finer scales than those reported with the genetic data currently available. Future work applying full genome sequencing may provide genetic information at finer geographical scales.

Genetic data strongly suggest that current assumptions for the North Sea advisory unit are violated. There is evidence for heterogeneity within the current North Sea advisory unit. There is also strong support for at least two separate reproductive populations in the North Sea. The Viking population is mainly in the northern, deeper parts of the North Sea (part of 4.a), and the Dogger population is mainly distributed in more shallow regions and in the south. Some studies have suggested genetic structure at even finer geographic scales within the North Sea, but these genetic signals are weaker and have not been consistently reported across studies. There is evidence for high degrees of connectivity with adjacent advisory units, particularly with the Skagerrak and the Kattegat, where North Sea cod may constitute a high proportion at juvenile life stages. There is support for separate reproductive units in Norway (1 and 2), the Faroe Islands (5.b.1 and 5.b.2), Kattegat (Subdivision 21) and the Western English Channel and southern Celtic Sea (7.e–k).

Further studies are recommended to refine our understanding of the geographical distributions of North Sea cod populations in spawning as well as feeding seasons. Data from some studies

(e.g. Heath *et al.*, 2014, Fairweather *et al.*, 2018; Wright *et al.*, 2020) could be reanalysed with a specific focus on the questions for North Sea stock assessment and management. Available data could also be mined as a first step towards identifying diagnostic genetic markers to develop a genetics based tool for routine use for stock identification of the major units as currently defined (i.e. Viking cod, Dogger cod, and Celtic cod; Heath *et al.*, 2014) in the North Sea and adjacent areas, as currently implemented for cod in the Baltic Sea and the Kattegat. In addition, new genomic data is expected to provide information about potential genetic structuring on finer geographical scales, elucidate patterns of neutral gene flow vs. adaptive genetic variation, and facilitate the development and implementation of high-powered tools for monitoring stock distributions and mixing.

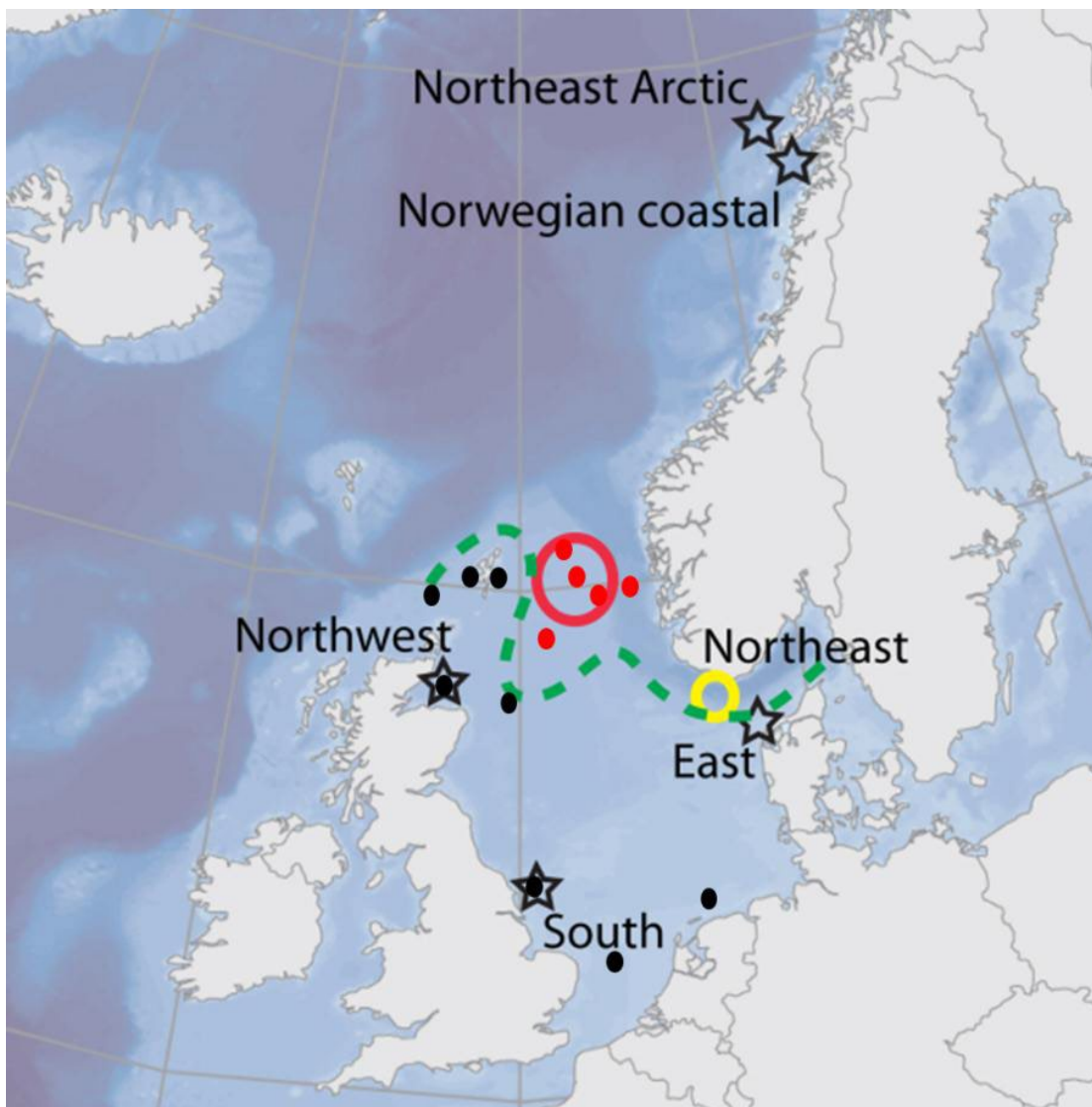


Figure 2.12. Location of areas included for genetic studies in the current North Sea advisory area (from Wright *et al.*, 2015). Red circle shows Viking Bank, where Nielsen *et al.* (2009b) identified a genetically unique population. Yellow circle represents the area analysed in Poulsen *et al.* (2011), Fairweather *et al.* (2018) and Sodeland *et al.* (2016). Dots and stars represent sample locations, which were assigned to different populations (here indicated in red and black, respectively) in Heath *et al.* (2014). Broken line indicates approximate location of break (100 m contour) between northern and southern populations in the North Sea, as suggested by Wright *et al.* (2011).

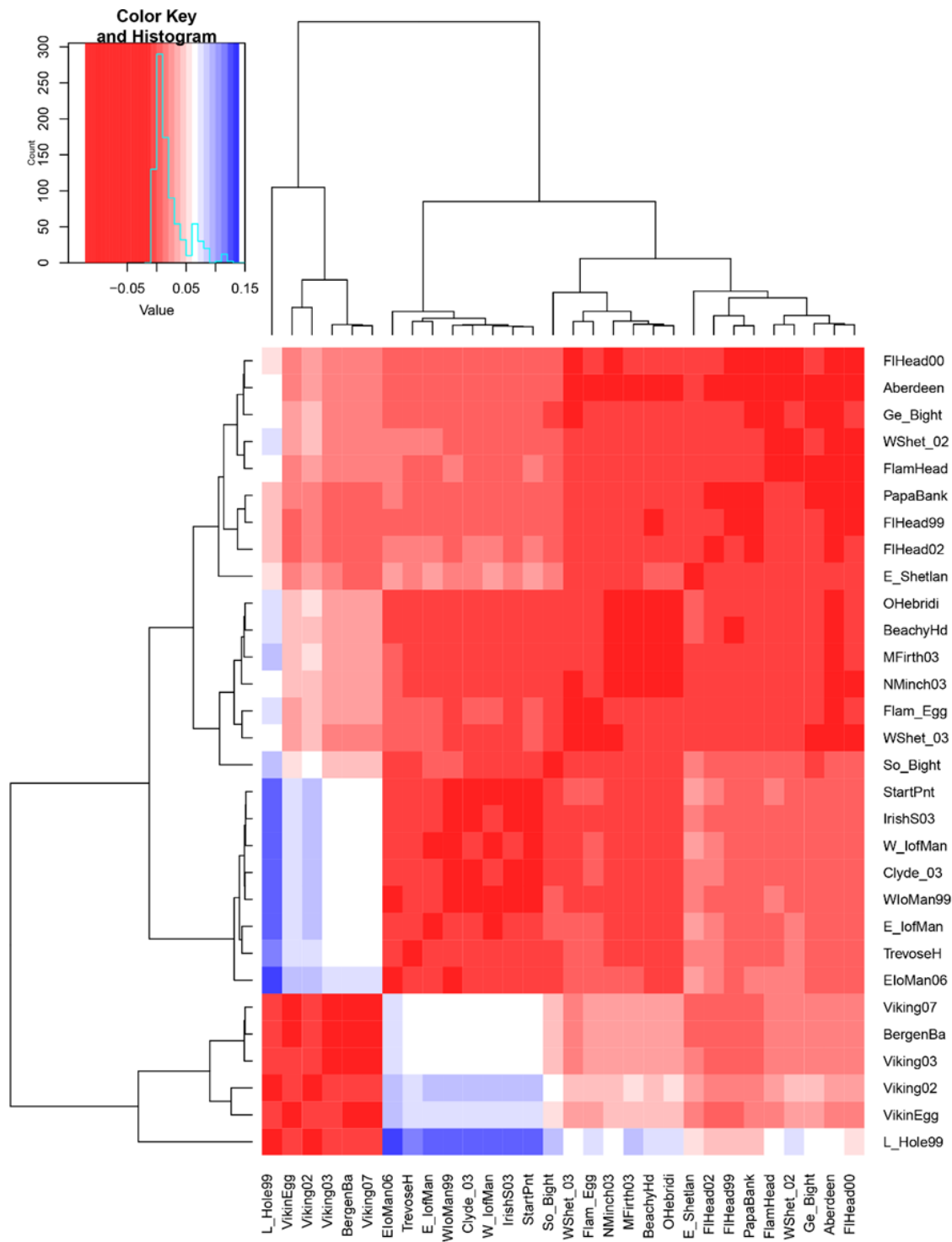


Figure 2.13. Heatmap of pairwise FST from re-analysis of data from Heath et al. (2014).

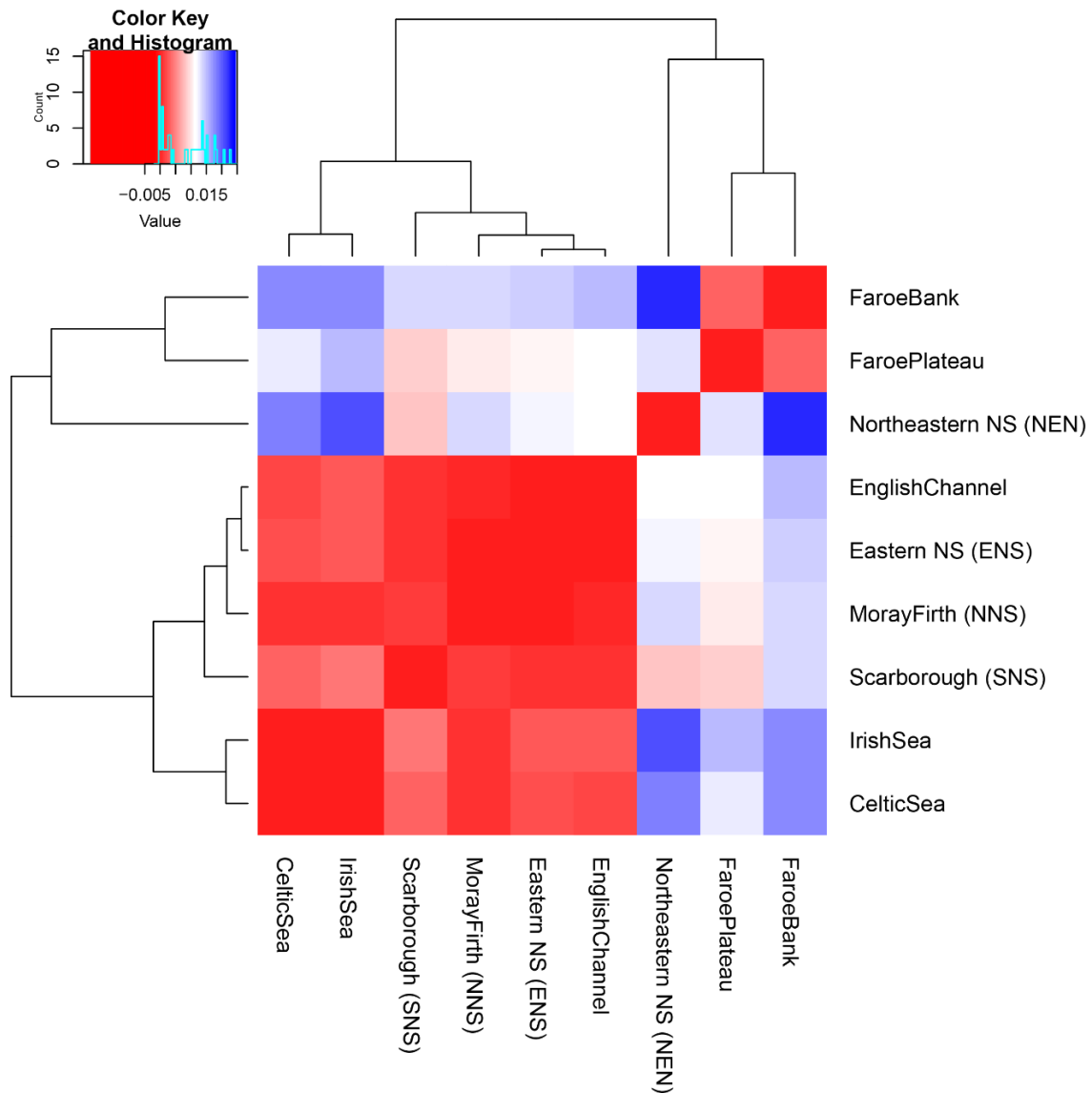


Figure 2.14. Heatmap of pairwise  $F_{ST}$  from re-analysis of data from Fairweather et al. (2018).

## 2.6 Otolith microchemistry (ToR 1 c.)

Otolith chemistry is useful in examining movements among life-stages in regions where there is detectable spatial variation (Thresher, 1999). Connectivity among life-stages has been estimated by comparing microchemistry in equivalent parts of the otolith from the same year-class, thus allowing post dispersed individuals to be assigned to sampled sources (Gillanders, 2002). However, this approach is challenging for studying marine larvae because of their relative abundance, wide dispersal and high mortality. These challenges have led to using unsupervised cluster analysis of near-core ablation chemistry to infer the number of distinct natal sources and the spatial scale over which larval dispersal takes place (Calò *et al.*, 2016; Gibb *et al.*, 2007). Otolith microchemistry profiles have also been used to track individual movements, although this approach can be biased, because temperature, salinity and physiological changes linked to ontogeny can also affect otolith chemistry (Walther *et al.*, 2010; Clarke *et al.*, 2011; Barnes *et al.*, 2013; Stanley *et al.*, 2015).

Regional variation in the otolith microchemistry of cod inhabiting the North Sea and adjacent areas has been examined in a number of studies. Gibb *et al.* (2007) tested differences in the cod

otolith microchemistry based on whole solution inductively coupled plasma mass spectrometry (ICPMS) of samples from around Scotland including three aggregations of settled 0-group in 4.a within the Northwest substock division identified by ICES (2015: Shetland, Moray Firth and Buchan, as well as 6.a (Firth of Clyde). Cod from all 0-group samples could be distinguished with >90% accuracy based on quadratic discriminant analysis, indicating no mixing between the nursery areas within the Northwest division or with the Clyde. The limited mixing of early life stages indicated by otolith microchemistry was consistent with the extent of movement based on tag-recapture evidence (see section 2.1), suggesting that the Northwest substock is comprised of a number of largely resident cod groups.

