Spatial patterns in the distribution and early life characteristics of North Sea cod - Influence from environmental factors and climate change

Höffle, Hannes; Munk, Peter; MacKenzie, Brian

Publication date:
2012

Citation (APA):
Höffle, H., Munk, P., & MacKenzie, B. (2012). Spatial patterns in the distribution and early life characteristics of North Sea cod - Influence from environmental factors and climate change. Charlottenlund: Technical University of Denmark, National Institute of Aquatic Resources.

Spatial patterns in the distribution and early life characteristics of North Sea cod

- Influence from environmental factors and climate change

Ph.D. thesis by

Hannes Höffle

April 2012

Technical University of Denmark

DTU Aqua – National Institute of Aquatic Resources

Section for Ocean Ecology and Climate

Cover photo: Eric Selander

Preface and Acknowledgements

The present thesis was prepared at DTU Aqua – National Institute of Aquatic Resources, the Technical University of Denmark in partial fulfillment of the requirements for acquiring the degree of Ph.D. Financial support for the research came from the project SUstaiNable FISHeries, climate change and the North Sea ecosystem (SUNFISH). The author is indebted to the Working Group on North Sea Cod and Plaice Egg Surveys in the North Sea (WGEGGS), which coordinated the many survey cruises that delivered data for this work. The Ph.D. study was taken up on 15th December 2008 and finished on 10th April 2010. The thesis consists of a summary report and 4 manuscripts written during the period. Three of the four manuscripts are submitted for publication in peer reviewed journals.

First and foremost, I would like to express my gratitude to my supervisors Peter Munk and Brian R. MacKenzie for their advice and encouragement during the project. Special thanks to Peter for his support during the final days of writing, while he could as well have enjoyed a pleasant Easter weekend. Sometimes I chose to ignore the advice of my supervisors; usually to my regret. In the end, I arrived somewhere but not necessarily in the direction I was pointed into in the beginning.

I spent several months at IMR in Bergen and I am indebted to Richard Nash who was my supervisor and invited me to a co-authored paper. Further I wish to thank Laura Rey for the excellent training she gave me in identifying fish larvae and Roger Bivand at NHH whose equally excellent course showed me how to deal with my data.

Of my other colleagues at DTU Aqua I would like to particularly thank my officemate Cornelia Jaspers and our librarian Carina Anderberg. Cornelia was very tolerant towards books, printouts, papers and other stuff that should have been on my desk, but spilled over onto hers. Carina promptly provided any literature one could ask for. I cannot thank all my other colleagues by name, but all of them provided help at some time, small increments which drove my work forward.

I may not have been the easiest person to cope with in those three years and I aim indebted to my friends who tolerated my behavioural glitches in that time.

Last, certainly not least, my family. Somewhere along the way, they have accepted that my calling was not to be an accountant and often had more trust into my abilities than I had myself.

Charlottenlund, April 2012

Hannes Höffle

Table of Contents

Summary

The North Sea cod stock, besides being fished down to its lowest level of spawning stock biomass in history, is also considered to be threatened by negative effects of climate change. As a stock close to the southern limit of the species' latitudinal range it may particularly suffer from increasing temperature. However, climate change would not only entail increasing temperatures, but also changes in freshwater inflow, wind stress and large scale changes in current flow. While information is accumulating on the environmental effects on the early life stages, there is still limited understanding of how effects interact during the early life, from the spawned egg to the settled juvenile.

The primary focus of the present PhD study was to investigate spatial patterns in the planktonic and early demersal stages of cod and relate these to biological and physical factors. The ultimate goal has been to enhance our understanding of interaction between factors in the light of potentially changing conditions due to climate change. Specifically addressed were i) the linkage between hydrography and the distributional patterns of cod eggs; ii) the influence of hydrography and the distribution of potential prey, on the horizontal and vertical distribution of fish larvae and iii) the description of suitable nursery grounds for settling juveniles in hydrographical and biological terms.

Traditional methods of field sampling and identification based on morphology were combined with statistical models for spatial data, using Generalized Additive Models (GAMs), to describe the environmental conditions in spawning and nursery areas. While the main focus was on cod, other common gadoids and flatfish were also investigated, and the vertical distribution of fish larvae was examined in a comparative approach between species.

During the study period for cod spawning in the North Sea the hydrographical patterns were quite stable, also in comparison to earlier studies. Likewise, the distribution of fish eggs and hence spawning exhibited only limited variation on the broad scale. This might stem from adults returning to the same spawning grounds. Within these grounds, there was some adaptability in spawning behaviour, as the centre of egg abundance varied in accordance with prevailing hydrographic conditions. Environmental conditions appeared to be more powerful descriptors for the presence/absence of fish eggs, while variations in the abundance were better explained by spatial dependency (i.e. greater similarity the closer two samples are together).

During the study of fish larvae in the northern North Sea, we found aggregations near frontal systems. The larvae were concentrated in the upper and middle water column, forming two distinct assemblages during the day. Prey was abundant in the upper 40 m of the water column, and fish larvae aggregated between 20 and 40 m for foraging. When not foraging, the larvae remained at the same relative depth in relation to other species.

During the 20-year period studied for the settlement distribution of 0-group cod, a strong decline in nursery area usage was observed. In later years, 0-group cod were mostly found in relatively shallow, warm and medium saline water. Modelling of the 0-group presence in these areas with a few temporally stable and temporally variable covariates allowed to predict the distribution in other periods to a fairly good level ($r_s>0.8$), but also revealed that for long term predictions the dynamics within the population have to be taken into account.

While the North Sea may have already become warmer, broad scale patterns of hydrography as depicted from bottom conditions have not changed substantially yet. However, more extreme climate forcing in the future, may change this. Effects of increased temperature and changes in Atlantic inflow, current patterns and freshwater influence might be beneficial for some species and at some stages during their life, but overall detrimental effects are likely, which may lead to reduced recruitment and stock size.

Resumé (Summary in Danish)

Nordsøens torskebestand er, udover at være fisket ned til den mindste gydebestand nogensinde, også truet af de negative effekter fra klimaændringer. Da bestanden er tæt på torskens sydligste udbredelse kan den tænkes at være særligt sårbare overfor temperaturstigninger. Klimaændringer vil dog ikke kun omfatte temperaturstigninger, men også ændringer i ferskvands-tilstrømning, vind samt større ændringer i havstrømmene. Mens der bliver mere og mere information tilgængelig om miljøets betydning for fiskenes tidligste livstadier, er der stadig begrænset forståelse for hvordan påvirkningerne spiller sammen under fiskenes opvækst – fra det gydte æg til den juvenile fisk der søger mod bunden.

Det primære fokus for nærværende Ph.d. har været at klarlægge de rumlige forhold for de planktoniske og tidlige demersale stadier af torskens liv, og at sammenholde disse med biologiske og fysiske omgivelsesforhold. Det ultimative mål har været at forbedre vores forståelse af samspillet mellem specifikke faktorer i lyset af potentielt nye vilkår på grund af klimaændringer. Specifikt er der set på: i) sammenhængen mellem hydrografi og fordelingen af torskeæg, ii) hydrografiens indflydelse på fordelingen af potentiel føde og fiskelarvers horisontal og vertikal fordelinger, og iii) hvorledes egnede opvækststeder for bund-slående juvenile torsk kan beskrives ved hydrografi og biologiske faktorer.

Studiet kombinerede traditionelle metoder for felt-indsamling og arts-identifikation med statistisk rumlig modellering, vha. GAM, i en beskrivelse af omgivelsesforholdene for gyde- og opvækstområder. Mens hoved-fokus var på torsk, undersøgte vi også andre arter, og fiskelarvernes vertikale fordeling blev beskrevet i et sammenlignende studie mellem arterne.

Gennem perioden hvor torskens gydning i Nordsøen blev undersøgt viste de hydrografiske forhold sig at være relativt stabile, også i sammenligning med tidligere perioder. På samme måde varierede fordelingen af fiskeæg, og dermed gyde-aktiviteten, ikke meget på den store skala. Det synes at have sammenhæng med at de voksne fisk vender tilbage til de samme gydepladser. Indenfor disse pladser var der dog en tilpasning af gyde aktiviteten, på den måde at centrum for æg forekomst lå forskellige steder alt efter den aktuelle hydrografi. Omgivelsesforholdene viste sig at kunne give den bedste beskrivelse af hvorvidt der var gydning i et område, mens variationen i den absolutte forekomst bedst kunne beskrives ved den rumlige afhængighed (at to forekomster ligger tættere eller længere fra hindanen)

Under studiet af fiskelarver i den nordlige Nordsø fandt vi larverne i de højeste forekomster tæt ved hydrografiske fronter. Larverne var koncentreret i den øverste og den midterste del af vandsøjlen, sådan at de om dagen dannede to distinkte grupper. Byttet var fordelt i de øverste 40 m af vandsøjlen, og fiskelarverne samledes mellem 20 og 40 m for at fouragere. Når de ikke fouragerede, havde de forskellige arter den samme respektive fordeling i forhold til de øvrige arter.

Gennem den 20-års periode hvor bund-slånings områderne for 0-gruppe torsk blev undersøgt, skete der et stærkt fald i forekomsterne. I de senere år forekom 0-gruppe torsk mest i relativt lavvandede, med relativt høj temperatur og medium saltholdighed. Ved modellering af 0-gruppernes forekomst i disse områder, med anvendelse af nogle få rumligt stabile og tidsmæssigt variable faktorer, kunne fremtidig fordeling forudsiges med en vis sikkerhed på kortere sigt (i.e. 5-år). Men for at kunne lave forudsigelser for længere perioder (i.e.10 år) skal selve populationsudviklingen sandsynligvis tages med i betragtning.

Mens Nordsøen allerede er blevet varmere, er de overordnede karaktertræk ved hydrografien, som de er analysered ved bund-forholdende, ikke ændret markant. Men mere ekstreme ændringer i fremtiden kan ændre dette. Effekterne af temperaturstigninger, og ændringer i indtrængning af Atlantisk vand, havstrømmene, og ferskvandsindflydelsen kan være positive for nogle arter og stadier i deres liv, men sandsynligvis vil mange effekter være negative og lede til faldende rekruttering og bestands-størrelser.

Abstract

Due to predictions for future climate change, there are rising concerns about the future of the North Sea cod stock. As this is one of the stocks close to the southern limit of the species' range, it may be among those most affected. Direct, as well as indirect effects, of climate forcing may have the greatest effects on early life stages. Hence, the present study examined the linkages between hydrography and distributional patterns of early life stages of cod as well as of several other gadoids and flatfish. Findings indicated that in the egg stage, the environment is more important for the probability of occurrence, while abundance is more under the control of spatial dependency. Larvae were found to be aggregated in the proximity of frontal structures and on the vertical axis, were forming distinct assemblages during the day, while they aggregated during the night. In the recent past, most 0-group cod were found in relatively shallow, warm and medium salinity water. Habitat models for the 0-group had fairly good predictive power on the sub-decadal scale, but were found lacking on a longer time scales. Climate change may have complex impacts on the early life stages, potentially detrimental for one stage and beneficial to another.

Kort Resumé

På grund af prognoser for fremtidige klimaændringer, er der stigende bekymringer om fremtiden i Nordsøens torskebestand. Da denne bestand er på den sydligste grænse af artens udbredelse, kan den være blandt de mest påvirkede. Direkte, såvel som indirekte, effekter af klimapåvirkningen kan få størst indvirkning på tidlige livsstadier. Derfor undersøgtes sammenhængen mellem hydrografi og de fordelingsmæssige mønstre hos de yngste livsstadier af torsk, foruden andre torskefisk og fladfisk. Resultaterne viste, at i ægfasen er miljøet vigtigere for sandsynligheden for forekomst, mens antallet er kontrolleret af den rumlige afhængighed. Larverne samledes i nærheden af fronter. Deres placering i vandsøjlen varierede over døgnet, hvor de i løbet af dagen deltes i to grupper og samledes om natten for at fouragere. I de seneste år er de fleste 0-gruppe torsk blev fundet i relativt lavt og varmt vand med medium saltholdighed. Habitat modeller for 0-gruppen havde rimelig god forudsigende effekt på indenfor årtier, men ikke på længere tidsskalaer. Klimaændringerne kan have komplekse indvirkninger på de tidlige livsstadier, hvor de kan være potentielt skadelige for ét livsstadie og gavnlige for et andet.

Thesis

"There is no great mystery about what happened to the codfish of the North Atlantic. The fishermen caught them, and the rest of us ate them."

Richard Ellis (2003)

1. King cod

In spite of the collapse of important stocks (Hutchings and Myers, 1994) and low levels of spawning stock biomass (ICES, 2010), cod is still an important food fish. The, one-sided, relationship between cod and man goes back a very long time, as cod was already fished in the stone age (Enghoff *et al.*, 2007). The abundance of cod off North America has contributed to the motivation for exploration, cod fishing rights have been disputed to the brink of war (Kurlansky, 1998) and cod is still staple in the diet of many coastal communities. The importance of cod as food fish, and the variable success in fishing for cod and herring (*Clupea harengus*), caused an early interest of science in the dynamics of fish stocks (e.g. Hjort, 1914; Hjort, 1926) and hence the foundation of fisheries science.

1.1 General description

Cod (*Gadus morhua* Linnaeus, 1758) is the largest species in the family of *Gadidae,* reaching a maximum length of around 2 metres (Cohen *et al.*, 1990). Its coloration is variable, but it can be easily distinguished from other fish in the family by its light lateral line. Cod can tolerate between -1°C and over 20°C but prefers waters between 0 and 12°C (Drinkwater 2005). It covers a wider range than the other Atlantic *Gadidae* species. Cod is a demersal fish, preferring depths of no more than 200 m but can be found down to depths of 600 m (Cohen *et al.*, 1990). In the adult form the fish has no preference for any particular substrate. Settling juveniles may settle onto any given substrate (Juanes, 2007), but nurseries with ground cover, like seagrass beds (Gorman *et al.*, 2009) promote survival in that stage. Within its range, cod belongs to the top predators and is a keystone species, having a large influence on the size distribution and abundance of its prey (Van Leeuwen *et al.*, 2008). The diet of cod varies between life stages. Larvae, pelagic and early benthic juveniles feed primarily on small crustaceans, especially copepods (Hüssy *et al.*, 1997; Pinnegar and Stafford, 2007). As the fish grows, decapods of increasing size and later fish, including younger conspecifics (Uzars and Plikshs, 2000), become important prey items (Cohen *et al.*, 1990).

1.2 Reproductive properties and behaviour

Part of its evolutionary success is based in cod's high fecundity, with on average 1 million eggs per female (Cohen *et al.*, 1990). However, egg production and egg quality are influenced by maternal size and condition (Marteinsdottir and Begg, 2002; Marteinsdottir and Steinarsson, 1998) and large females can produce a much higher number of eggs. Cod spawns in batches (Murua and Saborido-Rey, 2003) over an extended spawning season that can begin as early as December and end as late as September (Cohen *et al.*, 1990), depending on the stock. In stocks that cover several degrees latitude, the spawning peak may occur later the farther north one goes (e.g. in the North Sea; Brander, 1994b). In the spawning season, cod aggregates into spawning shoals, returning each year to the same spawning grounds. Males claim territory, which they dominate and spawning occurs near the surface after elaborate courtship (Brawn, 1961). After spawning the egg drifts in a depth determined by buoyancy (Stenevik *et al.*, 2008), passing through a series of development stages in the course of 2 to 3 weeks, depending on temperature (Geffen *et al.*, 2006; Thompson and Riley, 1981). After hatching the larvae take up feeding when their yolk sac is exhausted and later metamorphose into pelagic juveniles. When they reach a size between >3.5 cm and ca. 5 cm (Andrews *et al.*, 2006; Riley and Parnell, 1984), the juveniles seek proximity to the bottom and take up demersal life. After 2-4 years (Munk and Nielsen, 2005) they attain sexual maturity and recruit into the spawning stock. However, only very few fish survive to reach that stage. The pelagic stages and even the early demersal juveniles can have high mortality rates (McGurk 1986; Serchuck *et al.*, 1994). McGurk (1986) showed that the mortality rates of fish eggs and larvae are even above those for other organisms in their size range.

1.3 Ecological plasticity

Cod can survive and successfully reproduce in a wide range of temperatures (Drinkwater, 2005) and salinities (Cohen *et al.*, 1990). This is also visible from the species' geographic distribution, in relationship to temperature ranging from Cape Hatteras and the Bay of Biscay in the South to Ungava Bay and the Barents Sea in the North (Cohen *et al.*, 1990) and concerning salinity extremes including stocks in truly oceanic water (e.g. Icelandic stock) to the Baltic cod, which can withstand low salinities. Depending on definition by ICES/NAFO Divisions or by population, there are 21

(Mantzouni and MacKenzie, 2010) or 22 cod stocks (Drinkwater, 2005) in the North Atlantic (Table 1).

The differences in environmental conditions have their effects on the stocks. Spawning success of Baltic cod is limited by the effects of low salinity on the buoyancy of cod eggs (Nissling *et al.*, 1994) and by the hypoxic conditions below the halocline (Matthäus and Franck, 1992; Nissling, 1994).

Table 1: Cod stocks in the North Atlantic as defined in Drinkwater (2005). Stocks are presented in clockwise order from the Southwest to Southeast.

Western Stocks	Eastern Stocks
Georges Bank	East Greenland
Gulf of Maine	Iceland
Western Scotian shelf	Faroe Plateau
Eastern Scotian shelf	Faroe Bank
Southern Gulf of St. Lawrence	North East Arctic
Northern Gulf of St. Lawrence	White Sea
Southern Newfoundland	Baltic Sea
Grand Bank	Kattegat
Flemish Cap	North Sea-West Scotland-English Channel
Northern Newfoundland/Southern Labrador	Irish Sea
West Greenland	Celtic Sea

The wide temperature range covered, causes different effects of variation in temperature on growth, conditions and recruitment. Brander (1994a; 1995) has shown that greater mean bottom temperature accounts for 90% of the difference in growth rates between the stocks. Similarly, Rätz and Lloret (2003), examining ten different cod stocks, found those in warmer temperature regimes (e.g. North and Irish Seas) in better condition (Fulton's K), than those in colder temperature regimes (e.g. Labrador, Greenland). The rise of Fulton's K by around 0.02 for each 1°C entailed positive effects on the weight at age, the slope (a) of standardized Ricker's recruitment-SSB relationships and estimated biological management reference points (F_{med}). However, living in warmer waters has its ramifications. Planque and Frédou (1999) found that a meta-analysis across stocks, of the effects of temperature fluctuations, exhibited that recruitment at the extremes of the temperature range is more sensitive to these fluctuations, in warm water the relationship was negative and in cold water positive. For stocks in the middle of the range, like the Faeroes and the Georges Bank stocks, the temperature fluctuations were within the tolerance range and no relationship was found.

Taking long term predictions (until 2100) for changes in ocean temperature into account, Drinkwater (2005) predicted that stocks in the Celtic Sea and the English Channel would disappear when annual mean bottom temperature would rise above 12°C, while other southern stocks would decline (e.g. southern North Sea, Irish Sea). The stocks at the northern end of the range, in the Barents Sea, off Greenland and Canada would experience improved recruitment however. Other changes would be a range extension to the North, changed migration patterns and possibly an increase in overall production.