Connectivity between the North Sea cod nursery and spawning grounds has been conducted by comparing microchemistry in equivalent parts of the otolith from the same year-class, in two studies. Wright *et al.* (2006b) used this approach to consider the links between nursery and spawning areas in the west of Scotland (ICES division 6.a) and Shetland coastal waters (ICES division 4.a). Maximum likelihood assignments of juveniles to their site of origin indicated an error rate of  $\leq 12\%$ . Assignment of the juvenile component indicated a largely local origin of adults with a possible small contribution from the adjacent nursery grounds, which might reflect assignment error. Specific information was not available on the larval phase due to the use of whole otolith solution ICPMS, but the evidence of self-recruitment, supported by tagging data from this study and Neat *et al.* (2006), suggests that Shetland has a local coastal population, and there may be finer-scale population structure than the three substocks proposed by ICES (2015).

Wright *et al.* (2018) examined nursery to spawning links across the North Sea and Skagerrak. Whole otoliths from demersal young of the year (0-group) from ten sites in autumn 2007 ( $n=431$ ) were used to produce baseline chemical signatures. The corresponding portion was analysed from the same year-class of adults, sampled as spawning age-2 cod in 2009 and age-3 in 2010 ( $n=442$ ). Classification accuracy of whole otolith juvenile signatures to their sampling area was highest for the northern North Sea (4.a) and southern and central North Sea (4.c and 4.b), but chemical signatures of Scottish east coast and eastern Skagerrak partially overlapped, leading to lower classification accuracy. Assignment of adults to 0-group areas indicated different juvenile sources between the southern North Sea (4.c) and northern North Sea (4.a) spawning aggregations, exception for the Skagerrak and adults in the northern North Sea. The Skagerrak had a small contribution to the central and southern North Sea (4.b–c), where most adults originated from the east coast of 4.b and 4.c and none from the north. Some adults in 4.b were assigned to the Scottish east coast which may reflect some mixing or poor discrimination with the Skagerrak signature. The Skagerrak had the largest contribution to the northeast North Sea (*i.e.* Viking area, Heath *et al.*, 2014), while almost all the remainder had a northern juvenile signature.

In order to consider the number of distinct natal sources and the spatial scale over which larval dispersal takes place, Wright *et al.* (2018) conducted laser ablation (LA) ICPMS on the second sagitta otolith of the 0-group juveniles, with ablation pits near the core and edge, corresponding to the early larval and settled juvenile phases. The edge chemistry could be classified into four areas (northern: Shetland and Fisher Bank), Skagerrak sites (north and east), southern sites (Danish coast, German and Southern Bights) and Buchan, off the Scottish east coast. Unsupervised clustering analysis of the near-core ablation data using a random forest method suggested four potential natal sources. Two of these clusters accounted for nearly all juveniles in either the Southern Bight (4.c) or Shetland (4.a) juvenile samples, and the cluster chemistry was similar to that of the corresponding edge chemistry. Other juvenile samples were comprised of a mixture of the four natal clusters that may suggest larval mixing or a lack of geographic heterogeneity in the elemental signature. Taken together with the adult assignment results, the study supports the hypothesis of separate stocks in the northern North Sea (4.a) and southern North Sea (4.c), with the Skagerrak as a nursery area, particularly for 4.a. The mixed natal sources of juveniles in the Skagerrak were consistent with genetic and biophysical modelling evidence for mixed North

Sea and local juveniles. However, the mixed natal sources in some southern sites and Buchan are more difficult to interpret, because of no significant difference in Mn and Ba edge and near-core levels.

In another study of natal sources, Svedäng et al. (2010) used micro particle-induced X-ray emission to examine chemistry near the core otoliths from 40 cod tagged in the Kattegat (just east of the stock boundary). These cod were grouped into three areas based on their recapture position and comprised several age-classes. Canonical discriminant analysis (CDA) was used to test if natal chemistry differed among the three recapture sites. Differences in near core otolith chemistry among these sites were interpreted as reflecting early spatial segregation. This result might have been biased by the supervised nature of the CDA method, which is intended to find variables that discriminate among groups. Nevertheless, the combined results of otolith chemistry and tagging suggested the presence of multiple cod groups in the Kattegat with little mixing.

Hemmer-Hanssen et al. (2020) used otolith microchemistry to investigate interactions between North Sea and resident cod in the Kattegat. The study combined an extensive genetic analysis which allowed assignment of cod to Kattegat or North Sea genotypes. Transects across the otolith of juvenile and adult cod, from core to edge, were analysed using LA ICPMS. Edge chemistry for a range of elements was used as a baseline signature and compared to that for earlier life-stages evident in the otolith record. Otolith chemistry comparisons were made for the portion of the otolith corresponding to the pelagic juvenile, demersal juvenile and first and successive winters using ANOVA, MANOVA and linear discriminant analysis. The continuous measurement of Sr was used to reconstruct the fishes path using a combination of assignment of measured otolith strontium to salinity levels, an otolith Sr-salinity relationship and salinity data. The otolith classification success decreased from 83% for pelagic to 72% for demersal and 50% for first sea winter in the North Sea genotype and similarly from 68% to 62% and 51% in the Kattegat genotype. This suggests that there were early differences in the otolith chemistry of pelagic juveniles which subsequently declined as the two genotypes inhabited the same environment. Reconstructed migration patterns of adult cod based on this Sr state-space migration model also indicated that 45% of cod in the Kattegat remained resident, while some mixed with cod in the Skagerrak and North Sea. As such the study confirms previous evidence that the Kattegat acts as a nursery area for cod that have been transported in from the North Sea and Skagerrak.

### 2.6.1 Summary

Spatial variation in otolith microchemistry distinguishes cod among some areas of the North Sea and adjacent waters, most notably between the northern North Sea (4.a) and the southern North Sea (4.c). Unsupervised clustering of otolith chemistry indicates separate northern and southern natal sources. Assignment of adults to juvenile sites indicates largely separate nursery sources for the southern North Sea (4.c) and northern North Sea (4.a) adults, with some evidence of localised recruitment. Based on the reviewed studies, the Skagerrak and beyond into the Kattegat are suggested to be home to both resident groups as well as being used as nursery areas by North Sea cod mostly for 4.a (i.e. Viking), which mix with local coastal populations as juveniles.

## 2.7 Morphometrics and meristics (ToR 1 d.)

Little was found in the literature regarding meristics and morphometrics of cod in the North Sea and adjacent areas. The only two mentions of possible meristic differences among cod (vertebrae count) from different regions in the North Sea went back to the early seventies (ICES, 1970, 1971) and were inconclusive due to lack of data.

Galley et al. (2006) investigated the capacity of otolith shape to discriminate among fish originating from spawning grounds possibly hosting different subpopulations in the Northern North Sea (4.a: Viking Bank, Shetland, Papa Bank, Moray Firth), West of Scotland (6.a, South Minch, Firth of Clyde) and the Irish Sea (7.a) using both morphological and standardized Fourier harmonic descriptors. Using pairwise discriminant analysis, they evidenced high classification success among spawning grounds within 4.a and between 4.a and both 6.a and 7.a, driven mostly by comparisons of fish from Moray Firth against all other investigated locations. Fish spawning on the Viking Bank exhibited high classification success against other areas within 4.a (Shetland and Moray Firth) and in 6.a (South Minch). They also demonstrated that this capacity to predict the origin of individuals was only partially driven by differences in somatic growth, which is known to influence otolith shape (e.g. Wright *et al.*, 2002; Cardinale *et al.*, 2004), suggesting some alternative drivers to the highlighted differences. Based on pairwise randomisation analysis using all Fourier harmonics, Galley et al. (2006) also showed that fish originating from the Viking and Papa Bank areas had significantly different otolith shapes compared to other locations within and outside 4.a but not between them. This analysis was not size-independent and may include growth-driven differences. Although they did not use any correction for multiple testing, applying a false discovery rate correction (Benjamini and Hochberg, 1995) on the p-values reported in the article suggests that conclusions are mostly maintained. Although their conclusions regarding the partial independence of the highlighted differences in otolith shapes to differences of size at age among spawning ground seem robust, the link to reproductive isolation between locations is only speculative, and their study could not rule out the influence of other environmental factors. However, the results support stock structure within 4.a (i.e. resident population in Moray Firth, differentiation of Viking from most areas but Papa Bank), differences between 4.a and the areas West of Scotland (6.a), and possibly fine-scale, discrete stock structure.

## 2.8 Life-history and parasites (ToR 1 e.)

Persistent patterns of geographic variation in life-history traits can delineate phenotypic stocks that have limited inter-stock mixing and are relevant to determining spatial structure for stock assessment models that model growth and maturity rates (McBride 2014), and parasites can serve as natural tags (Sindermann, 1961). Eight papers were available on geographic variation in life history of North Sea cod (Graham, 1934; Harrald *et al.*, 2010; Kuparinen *et al.*, 2016; Roney *et al.*, 2016, 2018a, 2018b; Wright *et al.*, 2011; Yoneda and Wright, 2004), with a range of spatial resolution in the sampling designs. Three papers on cod parasites were reviewed (Perdiguero-Alonso *et al.*, 2008; Gay *et al.*, 2018; and Sokolova *et al.*, 2018), and a working document was prepared with further references (WD02 in Annex 4: below).

### 2.8.1 Life-history

At a broad-scale of spatial resolution within the North Sea, Graham (1934) delineated between faster-growing cod in the south and slower-growing cod in central areas of North Sea. This delineation was associated with a vertical thermocline in summer in the north and a well-mixed water column in the south throughout the year. The differences in growth were possibly linked to temperature, the position of the thermocline, or quantity and quality of food. The delineation suggested by Graham (1934) was strikingly similar to more recent studies (ICES, 2005; Núñez-Riboni *et al.*, 2019).

Harrald et al. (2010) tested whether spatial variability in reproductive traits of cod from two regions (northwest North Sea, and southern North Sea) is linked to intrinsic (genetic) differences in cod from these regions. They analysed field data (IBTS quarter 1 survey, supplemented with

commercial trawl sampling) to identify differences in size at maturity in wild cod in these regions. Once established, they then used a common-environment experiment on wild-caught juveniles raised through to maturity to demonstrate that cod from the southern North Sea mature at larger sizes than those from the northwest North Sea, despite broadly similar growth rates, and concluded that spatial variation in maturity–size relationships in the wild has a significant genetic component. Specifically, the study found that smaller female size at maturity partly reflected higher relative liver weight, with northwest North Sea females having a higher relative liver weight than Southern North Sea females. By investigating maturation under controlled conditions, the study provides evidence for life history trade-offs in energy allocation between growth, energy storage, and reproduction that may underlie the spatial variation observed in the field.

Also at a broad-scale of resolution, Wright *et al.* (2011) examined trends in maturation schedules from three subpopulations of North Sea cod (northwest, northeast, south), in relation to the biomass of conspecifics and bottom sea temperature around the summer maturation decision phase, using the demographic probabilistic maturation reaction norm (PMRN) approach. They used data on sex, maturity, age, length, and CPUE extracted from the first quarter IBTS databases (DATRAS), for the years 1971–2009, supplemented with additional research and commercial trawl sampling in the years 1999, 2002–2004, and 2008. They found declines in maturation probability with size and age, but the magnitude of decline differed among subpopulations (with little evidence of a net decline for the northeast subpopulation), leading to significant spatial differences in recent times. Changes in maturation probability could not be explained by colonization from adjacent regions, indicating a local response to conditions. Furthermore, temperature had a positive effect on maturation probability, but could only partially explain the decreasing trend in PMRN midpoints. Consequently, regional selection for early maturing genotypes provides the most parsimonious explanation for the declines in maturation probability observed.

Investigating at a fine-scale, and overlapping the geographic range considered for the next North Sea cod assessment, Yoneda and Wright (2004) considered how reproductive investment in cod (age/length at maturity, annual fecundity) changed during periods of high stock size (1969–70) versus low (2002–03) stock size, and how it differed among three areas (offshore North Sea, inshore North Sea, Scottish west coast). The study found that in recent years, maturity and fecundity in pre-spawning females differed among the three areas, which they argued may reflect population differences. Furthermore, they found temporal trends in inshore North Sea cod, maturing at a smaller size and younger age, and being more fecund, in 2002–03 compared to 1969–70 (high stock years). They rejected density-dependent mechanisms as inducing these temporal trends, instead suggesting that the change in the maturity-size relationship in inshore North Sea cod could partly be attributable to a genetic selection towards smaller size at maturity, which may be associated with truncated age distribution. They found spatial differences in maturity but not fecundity during 1969–1970, and spatial differences in length at maturity, but not age at maturity, and significant differences in fecundity during 2002–03. Finally, they concluded that spatial variation in fecundity in recent years cannot be solely explained in terms of nutrition because similar gutted body and liver weights for a given size were found in all three areas. Therefore, inshore North Sea cod could allocate more energy to reproduction than any other area examined.

Six papers (Olsen *et al.*, 2008; 2009; Kuparinen *et al.*, 2016; Roney *et al.*, 2016, 2018a, 2018b) provide information on fine-scale life history structuring of cod populations in Norwegian fjords of the Skagerrak (20), which are excluded from the North Sea cod assessment. The spatial scale of population structure in Norwegian fjords may not be comparable to the population structure of offshore cod in the North Sea and Skagerrak. Olsen *et al.* (2008) sampled cod on the Norwegian coast of the Skagerrak and found fine-scale spatial structuring of maturation reaction norms that were comparable to the differences in neutral genetic markers. Olsen *et al.* (2009) also analysed



cod samples from the Norwegian Skagerrak coast from a long year beach seine survey series and a mark-recapture study and found that juvenile size steadily decreasing across 90 years despite no trend in mean size.

Two related papers report fine-scale (< 10 km) differences in realized reproductive output of cod in the Skagerrak of coastal Norway. Roney et al. (2018a, b) examined daily estimates of parentage and offspring-quality metrics for thousands of cod larvae from a free-spawning group of several dozen wild-adult Atlantic cod in the Risør fjord. They report that cod spawning in the outer fjord produced fewer egg batches over shorter periods of time than those spawning in the inner fjord. These differences occurred after accounting for the number of individuals, average body size, sex ratio, initiation of spawning period, and body condition.

At the finest spatial scale, Kuparinen et al. (2016) examined differences in cod growth between the inner and outer Risør fjord on the Norwegian coast of the Skagerrak and found no significant sex differences, but differences in growth between inner/outer fjord, with the outer fjord fish on average one year younger at a given size. Life history differences, possibly linked to population structure, within the Norwegian Skagerrak was at a very fine spatial scale (10 km), but the authors could not quantify the relative roles of environment/genetics on the observed growth differences. Roney et al. (2016) used samples from autumn surveys (1984–2014) over a broader area of the southern Norwegian coast in general linear mixed-effects models to consider whether coastal populations of cod differ in life history, whether such differences persisted over time, and what factors were responsible for these differences. The authors found that the probability of being mature expanded spatially (along an increasing longitudinal cline) and increased temporally (throughout a 30-year time-series). However, in the absence of physical barriers, neither of these trends could be fully explained by variation in sea temperature or population density, and the authors argue that their work provides empirically defensible justification for studies on the ecological factors and evolutionary mechanisms responsible for producing and maintaining this variability.

In conclusion, several studies demonstrated how maturity varies between different subregions of the North Sea (e.g. southern, northwest, and northeast). These included evidence for an intrinsic (e.g. genetic) basis based on a common-environment experiment. There is also a historic record of a latitudinal difference in cod growth rate throughout much of the North Sea, with slow growers to the north and fast growers in the south, delineated by a thermocline in summer related to depth. Several papers also demonstrate fine-scale structuring of life-history parameters, particularly cod in Norwegian fjords of the Skagerrak (which are not included in the assessment of North Sea cod). These differences could not fully be explained with environmental variables, suggesting that they may be related to ecological factors and evolutionary mechanisms.