2. The North Sea cod stock

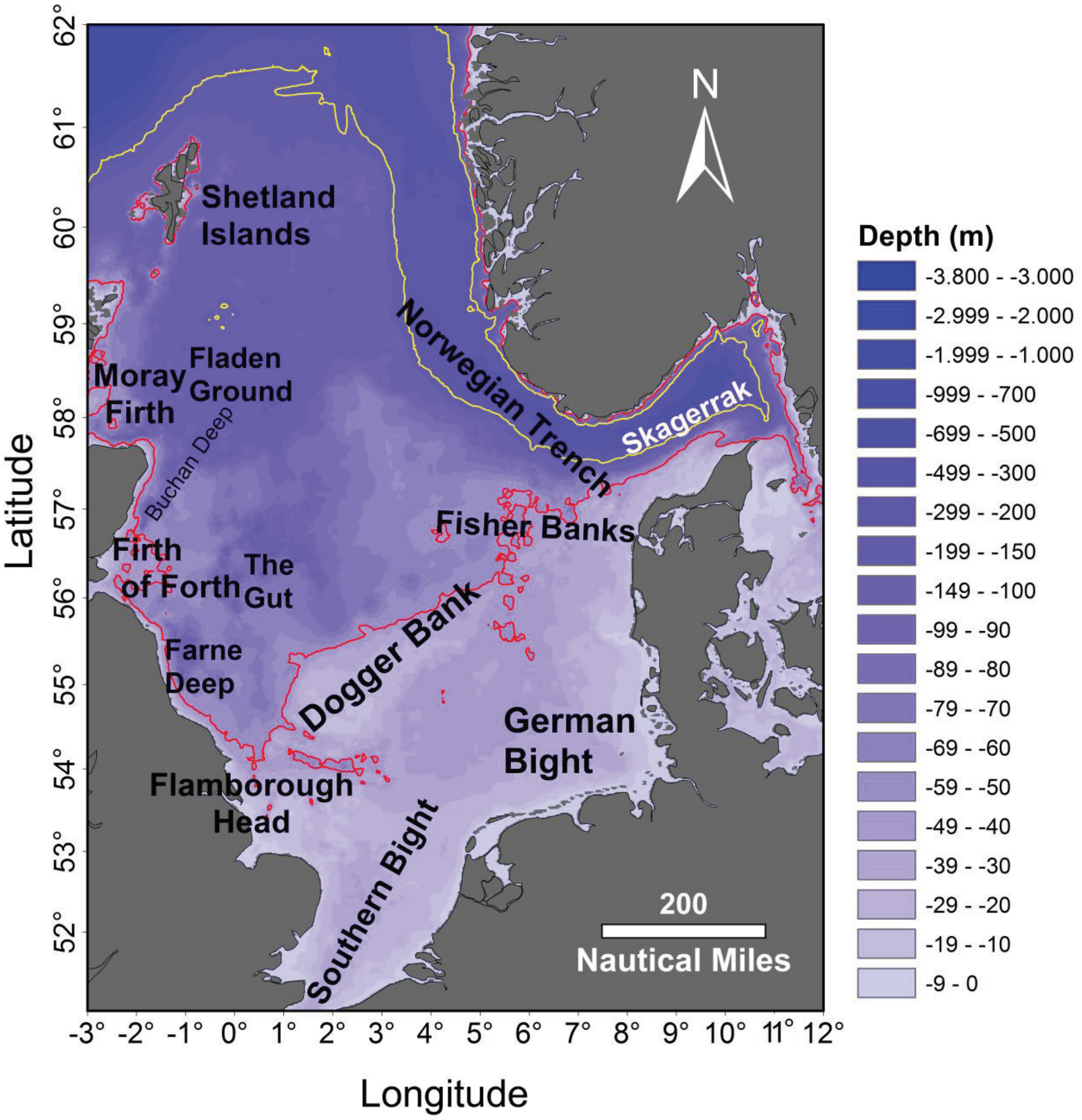


Figure 1: Overview of the North Sea for the geographic extent 3°W-12°E and 51-62°N. The 50 m isobath is depicted as a red line; the 200 m isobath is depicted as a yellow line. Important undersea features and fishing grounds which are named in the Papers are labelled.

2.1 Status and stock structure

The North Sea cod stock falls into the category of warm water stocks (Rätz and Lloret, 2003) and should include fish in good condition and of high fecundity that could sustain high levels of exploitation. The real state of the stock is however a very different one, as it is severely depleted. SSB was, apart from a good recruitment in 1996, in constant decline (Figure 2a) and reached a record low of about 30,000 t in 2006 (ICES, 2010), a tenth of peak catches in the early 1970s (Daan *et al.*, 1994). Likewise, recruitment was low since the mid-1980s (Fig. 1b; Beaugrand *et al.*, 2003).

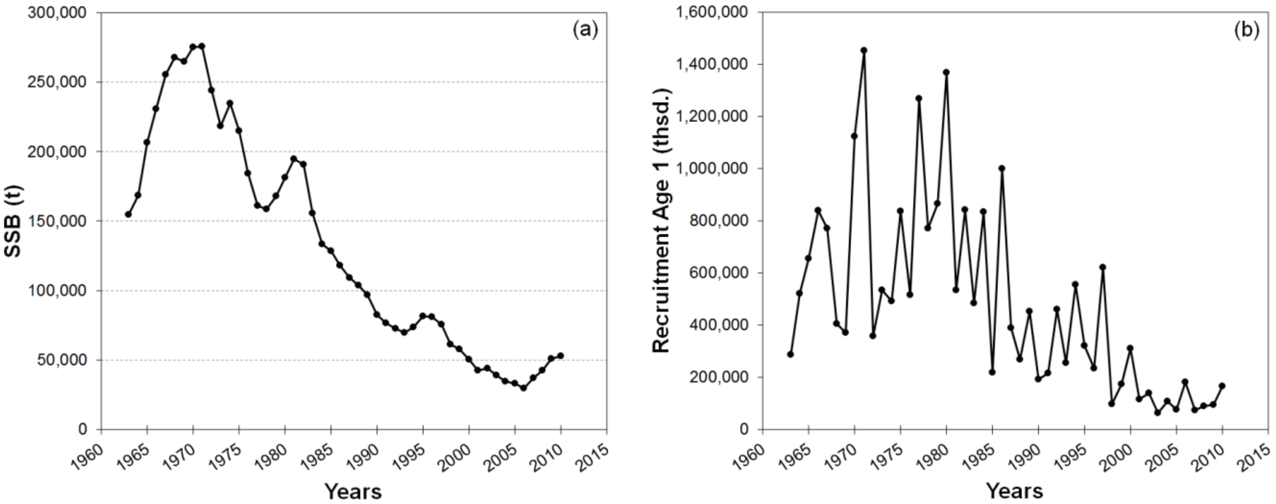


Figure 2: Spawning Stock Biomass (a) and recruitment at age 1 (b) of cod in the North Sea, Eastern Channel and the Skagerrak, from 1963 to 2010. SSB fell under the minimum biomass (B_{lim} = 70,000 t) in 1998 and did not recover since (Data: ICES, 2012).

Although the North Sea cod stock is managed as a single unit, including cod in the Eastern English Channel and the Skagerrak, recent studies have found evidence that the stock is a metapopulation, consisting of several fairly resident inshore groups and more mobile offshore spawners (Wright *et al.*, 2006). These authors found that up to 97% of tagged adults remained within 100 km of their spawning grounds, with only a small proportion straying between spawning grounds. Furthermore, elemental signature in otoliths indicated that most adults originated from local nurseries. Similarly, Hutchinson et al. (2001), using microsatellites from genes, a method which was more sensitive than methods available during earlier studies, found four distinct populations in the North Sea around Bergen Bank, Moray Firth, Flamborough Head and the Southern Bight. Gene flow to outside the North Sea appeared only to occur between the Southern Bight and the Eastern English Channel.

2.2 Direct and indirect influence of climate

The history of the North Sea cod stock during the 20th century was marked by two major events. First the ‘gadoid outburst’, which for cod may have begun in 1969 (Hislop, 1996) and ended in the mid-1980s, followed by a steep decline in SSB in what is sometimes termed a regime shift

(Beaugrand, 2004). Both events, the onset as well as the end of the gadoid outburst, have been attributed to variations in the abundance and size *of Calanus finmarchicus* in the North Sea (Beaugrand *et al.*, 2003; Cushing, 1984). Beaugrand (2003) additionally identified a reduced abundance of Euphausiids later in the year as a possible cause. Alternatives for the hypothesis of control by *C. finmarchicus* have been suggested for both cases. Daan (1994) suggested the collapse of pelagic fish stocks and subsequently reduced predation on gadoid eggs and larvae as the cause for the onset of the gadoid outburst. Brander (1992) re-examined the relationship between cod recruitment and the abundance of *Calanus finmarchicus* and found that Cushing's approach ignored spatial heterogeneity. Pitois and Fox (2008) came to the conclusion that the changes in zooplankton community would not so severely inhibit cod recruitment and stock recovery as suggested by Beaugrand (2003).

Sea Surface Temperature (SST) and a persistently positive North Atlantic Oscillation (NAO) are other possible drivers (Beaugrand, 2004). This is in agreement with the study by Stige *et al.* (2006) who integrated the NAO into Ricker S/R functions for all 22 cod stocks. Their results corroborated those of Brander and Mohn (2004) who found a positive NAO and related higher temperatures would negatively affect recruitment in the southernmost cod stocks, particularly on the eastern side of the Atlantic. The NAO does not only affect the temperature, but also the availability of *C. finmarchicus* as prey, as it overwinters along the European shelf break and is transported into the North Sea with the currents (Backhaus *et al.*, 1994). A positive NAO would hamper this transport (Fromentin and Planque, 1996).

Direct effects of climate change may be easier to recognize. Clark et al. (2003) coupled the Hadley general circulation model with simulations of the stock development. Even when simulation relatively low increases in temperature (0.005°C yr^{-1}) the rate of decline would increase and at an increase of 0.026°C yr^{-1} the stock would be practically gone by 2040.

The North Sea stock is under heavy fishing pressure and larger, older fish are severely depleted (Rindorf and Lewy, 2006). Exploited stocks may be more sensitive to changes in climate (Hsieh *et al.*, 2008) and Rindorf and Lewy (2006) hypothesized that the reduced age structure of the stock may make a stock recovery in the southern North Sea difficult. While a northward shift of spawning and of the population in general may have negative effects for fishing in the southern North Sea, it may partially abate the effects of higher temperature on recruitment (Clark *et al.*, 2003).

2.3 Spawning

North Sea cod does not undertake long distance spawning migrations, comparable to North East Arctic cod, but it does migrate seasonally between spawning and feeding grounds (Daan *et al.*, 1990) The spawning grounds appear, on the scale of the entire North Sea quite stable in time, and spawning has consistently been found in specific areas during studies often decades apart. Brander (1994b) subdivided the North Sea into three areas. In the West-central North Sea spawning began in early February along the southern edge of the Dogger Bank with egg distributions then spreading in NW-SE direction with the spawning period ending close to the coast in late April (data from 1976). In the Southern Bight the first eggs were found in early January and spawning peaked in mid-February. Spawning took place mostly in the central part of the Southern Bight where the water was more saline and more transparent. Finally in the German Bight the eggs were more dispersed. These findings agree with Daan (1978) who found the main spawning areas along the southern flank of Dogger Bank and in the Southern Bight. Other authors identified the area off Flamborough (Harding and Nichols, 1987), the eastern flank of Dogger Bank (Heessen and Rijnsdorp, 1989) or the area east of the Shetlands and the Moray Firth (Heath *et al.*, 1994; Raitt, 1967) as spawning grounds.

After an extended period with no further surveys for identification of spawning grounds an ICES-coordinated ichthyoplankton survey was conducted, covering the whole of the North Sea in the first quarter of 2004. Employing molecular TaqMan probes, to distinguish gadoid species in the early egg stage, Fox et al. (2008) found significant amounts of cod eggs in all of the previously described spawning grounds, except for the one off Flamborough Head which appeared defunct. Based on the same survey Munk *et al.* (2009) found that spawning mostly occurred near fronts, while the peak egg abundances where at the fronts themselves. These authors concluded that spawning near or at fronts may have long-term advantages for the stock, as the increased production at a front enhances food availability. Furthermore, the hydrographic conditions around frontal hydrography, like frontal jet currents, may promote transport to suitable nursery areas. The downside of such a spawning distribution might be that the fronts in late winter/early spring are primarily salinity driven and therefore variable by the amount of freshwater runoff from land. Hence the positioning of these fronts might be influenced by both annual variability and long term changes in climate. A second ichthyoplankton survey carried out in 2009 provided the possibility to study the variation in distribution of eggs on a sub-decadal scale. The study covered both, cod eggs and eggs of other common North Sea fishes, and considered temporal variability as well as the potential influence of hydrographic conditions (Höffle *et al.*, submitted (a); Höffle *et al.*, submitted (b)).

3. Variability in the distribution of fish eggs and the influence of hydrography – Paper I & Paper II

3.1 Motivation and Objectives

Significant survey resources are necessary to cover the ichthyoplankton distributions in a relatively large area as the North Sea. Targeted ichthyoplankton surveys have therefore been relatively few and separated in time. Therefore two surveys in 2004 and 2009, coordinated by the ICES working group PGEGGS (Planning Group on North Sea Cod and Plaice Egg Surveys in the North Sea), afforded unique opportunities for the analysis of spawning distributions. Firstly they were conducted at a time when distinguishing early egg stages of Gadidae with molecular techniques was sufficiently rapid and affordable to at least verify identification with visual methods (Fox *et al.*, 2008; Taylor *et al.*, 2002) and thus reducing the risk of misidentification and over- or underestimating the contribution of one species to the total number of eggs (Fox *et al.*, 2005). Secondly, while still being snapshots, the two surveys were sufficiently close together in time, to investigate whether the distribution of fish eggs changes in the course of a few years, elucidating the potential coupling to prevailing hydrographic conditions or to internal factors, like homing behaviour.

The first objective was to examine the stability in time and space of the spawning distribution for a number of fish species in the North Sea and whether the spawning occurred at one preferred place or in several patches within a spawning ground **(Paper I).** Secondly, recent developments in the field of analysing spatial data were used to construct statistical models, describing the distribution of fish eggs in the North Sea **(Paper II).**

Apart from cod the other species taken into consideration were haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and plaice (*Pleuronectes platessa*). All four species are common in the North Sea and are commercially important fishes. In the statistical approach, models were constructed using hydrographic data (temperature, salinity, density gradient) for the surface/upper water column and for the bottom, aiming to distinguish the influence of bottom hydrography working through the demersal adults, or of surface hydrography directly influencing the drifting eggs.

3.2 Main results

3.2.1 Variation in spawning area usage

On a broad scale the hydrography in the years 2004 and 2009 was quite similar, showing stable hydrographic conditions in winter, even in comparison with data collected in 1962 (Otto and Zimmerman, 1990). The winter distribution of water masses in the North Sea is marked by a decrease in temperature and salinity from North to South, as the Atlantic water coming from the North is warmer and more saline (Otto *et al.*, 1990). While in 2009 the water coming from the North was warmer by 0.4°C and extended less far south than in 2004, the main differences in hydrography occurred in the southern North Sea. There, the surface temperature in the German Bight was more than 1°C colder in 2009 and temperatures <5°C extended farther offshore. In 2004, the influence of freshwater extended farther out to sea but density gradients (in g m^{-3} NM^{-1}) were weaker than in 2009.

The broad scale distribution of fish eggs was similar in both years and also resembled the distribution described in the literature (e.g. Daan, 1978; Saville, 1959). However, there were regional variations between the years, mostly occurring in the southern North Sea. The Southern Bight exhibited the highest egg densities (in nos. m^{-2}) in 2009, higher than observed in the rest of the North Sea or in 2004 (Fig. 3). Overall, the eggs of the different species were found in the spawning areas which had been described in the literature and species specific differences in the relation to hydro- and bathymetry were observed. Analysing the influence of categorical variables in a multivariate ANOVA exhibited that the progress of spawning differed between spawning grounds (grouped after the ICES defined roundfish areas) as the abundance for a given development stage was always significantly different between at least two of these areas.

The interaction of species and spawning ground showed that for cod and plaice the German Bight was significantly different from all other spawning grounds, indicating that this was particularly important for the two species.

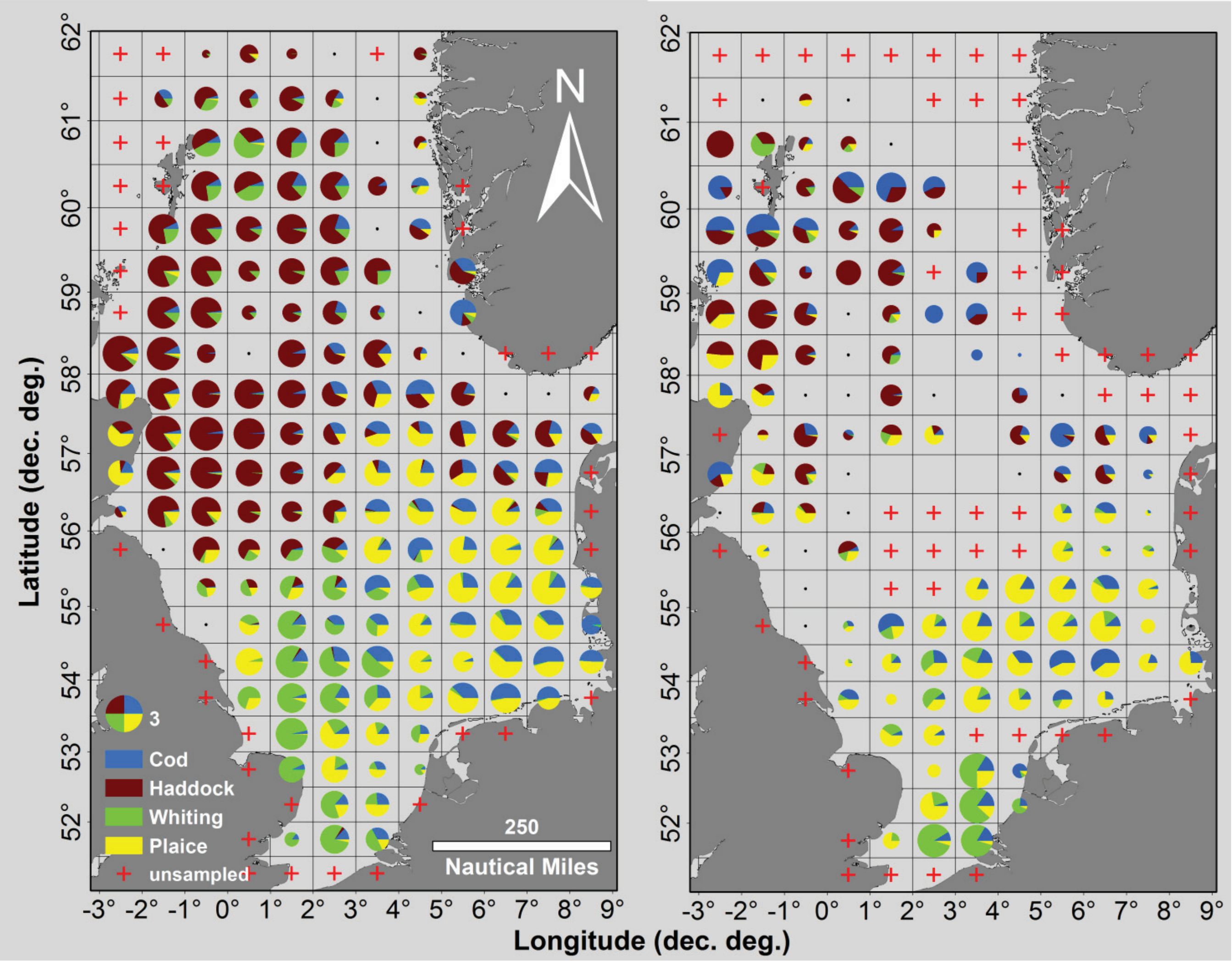


Figure 3: Distribution of fish eggs per ICES square in 2004 (left panel) and 2009 (right panel). Abundances are averaged per ICES square and log(N+1) scaled.