## 2.8.2 Parasites

The three available papers on parasites of North Sea cod were not that informative about cod population structure in the North Sea. Perdiguero-Alonso et al. (2008) found relatively rich and abundant regional macroparasite faunas in cod from six regions of the North-East Atlantic (stretching from the Baltic Sea to Iceland, including the North, Celtic and Irish Seas, and a Norwegian fjord), generally dominated by generalist parasites with Arctic-Boreal distribution. The high regional variation in the prevalence and abundance of the parasite species imply that differences may exist in the feeding behaviour between cod in the six regions, or alternatively, that these differences could be due to the variations in the abundance of the intermediate hosts. Gay et al. (2018) considered three regions (Barents, Baltic and North seas) and found the highest number of *Anisakis* in the North Sea, with the numbers and prevalence of *Anisakis* positively related to fish length/weight, and prevalence influenced by season. They also found differences among

the three regions, with highest prevalence of *Pseudoterranova* in the northern North Sea, *Contracaecum* in the Baltic Sea (none in the Central North Sea), and *Hysterothylacium* in the Barents and the Northern North Sea (none in Baltic Sea). Finally, Sokolova et al. (2018) focussed on the Skagerrak, Kattegat and Baltic Sea, and found that the prevalence of infection with *Contracaecum osculatum* differed significantly between areas (highest in the east, lowest in the southwest, and intermediate in the other areas).

All three papers investigated *Contracaecum* prevalence and suggested low values in the Central North Sea (4b) as compared to other areas. Gay et al. (2018) suggested low *Contracaecum* prevalence in the central North Sea (4b) in contrast to high prevalence found in the northern North Sea (4a) and Barents Sea. Perdiguero-Alonso et al. (2008; supplementary materials) identified low prevalence in the central North Sea (4b) but high prevalence of *Contracaecum osculatum* in the central Baltic, Irish and Celtic Seas. Sokolova et al. (2018) suggested both Kattegat and Skagerrak at similar intermediate values of *Contracaecum osculatum* prevalence and very high values in the Central Baltic.

### **Parasites of cod (*Gadus morhua*) in the North Sea as biological tags of stock structure**

Neil Campbell, WD02 (Annex 4: below)

The use of parasites as biological tags for stock identification studies has an extensive and well-documented history. Given its wide distribution in the north Atlantic and migratory nature, cod is one of the species to which this approach has been applied most frequently. This paper documents the principles of using parasites as biological tags, examples of the types of parasites used and the information on stock structuring which they can provide, throughout the range of the species, and details history of the application of this approach within the North Sea and associated waters. It finds that although this technique has been commonly applied to problems of cod population structuring, evidence of its use within the North Sea is inconclusive, and, other than a suggestion of some differences between the Skagerrak and Dogger Bank cod, there is little information available from parasitological studies on the stock structure of North Sea cod.

In conclusion, there is little information available from parasitological studies on the stock structure of North Sea cod. The high regional variation in the prevalence and abundance of the parasite species imply that differences may exist in the feeding behaviour of cod, or alternatively, that these differences could be due to the variations in the abundance of the intermediate hosts.

### 3 Plausible scenarios for cod stocks in the North Sea and adjacent areas (ToR 2)

WKNSCodID reaffirmed previous conclusions by ICES (1996, 2005, and 2015) that the current advisory unit of cod in the North Sea, Eastern English Channel, and Skagerrak (Subarea 4, Division 7.d, Subdivision 20) is not a closed, homogeneous, and well-mixed population. There is compelling evidence of distinct population structure of cod within the North Sea and substantial connectivity with other adjacent advisory units of cod.

Despite common trends and spatial synchrony of cod biomass and recruitment among subareas of the North Sea and Skagerrak (see Figure 2.6 and Figure 2.7), significant and persistent patterns of genetic variation provide evidence of reproductively isolated populations of Viking cod and Dogger cod (e.g. Nielsen *et al.*, 2009b, Poulsen *et al.*, 2011; Heath *et al.*, 2014, Sodeland *et al.*, 2016; Fairweather *et al.*, 2018). These populations generally inhabit different portions of the North Sea and adjacent areas, and cod in these different habitats have different phenotypic traits, such as rates of maturity and growth (e.g. Graham, 1934, Yoneda and Wright, 2004, Harrald *et al.*, 2010; Wright *et al.*, 2011). These reproductively isolated populations also exhibit some mixing after spawning (e.g. Figure 2.3–Figure 2.5). For example, genetics, otolith chemistry and demographic information offer evidence that the Skagerrak appears to be a nursery ground for both Viking and Dogger cod (e.g. Knutsen *et al.*, 2004, Svedäng and Svenson 2006; ICES, 2015; André *et al.*, 2016; Wright *et al.*, 2018; Hemmer-Hansen *et al.*, 2020), with most of the cod in the Skagerrak being Viking cod (Wright *et al.*, 2015). The common trends in biomass and recruitment among subareas suggest that there is some mixing of populations after spawning in some areas of the North Sea and common environmental factors throughout the region.

Viking cod is defined as a separate genetic population that primarily inhabits the northeast North Sea (on and near Viking Bank) that is reproductively isolated from Dogger cod. The Skagerrak (20) and the northern part of the Kattegat (21) are nursery areas for Viking cod. Viking cod mix with Dogger cod near the Shetlands (western portion of 4.a), and extend southward to near the 4.a–4.b border. This definition is based primarily on genetics but supported by tagging, larval dispersal, size and age at maturity, otolith chemistry, otolith shape and different recent trends in biomass than the southern North Sea.

The Dogger cod population inhabits the southern and central North Sea (on and near Dogger Bank). Dogger cod range from the English Channel (7.d–e), through the southern and central North Sea (4.a–b), along the Scottish coast (4.a) to West of Scotland (6.a.North). The Skagerrak (20) and northern portions of the Kattegat (21) are a nursery area for some Dogger cod from the central North Sea (4.b). There is a spatial boundary between the Dogger cod population and the Celtic cod population west of Scotland (between the Outer Hebrides and the Firth of Clyde, Heath *et al.*, 2014), and another boundary between these populations in the English Channel (between 7.d and 7.e; Heath *et al.*, 2004, 2014).

The available information does not provide clear evidence of genetic heterogeneity within the Dogger cod population (e.g. re-analysis of data from Heath *et al.* (2014) and Fairweather *et al.* (2018); Figure 2.13 and Figure 2.14), but the population has some spatial phenotypic and demographic structure. There appear to be two phenotypic stocks with different rates of growth and maturity, in which cod grow and mature faster in the shallower (<50 m) southern part of the North Sea (Graham, 1934, Harrald *et al.*, 2010; Wright *et al.*, 2011). These phenotypic groups exhibit different recent trends in biomass. Survey indices suggest recent rebuilding of cod in the northwest North Sea, but no rebuilding in the Southern subarea (Figure 1.1; ICES, 2015; 2019a; Figure 2.6), creating a shift in the distribution of cod to the north as indicated by surveys and

fishery data (ICES, 2005; Engelhard *et al.*, 2014; Graham and Olsen, 2020). Decadal changes in thermal suitability may explain the recent differences in biomass trends, with negative changes in thermal suitability in the southern North Sea, and positive changes in the northern North Sea, particularly for adult cod (Núñez-Riboni *et al.*, 2019). Geographic shifts in the distribution of North Sea cod and the low abundance of cod in the south (4.c) appear to result from the interaction of fishing and warming temperatures. The pattern of geographic variation and different recent trends in biomass are consistent with tagging data that indicates substantial mixing between the southern and central North Sea (4.b–4.c) and much less mixing between those areas and the northern North Sea (4.a, Figure 2.1 and Figure 2.2). Otolith chemistry also suggests local recruitment in the northwest North Sea (Gibb *et al.*, 2007; Wright *et al.*, 2006a).

North Sea cod are isolated from some adjacent advisory units of cod. Cod on the Faroe Plateau (5.b.1) are genetically distinct from those in the North Sea (Poulsen *et al.*, 2011). Despite some indications of mixing of cod in the North Sea with those in Norwegian fjords (subareas 1–2), the Norwegian Coastal and Northeast Arctic cod (1–2) are genetically distinct from those in the North Sea (Wright *et al.*, 2015; Fairweather *et al.*, 2018). Cod in Norwegian fjords of the Skagerrak (Subdivision 20) are also genetically distinct from North Sea cod (Knutsen *et al.*, 2004, 2011; Poulsen *et al.*, 2011; Barth *et al.*, 2017) and may display spatial phenotypic differences at smaller spatial scales.

There is evidence of considerable connectivity with other adjacent advisory units of cod. Most spawning cod in the Kattegat (21) are genetically distinct from North Sea cod, but there is some mixing of juveniles (André *et al.*, 2016). The Kattegat appears to be a spatial extension of the Skagerrak nursery area for both the Viking and Dogger cod populations.

The Dogger cod population extends westward from the North Sea along the coast of Scotland, into Division 6.a. ICES (2020) concluded that the ‘northern offshore component’ of cod in 6.a is part of the ‘Dogger cod’ population based on genetics, tagging and trends in abundance. Wright *et al.* (2019, 2020) found evidence of a continuous population of cod sampled in the northern part of 6.a in deep water (>100 m) and samples from Shetland (4.a). The focus of that investigation was on the ‘northern offshore component’ of cod in the northern part of 6.a, because it currently accounts for almost all the landings in area 6.a. However, WD 4.1 of ICES (2020) provided information from tagging that also shows mixing of inshore cod between the 4.a and the northern part of 6.a. In the waters inshore of 100 m in 6.a, there are a number of largely resident coastal groups, some of which have been found to recruit from local nurseries (Wright *et al.*, 2006 a,b). These inshore groups are found across the west, north and east coast of Scotland leading to some exchange between the northern part of 6.a and 4.a (Wright *et al.*, 2006a, 2019). Although the abundance of northern inshore 6.a cod groups is currently low, the potential for overlap with inshore cod in 4.a suggests it would be appropriate to consider both the northern offshore component and the northern inshore component of cod in 6.a in future benchmark assessments of this region.

Most cod in the western English Channel and southern Celtic Sea (7.e–k) are genetically distinct from the Dogger cod population (Heath *et al.*, 2014). However, some adult cod from the Dogger population migrate seasonally to the western English Channel (7.e) from the eastern English Channel (7.d; Righton *et al.*, 2007; Griffiths *et al.*, 2018).

In summary, there are reproductively isolated populations of Viking cod and Dogger cod in the North Sea, with some mixing after spawning (e.g. Skagerrak and Kattegat are nursery grounds for both populations), and the areas inhabited by these genetically different groups have different phenotypic traits (maturity, growth) despite generally common trends in biomass and recruitment among subareas. The Dogger cod population extends to the north and west of Scotland (northern part of 6.a) and adults seasonally migrate to the western English Channel (7.e–k). The

available information does not provide clear evidence of genetic heterogeneity within the Dogger cod population, but the population appears to have some spatial structure with a phenotypic boundary between the southern and northern North Sea. North Sea cod appear to be isolated from other adjacent cod populations on the Faroe Plateau (5.b.1) and Norwegian Coastal Cod (1–2).

## 4 Practical implications of cod stock scenarios (ToR 3)

The current advisory unit for North Sea cod (i.e. the North Sea, Eastern English Channel, and Skagerrak; Subarea 4, Division 7.d, and Subdivision 20) does not reflect the most plausible scenario of cod stock structure in the North Sea and adjacent areas, as described in section 3. Conventional stock assessment models implicitly assume that the spatial extent and structure of stock assessments represent the population structure of the resource, because a dynamic pool is assumed to be evenly distributed over the stock area. Several case studies and simulation tests demonstrate that accurately accounting for spatial structure in stock assessments can improve model performance (e.g. Kerr and Goethel 2014, Berger *et al.*, 2017; Punt 2019a). Conversely, ignoring spatial structure can lead to a risk of overexploitation of distinct population components, misperceptions of stock status and failures in fisheries management. For example, the collapse of the cod fishery off Newfoundland and Labrador has been partially attributed to the mismatch between the spatial management unit and population structure (Hutchings 1996, Smedbol and Stephenson, 2001; Lilly, 2008), and similar mismatches have led to misperceptions of stock status, depletion of spatial components and failure to achieve rebuilding plans for cod fisheries on the Scotian Shelf (Smedbol and Stephenson 2001) and off New England (Zemeckis *et al.*, 2014).

These general concerns about the consequences of ignoring spatial structure of populations are relevant to North Sea cod. Hutchinson (2008) concluded that ignoring evidence of genetically distinct groups of cod in the North Sea that have different productivities and resilience to fishing will result in overfishing and collapse of the weaker components. Jardim *et al.* (2018) developed an operating model for North Sea cod based on the spatial structure defined by ICES (2015), assuming varying degrees of connectivity between subareas, to test the performance of alternative stock assessment approaches. They found that when stocks are independent and relatively homogeneous, estimates from the one-area stock assessment were similar to the sum of estimates from subarea stock assessments, supporting the continued application of a single-area stock assessment for North Sea cod. However, the diffusion process simulated by Jardim *et al.* (2018) does not appear to represent the site fidelity and homing exhibited by North Sea cod.

The current assessment model for North Sea cod (ICES, 2019b) assumes a closed, homogeneous and well-mixed population, but recent ICES advice recognizes substock structure within the North Sea (ICES, 2019a). Some geographic variation in growth and maturity are accounted for by representing the heterogeneous cod resource with spatially stratified sampling, but estimation models and reference point models assume a homogenous dynamic pool. Reproductive isolation as well as geographic variation in maturity and growth suggest that alternative spatial (or explicit substock) approaches to assessment and advice may perform better for informing management of North Sea cod fisheries. The distinct population structure of cod within the North Sea and substantial connectivity with other advisory units of cod justify the consideration of alternative spatial or substock structure for assessment, advice and fishery management.

Although the Viking cod and Dogger cod populations are reproductively isolated, there is some spatial mixing after spawning particularly in the juvenile phase. Therefore, geographic boundaries between the populations are not distinct, and more precise population assignment would require stock composition analyses. Despite the challenges of spatially overlapping populations, alternative spatial definitions would represent the most plausible scenario of stock structure much more accurately than the current advisory unit delineation (4-7.d-20). ICES (2015) proposed a geographic boundary using latitude-longitude rectangles to delineate cod stock structure in the North Sea (Figure 1.1), which was a refinement of the subareas defined by Holmes *et al.* (2014). The Workshop generally accepted the ICES (2015) boundaries, with some minor revisions: the extension of the Viking area to the north and west of Shetland by ICES (2015) was

based on preliminary evidence on size at maturity, but subsequent evidence for significant genetic differences between Viking cod and those west of Shetland and fine-scale analysis of maturity at size do not support the westward extent of the Viking population (Wright *et al.*, 2020). Therefore, all ICES rectangles west of 0° should be included in the northwest subregion (Figure 4.1).

A geographic boundary between the northern and southern phenotypic stocks of the Dogger cod population is more difficult to define. Several independent studies identified a persistent boundary near the 50 m bathycline in the central North Sea, which is approximately delineated by the substock boundaries defined by ICES (2015; Figure 1.1 and Figure 4.1). The boundary between relatively fast-growing cod in the southern North Sea and slow-growing cod in the northern North Sea suggested by Graham (1934) was defined by a bottom isotherm as well as the geographic extent of the vertical thermocline in the northern North Sea, because the southern North Sea is relatively well-mixed throughout the year. Decadal patterns of distribution indicated by surveys of age-1 and age-2 cod suggested a boundary along the 50 m bathycline, approximately from Flamborough Head to Jutland Bank (ICES, 2005). Núñez-Riboni *et al.* (2019) identified a similar boundary in thermal suitability near the 10.5°C isotherm and 56°North, with an increasing time trend in suitability to the north and a decrease in suitability to the south (including the Southern and German Bights and the Dogger Bank). Neat *et al.* (2014) used archival tag data to confirm that cod in the northern North Sea inhabited colder waters than those in the southern North Sea, and those habitat differences may explain differences in growth rates. However, home ranges of cod in the southern North Sea extend to approximately 56°North (Neat *et al.*, 2014), and there was no evidence from archival tag data of a northward shift, suggesting that the northward shift of cod to cooler habitats was from the depletion of cod in the south (Neat and Righton, 2007). Information on movement from historical tagging also suggested limited movement of cod between the southern and northern North Sea, with a boundary near Flamborough Head (ICES, 1970, 1971). Re-analysis of conventional tags suggests that the boundary between northern and southern phenotypic groups is slightly more to the north (Figure 2.3–Figure 2.5), near the Firth of Forth (56°North).