3.2.2 Relation to the environment and the challenges of spatial data

Since the location of spawning fish is governed by spatially autocorrelated environmental conditions, the spawning distribution and subsequently the distribution of eggs itself is under the influence of Tobler's first law of geography (Tobler, 1970), saying: "Invoke the first law of geography: everything is related to everything else, but near things are more related than distant things." (as cited in Miller, 2004). Hence, the data violates the assumption of independent observations, which is necessary for most statistical procedures. The autocorrelation must be accounted for to achieve a meaningful analysis (Legendre, 1993). The method as used in **Paper II**,

formerly called Principal Coordinates of Neighbour Matrices (PCNM) and now integrated into the broader framework of Moran's Eigenvector Maps (MEM, Dray *et al.*, 2006) allows to model spatial structures on several scales (Borcard *et al.*, 2011). The procedure is explained in great detail in Borcard and Legendre (2002) and its output, in the form of eigenvectors which describe the spatial structures, can be easily integrated as explanatory variables in statistical analysis. Another problem that often occurs with distribution data is that it is severely skewed to low values, so-called 'zero-inflation'. To deal with that problem it was chosen to follow the approach of Loots et al. (2010), splitting the data into presence/absence and non-zero abundance. For both set, Generalized Additive Models (GAMs) were fitted to construct a binomial and a Gaussian model, respectively.
PCNM analysis found significant spatial structures on four scales (Fig. 4).

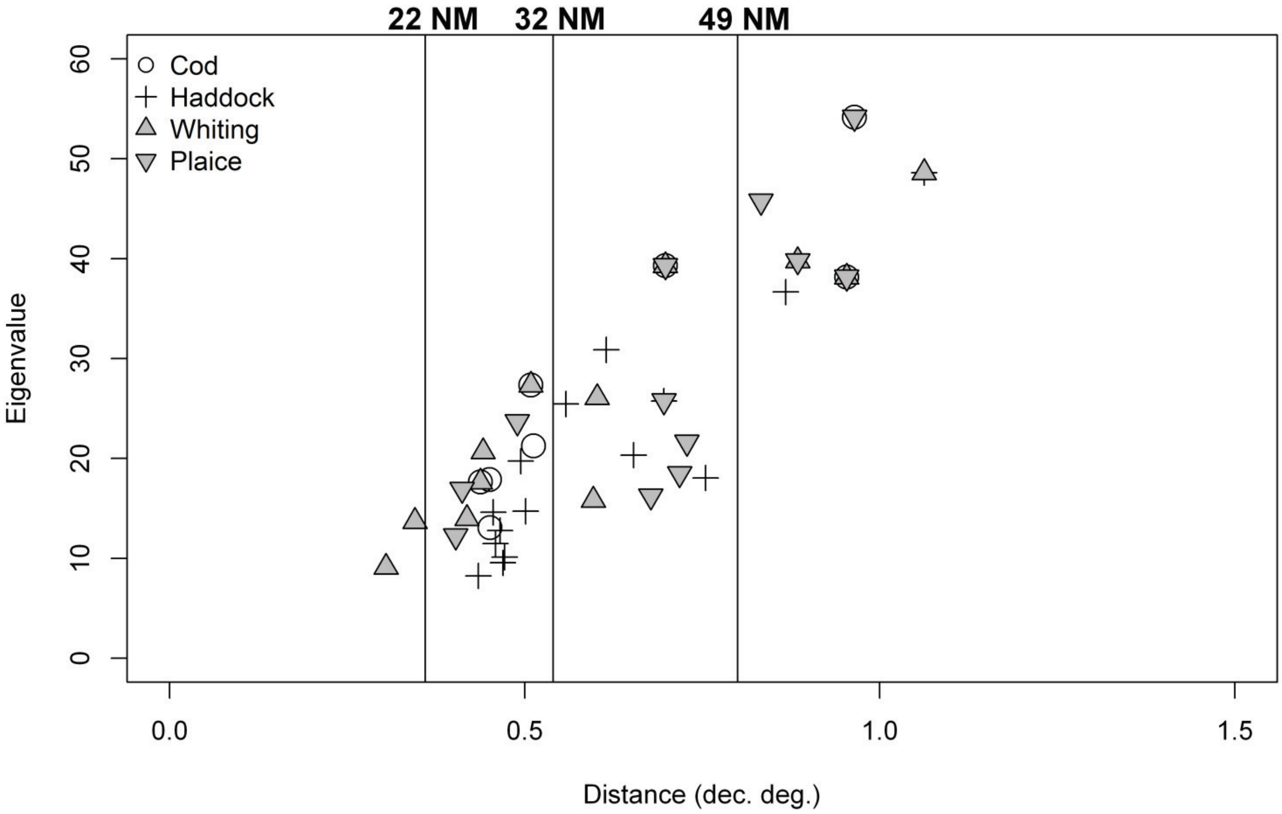


Figure 4: Range in decimal degrees of spatial sub-models for the eggs of cod, haddock, whiting and plaice on very fine (0-22 NM), fine (22-32 NM), medium (32-49 NM), and broad (>49 NM) scales. The solid lines define the thresholds for the spatial sub-models of the eggs. The boundaries between scales are denoted in nautical miles on the top axis. Eigenvalues are non-dimensional and proportional to Moran's I. **(reproduced from Paper II).**

When comparing these models, based on Akaike's Information Criterion (AIC), models for abundance, including hydrography for the upper water column were mostly superior and explained more of the deviation in the data. The sole exception was haddock, where the model for bottom hydrography fit better. For presence/absence the relationships were more equally distributed with cod and plaice better explained when using bottom hydrography and haddock and whiting having a better fit when using surface hydrography. Variation partitioning showed that combined on all scales spatial dependency explained more of the variation in the abundance data than the environment, while the environment was superior in explaining the variation in presence/absence. Haddock, which, when adult, is limited by its environmental preferences to the northern North Sea (Hedger *et al.*, 2004), exhibited a particularly high explanatory power of the environment for the abundance. This might be due to the limitation by the environment, as the opposite case (large influence of spatial dependency in comparison to environment) has been shown for plaice (Loots *et al.*, 2010), which is well within its environmental range in the North Sea.

In summary, while the spawning distribution of the four species was similar to previous studies, on the scale of the single spawning ground it exhibited some adjustment to hydrographic conditions, as was apparent in the southern North Sea in relation to the front between freshwater influenced water along the continental coast and the oceanic water farther out to sea. Controls on presence/absence were primarily environmental, while the abundance relied more on spatial dependency. Exceptions from this rule are however the species which are at the edge of their habitat, like haddock in this study. Abundance was apparently more under the influence of the surface hydrography indicating that the eggs are primarily transported in the upper water column.

4. Relationships between fish larvae and physics

As for all pelagic eggs, cod eggs will drift with the prevailing currents. The time to hatching is on the order of 2 to 3 weeks, depending on temperature (Geffen *et al.*, 2006; Thompson and Riley, 1981). After hatching the larva is sustained by the yolk sac but has find prey within a short time in order not to starve (Kjorsvik *et al.*, 1991).

Spawning is hypothesized to occur in areas where eggs and larvae are retained or transported to water masses with favourable conditions, which in many cases are upwelling and frontal areas. This interpretation is influenced by the retention hypothesis which was based on spawning of different herring stocks in the Atlantic (Iles and Sinclair, 1982; Sinclair and Tremblay, 1984). Ocean banks appear to promote retention, either by clockwise frontal gyres around large banks (O'Boyle *et al.*, 1984) or in case of small, low-energy banks in form of frontal currents originating from the interactions of spawning locations, geostrophic currents and bathymetric steering (Reiss *et al.*, 2000). In other regions of the North Atlantic transport of eggs and larvae with currents, may play a larger role. An example is given by Townsend & Pettigrew (1996) who observed two patches of cod larvae sampled on Georges Bank of which one was advected only over a short distance (25 km), while the other one was advected 75 km along a frontal boundary. From their observations they formulated the hypothesis that clockwise frontal currents around the Georges Bank are highly important for the transport of fish larvae and that variations in recruitment can be due to variations in intrusions of other water masses causing changes in the frontal current. Lough et al. (2006) examined the spawning of cod and haddock on the same offshore bank over several years and identified two areas with good retention in different seasons. They came to the conclusion that retention may become more important with smaller stock size but is otherwise only one factor of many. Similar conditions can occur along coasts. Begg and Marteinsdottir (2002) suggested that cod recruitment around Iceland depends on a combination of regional spawning components close to the nursery areas in the North and inflow to the nursery grounds from the main spawning area in the Southwest, with the clockwise coastal current. This would be promoted by larger, more fecund cod which spawn closer to the coast as the current is stronger there. Depending on the strength, of the Irminger current, the eastern Greenlandic stock can be supplied with Icelandic larvae.

North Sea cod undertakes only relatively short spawning migrations, hence the spawning grounds are close to nursery areas (Daan *et al.*, 1990). Frontal hydrography is also important for the retention of fish larvae in the North Sea, which is apparent along the shelf break front in the northeastern North Sea where primary production and zooplankton concentrations are high (Munk *et al.*, 1995). It was also noted that there are spatial and temporal variations between different gadoids (Munk *et al.*, 1999) in relation to the frontal zone. A similar gradient, but related to bottom depth, was found in the International 0-group Gadoid Survey (Holden, 1981). Hence it is hypothesized that the frontal dynamics are important for the spatial separation of gadoid species, presenting each with suitable physical and biological regimes and having different effects on each (Munk *et al.* 1999).

While the swimming ability of fish larvae is limited in relation to the mesoscale horizontal variability in hydrography, different vertical environments are within reach of the larvae, as vertical hydrographic changes take place within a few metres distance. Through a change of depth fish larvae may find suitable abundances of preferred prey and it may influence their horizontal drift, because current speed and direction can be different in different depth strata. This is especially important for species related to estuaries, where the depth can determine whether the larvae are flushed out into the open sea, or transported shoreward to their nursery areas (Fortier and Leggett, 1982; Fortier and Leggett, 1983; Govoni and Pietrafesa, 1994). The interaction of vertical distribution and currents also poses a problem to modelling studies. Larvae are often modelled as passive drifters without any vertical migration behaviour (e.g. Christensen *et al.*, 2008; Christensen *et al.*, 2007). This approach can be problematic, when the larvae depend on being transported with a particular current at a particular depth. Sclafani *et al.* (1993) showed that modelling the buoyancy dependent depth distribution of larvae can already improve the representation of the depth distribution and differential drift of larvae in good condition and starving larvae. Therefore understanding of key spatial processes may be improved by combined information on the horizontal and vertical distribution/migration of larvae.

A cruise by R/V G. O. Sars (IMR, Bergen, Norway) in April and May 2010, took depth integrated (with GULF VII high speed sampler) samples in two transects across the northern North Sea and depth discrete samples (with MOCNESS) east of the Shetland Isles affording to study the horizontal distribution in a larger area, combined with the analysis of the vertical distribution on a finer scale, in an area that has been found to be particularly species rich (Economou, 1987).

5. Differences in vertical distribution of larval fishes in relation to hydrography and prey – Paper III

5.1 Motivation and Objectives

Vertical distribution patterns of fish larvae can be classified into three categories. Neilson and Perry (1990) identified two types: Type I migrations where the larvae move upward at the beginning of night and downward at the beginning of day; type II migrations which are simply the reverse of type 1. A third pattern exists, where the larvae are aggregated during the day and disperse at night (Gray, 1998; Leis, 1991). Controls governing the vertical distribution of fish larvae can be variable.

Several kinds of cues have been discussed, from control by a preferred isolume (Woodhead, 1966), hydrographic conditions (Lough and Potter, 1993) or the balance of hunger, satiation and the need to avoid predators (Pearre, 2003), to a simple control by the interaction of buoyancy with the density of the water mass (Sclafani *et al.*, 1993).

The objective of the study was to examine how the different species are vertically distributed in relation to their prey, hydrography and each other and to elucidate whether the segregation in the horizontal plain is resembled by segregation on the vertical axis. The comparative approach should reveal the key factors governing the vertical distribution of fish larvae.

5.2 Main results

The overall trend in the two transects at 59.3°N and 60.75°N was an increased species richness and abundance in east-west direction, while mean standard length declined, indicating that larvae in the East were older and that the primary nursery was in the West from where the larvae drifted southeast, similar to what has been described for Norway pout (Nash *et al.*, submitted). Peak larval abundances, together with peak concentrations of zooplankton, were observed in the vicinity of frontal hydrography (Fig. 5). Especially on the western margins of the transects, were the area for depth discrete sampling was located too.

The depth discrete sampling was carried out in an area of 5 X 5 NM, located to the Southeast of Mainland Shetland. Five depth discrete samples were taken over 18 hours between the evening of 2nd to the late morning of 3rd May 2010. The hydrography at this station was of little variability in time and depth. Salinity changed only by 0.01 over the 120 m of measured water column. Temperature was stable at ca. 8°C down to 50 m and at greater depths declined continuously to 7.6°C. Fluorescence was more variable than either temperature or salinity and peaked at about 40 m depth. (**Paper III).** In depth integrated samples (with GULF VII high speed sampler), 23 fish species in 9 families were identified **(Paper III)**. The larvae of ten species were found in sufficient numbers to study their vertical distribution. During the day these larvae constituted two assemblages. One assemblage consisting of cod, haddock, whiting, pollock (*Pollachius pollachius*) was found in the upper water column (0-40 m). The other assemblage contained saithe (*Pollachius virens*), Norway pout (*Trisopterus esmarkii*), poor cod (*Trisopterus minutus*) and the flatfish witch (*Glyptocephalus cynoglossus*), long rough dab (*Hippoglossoides platessoides*) and brill (*Scophthalmus rhombus*). This second assemblage was found below 40 m. A similar distinction into different assemblages was found in previous studies (Gray and Kingsford, 2003; Olivar and Sabatés, 1997). Based on centre of abundance cod was deeper during the night, hence a type II distribution, while all other species were at shallower depth during the night (type I). Most of these species ascended between dusk and night, while Norway pout and brill ascended earlier, reaching their shallowest centre of mass at dusk. Most species ascended no more than to the 20-40 m stratum, probably indicating that they found sufficient prey there. This would support the idea that a starving population would not rise farther than necessary to find sufficient prey (Pearre, 2003).

In relation to each other the different species mostly kept to their position in the water column, while they aggregated in one depth stratum when they were foraging (Fig. 6).

The horizontal distribution indicates that, like in the northeastern North Sea, the fish larvae aggregate near fronts. Similar to the segregation in the horizontal plain which was observed earlier (Munk *et al.*, 1995) the fish larvae appeared to keep to a certain distribution in depth, which was probably governed by the interaction of the physical water column with the buoyancy of the larvae (Sclafani *et al.*, 1993). However, governing cues seem to change in relation to feeding, as the vertical hierarchy broke down during foraging.

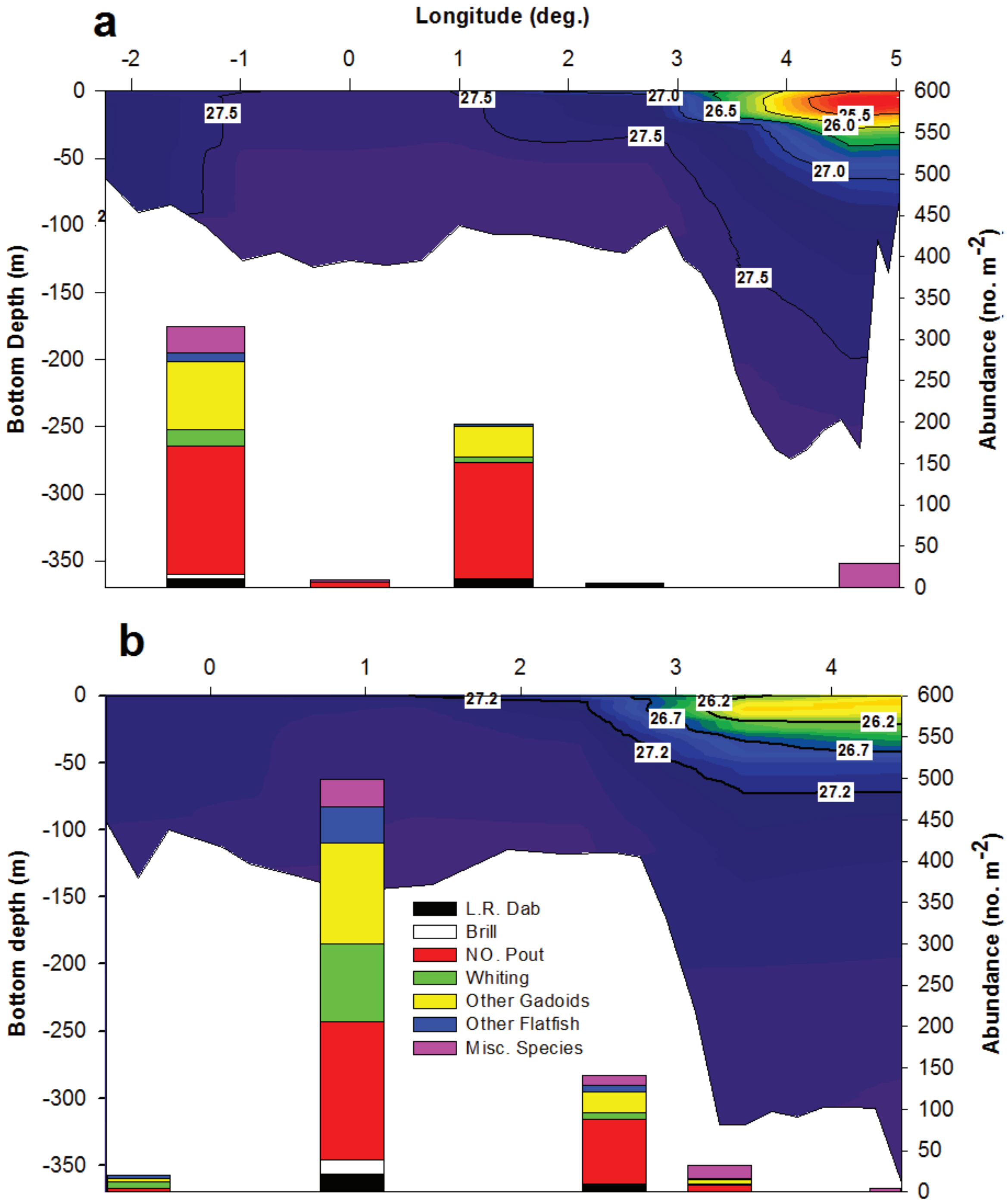


Figure 5: Profiles of water density (0.5 kg m^{-3} contours) and abundance of fish larvae along the transects at 59.3°N (panel a) and 60.75°N (panel b). Only the most common species are presented. Miscellaneous species comprise Clupeidae, Argentinidae, Ammodytidae, Lotidae and Gobidae. **(Colour reproduction of figure 2, Paper III)**