The spatial resolution of stock boundaries depends on the data used for stock assessment. From a practical perspective, historical survey and fishery data can be compiled based on ICES divisions (e.g. 4.a, 4.b, 4.c, 7.d) and subdivisions (e.g. 20). Surveys and possibly recent fishery data can be disaggregated by latitude-longitude rectangles, but further disaggregation of historical fishery data (landings, discards, effort) is difficult. Relatively simple groupings of latitude-longitude rectangles allow for raising samples of landings and discards to total catch at size or age.

In addition to the challenges of providing a time series of spatially explicit data at a high spatial resolution, complicated stock boundaries can lead to problems with managing fisheries and providing advice. Therefore, the workshop considered more practical boundaries that approximately represent the most plausible stock structure scenario, including a subdivision of Division 4.a at the prime meridian into 4.a.East and 4.a.West (Figure 4.1) and a division of 6.a at 56°N to delineate Dogger cod off the outer Hebrides from Celtic cod in the Clyde (as implemented in the 6.a.North herring assessment):

- The 4.a.East–20 area encompasses almost all of the Viking cod population.
- The 4.a.West–4.bc–7.d–6.a.North area encompasses almost all of the Dogger cod population.
- The 4.a.West–6.a.North area encompasses almost all of the northern phenotypic stock of Dogger cod.
- The 4.bc–7d area encompasses almost all of the southern phenotypic stock of Dogger cod.

These practical delineations are intended to facilitate data collation, stock assessment, advice, fishery management, and enforcement of regulations. Data compiled by ICES divisions (i.e. 4.b,

4.c, 7.d) and subdivisions (20, 4.a.East, 4.a.West, 6.a.North) would support a range of stock assessment options:

1. The current stock assessment method (4-7d–20) implicitly assumes that spatially stratified sampling accounts for spatial heterogeneity and that spatial advice (e.g. ICES, 2019a) are effective for avoiding local depletion. However, spatial advice is empirical (i.e. based on survey and catch trends) with no reference points or projections, and spatial patterns in catch can lead to local depletion or failure to achieve rebuilding plans.
2. Separate stock assessments and advice for Viking Cod (4.a.East–20) and Dogger cod (4.a.West–4.bc–7.d–6.a.North), or northern Dogger cod (4.a.West–6.a.North) and southern Dogger cod (4.bc–7d) would provide an analytical basis for spatial advice (e.g. stock-specific estimates of fishing mortality, stock biomass, recruitment, reference points and projections) to meet management objectives for each stock. However, these separate assessments would ignore mixing across stock boundaries, and data may be insufficient to estimate independent parameters for each stock.
  - a. If data from 6.a.North cannot be considered in the 2020–2021 benchmark workshop, separate stock assessments and advice for North Sea Dogger cod (4.a.West–4.bc–7.d), or northern North Sea Dogger cod (4.a.West) could be considered as alternatives.
  - b. If historical fishery data cannot be partitioned into 4.a.East and 4.a.West, alternative stock definitions of northern North Sea-Skagerrak (4.a–20) and southern North Sea-Eastern Channel (4.bc–7d) could be considered as an alternative.
3. A fleet-structured stock assessment model of cod in the entire area (4-7.d–6.a.North–20), with fleets defined by metier and stock area, would apply an ‘areas-as-fleets’ approach (e.g. Hurtado-Ferro *et al.*, 2014; Waterhouse *et al.*, 2014), which is commonly applied to fisheries with spatial structure. The approach accounts for spatial fishing patterns, has the efficiency of estimating some ‘shared’ parameters (e.g. recruitment) among stock areas, offers an analytical basis for spatial advice, and can identify areas with higher fishing mortality. However, the approach implicitly assumes a spatially uniform resource distribution and may not avoid local depletion.
4. A spatially structured stock assessment model, with spatial strata delineating stocks, would account for spatial fishing patterns and stock structure. Spatial models reflect the spatiotemporal dynamics of fleet behaviour, catch and effort, population structure, management regulations, and spatial zoning (Berger *et al.*, 2017). However, spatially structured models commonly require more data and structural complexity as well as the computational demands of estimating many additional parameters (Berger *et al.*, 2017; Punt 2019b). Accurately representing the dynamics of the Skagerrak nursery area would require a movement submodel to allow juveniles from the Skagerrak to move to North Sea areas as they mature, which may require some simplifying assumptions (e.g. an assumed high portion of cod in the Skagerrak move to the North Sea when they reach maturity).

If data are compiled by ICES divisions (i.e. 4.b, 4.c, 7.d) and subdivisions (20, 4.a.East, 4.a.West, 6.a.North), all of these options can be explored, including an ensemble approach, which would help to understand the strengths and weaknesses of each method and to communicate the implications of stock structure in advice. Eventually, data quality and model diagnostics of alternative stock assessment models will help to determine the optimal approach. Ideally, simulation testing (e.g. Jardim *et al.*, 2018) would help to evaluate performance of assessment approaches that accurately reflect the most plausible population structure vs. those based on practical considerations as well as the associated trade-offs among approaches. If the benchmark workshop concludes that spatially structured stock assessment models are too complex for regular updates, the spatially structured models developed at the benchmark might serve to condition spatial



operating models for testing the performance of simpler models (e.g. Kerr and Goethel 2014, Goethel *et al.*, 2016). For example, movement rates among areas and estimates of recruitment, fishing mortality, and selectivity by area estimated from spatially-structured models can provide parameter values for operating models that are generally consistent with the available data (e.g. Carruthers and Butterworth 2018), and the spatially-structured operating models can be used to test performance of simpler estimation models.

If spatial disaggregation of historical fishery data is uncertain or impossible, survey-based assessments (e.g. SURBAR, Needle 2015) may offer another alternative for separate stock assessments of subareas. As a demonstration, survey data were disaggregated by roundfish sampling areas to represent cod in the northern and southern North Sea, with a boundary near 56°North to provide estimates of mortality, relative stock biomass and recruitment (Figure 4.2). SURBAR also provides diagnostics on cohort tracking (Figure 4.3) which may help to evaluate data quality for stock assessment and the practicality of alternative spatial groupings.

Beyond these spatial approaches to assessment and advice, there are several options for addressing mismatches between management units and the most plausible scenario of population structure (ICES, 2011; Kerr *et al.*, 2017). Options include status-quo assessment and management, managing the “weakest link” population component, spatiotemporal fishing closures, stock composition analysis, and revised stock boundaries. Several factors should be considered in the choice among these alternatives, including the spatial resolution of historical fishery data, the challenge of delineating Viking and Dogger cod populations and phenotypic stocks of the Dogger population, and the strengths and weaknesses of a range of spatial alternatives. The benchmark stock assessment should provide valuable information on the viability of alternative assessment options.

As procedural practicality, considering the connectivity of cod between 6.a.North and 4.a.West is beyond the scope of the 2020–2021 North Sea cod Benchmark, and considering that aspect of the most plausible stock structure scenario would have to be considered at future benchmark workshop.

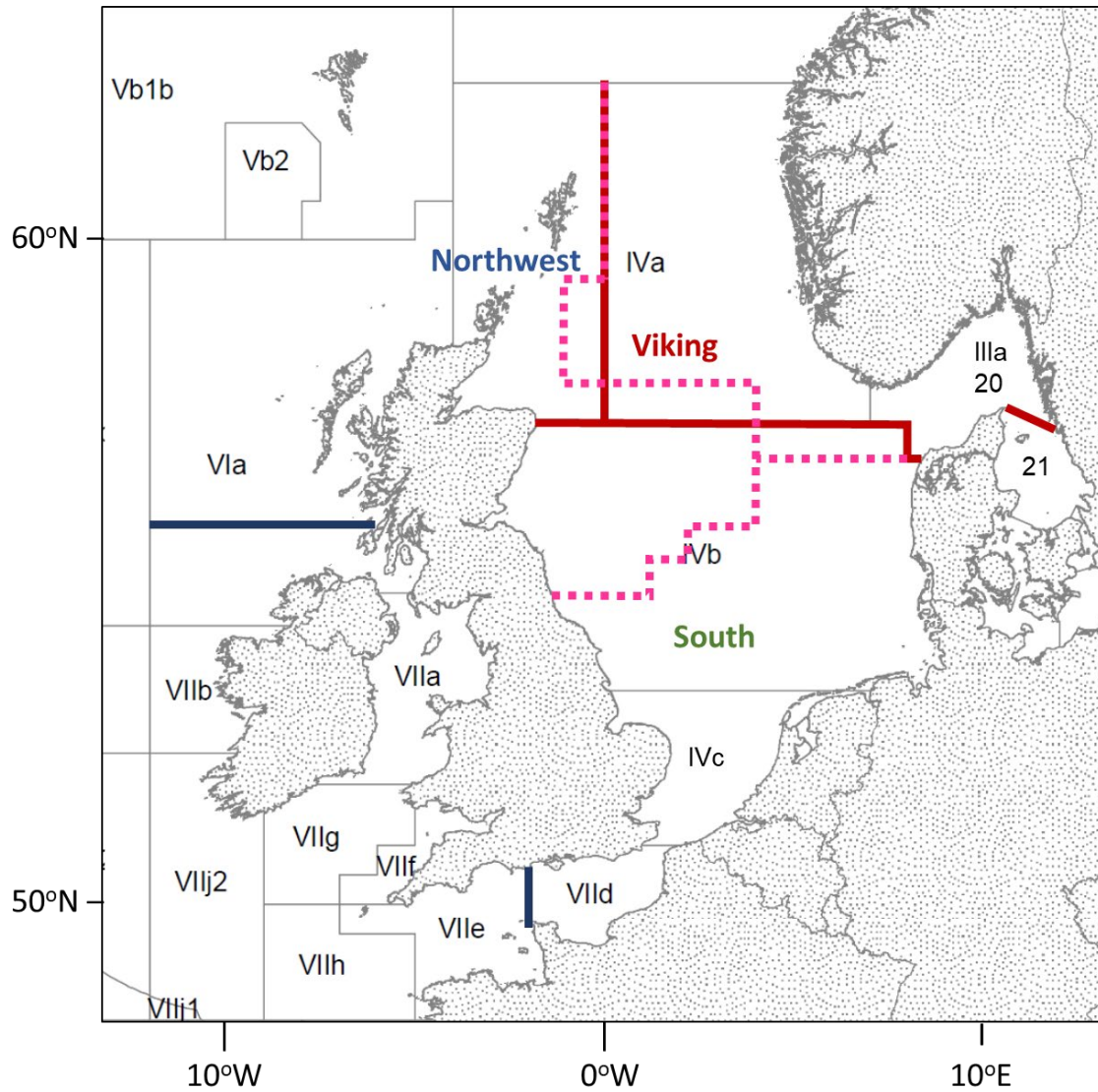


Figure 4.1. Geographic delineation of the most plausible scenario of cod stock structure in the North Sea and adjacent areas. The pink dotted line indicates the most likely border between the Viking population and the Northwest and South components of the Dogger population based on ICES latitude/longitude rectangles. The red line indicates a more practical approximation of the same border for compiling fishery and survey data and defines subdivisions 4.a.East and 4.a.West. The blue lines indicate the western boundaries for the Dogger cod population, including Subdivision 6.a.North.

Northern and Southern Area

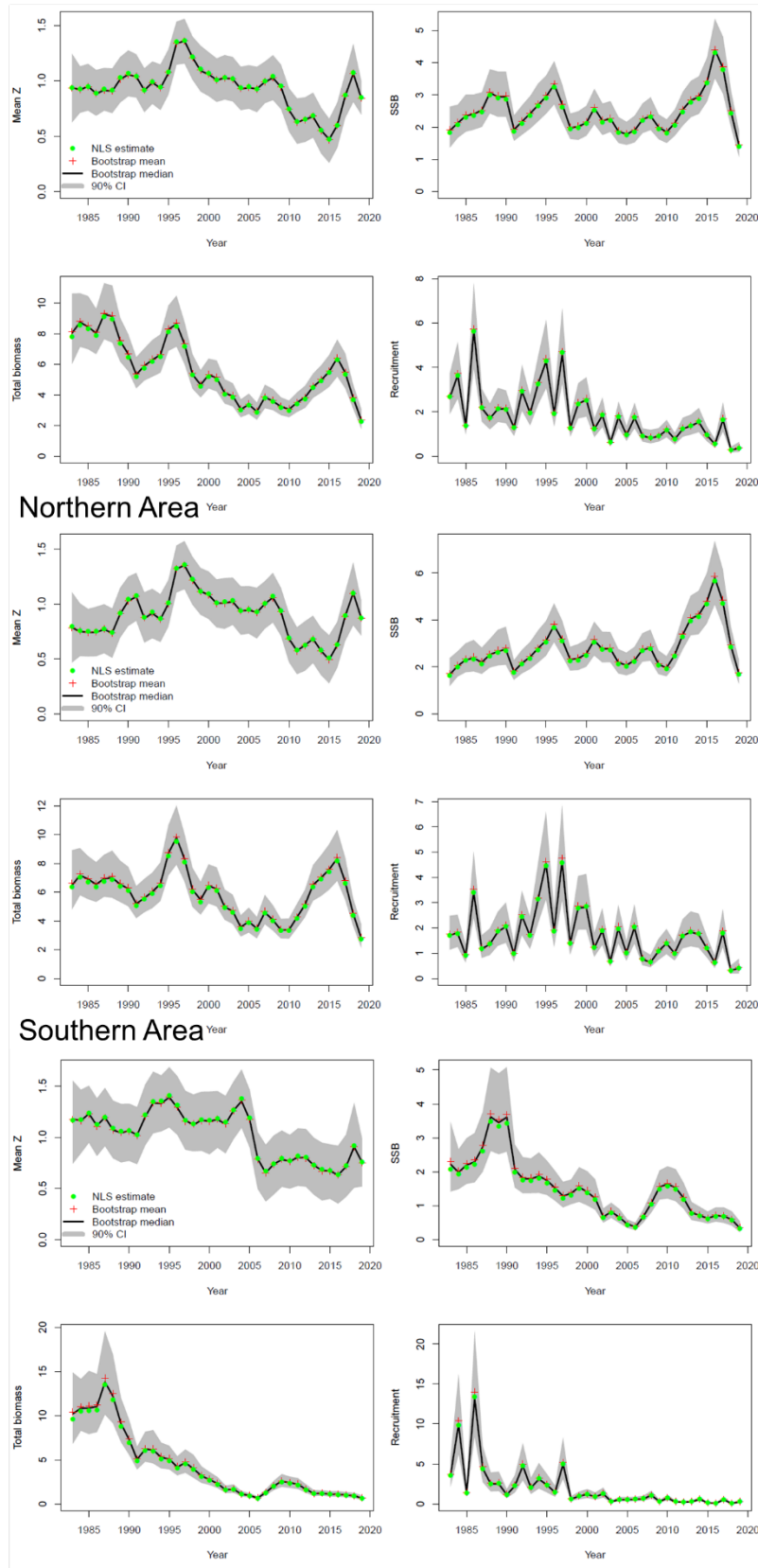
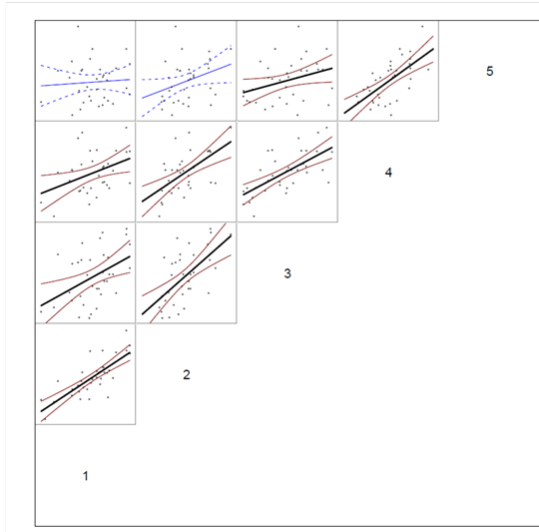
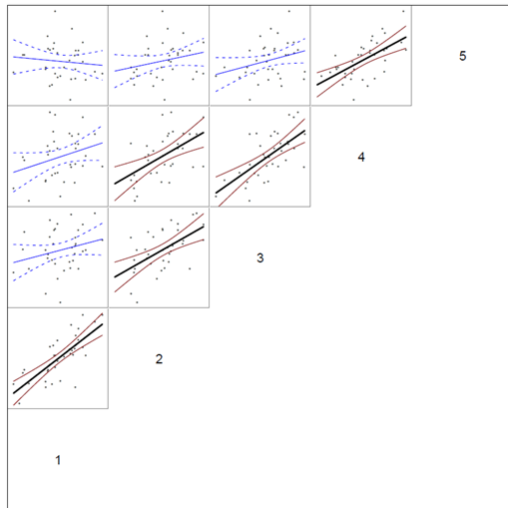


Figure 4.2. SURBAR estimates of total mortality (Z), relative spawning stock biomass (SSB), total biomass and recruitment of cod in the North Sea and Skagerrak (4-7-20, top) as well as estimates for the area north and south of approximately 56°N.

## Northern and Southern Area



## Northern Area



## Southern Area

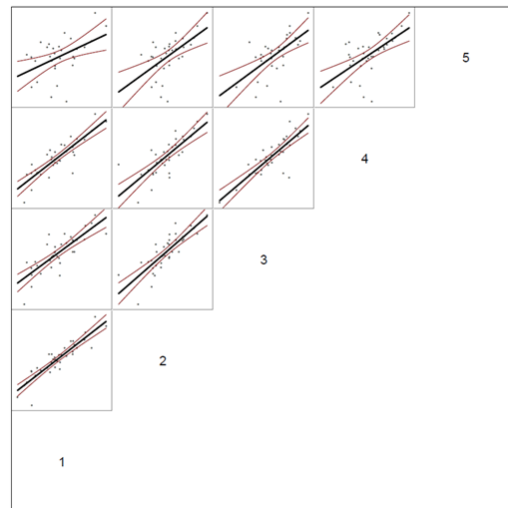


Figure 4.3. Correlation of survey indices for cohort tracking from SURBA of cod in the North Sea and Skagerrak (4-7-20, top) as well as estimates for the area north and south of approximately 56°N.

## 5 Recommendations for North Sea cod benchmark (ToR 4)

The most plausible scenario of cod population structure in the North Sea and adjacent areas should be accurately represented in ICES assessments and advice. The stock assessment should support advice for managing the genetically distinct Viking cod and Dogger cod populations. Representing phenotypic stocks of northern and southern Dogger cod should also be considered.

A range of spatial approaches to stock assessment methods and advice should be developed by the 2020–2021 North Sea cod benchmark workshop. As a minimum spatial resolution, survey and fishery data should be compiled spatially by divisions (4.b, 4.c, 7.d), Subdivision 20, and a practical subdivision of 4.a.East and 4.a.West (with a boundary at 0° longitude, Figure 4.1), with as long a time-series as possible. The range of spatial approaches should include a single assessment of the current advisory unit as a unit stock, separate-area assessments, fleets-as-areas, spatially structured assessments, and survey-based assessments.

Beyond the 2020–2021 North Sea cod benchmark assessment, genetic stock composition sampling and analysis should be considered, because geographic boundaries do not account for mixing of distinct genetic populations. The composition of Viking cod and Dogger cod should be estimated for fisheries and surveys in areas of mixing. If possible, archived samples should be analysed to estimate historical stock compositions in those areas. For example, stock composition analysis to assign catches in the Kattegat to North Sea cod should be considered in stock assessments. Stock composition analyses should also be developed for Dogger cod in Western English Channel. Genetic stock composition analysis has proven to be cost-effective for other fisheries, and the costs continue to decrease such that investments may be justified for North Sea cod.

The connectivity of cod in 4.a.West with ‘northern inshore and offshore components’ of cod in 6.a.North should be considered in future benchmark assessment workshops. Once spatial assessment approaches are developed, they should be simulation-tested to evaluate the relative performance of alternative spatial assessment approaches for providing accurate advice.

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## Annex 1: List of participants

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Peter Wright	United Kingdom	Marine Scotland Science

## Annex 2: Recommendations

Recommendation	Recipient	Has this recommendation been communicated to the recipient?
Survey and fishery data should be compiled spatially by divisions (4b., 4c, 7d), subdivision 20, and a practical subdivision of 4aEast and 4aWest	WGNSSK	Via ACOM chair and secretariat
A range of spatial approaches to stock assessment and advice should be explored at the 2020-2021 benchmark, including a single assessment of the current advisory unit as a unit stock, separate-area assessments, fleets-as-areas, spatially structured assessments, and survey-based assessments	WGNSSK	Via ACOM chair and secretariat
Genetic stock composition sampling and analysis should be considered	SCICOM	Via secretariat
The connectivity of 'northern inshore and offshore components' of cod in 6.a.North and 4.a.West should be considered in a future benchmark assessment workshop.	ACOM	Via ACOM chair and secretariat

## Annex 3: Working document 01

### WD01: Survey Indices and Abundance Maps for North Sea Cod

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#### Summary

The current advisory unit for North Sea cod is ICES Subarea 4 (North Sea), Division 7.d (English Channel) and Subdivision 20 (Skagerrak), although many studies suggest finer scale population structuring. Given indications of subpopulations inhabiting different regions of the North Sea, the last benchmark for North Sea cod proposed four subregions for comparison of substock differences and recommended that these be monitored going forward. Here, we present updated biomass indices by subregion showing continued differences in trend between the South and subregions further north, but a high level of synchrony in recruitment with significant correlations in both biomass and recruitment between all subregions.

In recent years, assessments of North Sea cod have shown a persistent downward revision of SSB and upward revision of fishing mortality. This retrospective pattern is caused by lower catch rates of older fish in the surveys compared to commercial catches, with misconception of spatial structure being one possible cause. Here we combine survey data from the North Sea with adjacent Division 6.a (West of Scotland) and Subdivision 21 (Kattegat) to map the spatiotemporal distribution of cod in the North Sea and surrounding areas, indicating a north-westwards shift of older cod towards the west of Scotland. Although combined indices display the same trends associated with the retrospective pattern, they suggest considerable migration of older cod from the North Sea to 6.a.

#### Delta-GAM model

Analyses were conducted using a model-based approach to account for nuisance factors caused by changes or differences in experimental conditions. The methodology is described in Berg and Kristensen (2012) and Berg et al. (2014) but consists of (1) calculating numbers-at-age from observed numbers-at-length and spatially varying ALKs and (2) estimating abundance-at-age using a delta-GAM model:

$$g(\mu_i) = \text{Year}(i) + \text{Gear}(i) + U(i)_{\text{ship}} + f_1(\text{Year}_i, \text{lon}_i, \text{lat}_i) + f_2(\text{depth}_i) + f_3(\text{time}_i) + \log(\text{HaulDur}_i)$$

where  $\mu_i$  is the expected numbers-at-age in the  $i^{\text{th}}$  haul (or probability of non-zero catch for the presence-absence part),  $g$  is the link function, Year and Gear are categorical effects,  $U$  is a random vessel effect,  $f_1$  is a three-dimensional tensor product spline,  $f_2$  a thin plate spline and  $f_3$  a cyclic cubic regression spline.

Maps were obtained by predicting abundance on a grid of haul positions while indices were obtained by summing model predictions over the relevant parts of the grid, where nuisance parts of the model, such as gear, ship, and haul duration, were held constant to remove their effect.

#### Subregion indices

Biomass indices by subregion were calculated from North Sea International Bottom Trawl data for Quarter 1 (NS-IBTS-quarter 1) and Quarter 3 (NS-IBTS-quarter 3) downloaded from the



DATRAS database. The methodology follows that of the North Sea working group (WGNSSK): the delta-GAM was fit to the entire dataset then re-computed on subsets of the spatial grid corresponding to each subregion (Figure A1) to obtain indices-at-age. These were then multiplied by smoothed weight-at-age estimates and summed to get biomass indices.

Biomass indices continue to follow the same trends as noted by WGNSSK (ICES, 2020). There was a general decline in all areas prior to the mid-2000s, followed by an increase to 2015–2017 for the Viking and Northwest subregions and a sharp decline thereafter. Biomass in the South has declined steadily over the entire time series (Figure 1); however, there are high and significant correlations in first order differences between all subregions despite differing trends (Figure 2).

Recruitment indices show similar trends in all subregions with no major asynchronies, but with indications of increased recruitment in the northern North Sea (Figure 3). Correlations between all subregions are strong and highly significant in both quarters (Figure 4).

### Abundance maps

To obtain abundance maps, the delta-GAM model was fit to data from six surveys: the NS-IBTS-quarter 1 and quarter 3, the Scottish West Coast Groundfish Survey in Division 6.a (West of Scotland) in Quarter 1 (ScoWCGFS-quarter 1) and Quarter 4 (ScoWCGFS-quarter 4) and the Baltic International Trawl Survey covering Subdivision 21 (Kattegat) in Quarter 1 (BITS-quarter 1) and Quarter 4 (BITS-quarter 4). The model was applied separately to all data for Quarter 1 from 1983 and all data for Quarters 3 and 4 from 1992 (for consistency with assessment indices; Appendix 2) but maps are presented only for ages and years with adequate age sampling across surveys. A change to the rig of the ScoWCGFS gear in 2011 was accounted for via the ship effect of the delta-GAM model.

Maps for Quarter 1 from 1996–2020 (Figure 5 and Appendix 3) show the highest abundances of recruits (age 1) to be in the Skagerrak and Kattegat throughout the time series. There are also areas of higher recruitment extending the east coast of the UK, with hotspots appearing to the east of Scotland from 2010. Arcs of higher abundances of ages 1–3 from Flamborough across Fisher to the Viking Bank diminished during the 2000s while hotspots of age 2–4 abundance in the south disappeared. We did not consider surveys in the Channel, so cannot make inferences about whether this disappearance is a consequence of migrations or local depletion in the south. The distribution of older ages (3+) appears to have contracted north and west over the time series with relatively high abundances of 3+ cod to the north of Scotland over the last 10 years.

Maps for Quarters 3–4 from 1999–2019 and ages 1–4 (Figure 6 and Appendix 4) show similar trends to those of Quarter 1. Arcs of abundance from the east coast of the UK across Fisher to the Viking bank have diminished with a hotspot of recruitment appearing to the east of Scotland over the last 10 years. Although the model predicts slightly higher abundances of ages 1 and 2 in the south towards the beginning of the time series, this is not as strong as for the Quarter 1 analysis. Increased abundances of 2+ fish extending from the Skagerrak to Shetland appear to shift westwards over the time series.

### Boundary effects

*West of Scotland* - As the highest concentrations of older cod are found near the border of the assessment area towards the west of Scotland, it could be hypothesized that migrations in and out of the assessment area are causing year effects in the survey indices. The last benchmark for cod investigated this issue by combining the NS-IBTS survey with the ScoWCGFS survey to include a major part of Division 6.a in an alternative index (ICES, 2015). Here we derive similar alternative indices by summing model predictions from the combined delta-GAM over Subarea 4 (North Sea), Division 6.a (west of Scotland) and both areas combined, showing that abundance of 3+ cod in 6.a has increased more than in the North Sea in recent years (Figure 7). However, the

combined index shows the same trends that have been associated with the retrospective pattern in the assessment of North Sea cod (ICES, 2020). That is a disappearance of the strong 2013 year-class coinciding with a peak in the 2012 year-class at age 5 in Quarter 1 and age 4 in Quarters 3 & 4. While this may not resolve the issues associated with the retrospective pattern, relative differences between the combined and North Sea indices suggest that movements from the North Sea to 6.a could be important and should be investigated further (Figure 8).

*Kattegat* - The same method was used to investigate potential links between the North Sea stock and adjacent Kattegat advisory unit. Again, predictions from the combined delta-GAM were summed over the relevant management areas: Subarea 4 and Subdivision 20 (North Sea and Skagerrak), Subdivision 21 (Kattegat) and both areas combined (Subarea 4 and Division 3.a). Differences between indices for the North Sea assessment area and combined management areas mostly appear small (Figure 9) but with a decrease in relative differences suggesting a larger increase of age 1 cod in the North Sea assessment area compared to the Kattegat in recent years (Figure 10).

### Conclusions

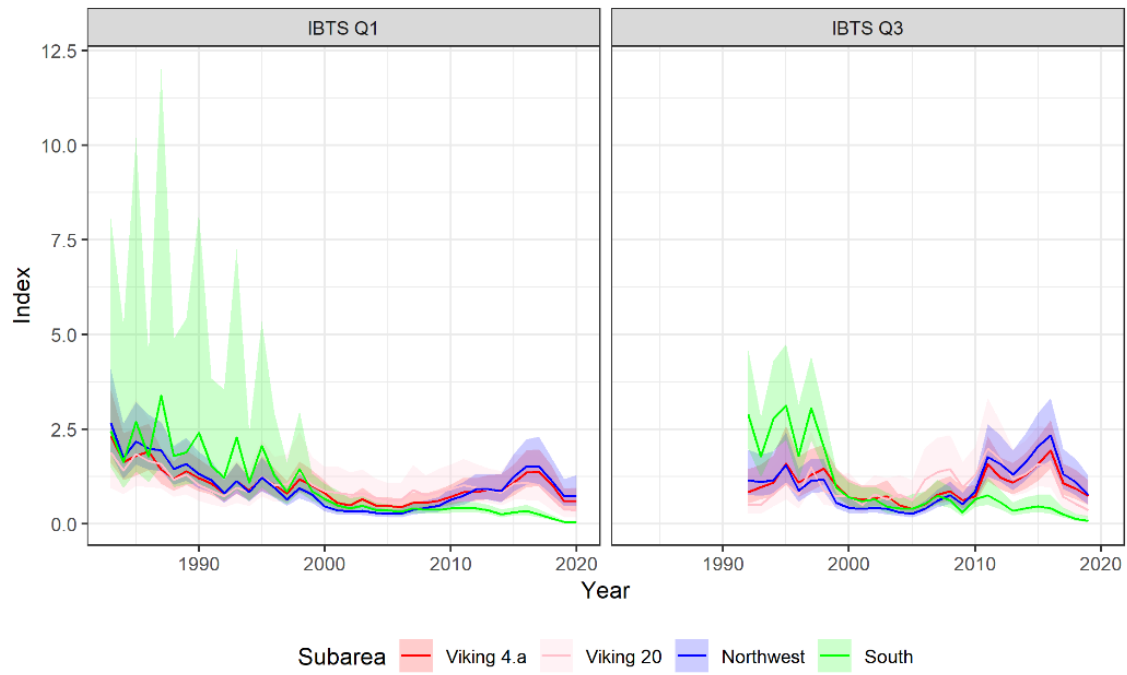
There are high correlations between subregion biomasses despite recent differences in index trends. Recruitment trends are similar in all subregions with no major asynchronies and strong and significant correlations.

Maps of abundance show a perceived north-westwards shift of older cod and reduced abundances in the south. The highest abundances of recruits are in the Skagerrak and Kattegat with a hotspot of recruitment appearing to the east of Scotland over the last 10 years.

Differences between indices for the assessment area and combined indices including adjacent management areas suggest increased movements of older cod towards the West of Scotland. While a combined North Sea and 6.a index may not resolve the issues associated with the retrospective pattern in the assessment, migrations from the North Sea into 6.a seem to be substantial and should be investigated further.