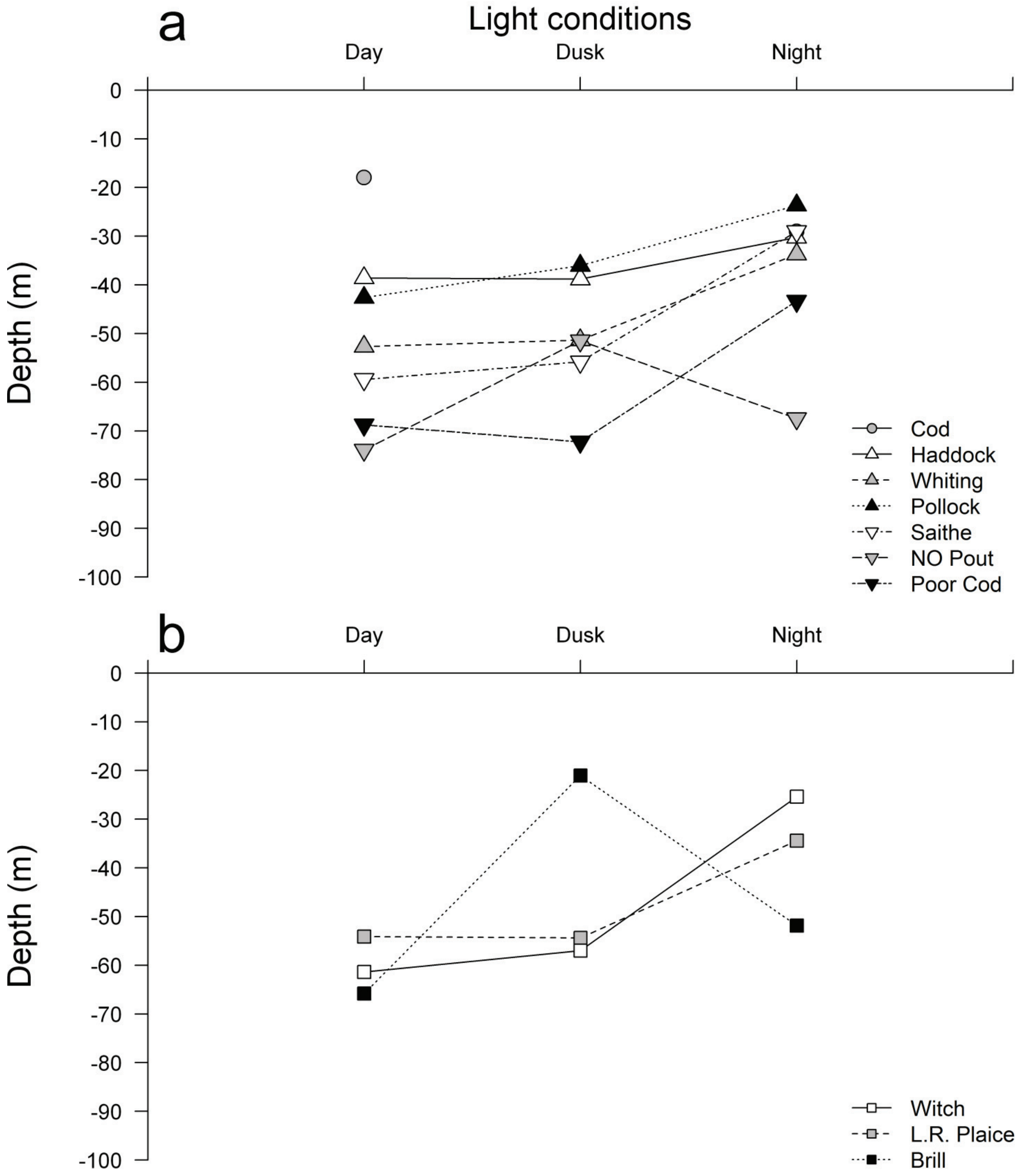


Figure 6: Depth of the centre of abundance for gadoid (a) and flatfish larvae (b) during three different light environments. Due to the long days at this time of the year, there was only one station at dusk (21:52 hours) and night (23:56 hours), while three stations were in daylight (19:14 hours, 06:20 hours and 08:22 hours). **(Reproduction of Figure 6, Paper III).**

6. Settlement of juvenile cod in the North Sea

During their drift cod larvae feed on increasingly larger food items (Godiksen, 2005; Nielsen and Munk, 1998) subsequently they undergo metamorphosis at a length of slightly more than 8 mm (Rowlands *et al.*, 2008). The juveniles gain increasing swimming ability and become able to influence their location on a larger scale. The threshold at which the swimming ability becomes more important than transport with the currents is found to be at about 35 mm (Andrews *et al.*, 2006). From this size juveniles cod might start the transition from a pelagic to a demersal lifestyle, but what determines the settlement of juvenile cod is not fully understood. The availability of sufficiently large and nutritious prey may play an important role. Munk (1997) determined a preferred prey size of cod larvae to 5.1 % of their standard length, a relationship which stayed more or less constant during the larval phase. While the cod larvae consume increasingly older stages of increasingly larger sized copepod species (Nielsen and Munk, 1998), Euphausiids and other large zooplankters become more prominent in the diet of the pelagic juveniles in the size range of 25-35 mm (Godiksen, 2005), while the size relationship between prey and predator stays about the same as in the larval phase. Fish larvae have been found in the stomachs of juvenile gadoids at lengths of only 11 mm (Economou, 1991), but the onset of feeding on fish larvae appears more commonly when cod is above 30 mm (Bromley *et al.*, 1995). Godiksen (2005) identified sandeel (*Ammodytes* spp.) as the primary fish larval prey, which is consistent with later studies (Demain *et al.*, 2011). The relative size of larval prey in the cod stomachs was substantially larger, on average 44% for gadoid larvae and 64% for sandeel larvae and also the weight of stomach contents increased. The need to fulfil requirements for prey of larger and larger sizes might be one of the driving forces for the initially pelagic juveniles to include the near-bottom in their search for prey.

Another driver could be a search for territory which offers more protection (Tupper and Boutilier, 1995). Such protection might be advantageous for juveniles when at about 35 mm, the size that is used in several modelling studies (Andrews *et al.*, 2006; Heath *et al.*, 2008). Settling of cod appears not to be selective about the type of bottom (Juanes, 2007), however post-settlement survival apparently depends on the complexity of the relief in the habitat (Lough, 2010).

Dedicated surveys for research on the early juvenile stage of North Sea cod like the International 0-group Gadoid Survey (IOGS) from the 1970s and early 1980s, gave a comprehensive overview of the distribution of late pelagic 0-group cod. These were consistently aggregating off the Danish west coast, east of Shetland and east of the Firth of Forth (Holden, 1981). A later survey series, the 3rd quarter surveys of the International Bottom Trawl Survey (IBTS), was initiated in 1991 targeting primarily older stages of a range of commercial fish species. However during these surveys also 0-group stages are caught and hence these surveys afford the opportunity to study the distributional patterns of cod when settling to the bottom. This opportunity was used in Paper IV (Höffle and Munk, manuscript).

7. Settlement distribution of 0-group cod – Paper IV

7.1 Motivation and Objectives

One reasons for decline in the North Sea cod stock is its low recruitment (Figure 1b). This decline in recruitment is also reflected in the catches of 0-group cod during the IBTS 3rd quarter survey Similarly, other observations indicated a northward shift of the centre of abundance of juvenile (Rindorf and Lewy, 2006) as well as of adult cod (Perry *et al.*, 2005). It is debated whether this shift is due to wind driven transport of larvae and subsequent homing of the juveniles that settled in the northern North Sea (Rindorf and Lewy, 2006), or whether it is due to increase/decrease in different sub-populations (Holmes *et al.*, 2008; Righton *et al.*, 2007). The data collected during the IBTS survey in the 3rd quarter, between 1991 and 2010, allows modelling of the potential habitat of newly settled 0-group cod with GAMs. This would allow to identify the characteristics of settling sites and to make an attempt to elucidate whether changes in the distribution of settled juveniles can be explained by changes in the hydrography.

7.2 Main results

Averaged for 5-year periods throughout the 20 years covered by the study, the hydrography during the 3rd quarter was remarkably stable. The most prominent hydrographic feature was a thermal front, roughly along the 50 m depth contour between the northern tip of Jutland and Flamborough Head, then extending northwards and around the Shetland Isles. Water of temperatures >10°C was south of the front, while cooler water was to the North. Water with salinity >34 entered the North

Sea from the North and the South. While the tongue of saline water entering from the English Channel and the 34.5 salinity line were relatively variable, the 35 salinity line never came farther south than about 56°N. Its extension into the Skagerrak however was variable between the periods and appeared to be somewhat reduced in the 2000s. Freshwater influence along the continental coast produced a salinity driven front between coastal waters and the central North Sea.

Between 1991 and 2010, the distribution of 0-group cod changed substantially. Catch Per Unit Effort (CPUE) was decreasing, particularly in the offshore areas like the Fisher Banks and East of Shetland. In the German Bight CPUE decreased and the centre of abundance shifted northward along the coast of Jutland. In the Skagerrak a noticeable decrease only occurred in the last period, 2006-2010. It is likely that the population of 0-group cod was supported by inflow from the North Sea, as was suggested in previous studies (Stenseth *et al.*, 2006; Svedäng and Svenson, 2006). The composition of covariates when fitting GAMs to the presence/absence of 0-group cod was very similar, whether the model was fitted to a 5-year period (1991-1995 and 2001-2005) or to a 10-year period (1991-2000). The best fit was achieved with the covariates: Geographic position, bottom depth, interaction of temperature and salinity as well as both as single terms and presence/absence of age-2 cod. In the period 2001-2005 the slope of the bottom was additionally included. Predicting the following five or ten year period from the fitted GAM, produced fairly good correlation between predictions and observations (Fig. 7), although predictions over a shorter time were better (Fig. 8), particularly as the prediction for ten years could not fully capture the decline in the probability to find cod in the central and western North Sea during the 2000s.

The stable hydrography over most of the North Sea in the study period indicates that the observed changes in CPUE and distribution can only be partially explained by the hydrographic conditions, or alternatively by changes in hydrography that have occurred before the study period (c.f. Beaugrand, 2004) which influenced the distributional patterns of 0-group cod during the following years. Including only external covariates into a model of the juveniles' habitat appeared useful, as it provided good prediction on sub-decadal time scales. Hydrographic variables (temperature, salinity) apparently served as modifiers for the influence of time invariable covariates, i.e. geographic positions and bottom depth.

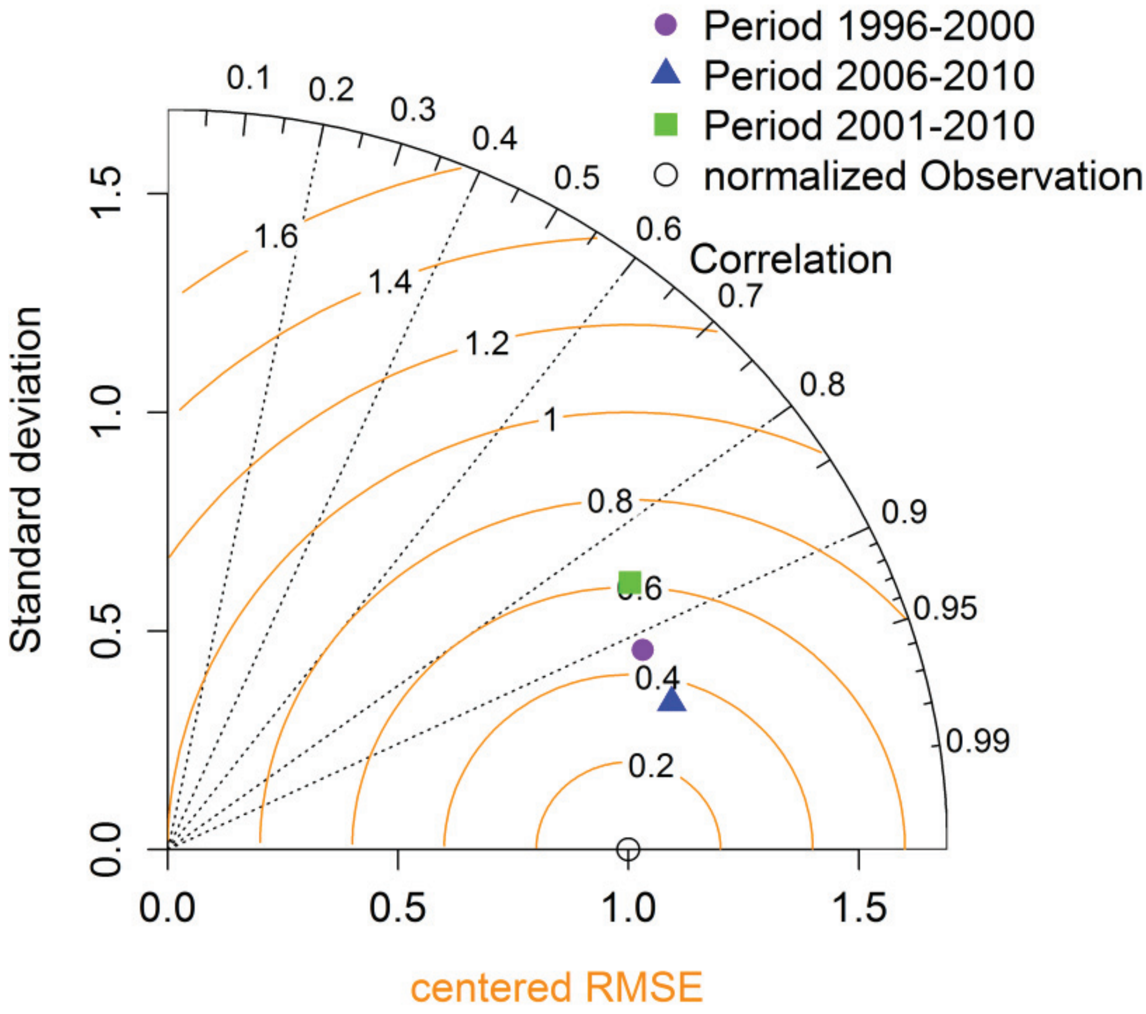


Figure 7: Taylor diagram, comparing the probability of occurrence predicted from the selected GAM models with the observations in 1996-2000, 2006-2010 and 2001-2010. Standard deviation for the observed values was normalized to 1 and the Root Mean Square Error (RMSE) normalized to 0. Standard deviation of the predictions is depicted on the y-axis, while the radii of the circle represent the correlation. The RMSE is plotted on the concentric circles around the normalized standard deviation of the observations. Only the segment of the diagram which depicts

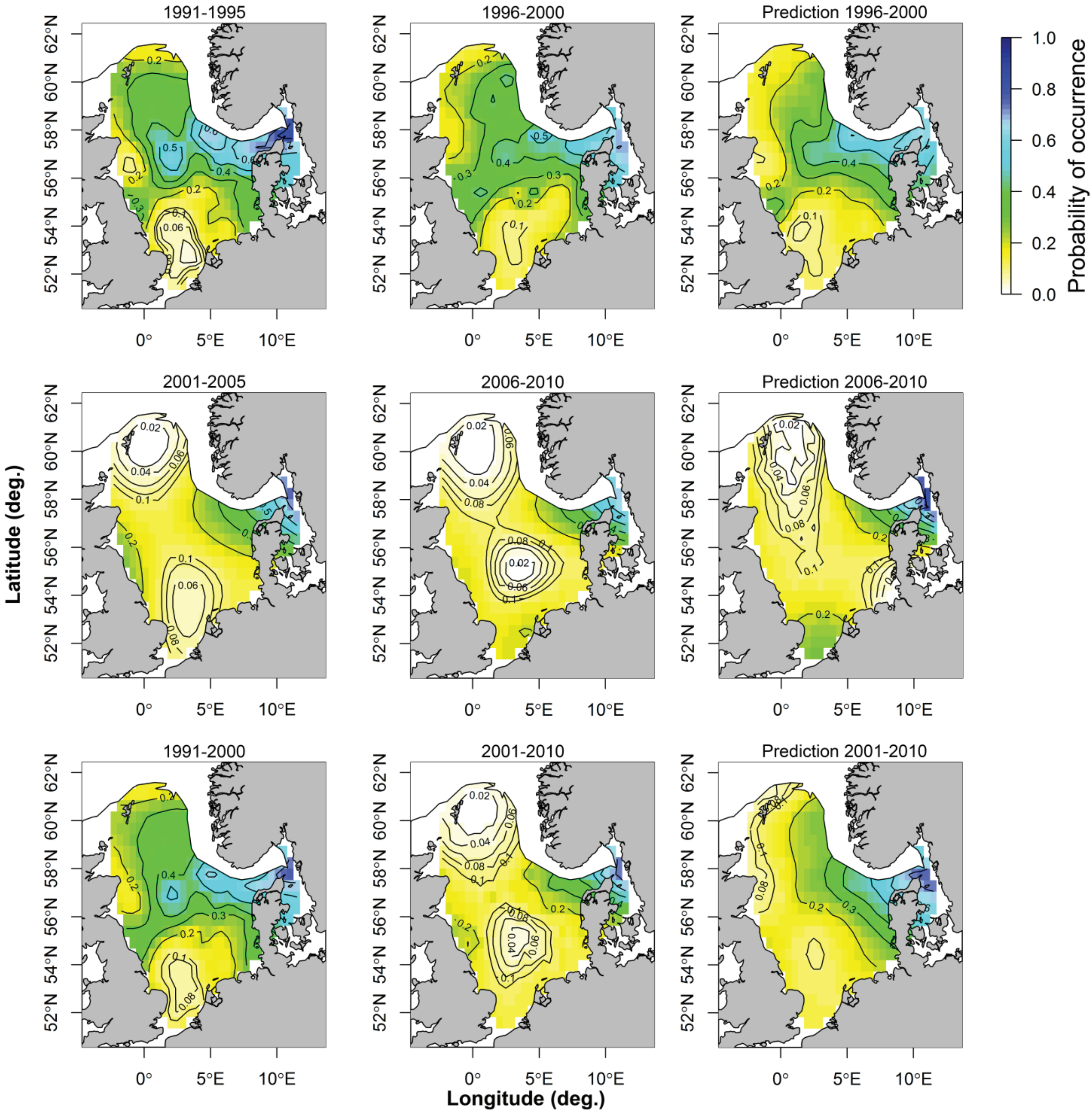


Figure 8: Interpolated probabilities of the occurrence of 0-group cod. The left column shows the probability for the periods GAMs were fitted to, the middle column shows the periods for which predictions were made and the right column shows the predictions. Areas deeper than 200 m are masked, because of lack of data. **(reproduction of figure 11, Paper IV)**

8. Synthesis

8.1 Rationale and aims

The primary aim of the present PhD study was to investigate how spatial patterns in the early life of cod are influenced by the physical environment and how changes in climate may indirectly, via effects on hydrography, influence these distribution patterns. Particular focus was given to i) establish a linkage between hydrographic characteristics and the distributional patterns of cod eggs and to set it into relation with spawning patterns and the drift of eggs and larva. ii) To examine the influence of hydrography and potential zooplankton prey distribution on horizontal and vertical distribution of fish larvae. iii) To investigate processes during the change from pelagic to demersal life with a particular focus on the description of appropriate nursery grounds in hydrographical and biological context.