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**Figure A1. Biomass indices by subregion together with 95% confidence intervals based on NS-IBTS-quarter 1 and quarter 3 data. The indices and confidence intervals are standardised by the mean of the index for each subregion.**

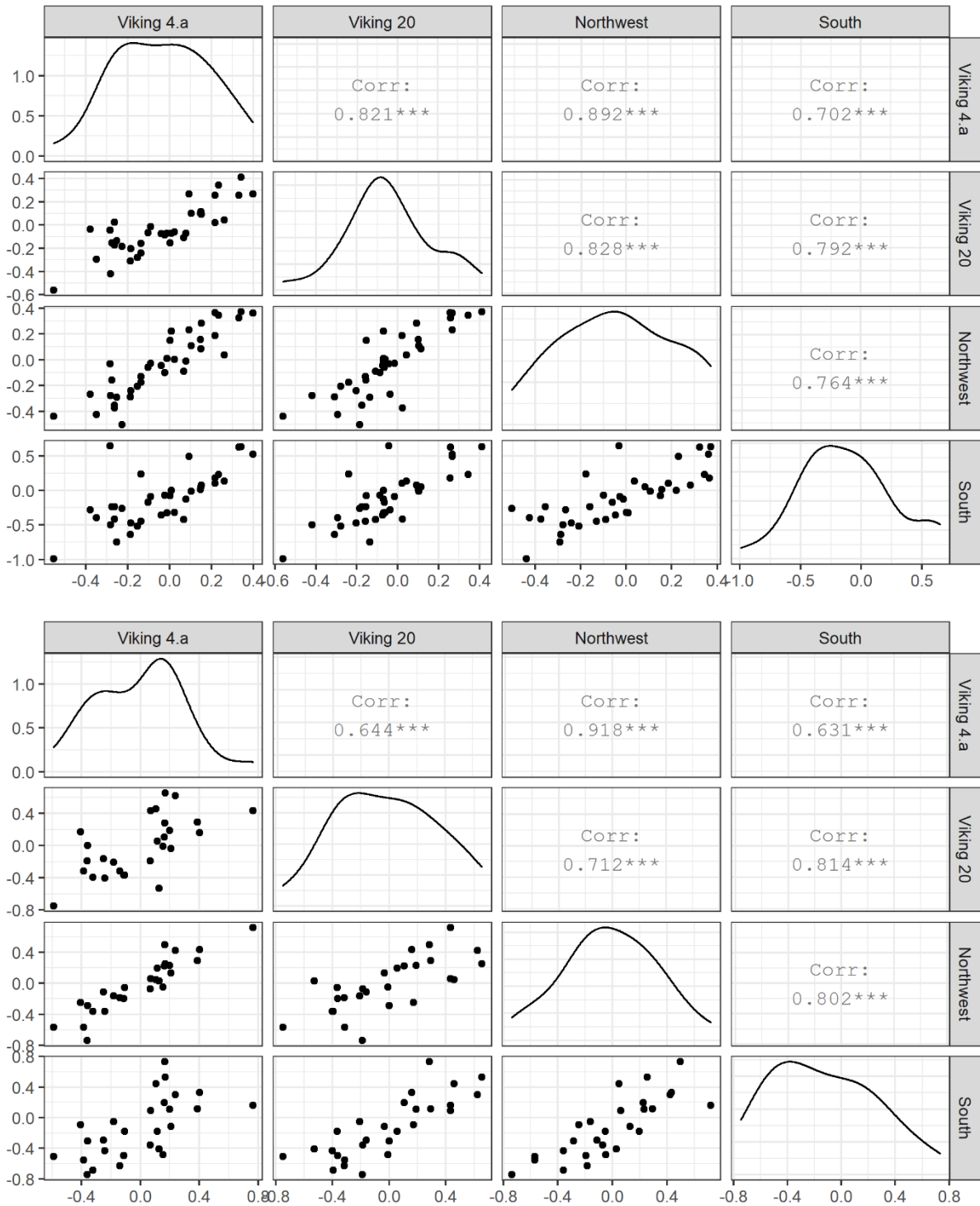
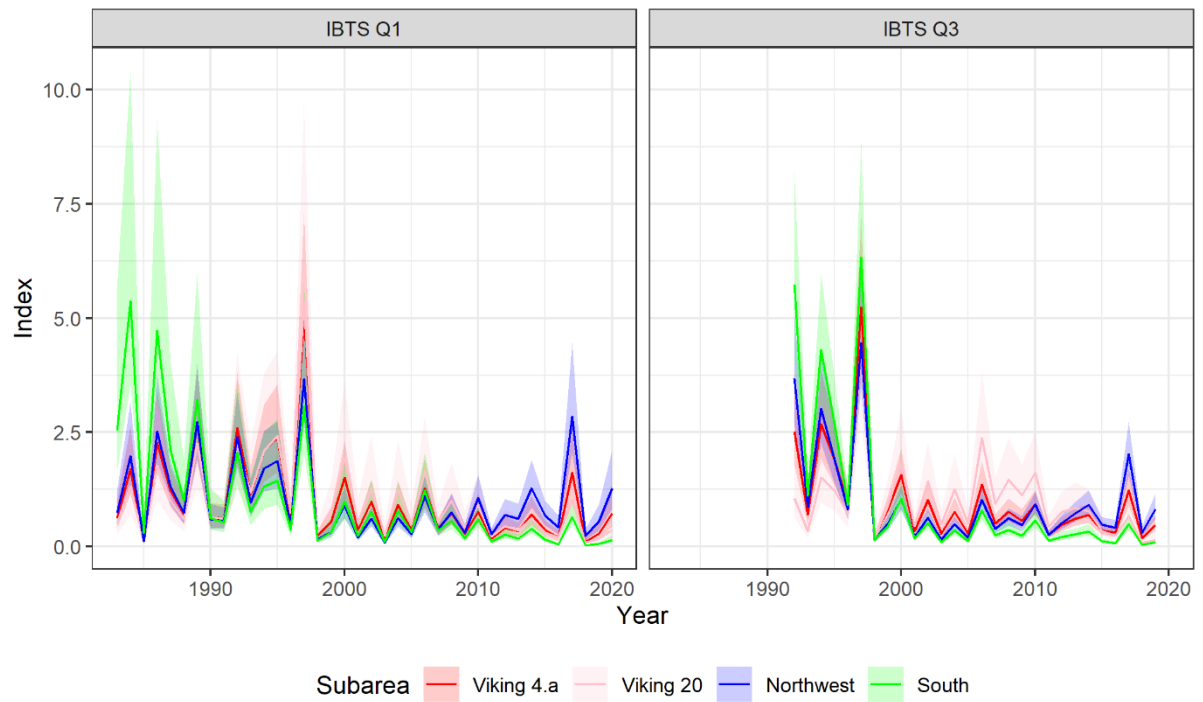


Figure A2. Correlations between differenced log biomass indices by subregion for (top) Quarter 1 and (bottom) Quarter 3. The lower triangle of subplots shows scatterplots of differenced (lag 1 year) log biomass for each pair of subregions, the top triangle the Pearson correlation coefficient and the diagonal the distribution of differenced log index values for each subregion.



**Figure A4. Recruitment (age 1) biomass indices by subregion together with 95% confidence intervals based on NS-IBTS-quarter 1 and quarter 3 data. The indices and confidence intervals are standardised by the mean of the index for each subregion.**

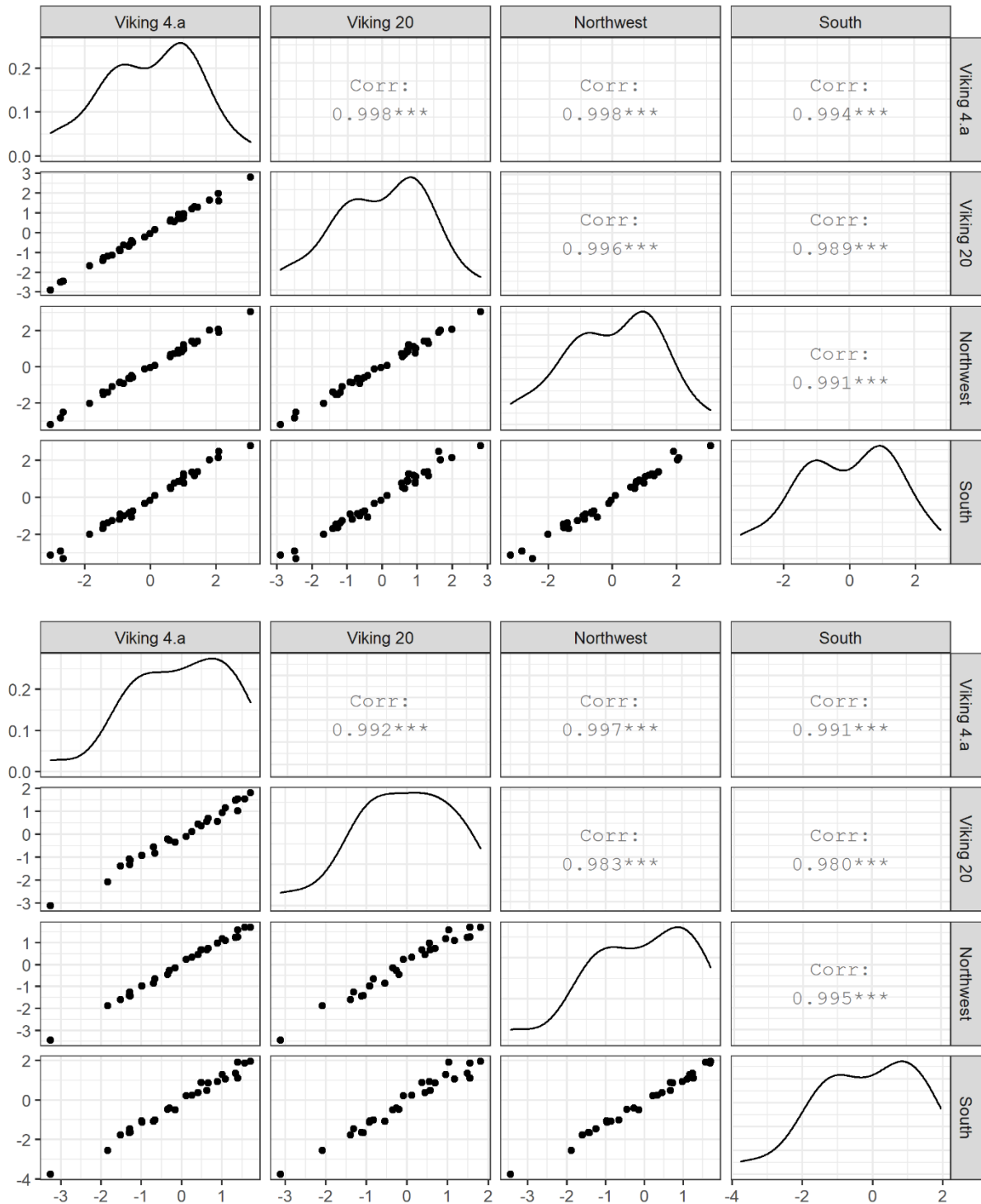


Figure A5. Correlations between differenced log recruitment (age 1) indices by subregion for (top) Quarter 1 and (bottom) Quarter 3. The lower triangle of subplots shows scatterplots of differenced (lag 1 year) log recruitment biomass for each pair of subregions, the top triangle the Pearson correlation coefficient and the diagonal the distribution of differenced log recruitment index values for each subregion.

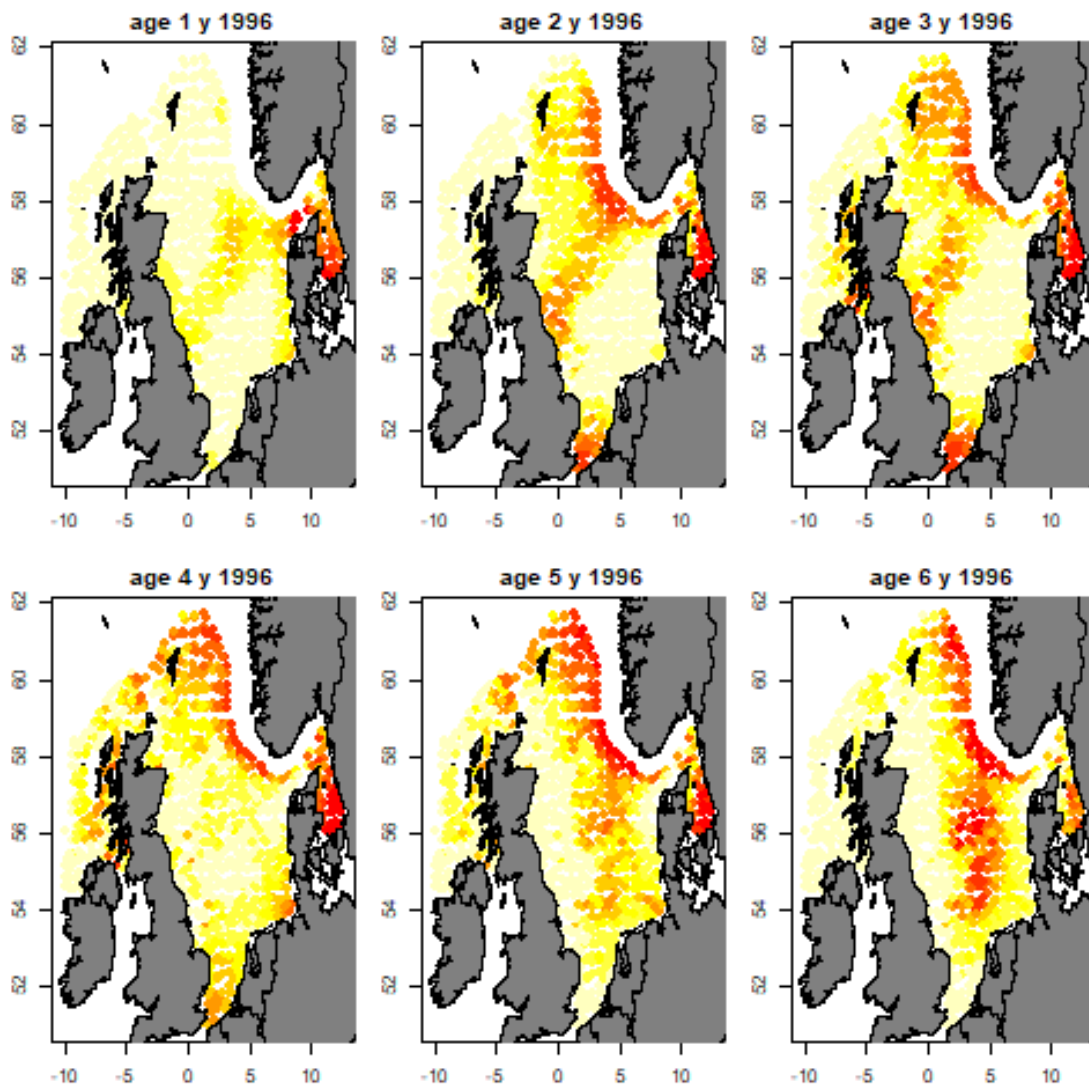


Figure A6. Animated abundance maps based on Quarter 1 data from the NS-IBTS, ScoWCGFS and BITS surveys (a subset of years are presented in Appendix 3). Individual subplots are produced separately hence the colours are indicative of trends only.