8.2 Findings of the PhD study in context

The distribution of spawning grounds in the North Sea, as observed in the course of this study exhibited their persistency over time, as it was similar to earlier studies (Brander, 1994b; Daan, 1978). Considering that genetically distinct sub-populations were recently identified (Hutchinson *et al.*, 2001) it appears that on the broad scale cod are bound to return to a specific spawning ground. Locally, within spawning grounds, there is some adaptability. The comparison of the spawning seasons, which were only separated by a few years, showed that the centre of egg abundance was shifting in accordance with the prevailing hydrographic conditions **(Paper I)**. Such local adaptability may partially balance effects of climate change on the position of frontal systems through changes in precipitation (Meehl *et al.*, 2007), while it may not entail a shift in the population centre, like suggested by Clark et al. (2003). The statistical models **(Paper II)** exhibited that the influence of changes in temperature would likely be larger than that of salinity. An increase in temperature may accelerate egg development (Thompson and Riley, 1981), influencing the location upon hatching and thus may not guarantee that the larvae hatch into favourable conditions. Such conditions may occur in frontal zones as indicated from the aggregation of larvae and zooplankton close to fronts, found in the present study **(Paper III)** as it was found in earlier studies (e.g. Lochmann *et al.*, 1997).

For the juveniles, salinity appears somewhat more important than temperature **(Paper IV).** Typical settling areas, were relatively shallow, warm and low in salinity. Such conditions which may ensure spatial separation from older, cannibalistic, conspecifics (Riley and Parnell, 1984). The models constructed to describe the potential habitat of juveniles were able to predict the probability distribution of occurrence on a sub-decadal time scale, but on the longer term knowledge about the population dynamics of North Sea sub-stocks is necessary.

8.3 Perspective

On the scale of the species' entire range, cod may be among the benefactors of climate change (Drinkwater, 2005), with increased productivity and biomass in the stocks on the northern edge of its range. This may be good news on the Lofoten Islands and on Greenland but it is certainly not well received in traditional fishing ports of the southern North Sea like Grimsby, Lowestoft or Esbjerg.

Changes in temperature and hydrography may have different effects on different stages of the early life or on the same stage in different locations. When temperature influences the time and location of hatching, it may therefore also influence if the larvae arrive in an area (e.g. a front) with sufficient prey in time to start feeding successfully. Since cod larvae in the northern North Sea feed primarily on *Calanus* spp., which does not occur in high abundance south of the Fisher Bank (Krause *et al.*, 1995), effects on the variability in supply of these copepods may affect these larvae more. In the South, where cod larvae are more dependent on other species, the effects of temperature and changes in hydrography may be more important.

In the juvenile stage, being in warmer water may have an advantage as the fish grow faster (Björnsson and Steinarsson, 2002) and an extended Region Of Freshwater Influence (ROFI) may increase the refuge from predation by older conspecifics (Riley and Parnell, 1984). Additionally, given that there appears to be competition for suitable habitats (Tupper and Boutilier, 1995), enhanced mortality in the planktonic stage may reduce density dependent mortality during the settled 0-group.

It has been shown that the velocity of climate change (the movement of isotherms in km/decade) north of 45°N is much faster in the ocean than on land and that spring temperatures arrive in the North Sea 5-10 days/decade earlier (Burrows *et al.*, 2011). Furthermore, the North Say may be particularly vulnerable to change, since it appears to be under the influence of a shifting biome boundary in the North Atlantic (Beaugrand *et al.*, 2008) and even with strict management of fishing, recruitment of North Sea cod may not return to earlier levels.

8.4 Future work

It must be noted that only the part of this study, covering the first two papers is based on dedicated surveys. The samples that were used for Papers III and IV, as valuable as they are, were not collected for the specific purpose. Hence, much work can still be done. Time and restrictions on the use of research vessels did not allow to conduct a study on the pelagic juvenile phase of cod and this, together with the analysis of stomach data collected during the 3rd quarter IBTS in 2009, may be the focus of another study which would close the arc from the egg to the settled juvenile completely.

As the area east of the Shetland Isles appears to be a hotspot for the larvae of a wide range of species, it may be beneficial to sample this area more often than the snapshots taken in the past (Economou, 1987; Höffle *et al.*, submitted (c)). A longer time series would afford the opportunity to conduct a thorough statistical analysis of the vertical distribution of fish larvae in the northern North Sea (like in Hernandez *et al.*, 2009) and in combination with areas in the southern North Sea may inform how different or similar changes in the southern and northern North Sea are. Much of the motivation for this study within the framework of the larger project **Sustainable fisheries, climate change and the North Sea ecosystem (SUNFISH)** was to deliver real world information for the validation of models or data sets sampled with non-standard methods (e.g. fish larval data from CPR). Partially this value is already realized (Lynam *et al.*, in prep.) and it will continue to be useful in future publications.

9. Concluding remarks

9.1 The king is dead – long live the cod

Blaming all change in cod stocks on climate may be convenient for some (see reactions to Schiermeier, 2004). However, it does nothing for the recovery of depleted stocks. Much of the problem with regulating fishing for cod in the North Sea is due to the high fishing mortality the stock could sustain in the 'golden age' of the gadoid outburst. Fisheries management was slow to pick up on the natural decline in the stock and therefore fishing pressure was, and still is, much too high. However, fisheries management shows signs of improvement (Brander, 2010).

Cod persevered through an earlier warm period (Enghoff *et al.*, 2007) and given reasonable management, it may continue to be an important species, in a future, warmer North Sea ecosystem. Even in the worst case, with unchecked fishing pressure, it would likely not go physically extinct, but would ‘only’ be reduced to commercial extinction. However, like the Canadian seabed which *“… today feels the scratch and suck of legions of invertebrate feet where fish once dominated.”* (Roberts, 2007), the North Sea would be a different sea.

10. References

Andrews, J.M., Gurney, W.S.C., Heath, M.R., Gallego, A., O'Brien, C.M., Darby, C. and Tyldesley, G. (2006) Modelling the spatial demography of Atlantic cod (*Gadus morhua*) on the European continental shelf. *Can. J. Fish. Aquat. Sci.* **63**(5)**:**1027-1048.

Backhaus, J.O., Harms, I.H., Krause, M. and Heath, M.R. (1994) An Hypothesis Concerning the space-time succession of *Calanus finmarchicus* in the northern North Sea. *Ices. J. Mar. Sci.* **51**(2)**:**169-180.

Beaugrand, G. (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog. Oceanogr.* **60**(2-4)**:**245-262.

Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S. and Reid, P.C. (2003) Plankton effect on cod recruitment in the North Sea. *Nature* **426**(6967)**:**661-664.

Beaugrand, G., Edwards, M., Brander, K., Luczak, C. and Ibanez, F. (2008) Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecol. Lett.* **11**(11)**:**1157-1168.

Begg, G.A. and Marteinsdottir, G. (2002) Environmental and stock effects on spawning origins and recruitment of cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* **229:**263-277.

Björnsson, B. and Steinarsson, A. (2002) The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **59**(3)**:**494-502.

Borcard, D., Gillet, F. and Legendre, P. (2011) *Numerical Ecology with R. Use R!* Gentleman, R., Hornik, K., and Parmigiani, G. New York: Springer, 249pp.-

Borcard, D. and Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Model.* **153**(1-2)**:**51-68.

Brander, K. (1992) A re-examination of the relationship between cod recruitment and *Calanus finmarchicus* in the North Sea. *ICES mar. Sci. Symp.* **195:**393-401.

Brander, K. and Mohn, R. (2004) Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **61**(9)**:**1558-1564.

Brander, K.M. (1994b) The Location and Timing of Cod Spawning Around the British Isles. *Ices. J. Mar. Sci.* **51**(1)**:**71-89.

Brander, K.M. (1994a) Patterns of distribution, spawning and growth in North Atlantic cod: the utility of inter-reginal comparisons. *ICES mar. Sci. Symp.* **198:**406-413.

Brander, K.M. (1995) The Effect of Temperature on Growth of Atlantic Cod (*Gadus morhua* L). *Ices. J. Mar. Sci.* **52**(1)**:**1-10.

Brander, K.M. (2010) Cod *Gadus morhua* and climate change: processes, productivity and prediction. *J Fish Biol.* **77**(8)**:**1899-1911.

Brawn, V.M. (1961) Reproductive Behaviour of the Cod (*Gadus callarias* L.). *Behaviour* **18**(3)**:**177-198.

Bromley, P.J., Watson, T. and Hislop, J.R.G. (1995) Feeding interactions and the development of food webs in pelagic 0-group gadoids (cod, haddock, whiting, saithe and Norway pout) in the northern North Sea. ICES, *Demersal Fish Committee G:29, Ref H.L.,*

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J. and Richardson, A.J. (2011) The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. *Science* **334**(6056)**:**652-655.

Christensen, A., Jensen, H., Mosegaard, H., John, M.S. and Schrum, C. (2008) Sandeel (*Ammodytes marinus*) larval transport patterns in the North Sea from an individual-based hydrodynamic egg and larval model. *Can. J. Fish. Aquat. Sci.* **65**(7)**:**1498-1511.

Christensen, A., Daewel, U., Jensen, H., Mosegaard, H., St, J. and Schrum, C. (2007) Hydrodynamic backtracking of fish larvae by individual-based modelling. *Mar. Ecol. Prog. Ser.* **347:**221-232.

Clark, R.A., Fox, C.J., Viner, D. and Livermore, M. (2003) North Sea cod and climate change - modelling the effects of temperature on population dynamics. *Glob. Change Biol.* **9**(11)**:**1669-1680.

Cohen, D.M., Inada, T., Iwamoto, T. and Scialabba, N. (1990) *FAO Species Catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes know to date. FAO Fish. Synop. No. 125.* **10** Rome: FAO, 442pp.

Cushing, D.H. (1984) The Gadoid Outburst in the North-Sea. *J. Conseil.* **41**(2)**:**159-166.

Daan, N. (1978) Changes in cod stocks and cod fisheries in the North Sea. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **172:**39-57.

Daan, N., Bromley, P.J., Hislop, J.R.G. and Nielsen, N.A. (1990) Ecology of North Sea Fish. *Neth. J. Sea. Res.* **26**(2-4)**:**343-386.

Daan, N., Heessen, H.J.L. and Pope, J.G. (1994) Changes in the North Sea Cod Stock During the twentieth Century. *ICES mar. Sci. Symp.* **198:**229-243.

Demain, D., Gallego, A., Jaworski, A., Priede, I. and Jones, E. (2011) Diet and feeding niches of juvenile *Gadus morhua, Melanogrammus aeglefinus* and *Merlangius merlangus* during the settlement transition in the northern North Sea. *J Fish Biol.* **79**(1)**:**89-111.

Dray, S., Legendre, P. and Peres-Neto, P.R. (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Model.* **196**(3-4)**:**483-493.

Drinkwater, K.F. (2005) The response of Atlantic cod (*Gadus morhua*) to future climate change. *Ices. J. Mar. Sci.* **62**(7)**:**1327-1337.

Economou, A.N. (1987) Ecology of survival in some gadoid Larvae of the Northern North Sea. *Env. Biol. Fish.* **19**(4)**:**241-260.

Economou, A.N. (1991) Food and feeding ecology of five gadoid larvae in the northern North Sea. *J Conseil* **47**(3)**:**339-351.

Ellis, R. (2003) *The empty ocean - plundering the world's marine life.* Washington: Shearwater Books, 375pp.

Enghoff, I.B., MacKenzie, B.R. and Nielsen, E.E. (2007) The Danish fish fauna during the warm Atlantic period (ca. 7000-3900 BC): Forerunner of future changes? *Fish. Res.* **87**(2-3)**:**167-180.

Fortier, L. and Leggett, W.C. (1982) Fickian Transport and the Dispersal of Fish Larvae in Estuaries. *Can. J. Fish. Aquat. Sci.* **39**(8)**:**1150-1163.

Fortier, L. and Leggett, W.C. (1983) Vertical Migrations and Transport of Larval Fish in a Partially Mixed Estuary. *Can. J. Fish. Aquat. Sci.* **40**(10)**:**1543-1555.

Fox, C.J., Taylor, M., Dickey-Collas, M., Fossum, P., Kraus, G., Rohlf, N., Munk, P., van Damme, C.J.G., Bolle, L.J., Maxwell, D.L. and Wright, P.J. (2008) Mapping the spawning grounds of North Sea cod (*Gadus morhua*) by direct and indirect means. *P. Roy. Soc. B-Biol. Sci.* **275**(1642)**:**1543-1548.

Fox, C.J., Taylor, M.I., Pereyra, R., Villasana, M.I. and Rico, C. (2005) TaqMan DNA technology confirms likely overestimation of cod (*Gadus morhua* L.) egg abundance in the Irish Sea:

implications for the assessment of the cod stock and mapping of spawning areas using egg-based methods. *Mol. Ecol.* **14**(3)**:**879-884.

Fromentin, J.M. and Planque, B. (1996) *Calanus* and environment in the eastern North Atlantic II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.* **134**(1-3)**:**111-118.

Geffen, A.J., Fox, C.J. and Nash, R.D.M. (2006) Temperature-dependent development rates of cod *Gadus morhua* eggs. *J Fish Biol.* **69**(4)**:**1060-1080.

Godiksen, J.A. (2005) Diet changes during the Pelagic Juvenile Stage of North Sea cod *(Gadus morhua)*. Department for Marine Ecology - University of Aarhus Thesis: 19992897 41pp.

Gorman, A.M., Gregory, R.S. and Schneider, D.C. (2009) Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*). *J Exp. Mar. Biol. Ecol.* **371**(1)**:**1-9.

Govoni, J.J. and Pietrafesa, L.J. (1994) Eulerian views of layered water currents, vertical distribution of some larval fishes, and inferred advective transport over the continental shelf off North Carolina, USA, in winter. *Fish. Oceanogr.* **3**(2)**:**120-132.

Gray, C.A. (1998) Diel changes in vertical distributions of larval fishes in unstratified coastal waters off southeastern Australia. *J. Plankton Res.* **20**(8)**:**1539-1552.

Gray, C.A. and Kingsford, M.J. (2003) Variability in thermocline depth and strength, and relationships with vertical distributions of fish larvae and mesozooplankton in dynamic coastal waters. *Mar. Ecol. Prog. Ser.* **247:**211-224.

Harding, D. and Nichols, J.H. (1987) Plankton surveys off the north-east coast of England in 1976: An introductory report and summary of the results. Directorate of Fisheries Research, *MAFF-DFR-TR-86,* 56pp.

Heath, M., Rankine, P. and Cargill, L. (1994) Distribution of Cod and Haddock Eggs in the North Sea in 1992 in Relation to Oceanographic Features and Compared with Distributions in 1952-1957 (Abstract). *ICES mar. Sci. Symp.* **198:**438-439.

Heath, M.R., Kunzlik, P.A., Gallego, A., Holmes, S. and Wright, P.J. (2008) A model of meta-population dynamics for North Sea and West of Scotland cod - The dynamic consequences of natal fidelity. *Fish. Res.* **93**(1-2)**:**92-116.

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A. and Andrews, J. (2004) Analysis of the spatial distributions of mature cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980-1999) using generalised additive models. *Fish. Res.* **70**(1)**:**17-25.

Heessen, H.J.L. and Rijnsdorp, A.D. (1989) Investigation on egg production and mortality of cod (*Gadus morhua* L.) and plaice (*Pleuronectes platessa* L.) in the southern and eastern North Sea in 1987 and 1988. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **191:**15-20.

Hernandez, F.J., Hare, J.A. and Fey, D.P. (2009) Evaluating diel, ontogenetic and environmental effects on larval fish vertical distribution using Generalized Additive Models for Location, Scale and Shape. *Fish. Oceanogr.* **18**(4)**:**224-236.

Hislop, J.R.G. (1996) Changes in North Sea gadoid stocks. *Ices. J. Mar. Sci.* **53**(6)**:**1146-1156.

Hjort, J. (1914) Fluctuations in the great fisheries of northern Europe. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **20:**1-228.

Hjort, J.O.H.A. (1926) Fluctuations in the year classes of important food fishes. *J Conseil* **1**(1)**:**5-38.

Höffle, H., Fox, C., Loots, C., Nash, R.D.M., Vaz, S., Wright, P. and Munk, P. (submitted (a)) Egg distribution of four common North Sea fishes - Local variation in spawning area usage *Fish. Oceanogr.* 28pp.

Höffle, H. and Munk, P. (manuscript) Distribution of juvenile cod settlement sites in the North Sea during the period 1991 to 2010. 29pp.

Höffle, H., Nash, R.D.M., Falkenhaug, T. and Munk, P. (submitted (c)) Differences in vertical distribution of larval fishes in relation to hydrography and prey *Mar. Biol. Res.* 25pp.

Höffle, H., van Damme, C.J.G., Lelièvre, S., Loots, C., Vaz, S. and Munk, P. (submitted (b)) Egg distribution of four common North Sea fishes - Hydrographic and geographic influence on distribution *Fish. Oceanogr.* 31pp.

Holden, M.J. (1981) The North Sea International 0-Group Gadoid Surveys 1969-1978. *ICES Coop. Res. Rep. No. 99,* 74pp.

Holmes, S.J., Wright, P.J. and Fryer, R.J. (2008) Evidence from survey data for regional variability in cod dynamics in the North Sea and West of Scotland. *Ices. J. Mar. Sci.* **65**(2)**:**206-215.

Hsieh, C.H., Reiss, C.S., Hewitt, R.P. and Sugihara, G. (2008) Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. *Can. J. Fish. Aquat. Sci.* **65**(5)**:**947-961.

Hüssy, K., Stjohn, M.A. and Bottcher, U. (1997) Food resource utilization by juvenile Baltic cod *Gadus morhua*: a mechanism potentially influencing recruitment success at the demersal juvenile stage? *Mar. Ecol. Prog. Ser.* **155:**199-208.

Hutchings, J.A. and Myers, R.A. (1994) What Can be Learned from the Collapse of a Renewable Resource Atlantic Cod, *Gadus morhua*, of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.* **51**(9)**:**2126-2146.

Hutchinson, W.F., Carvalho, G.R. and Rogers, S.I. (2001) Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. *Mar. Ecol. Prog. Ser.* **223:**251-260.

ICES (2010) Report of the ICES Advisory Committee 2010. *Book 6,* 309pp.

ICES (4-4-2012) Stock Assesment Summary/Standard Graph Database. *http://www.ices.dk/datacentre/StdGraphDB.asp*

Iles, T.D. and Sinclair, M. (1982) Atlantic Herring - Stock Discreteness and Abundance. *Science* **215**(4533)**:**627-633.

Juanes, F. (2007) Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. *J Fish Biol.* **70**(3)**:**661-677.

Kjorsvik, E., Vandermeeren, T., Kryvi, H., Arnfinnson, J. and Kvenseth, P.G. (1991) Early Development of the digestive tract of cod Larvae, *Gadus morhua* L, during start-feeding and Starvation. *J Fish Biol.* **38**(1)**:**1-15.

Krause, M., Dippner, J.W. and Beil, J. (1995) A Review of Hydrographic Controls on the Distribution of Zooplankton Biomass and Species in the North-Sea with Particular Reference to A Survey Conducted in January March 1987. *Prog. Oceanogr.* **35**(2)**:**81-152.

Kurlansky, M. (1998) *Cod: a biography of the fish that changed the world.* New York: Penguin Books, 294pp.

Legendre, P. (1993) Spatial Autocorrelation - Trouble Or New Paradigm. *Ecology* **74**(6)**:**1659-1673.

Leis, J.M. (1991) Vertical distribution of Fish Larvae in the Great Barrier Reef Lagoon, Australia. *Mar. Biol.* **109**(1)**:**157-166.

Lochmann, S.E., Taggart, C.T., Griffin, D.A., Thompson, K.R. and Maillet, G.L. (1997) Abundance and condition of larval cod (Gadus morhua) at a convergent front on Western Bank, Scotian Shelf. *Can. J. Fish. Aquat. Sci.* **54**(7)**:**1461-1479.

Loots, C., Vaz, S., Planque, B. and Koubbi, P. (2010) What controls the spatial distribution of the North Sea plaice spawning population? Confronting ecological hypotheses through a model selection framework. *Ices. J. Mar. Sci.* **67**(2)**:**244-257.

Lough, R.G. (2010) Juvenile cod (*Gadus morhua*) mortality and the importance of bottom sediment type to recruitment on Georges Bank. *Fish. Oceanogr.* **19**(2)**:**159-181.

Lough, R.G., Hannah, C.G., Berrien, P., Brickman, D., Loder, J.W. and Quinlan, J.A. (2006) Spawning pattern variability and its effect on retention, larval growth and recruitment in Georges Bank cod and haddock. *Mar. Ecol. Prog. Ser.* **310:**193-212.

Lough, R.G. and Potter, D.C. (1993) Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. *Fisher. Bull.* **91**(2)**:**281-303.

Lynam, C.P., Halliday, N.C., Höffle, H., Wright, P.J., van Damme, C.J.G., Edwards, M. and Pitois, S.G. (in prep.) Spatial patterns and trends in abundance of larval sandeels in the North Sea: 1950-2005 *ICES J Mar. Sci.*

Mantzouni, I. and MacKenzie, B.R. (2010) Productivity responses of a widespread marine piscivore, *Gadus morhua*, to oceanic thermal extremes and trends. *P. Roy. Soc. B-Biol. Sci.* **277**(1689)**:**1867-1874.

Marteinsdottir, G. and Begg, G.A. (2002) Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* **235:**235-256.

Marteinsdottir, G. and Steinarsson, A. (1998) Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. *J Fish Biol.* **52**(6)**:**1241-1258.

Matthäus, W. and Franck, H. (1992) Characteristics of major Baltic inflows - a statistical analysis. *Cont. Shelf Res.* **12**(12)**:**1375-1400.

Mcgurk, M.D. (1986) Natural Mortality of Marine Pelagic Fish Eggs and Larvae - Role of Spatial Patchiness. *Mar. Ecol. Prog. Ser.* **34**(3)**:**227-242.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J. and Zhao, Z.-C. (2007) Global Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., and Miller, H.L. (eds) Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press, Chap. 10

Miller, H.J. (2004) Tobler's First Law and spatial analysis. *Ann. Assoc. Am. Geogr.* **94**(2)**:**284-289.

Munk, P. (1997) Prey size spectra and prey availability of larval and small juvenile cod. *J Fish Biol.* **51:**340-351.

Munk, P., Fox, C.J., Bolle, L.J., van Damme, C.J.G., Fossum, P. and Kraus, G. (2009) Spawning of North Sea fishes linked to hydrographic features. *Fish. Oceanogr.* **18**(6)**:**458-469.

Munk, P., Larsson, P.O., Danielsen, D. and Moksness, E. (1995) Larval and Small Juvenile Cod *Gadus morhua* Concentrated in the Highly Productive Areas of A Shelf Break Front. *Mar. Ecol. Prog. Ser.* **125**(1-3)**:**21-30.

Munk, P., Larsson, P.O., Danielssen, D.S. and Moksness, E. (1999) Variability in frontal zone formation and distribution of gadoid fish larvae at the shelf break in the northeastern North Sea. *Mar. Ecol. Prog. Ser.* **177:**221-233.

Munk, P. and Nielsen, J. (2005) *Eggs and Larvae of North Sea Fishes.* Frederiksberg: Biofolia, 224pp.

Murua, H. and Saborido-Rey, F. (2003) Female reproductive strategies of marine fish species of the North Atlantic. *J Northwest Atl. Fish. Sci.* **33**(December)**:**23-31.

Nash, R.D.M., Wright, P., Matejusova, I., Dimetrov, S., O'Sullivan, M., Augley, J. and Höffle, H. (submitted) Spawning location of Norway pout (*Trisopterus esmarkii* Nilsson) in the North Sea. *Ices J. Mar. Sci.*

Neilson, J.D. and Perry, R.I. (1990) Diel Vertical Migrations of Marine Fishes - An Obligate Or Facultative Process. *Adv. Mar. Biol.* **26:**115-168.

Nielsen, T.G. and Munk, P. (1998) Zooplankton diversity and the predatory impact by larval and small juvenile fish at the Fisher Banks in the North Sea. *J. Plankton Res.* **20**(12)**:**2313-2332.

Nissling, A. (1994) Survival of eggs and yolk-sac larvae of Baltic cod (*Gadus morhua* L.) at low oxygen levels in different salinities. *ICES mar. Sci. Symp. 198,* pp. 626-631.

Nissling, A., Kryvi, H. and Vallin, L. (1994) Variation in Egg Buoyancy of Baltic Cod *Gadus morhua* and its Implications for Egg Survival in Prevailing Conditions in the Baltic Sea. *Mar. Ecol. Prog. Ser.* **110**(1)**:**67-74.

O'Boyle, R.N., Sinclair, M., Conover, R.J., Mann, K.H. and Kohler, A.C. (1984) Temporal and Spatial Distribution of Ichthyoplankton Communities of the Scotian Shelf in Relation to Biological Hydrological and Physiographic Features. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **183:**27-40.

Olivar, M.P. and Sabatés, A. (1997) Vertical distribution of fish larvae in the north-west Mediterranean Sea in spring. *Mar. Biol.* **129**(2)**:**289-300.

Otto, L. and Zimmerman, J.T.F. (1990) Review of the Physical Oceanography of the North Sea Part 1. General Review. *Neth. J. Sea. Res.* **26**(2-4)**:**163-193.

Otto, L., Zimmerman, J.T.F., Furnes, G.K., Mork, M., Saetre, R. and Becker, G. (1990) Review of the Physical Oceanography of the North-Sea. *Neth. J. Sea. Res.* **26**(2-4)**:**161-238.

Pearre, S. (2003) Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biol. Rev.* **78**(1)**:**1-79.

Perry, A.L., Low, P.J., Ellis, J.R. and Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science* **308**(5730)**:**1912-1915.

Pinnegar, J.K. and Stafford, R. (30-9-2009) DAPSTOM - An Integrated Database & Portal for Fish Stomach Records. Database version 1.5. Phase 1 Final Report. *http://www.cefas.co.uk/data/an-integrated-database-and-portal-for-fish-stomach-records-(dapstom)/prey-of-specified-predators.aspx*

Pitois, S.G. and Fox, C.J. (2008) Empirically modelling the potential effects of changes in temperature and prey availability on the growth of cod larvae in UK shelf seas. *Ices. J. Mar. Sci.* **65**(9)**:**1559-1572.

Planque, B. and Frédou, T. (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **56**(11)**:**2069-2077.

Raitt, D.F.S. (1967) Cod spawning in Scottish waters. Preliminary investigations. *ICES CM 1967/F:29,* 3pp. + 13 figures.

Rätz, H.J. and Lloret, J. (2003) Variation in fish condition between Atlantic cod (*Gadus morhua*) stocks, the effect on their productivity and management implications. *Fish. Res.* **60**(2-3)**:**369-380.

Reiss, C.S., Panteleev, G., Taggart, C.T., Sheng, J. and deYoung, B. (2000) Observations on larval fish transport and retention on the Scotian Shelf in relation to geostrophic circulation. *Fish. Oceanogr.* **9**(4)**:**377-377.

Righton, D., Quayle, V.A., Hetherington, S. and Burt, G. (2007) Movements and distribution of cod (*Gadus morhua*) in the southern North Sea and English Channel: results from conventional and electronic tagging experiments. *J. Mar. Biol. Assoc. UK* **87**(2)**:**599-613.

Riley, J.D. and Parnell, W.G. (1984) The distribution of young cod. *Flødevigen rapportser. 1,* pp. 563-580.

Rindorf, A. and Lewy, P. (2006) Warm, windy winters drive cod north and homing of spawners keeps them there. *J. Appl. Ecol.* **43**(3)**:**445-453.

Roberts, C. (2007) *The unnatural history of the sea.* Washington: Island Press, 435pp.

Rowlands, W.L., Dickey-Collas, M., Geffen, A.J. and Nash, R.D.M. (2008) Diet overlap and prey selection through metamorphosis in Irish Sea cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*). *Can. J. Fish. Aquat. Sci.* **65**(7)**:**1297-1306.

Saville, A. (1959) The planktonic stages of the haddock in Scottish waters. *Mar. Res.* **3:**1-23.

Schiermeier, Q. (2004) Climate findings let fishermen off the hook. *Nature* **428**(6978)**:**4-4.

Sclafani, M., Taggart, C.T. and Thompson, K.R. (1993) Condition, Buoyancy and the Distribution of Larval Fish - Implications for Vertical Migration and Retention. *J. Plankton Res.* **15**(4)**:**413-435.

Serchuck, F.M., Grosslein, M.D., Lough, R.G. and Mountain, D.G. (1994) Fishery and environmental factors affecting trends and fluctuations in the Georges Bank and Gulf of Maine Atlantic cod stocks: an overview. *ICES mar. Sci. Symp.* **198:**77-109.

Sinclair, M. and Tremblay, M.J. (1984) Timing of Spawning of Atlantic Herring (*Clupea harengus harengus*) Populations and the Match-Mismatch Theory. *Can. J. Fish. Aquat. Sci.* **41**(7)**:**1055-1065.

Stenevik, E.K., Sundby, S. and Agnalt, A.L. (2008) Buoyancy and vertical distribution of Norwegian coastal cod (*Gadus morhua*) eggs from different areas along the coast. *Ices. J. Mar. Sci.* **65**(7)**:**1198-1202.

Stenseth, N.C., Jorde, P.E., Chan, K.S., Hansen, E., Knutsen, H., Andre, C., Skogen, M.D. and Lekve, K. (2006) Ecological and genetic impact of Atlantic cod larval drift in the Skagerrak. *P. Roy. Soc. B-Biol. Sci.* **273**(1590)**:**1085-1092.

Stige, L.C., Ottersen, G., Brander, K., Chan, K.S. and Stenseth, N.C. (2006) Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. *Mar. Ecol. Prog. Ser.* **325:**227-241.

Svedäng, H. and Svenson, A. (2006) Cod *Gadus morhua* L. populations as behavioural units: inference from time series on juvenile abundance in the eastern Skagerrak. *J Fish Biol.* **69:**151-164.

Taylor, M.I., Fox, C., Rico, I. and Rico, C. (2002) Species-specific TaqMan probes for simultaneous identification of (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.) and whiting (*Merlangius merlangus* L.). *Mol. Ecol. Notes* **2**(4)**:**599-601.

Thompson, B.M. and Riley, J.D. (1981) Egg and larval development studies in the North Sea cod (*Gadus morhua* L.). *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **178:**553-559.

Tobler, W.R. (1970) A Computer Movie Simulating Urban Growth in Detroit Region. *Economic Geography* **46**(2)**:**234-240.

Townsend, D.W. and Pettigrew, N.R. (1996) The role of frontal currents in larval fish transport on Georges Bank. *Deep-Sea Res. (2 Top. Stud. Oceanogr.)* **43**(7-8)**:**1773-1792.

Tupper, M. and Boutilier, R.G. (1995) Size and Priority at Settlement Determine Growth and Competitive Success of Newly Settled Atlantic Cod. *Mar. Ecol. Prog. Ser.* **118**(1-3)**:**295-300.

Uzars, D. and Plikshs, M. (2000) Cod (*Gadus morhua* L.) cannibalism in the Central Baltic: interannual variability and influence of recruit abundance and distribution. *Ices. J. Mar. Sci.* **57**(2)**:**324-329.

Van Leeuwen, A., De Roos, A. and Persson, L. (2008) How cod shapes its world. *J. Sea. Res.* **60**(1-2)**:**89-104.

Woodhead, P.M.J. (1966) The behaviour of fish in relation to light in the sea. *Oceanogr. Mar. Biol. Annu. Rev.* **4:**337-403.

Wright, P.J., Neat, F.C., Gibb, F.M., Gibb, I.M. and Thordarson, H. (2006) Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *J Fish Biol.* **69:**181-199.

Appendix

Paper I

Höffle, H., Fox, C., Lelièvre, S., Loots, C., Nash, R.D.M., Vaz, S., Wright, P. and Munk, P. (submitted (a)) Egg distribution of four common North Sea fishes - Local variation in spawning area usage. *Fish. Oceanogr*. 28pp.

Paper II

Höffle, H., van Damme, C.J.G., Lelièvre, S., Loots, C., Vaz, S. and Munk, P. (submitted (b)) Egg distribution of four common North Sea fishes - Hydrographic and geographic influence on distribution. *Fish*. *Oceanogr*. 31pp.

Paper III

Höffle, H., Nash, R.D.M., Falkenhaug, T. and Munk, P. (submitted (c)) Differences in vertical distribution of larval fishes in relation to hydrography and prey. *Mar*. *Biol*. *Res*. 25pp.

Paper IV

Höffle, H. and Munk, P. (manuscript) Distribution of juvenile cod settlement sites in the North Sea during the period 1991 to 2010. 29pp.

Paper I

Running title: Variation in fish egg distribution in North Sea

Egg distribution of four common North Sea fishes – Local variation in spawning area usage

HANNES HÖFFLE[1*], CLIVE FOX[2], STÉPHANIE LELIÈVRE[3], CHRISTOPHE LOOTS[3], RICHARD D. M. NASH[4], SANDRINE VAZ[3], PETER J. WRIGHT[5] AND PETER MUNK[1]

[1]DTU Aqua, National Institute of Aquatic Resources, Technical University of Denmark, Kavalergården 6, DK-2920 Charlottenlund, DENMARK
[2]Scottish Association for Marine Science, Scottish Marine Institute, Oban, PA37 1QA, UK
[3]Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), Laboratoire Ressources Halieutiques, 150 quai Gambetta, BP699, F-62321, Boulogne sur Mer, France
[4]Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway.

[5]Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen, Scotland, AB11 9DB

**Correspondence.* e-mail: hhoe@aqua.dtu.dk

Abstract

The location and diversity of spawning areas is a key element in the life strategy of fish. Their offspring are under strong environmental influence, hence climate driven changes in conditions at the spawning and nursery grounds are likely to affect recruitment to the fish stocks. Here we investigate the variability in spawning ground conditions and use, comparing the hydrography and egg distribution of common North Sea fishes from surveys in 2004 and 2009. The analysis revealed little change in the overall hydrographic structure and distributional patterns of early life stages of cod (*Gadus* *morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and plaice (*Pleuronectes platessa*), between the two years of investigation. Likewise comparison to earlier studies indicated quite persistent spawning strategies. However, overall egg abundance and patchiness varied between the two years, most pronounced in the Southern Bight. Observations also illustrated differential progress of spawning activity, as the abundance of a given development stage differed significantly between the spawning grounds. The observed regional variation in the distribution between 2004 and 2009 suggested, however, some adjustment of timing of spawning to accommodate to prevailing hydrographic conditions.

Keywords: Fish eggs, Gadidae, *Pleuronectes platessa*, Early life, Geographical distribution

Introduction

Studies of spawning distributions of important commercial fish species such as cod in the North Sea generally suggest a persistent use of specific spawning areas over time (e.g. Brander, 1994; Daan, 1981; Raitt, 1967). Such stability has likely evolved to ensure that on average offspring enter suitable environmental conditions in a sufficient number of years to ensure reproductive success, thus promoting survival chances of the offspring. Areas where enrichment, concentration and retention in favourable conditions co-occur have been termed ‘ocean triads’ (Bakun, 1996). On the scale of the entire North Sea, it has been suggested that these areas are spatially stable over years and thus revisited by spawning fish (Cushing, 1990; Fox *et al.*, 2008). Primary and secondary productivity at ocean fronts is often also enhanced, compared with surrounding waters, so these areas may provide favourable feeding conditions for fish larvae (Munk, 2007). The North Sea with a combination of high tidal amplitudes and shallow areas (e.g. Dogger Bank) contains many tidal fronts (Pingree and Griffiths, 1978). Compared to temperature or salinity fronts, tidal fronts are stable over time. However, the importance of tidal fronts is greatest in summer, when these fronts break up the thermal stratification (Brown *et al.*, 1999), while many commercially important species spawn in late winter and early spring (Munk and Nielsen, 2005). In this period, salinity fronts have greater importance, particularly in the Regions Of Freshwater Influence (ROFI;

Simpson *et al.*, 1993) where the saline offshore water mixes with the outflows from Western Europe's major river systems. The location and intensity of these fronts might be more variable compared with tidal fronts since they are affected by variations in precipitation. Predictions of the Intergovernmental Panel on Climate Change (IPCC, Meehl *et al.*, 2007) suggest that the North Sea may experience both rising temperatures and a greater amount of freshwater runoff. Hence environmental conditions of spawning grounds might be changing and it is important to monitor the performance of the major spawning grounds over time, at least periodically.

In order to assess the extent of spawning areas in the North Sea and the potential linkage to frontal hydrography a North Sea wide international survey under the auspices of ICES was conducted in 2004. As well as mapping the distribution of all species caught (ICES, 2007), analyses from this survey compared the distribution of stage I cod eggs with the historic spawning grounds (Fox *et al.*, 2008) and investigated the relation between spawning locations and hydrography (Munk *et al.*, 2009). Spawning was shown to occur mostly near fronts while the peak egg abundances were located at the fronts themselves. A subsequent survey in 2009 made a second coverage of the North Sea, allowing comparison over a shorter period than between previous studies. In the present paper we examine the spawning distribution of four common, commercially important, species for spatial stability and whether spawning occurs aggregated or in several patches within each spawning ground. We describe the distribution of fish eggs across the North Sea in the surveys of 2004 and 2009 and compare the distribution with historical reports. While the observed hydrography is described, its relationship to egg distribution is statistically tested in a sibling study (Höffle *et al.*, submitted). Here we test for differences in the non-zero abundance induced by species, development stage, sampling and spawning ground.