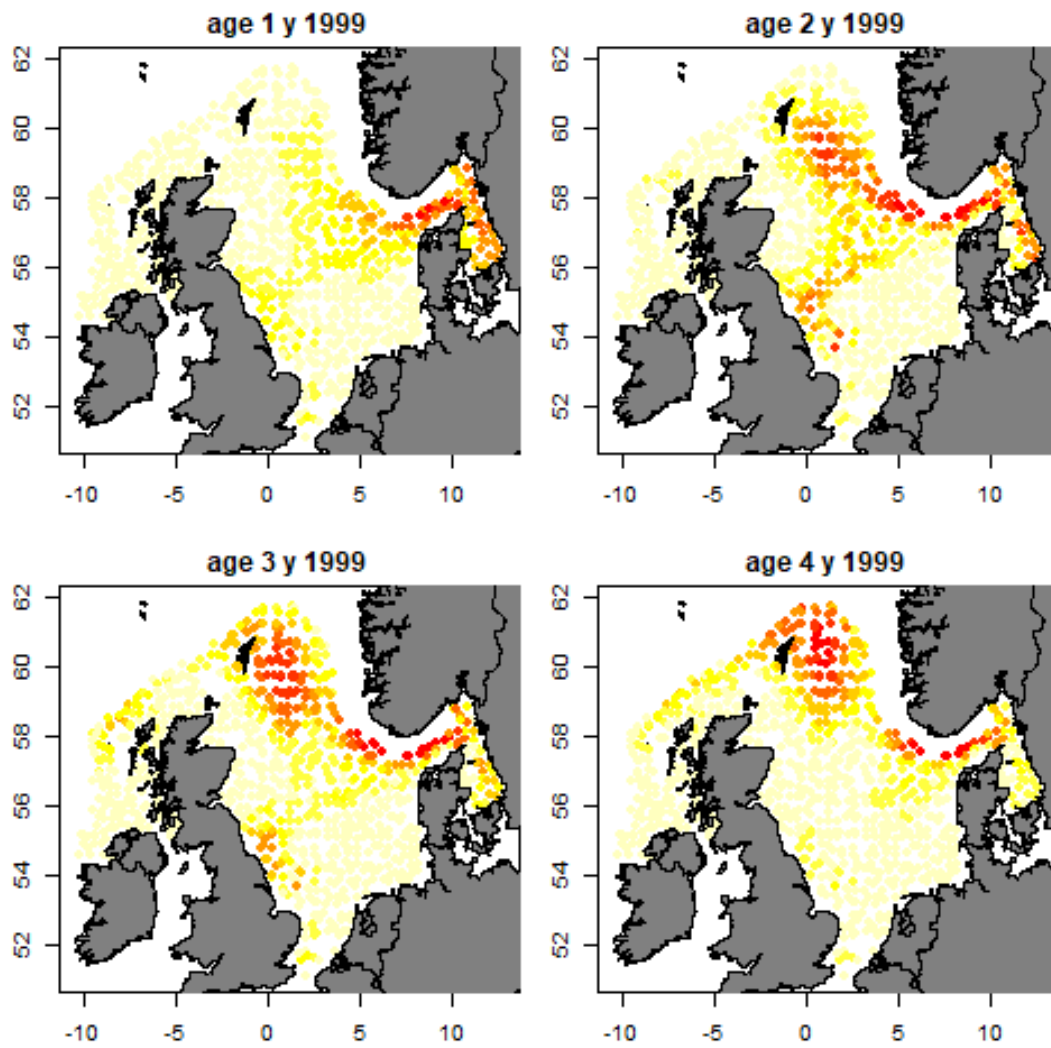


Figure A7. Animated abundance maps based on Quarter 3 data from the NS-IBTS survey and Quarter 4 data from the ScoWCGFS and BITS surveys (a subset of years are presented in Appendix 4). Individual subplots are produced separately hence the colours are indicative of trends only.



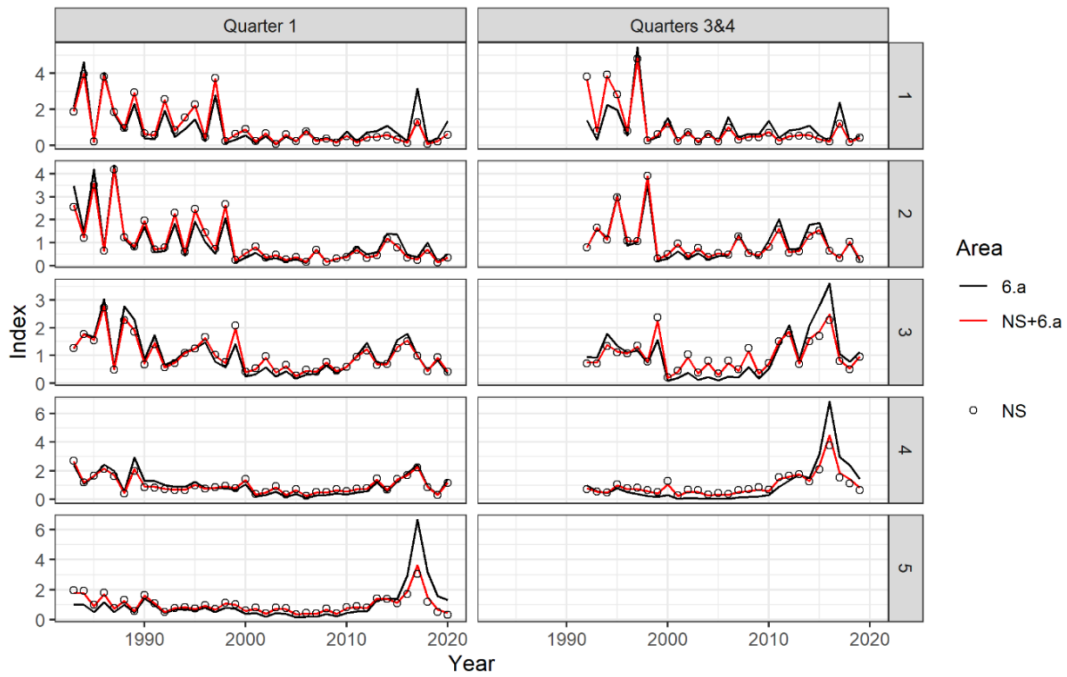


Figure A8. Indices derived from a delta-GAM model fit to data from the NS-IBTS, ScoWCGFS and BITS surveys. Indices are derived by summing model predictions on subsets of a spatial grid corresponding to the North Sea (NS), Division 6.a (6.a) and both areas combined (NS+6.a). Note that indices for the North Sea are not exactly the same as for the assessment due to inclusion of the Skagerrak in the assessment and a slightly different delta-GAM configuration (the assessment assumes a stationary spatial model). The indices are mean-standardised.

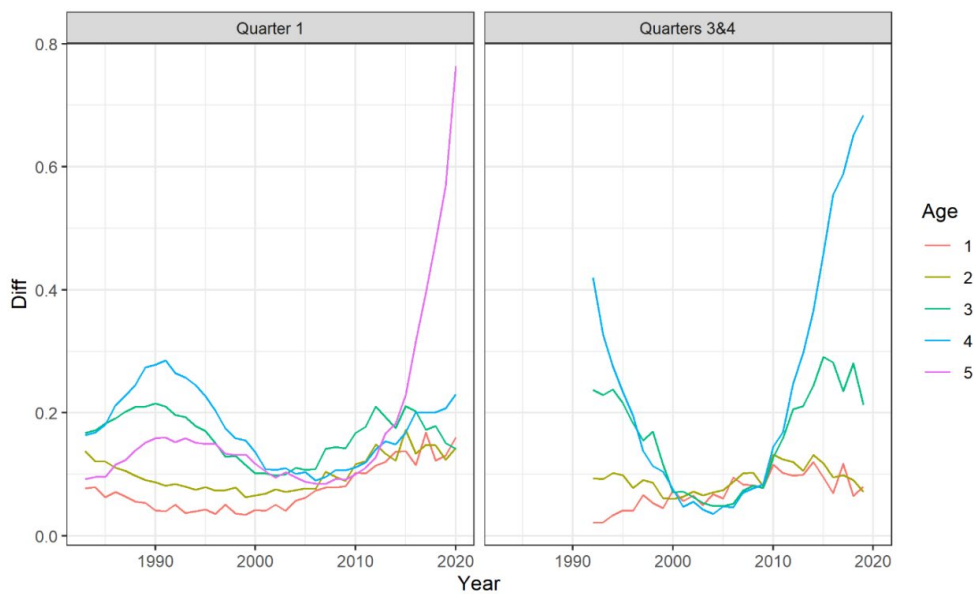
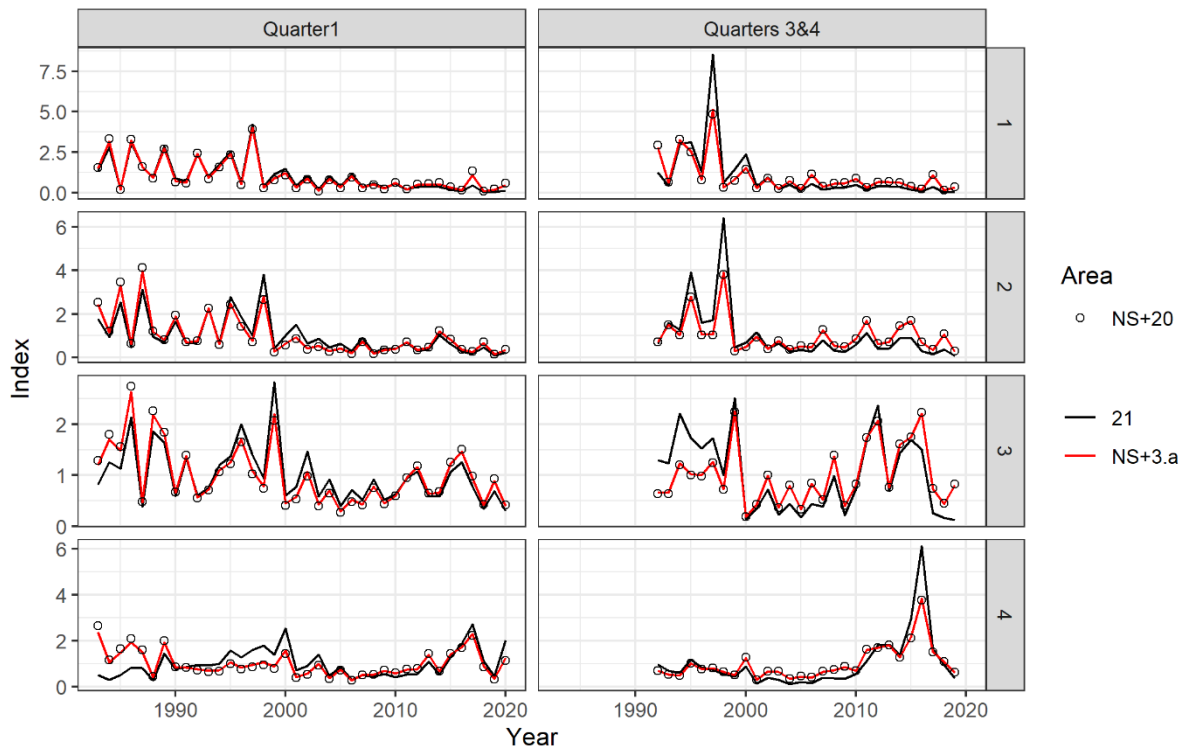
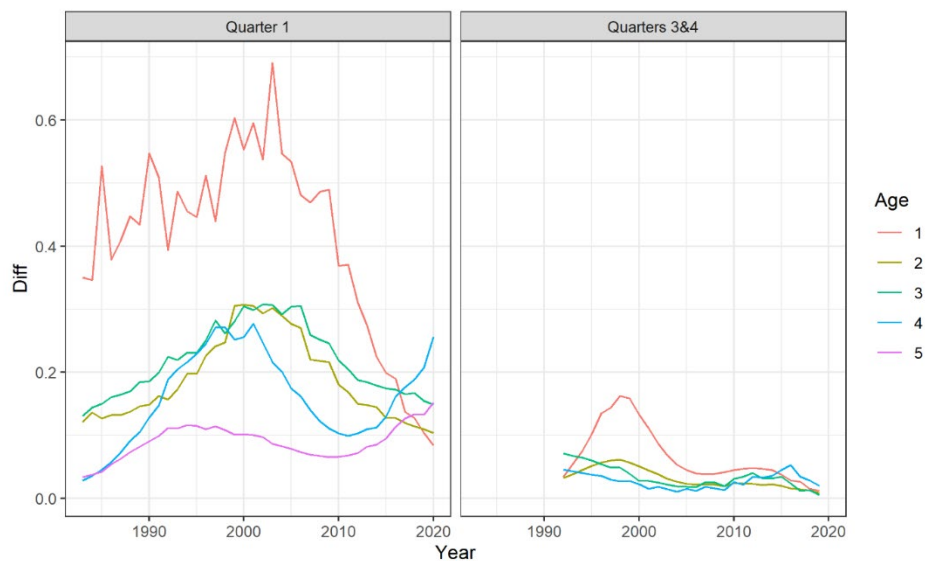


Figure A9. Relative differences between the untransformed indices for combined management areas (NS+6.a) and the North Sea (NS), calculated as  $(NS+6.a/NS) - 1$ . See caption to *Error! Reference source not found.* for details of the indices.



**Figure A10.** Indices derived from a delta-GAM model fit to data from the NS-IBTS, ScoWCGFS and BITS surveys. Indices are derived by summing model predictions on subsets of a spatial grid corresponding to the North Sea and Skagerrak (NS+20), Subdivision 21 (21) and both areas combined (NS+3.a). Note that indices for the North Sea and Skagerrak are not exactly the same as for the assessment due to a slightly different delta-GAM configuration (the assessment assumes a stationary spatial model). The indices are mean-standardised.



**Figure A.11.** Relative differences between the untransformed indices for combined management areas (NS+3.a) and the North Sea and Skagerrak (NS+20), calculated as  $(NS+3.a/NS+20) - 1$ . See caption to Error! Reference source not found. for details of the indices.

WD01 Appendix 1: Subregions

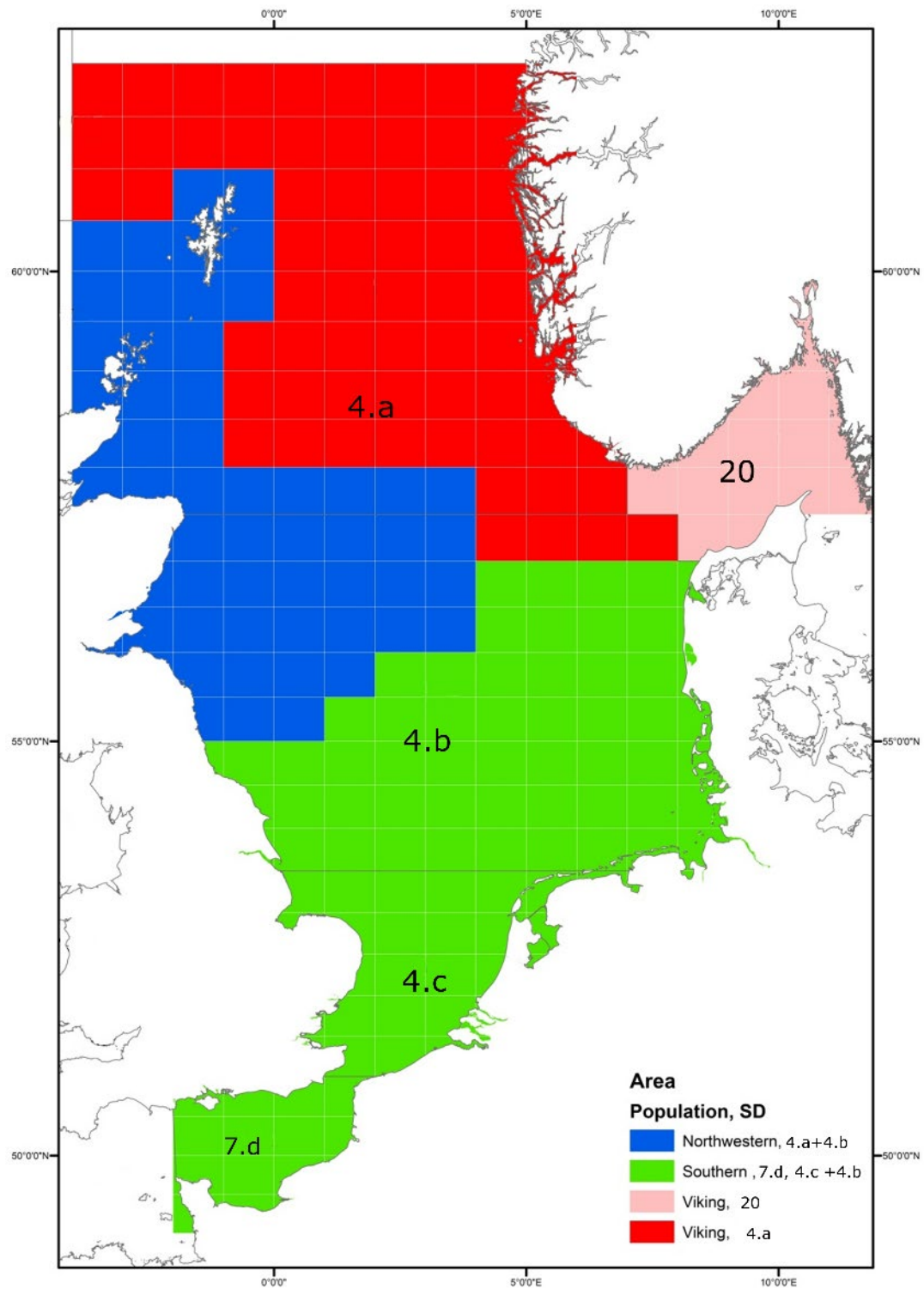


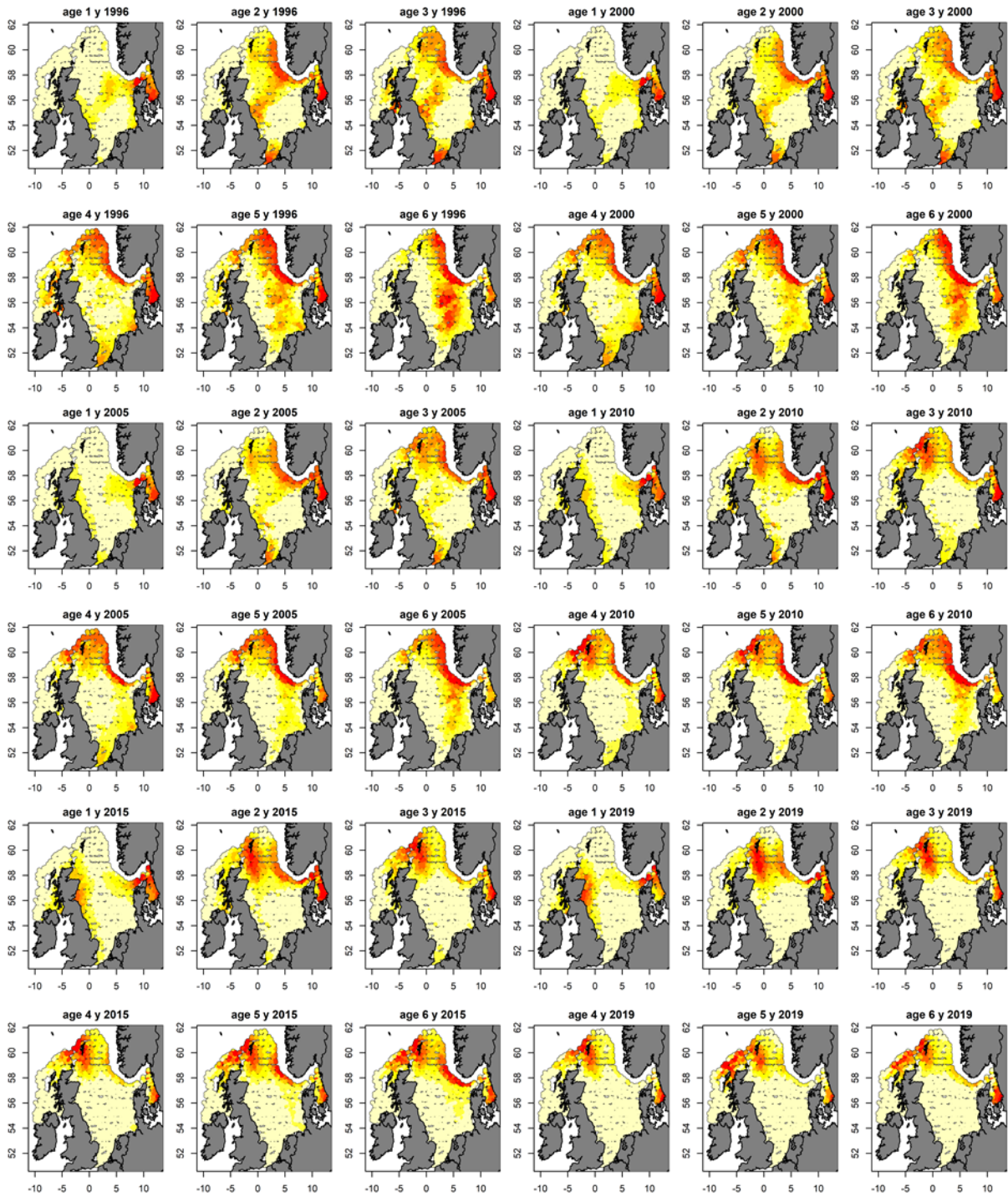
Table A12. Subregions used to derive area-specific biomass indices for North Sea cod based on NS-IBTS-quarter 1 and quarter 3 data (ICES, 2015).

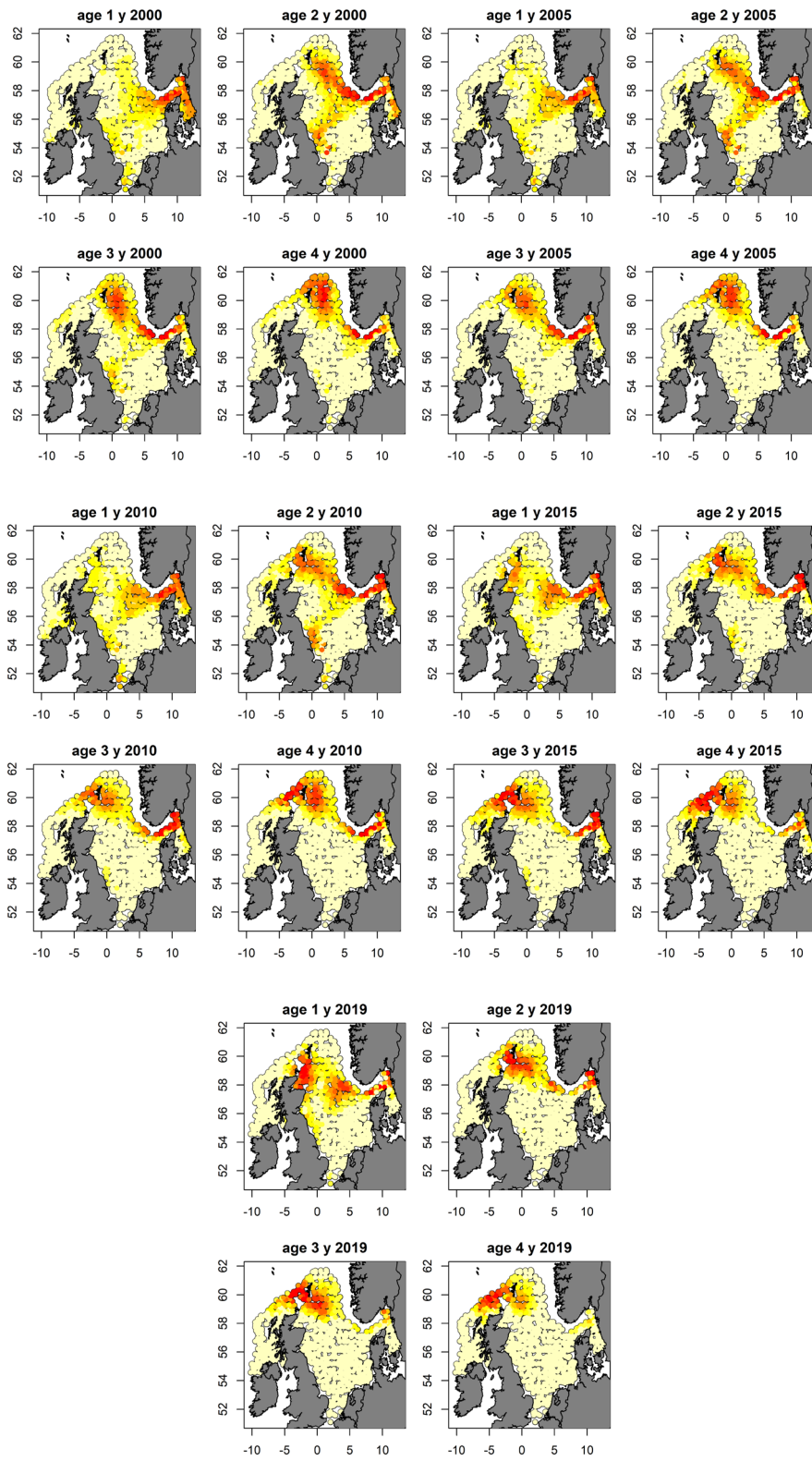
### WD01 Appendix 2: Survey data

**Table A1: Survey data used in the analyses together with management area covered, survey acronym (as used in this study), years with data for cod and years with age samples for cod.**

Survey	Management area	Acronym	Years	Age sampling
North Sea International Trawl Survey – quarter 1	4, 3.a	NS-IBTS-quarter 1	1983+	1983+
Scottish West Coast Groundfish Survey – quarter 1	6.a	ScoWCGFS-quarter 1	1986+	1986+
Baltic International Trawl Survey – quarter 1	Only data for Subdivision 21 included	BITS-quarter 1	1992+	1996+
North Sea International Trawl Survey – quarter 3	4, 3.a	NS-IBTS-quarter 3	1992+	1992+
Scottish West Coast Groundfish Survey – quarter 4	6.a	ScoWCGFS-quarter 4	1992+	1996–2009 2011+
Baltic International Trawl Survey – quarter 4	Only data for Subdivision 21 included	BITS-quarter 4	1993+	1999+

WD01 Appendix 3: Quarter 1 Abundance Maps



WD01 Appendix 4: Quarter 3 & 4 Abundance Maps

## Annex 4: Working document 02

### **WD02: Parasites of cod (*Gadus morhua*) in the North Sea as biological tags of stock structure**

Neil Campbell, Marine Scotland Science.

#### Abstract

The use of parasites as biological tags for stock identification studies has an extensive and well documented history. Given its wide distribution in the north Atlantic and migratory nature, Cod (*Gadus morhua*) is one of the species to which this approach has been applied most frequently. This paper documents the principles of using parasites as biological tags, examples of the types of parasites used and the information on stock structuring which they can provide, throughout the range of the species, and details history of application of this approach within the North Sea and associated waters. It finds that although this technique has been commonly applied to problems of cod population structuring, evidence of its use within the North Sea is inconclusive, and, other than a suggestion of some differences between the Skagerrak and Dogger Bank cod, there is little information available from parasitological studies on the stock structure of North Sea cod.

#### Introduction

The use of parasites as tags or markers for discriminating fish stocks is a widely accepted and applied approach, primarily developed during the 1960's (Kabata, 1963; Sindermann, 1961; Margolis, 1965). These authors critically assessed the value of particular parasites in terms of providing information on host biology and distributions, and developed criteria for the appropriate use of a parasite as a stock indicator. These criteria were later re-evaluated by MacKenzie (1987) and Lester (1990).

There have since been numerous papers describing the use of parasites to identify and discriminate fish stocks, many of which began as surveys of parasites in a fish species and proceeded with statistical analysis of the whole data set. Different areas can be shown to have different parasite faunas, but this does not necessarily equate to a stock separation. Choice of parasite species as tags is dependent on the life cycle and mode of infection of the parasite, and also the question being addressed. Typically, parasites which make a permanent infection or mark upon the host, such as nematode or cestode larvae which encyst in the body cavity or musculature are preferable tags to those which have annual or seasonal infections, such as digenean or monogenean trematodes in the gut lumen or on the gills.

#### Parasites as tags of cod

The use of parasites as biological tags for cod was reviewed by Hemmingsen and MacKenzie (2001) and Mackenzie and Hemmingsen (2015).

Shulman (1950) observed the gradual reduction in the parasite fauna of Baltic cod from west to east, marked by the sequential loss of parasites of marine origin. Based on the knowledge of life cycles and ecology existing at the time, Reimer (1970) drew approximate boundary lines marking the eastern limits of these endemic areas. One of the parasites listed by Reimer was the digenean *Cryptocotyle lingua*, and Buchmann (1986) suggested that the low level infection of cod with metacercariae of *C. lingua* in the Bornholm basin was the result of mixing of the uninfected resident stock with migrants from more saline waters further west.

In the Barents Sea, Polyansky and Kulemina (1963) found significant differences in the parasite communities of juvenile cod from different inshore areas, indicating that juvenile cod form local stocks with little migration between them. Along the north Norwegian coast of the Barents Sea, two distinct types of cod are recognized – coastal and Arcto-Norwegian – identifiable by differences in their otolith structure and differing in their migratory behaviour. These two types of cod form mixed populations in the fjords and offshore. Hemmingsen et al. (1991) found significant differences in the prevalences of seven parasite species in samples of cod caught at three locations in this area—two fjords and one offshore. Their results suggested that cod in one of the fjords may represent a population separate from the other two. In a follow-up study in the same general area, Larsen et al. (1997) used four parasite species – two myxosporeans, an adult digenean and a parasitic copepod—to investigate the stock structure and migrations of coastal and Arcto-Norwegian cod from two fjords and one offshore location. They found evidence that the fjords contained local resident populations of Arcto-Norwegian cod and that only the coastal cod migrated between the fjords and offshore. Karasev (1998) reviewed the literature on parasites of Arcto-Norwegian cod in Norwegian and Russian coastal waters of the Barents Sea but failed to find any good tag parasites for identifying local stocks.

Platt (1976) found that larvae of the nematode *Pseudoterranova decipiens* were abundant in cod caught in Icelandic waters but absent from those caught at Greenland. He attributed a reduction in the level of infection of Icelandic cod to immigration of uninfected cod from Greenland and was able to estimate the relative proportions of the two components on spawning grounds to the southwest of Iceland.

Latitudinal variations in the occurrence of four parasites of cod along the west coast of Norway between Finnmark and Ålesund prompted Hemmingsen and Mackenzie (2013) to suggest their use as biological tags. Infection data revealed discontinuous distributions of these parasites, while information on the lifecycles and geographical distributions of their intermediate and final hosts enabled the authors to identify the approximate geographical boundaries of their endemic areas. Metacercariae of the digenean *Proserhynchoides borealis* and plerocercoids of the cestode *Diphyllobothrium phocarum* are long-lived in cod and could be used for stock identification and to follow migrations.

McClelland and Melendy (2011) examined parasites of cod collected from the southern Gulf of St. Lawrence, NAFO (Northwest Atlantic Fisheries Organization) division 4T, and Cape Breton Shelf (NAFO subdivision 4Vn) and found that within the 4T samples, the nematodes, *Hysterothylacium aduncum*, and *Pseudoterranova decipiens* and the acanthocephalans *Echinorhynchus gadi* and *Corynosoma strumosum* were significant in the classification of cod to eastern or western 4T, supporting the findings of earlier mark-recapture studies which have indicated that 4T cod are comprised of discrete eastern and western spawning groups. Further analyses indicated that western 4T cod was distinct not only from eastern 4T cod, but also differed from cod from 4Vn, with rates of misclassification ranging from 6% to 9%. In US waters, the “two stocks” hypothesis was supported by the work of Sherman and Wise (1961), who found significant differences in the incidence of the copepod, *Lernaeocera branchialis*, between cod sampled from the Gulf of Maine and Georges Bank areas.

#### Evidence from North Sea

Although there are numerous studies comparing the parasitofauna of cod from the North Sea with those from other seas (e.g. MacKenzie *et al.*, 2005; Higgins *et al.*, 2010; Gay *et al.*, 2018), within the North Sea there are relatively few parasitological studies on structuring within it. Perdiguer-Alonso et al. (2008) studied the parasite fauna of cod from sites across the northeast Atlantic, including two sites within the North Sea - Dogger Bank and Skagerrak. The parasite fauna of fish collected from the former was dominated by *Stephanostomum* spp., *Anguicollia morhuae*, *Centracaeum osculatum* while that of the latter *Hemiuris communis* and *Anguicollia*



crassicollis. Further work by this author found classification algorithms were less successful at assigning fish to the North Sea sample, compared to the others where cod had been collected, and hypothesised that there was limited mixing between these two sites, with different salinity regimes, resulting in different parasite faunas, and reflecting a structuring of the cod population within the North Sea.

### Conclusions

While there is ample evidence for structuring of cod populations using parasites as biological tags on an ocean basin scale, within the North Sea, evidence is scarce, not necessarily because such structuring is absent - there are no studies showing a homogenous cod parasite fauna across the North Sea either - but because such work has not been carried out or published. Those results which are available suggest at least some separation between cod in the Skaggerak and on Dogger Bank. In general, it is not possible to establish firm conclusions about population structuring of cod in the North Sea on the basis of parasites as biological tags due to the paucity of work which has been done in this area using this approach.

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