Materials and Methods

Field sampling and egg identification

Sampling was conducted by five participating countries either during the annual International Bottom Trawl Survey for the first quarter (IBTS 1Q) or in dedicated surveys between the 16th February and 23rd of March 2004 and between the 17th of January and 6th of March 2009 (Table 1).

The samples were taken with Gulf III (Gehringer, 1962; Nellen and Hempel, 1969) and VII (Nash *et al.*, 1998), BONGO (Posgay and Marak, 1980) and WP2 (Fraser, 1968; UNESCO, 1968) nets, covering the entire North Sea from 51.5°N to 62°N. The Gulf and BONGO Nets were deployed in double oblique hauls, while the WP2 was deployed in vertical trawls, in both cases down to five metres above sea bottom or a maximum of 100 m depth. Deployment lasted at least 10 minutes with multiple hauls ensuring the minimum deployment time in shallow water (ICES, 2008). To determine cod-like eggs to species level, single eggs without oil globules and diameters of 1.1-1.75 mm (Fox *et al.*, 2008) or 0.97-1.89 mm (Lelièvre *et al.*, 2010) were fixed for later genetic analysis, either in 96% ethanol (Fox *et al.*, 2008; Taylor *et al.*, 2002) or in buffered 0.864% formalin/seawater Solution (Lelièvre *et al.*, 2010).

Table 1: Survey cruises for this study. For the BONGO nets only the mesh size for the samples used in the analysis is given.
Abbreviations: add. IBTS = Additional IBTS-Sampling, IHLS = International Herring Larvae Surveys, PLACES = Plaice and Cod Egg Surveys, PGEGGS = Planning Group on North Sea Cod and Plaice Egg Surveys

Year	Country	Survey	Ship	Start Date	End Date	Gear	Mesh (µm)	Nos. Hauls
2004	NL	PLACES	Tridens II	1.3.04	4.3.04	Gulf VII	270	41
	DE	PLACES	Heinke	16.2.04	23.2.04	BONGO	500	40
	UK	PLACES	Corystes	18.2.04	8.3.04	Gulf VII	270	134
	DK	PLACES	Dana	25.2.04	6.3.04	BONGO	330	92
	NO	PLACES	H. Mosby	8.3.04	23.3.04	Gulf III	330	86
2009	SC	PGEGGS	Scotia	20.2.09	6.3.09	BONGO	350	53
	FR	add. IBTS	Thalassa	17.1.09	13.2.09	WP2	500	103
	NO	add. IBTS	G. O. Sars	8.2.09	21.2.09	Gulf VII	280	59
	NL	IHLS	Tridens II	19.1.09	22.1.09	Gulf VII	280	83
	DK	add. IBTS	Dana	31.1.09	17.2.09	BONGO	330	68

In the laboratory, subsamples of at least a 100 eggs in the desired size range (>1.16 mm; Russel, 1976) were staged and determined to the lowest possible taxonomic level (Ryland et al., 1975; Thompson and Riley, 1981). The preserved eggs were identified either with TaqMan probes (Fox et al., 2008 - Taylor et al., 2002) or cytochrome b PCR – RFLP (Lelièvre et al., 2010). Accuracy of TaqMan probes is >98% for cod, haddock and whiting (Taylor et al., 2002) while compared to visual identification the cytochrome b PCR-RFLP was 98% accurate for cod and 71% accurate for whiting (Lelièvre et al., 2010). The obtained proportion of cod, haddock and whiting was used to apportion the visually identified cod-like eggs to the species. In 2004, cod-like eggs in samples for which no proportion could be established were apportioned according to a multinomial Generalized Additive Model (GAM) over the whole survey area (Fox et al., 2008). In 2009 a simpler procedure was used by apportioning them according to the average proportion for other stations in the same ICES square. Density of fish eggs, in Nos. m^{-2}, was calculated by dividing the numbers caught by the filtered volume and multiplying with the sampled depth and the raising factor. For statistical analysis the non-zero abundances were log-transformed.

Hydrography and Geostatistics

Hydrographic data was obtained from CTD hauls during the surveys and augmented with data from the ICES oceanographic data base (ICES, 2009). Data sets containing erroneous pressure measurement, temperatures (<0°C or >11°C) and salinities (<20 or >37) were excluded from further analysis, while the retained values were used to calculate density as σ_t (kg m^{-3}-1000) according to UNESCO standards (Millero and Poisson, 1981). For each hydrographic variable at three depths (5 m, 20 m and bottom), an experimental variogram was calculated in Surfer 8 (Golden Software, 2002), based on the equation (Webster and Oliver, 2001):

$$\gamma(h) = \frac{1}{2 \times n(h)} \times \sum [z(x+h) - z(x)]^2 \qquad (1)$$

Where *n(h)* is the number of pairs of observation for the distance *h, z(x)* is the observed value for the respective hydrographic variable at a given location *x, h* is the distance calculated from latitude and longitude and $\gamma(h)$ is the resulting experimental variogram. A theoretical variogram $\gamma' = F_{(\gamma)}$ was fit to the data based on a linear model with least square regression. Using that theoretical variogram, the hydrographic data was interpolated by ordinary kriging on a regular grid of 0.25 by 0.25 decimal degrees (dec. deg.). These grids were used to calculate the horizontal density gradient in g m^{-3} per nautical mile (NM^{-1}, =1.852 km^{-1}) with the formula (Golden Software, 1999):

$$\|\vec{g}\| = \sqrt{\left(\frac{Z_E - Z_W}{2\Delta x}\right)^2 + \left(\frac{Z_N - Z_S}{2\Delta y}\right)^2} \qquad (2)$$

where $\vec{g}$ is the density gradient, Z_E and Z_W are adjacent grid points in East-West direction, Z_N and Z_S are adjacent grid points in North-South direction, and Δx and Δy are the distances in longitudinal and latitudinal direction, respectively.

To graphically compare the distribution of eggs in 2004 the log(n+1)-transformed abundance data, including zero values, was similarly treated in R. The best fitting theoretical variograms were chosen between Gaussian, spherical, exponential, linear, hole-effect or Bessel models. Coverage in 2009 alone was too poor for sensible kriging results.

Statistical analysis

The log-transformed non-zero abundance was examined for significant differences in a multivariate ANOVA with the factors; species, spawning area, stage, year and sampling gear. For the description of larger areas of spawning we used the so-called roundfish areas (Fig. 1; ICES, 2010a). The roundfish areas 1, 2 and 6 were kept as such, representing the spawning areas east of the Shetland Isles, the northern part of Dogger Bank and the German Bight with the southeast of Dogger Bank, while the roundfish areas 7, 8 were merged to represent the Skagerrak and the Fisher Banks. The east coast of Britain was covered by merging the areas 3, 4 and 5, including the spawning area in the Moray Firth and the probably defunct spawning area off Flamborough (Fox *et al.*,

2008) as well as the Southwest of Dogger Bank. Although these aggregated areas are based on the known spawning areas for cod, they also include the hotspots of spawning for plaice (Loots *et al.*, 2010a), whiting (Loots *et al.*, 2011) and haddock (Heath and Gallego, 1998). Since, except for the years, all variables had more than two categories, Tukey's test was conducted post-hoc to determine which of the categories were significantly different.

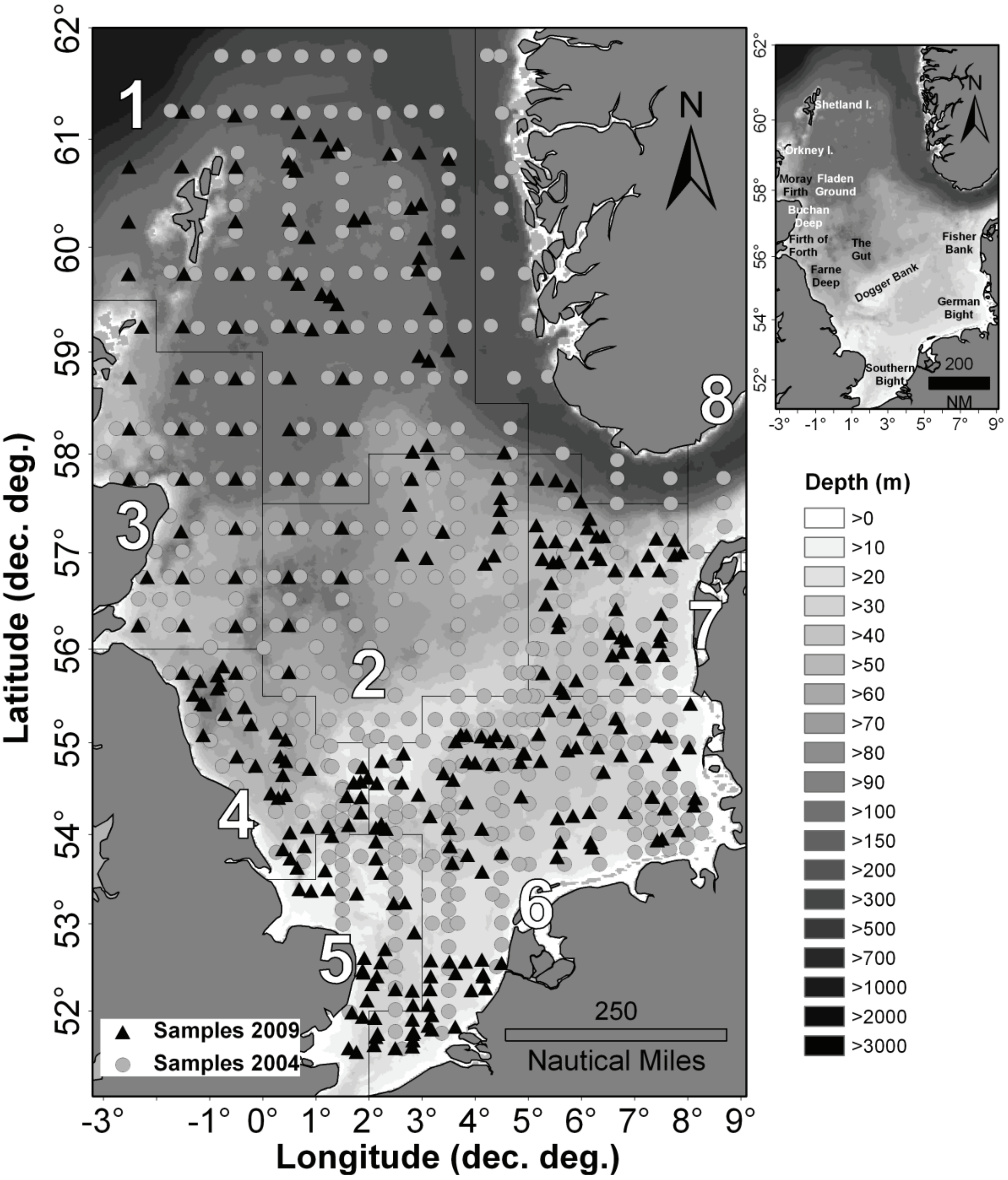


Figure 1: Sampling positions, in 2004 (grey circles) and in 2009 (black triangles). The underlying contour map shows the topography of the North. Lines delineate the ICES roundfish areas, numbered counter clockwise 1 to 8. The inset map names prominent undersea features, which are important fishing and/or spawning grounds.

Results

Hydrography

Temperature and salinity were generally homogenous throughout the water column and decreased from North to South (Fig. 2). In 2004 offshore waters were relatively warm (>7^{o}C) with salinities above 34.4, along the eastern margins waters were substantially cooler and fresher. In 2009, water in the northern North Sea was slightly warmer (0.4^{o}C) and more saline but extended only as far south as Flamborough. The more prominent differences between 2004 and 2009 were along the eastern margins of the North Sea, where water in the German Bight was more than 1^{o}C colder and more saline than in 2004. Temperatures below 5^{o}C extended also further eastwards in 2009. The horizontal density gradient (Fig. 2E, F) was mainly driven by salinity. The strongest density gradients were along the eastern margins with peak values above 2.3 g m^{-3} NM^{-1}. Along the Norwegian coast the density gradient between coastal and oceanic water was steeper in 2009 and peaked further offshore than in 2004. Between the German Bight and the central North Sea the peak density gradient also occurred further offshore in 2009, but it was not as strong as in 2004.

Egg distribution

Eggs of all four species (cod, haddock, whiting and plaice) combined showed the highest abundance in and adjacent to the German Bight, between the Orkney and Shetland Isles and to the East of the Shetland Isles (Figs 4C, D). In 2009 the highest egg abundances were found in the Southern Bight in contrast to 2004. While abundances averaged over the whole North Sea were similar between years, the distribution in 2009 was patchier with high densities in more restricted areas.

Plotted against the latitude (Figs 5A, B), the egg abundances for all stages combined exhibited similar patterns between the years, peaks occurred at the latitudes of all the major spawning areas, e.g. at 58^{o}N for the Moray Firth or at 60^{o}N reflecting the concentration near the Shetland Isles. The most striking difference, were the over 200 eggs m^{-2} in the Southern Bight (ca. 53^{o}N) in 2009.

The distribution patterns of individual species differed. Cod, which was the only gadoid fish spawning over the whole North Sea, had egg centres in the Southern Bight and east

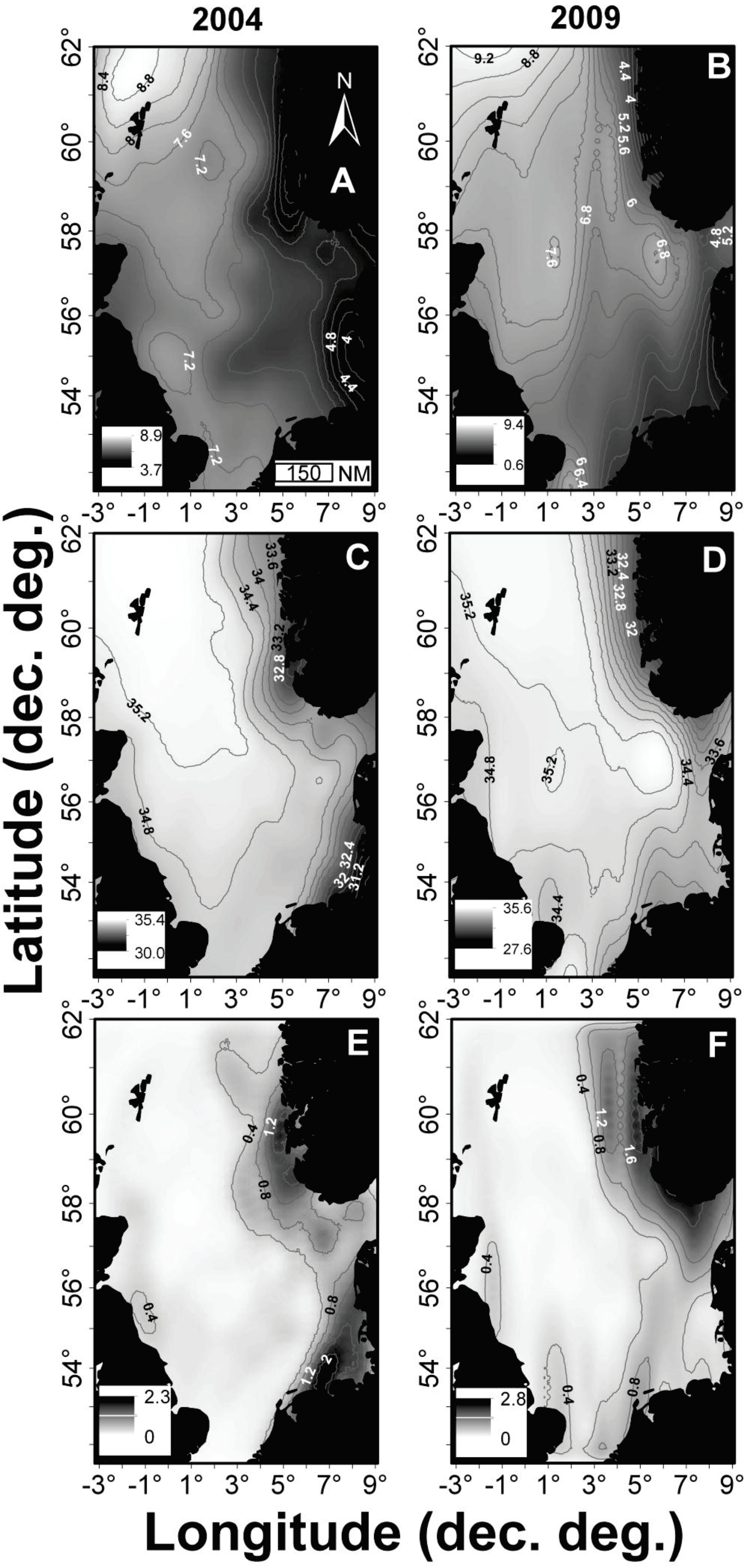


Figure 2: Hydrography for 2004 and 2009. Panels A and B represent the average surface temperature (°C) for the respective sampling periods. Panels C and D show the average salinity at 20 m depth and E and F the average density gradient (g m^{-3} NM^{-1}) at 20 m. For temperature and salinity lighter shades represent higher values, while for the gradient dark shades represent higher values.

of the Shetland Isles in 2009 (Fig. 3B), while the southern centre of egg abundance was in the German Bight and at the Dogger Bank in 2004 (Fig. 3A). The krigged log(n+1)-transformed abundances for 2004 exhibited highest abundances for stage I (2.1 m^{-2}) and persistent centres in the German Bight and at the Dogger Bank while high abundances around the Orkney and Shetland Isles were found mostly for the later stages (Fig. S1). Position and size of these abundance centres did not substantially differ between the stages, except for stage V where high and medium abundances contracted to small areas. Cod egg abundances along the east coast of England, were always low.

Haddock was hardly ever found south of 56^{o}N and had clear centres of abundance off the Orkney and Shetland Isles and the Moray Firth (Figs 3C, D). The maximum log-abundances were at 2.1 m^{-2} for stage IV. The extent of centres of abundance was more or less stable over all stages, while the medium abundances contracted continuously from stage I to V (Fig. S1). Whiting had two centres for all stages, one east of the Shetland Isles and the second between the English coast and the Dogger Bank (Figs 3E, F; S1). The one in the North was more prominent for the later stages, while it was the opposite for the South. The peak abundances were measured for stage I (2.6 m^{-2}).

Plaice spawning was centred on Moray Firth, the German and the Southern Bight in both years (Figs 4A, B), with very low abundances elsewhere. Plaice eggs in 2004 were more dispersed than the eggs of other species, with peak abundances between 1.5 m^{-2} and 1.9 m^{-2} which were overall lower than in the other species. While the distribution of the early development stages was homogenous, stages IV and V exhibited a distribution more similar to the other species, with several patches of high density off the Dutch and Danish coasts and otherwise medium or low densities (Fig. S1).

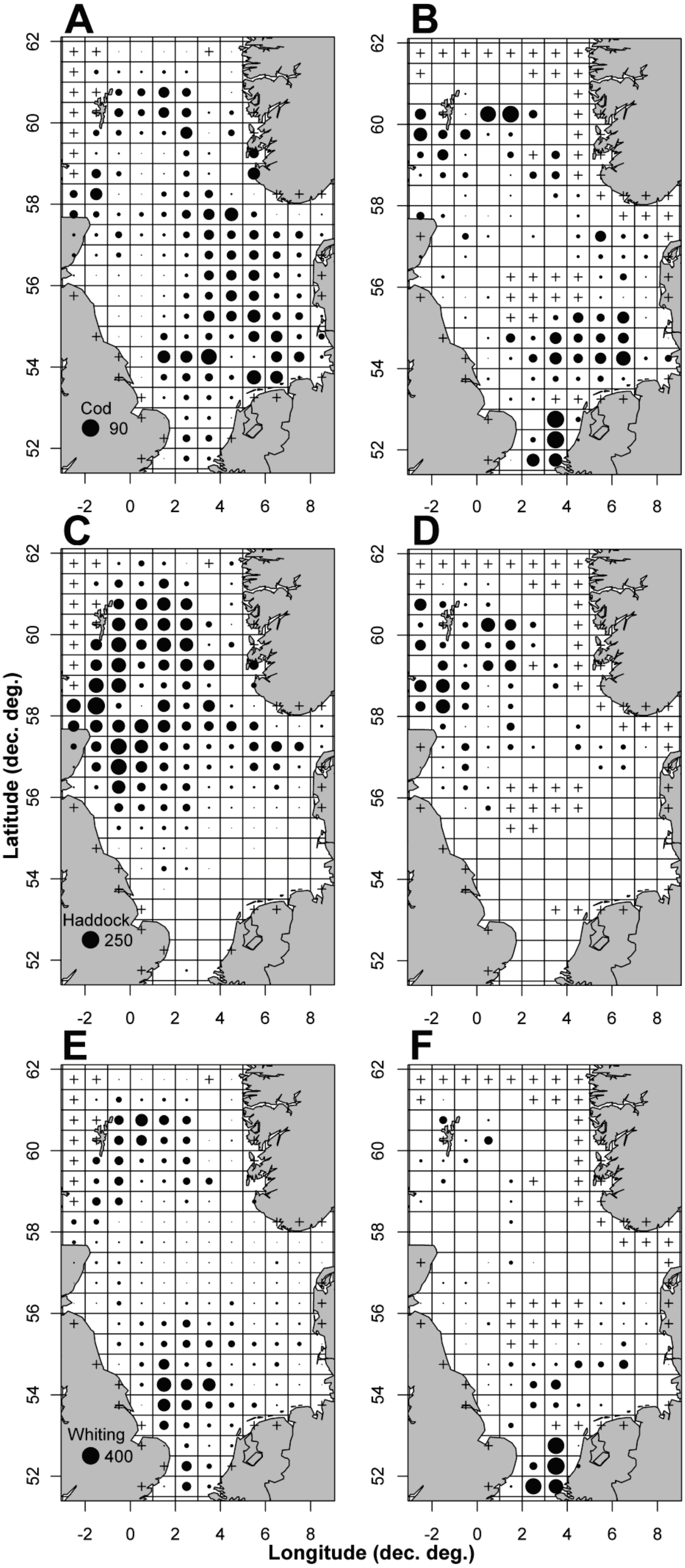


Figure 3: Abundance of fish eggs (Nos. m^{-2}) for the gadoid fishes. The left panels are for 2004, the right panels for 2009. The reference dot in each panel represents the next higher multiple of ten to the peak abundance of both years. Empty ICES rectangles were sampled without result, while rectangles marked with a cross were not sampled in the respective year.

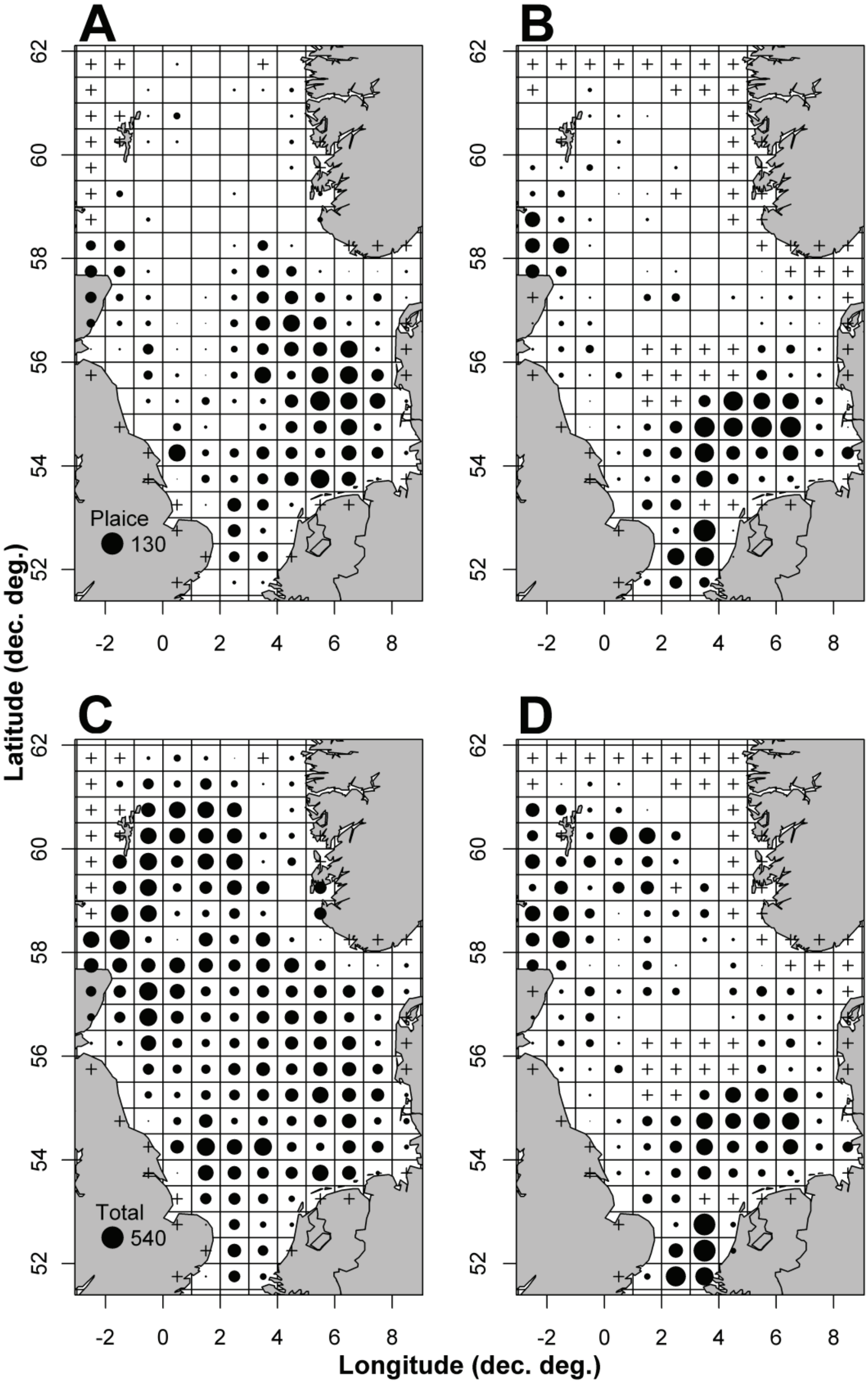


Figure 4: Abundance of fish eggs (Nos. m^{-2}) for plaice and all four species combined. The left panels are for 2004, the right panels for 2009. The reference dot in each panel represents the next higher multiple of ten to the peak abundance of both years. Empty ICES rectangles were sampled without result, while rectangles marked with a cross were not sampled in the respective year.

Relation to environmental conditions

Eggs were primarily found in water less than 200 m deep (Figs 5C, D), with highest abundances in areas with bottom depths of 30-40 m in 2009 and around 100 m in 2004. This difference was mostly due to the high abundances in the Southern Bight in 2009. Whiting contributed most to the peak at 30-40 m while haddock was most abundant at >80 m bottom depth and cod was abundant in 100-150 m too, more so in 2009 than in 2004. Similar to whiting, plaice eggs were mostly found in waters of less than 50 m.

In 2004 highest egg abundances were found in water of 5.5-8.5^{o}C, while in 2009 they were mostly between 4 and 6^{o}C, (Figs 6A, B). Whiting exhibited the strongest difference between the years with peak abundances at ~8^{o}C in 2004 and in the 4-6^{o}C range in 2009. Haddock was abundant between 6.5^{o}C and 8.5^{o}C in both years and was close to zero densities in lower temperatures. Cod was most abundant between 4 and 6^{o}C in both years and plaice was restricted to the same range with almost zero abundance outside.

Below a salinity of 32, egg densities were low in both years (Figs 6C, D). Highest abundances were between salinities of 34 and above 35. Haddock was at highest abundances in salinities above 35 while all the other species peaked in the 34-35 salinity range. Distribution over the density gradient was similar between the years with most eggs in gradients between 0.5 and 1.5 g m^{-3} NM^{-1} (Figs 6E, F), again mostly due to whiting, while cod preferred the higher range above 2 g m^{-3} NM^{-1} and haddock the lowest gradients around 0.25 g m^{-3} NM^{-1}. Plaice was evenly distributed across the range and apart from cod was the only species abundant >2 g m^{-3} NM^{-1}.

Statistical analysis

The overall non-zero abundance was significantly ($p<0.001$ overall) influenced by all of the factors and by all 2-factorial interactions (Table 2). In post-hoc Tukey's test, significant differences were found between all species and all spawning areas, except the area in the central North Sea (round fish area 2) and the east coast of Britain (roundfish areas 3, 4 and 5; $p=0.986$). When examining the interaction of species and spawning in roundfish area 6, containing the German Bight, the eastern part of the Southern Bight and the Southeast of Dogger Bank, exhibited significantly higher abundances for cod and plaice. No other spawning areas were significantly different for these species. Conversely, haddock exhibited significant differences between all spawning areas, except the Shetland Isles area (roundfish area 1) and the Skagerrak/Fisher Banks area (roundfish areas 7 and 8). Contrary to all other species its abundance was the lowest in roundfish area 6. In case of whiting, neighbouring areas were never significantly different and the highest abundances were found in roundfish area 6.

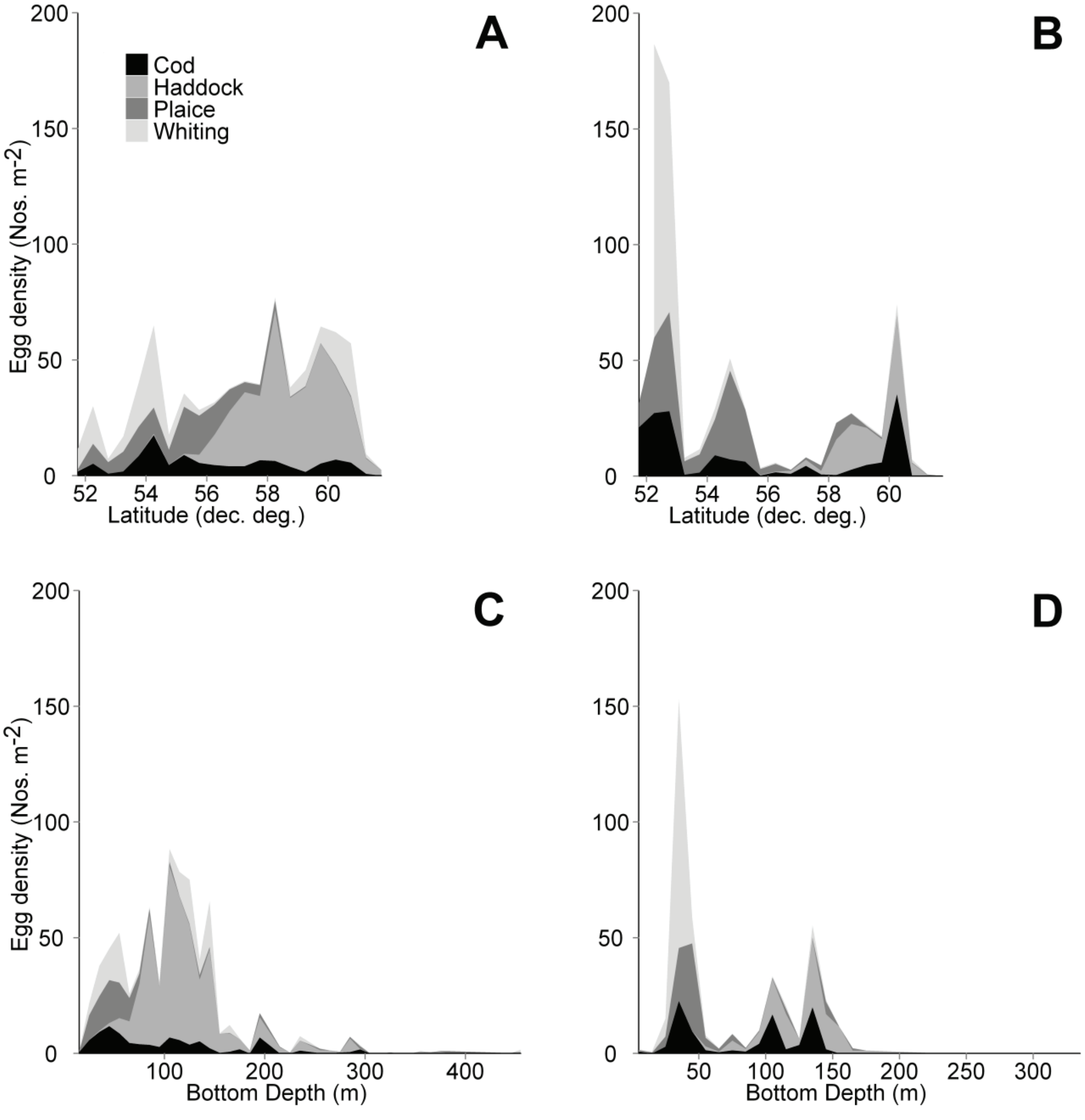


Figure 5: Average density of fish eggs (Nos. m^{-2}) compared to latitude (decimal degrees) and bottom depth (m). The left column is for 2004, the right column for 2009.

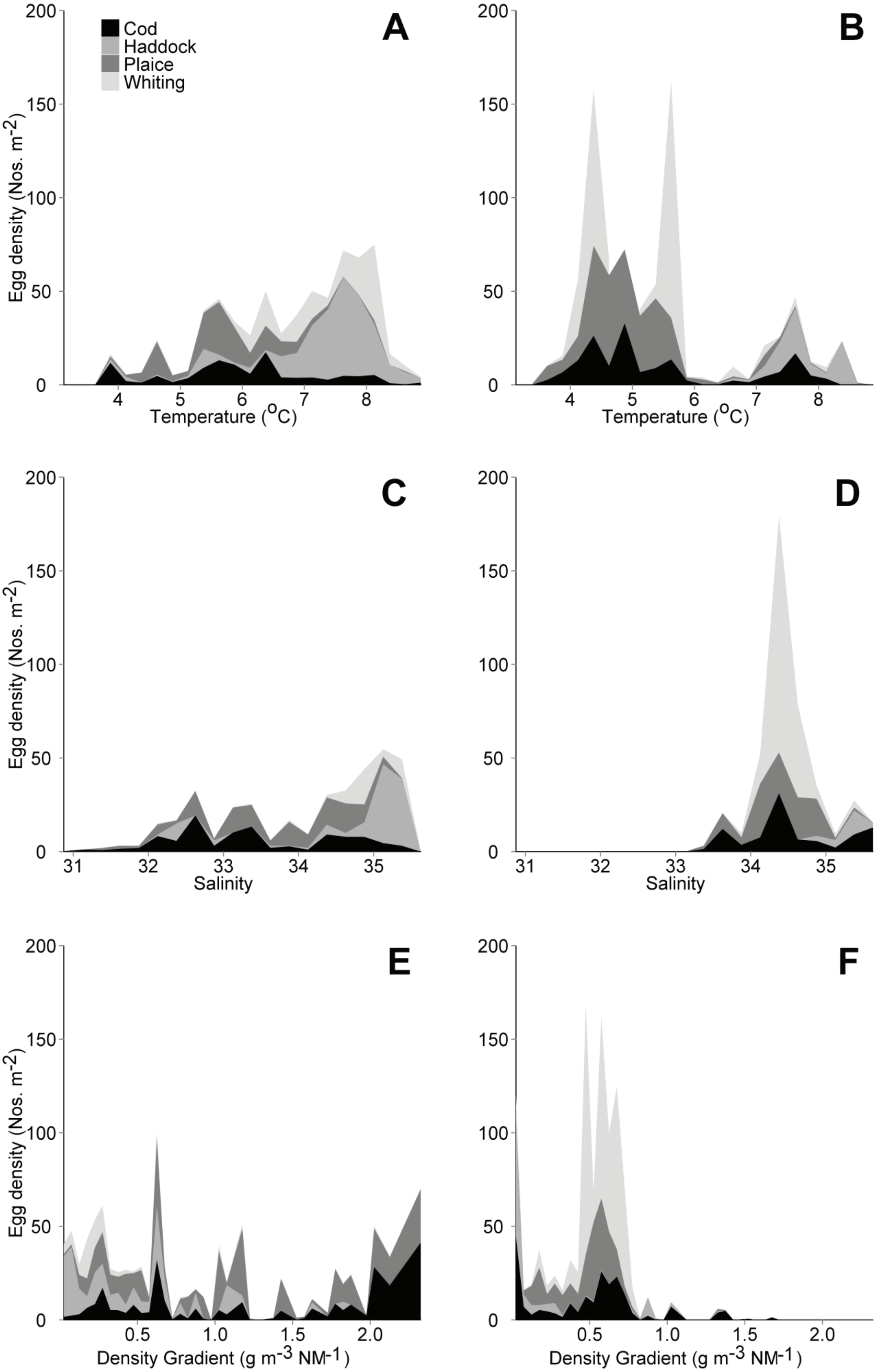


Figure 6: Average density of fish eggs (Nos. m^{-2}) compared to hydrographic indicators. The left column is for 2004, the right column for 2009.

The abundances of stages I and II eggs were significantly different to each other and the other stages, except II and V (p=0.228). The later stages III-V exhibited no significant difference among them in any of the species. The interaction between egg stage and spawning area exhibited significant differences between roundfish area 2 and areas 1 and 6. These differences occurred in all stages. For most development stages the highest and lowest abundances were found in the same spawning area than for all stages combined. The 3-factorial interaction of species, stage and spawning area was not significant (p=0.896).

Abundances were highly significantly different (p<0.001) between the years and the different sampling gears, except BONGO and GULF VII (p=0.082).

Table 2. Results of multi-factorial ANOVA on the abundance of fish eggs. Asterisks denote significant differences.

Factors	Df	Sum Sq.	Mean Sq.	F	P	
Species	3	334.60	111.52	217.04	<0.001	*
Stage	4	93.10	23.28	45.31	<0.001	*
Spawning area	4	218.20	54.55	106.15	<0.001	*
Year	1	22.00	22.03	42.88	<0.001	*
Gear	3	139.20	46.45	90.31	<0.001	*
Species × Stage	12	21.30	1.78	3.46	<0.001	*
Species × Spawning area	12	324.90	27.07	52.69	<0.001	*
Stage × Spawning area	16	33.80	2.11	4.11	<0.001	*
Year × Gear	1	30.20	30.24	58.86	<0.001	*
Species × Stage × Spawning area	48	18.60	0.39	0.75	0.896	
Residuals	6286	3229.9	0.51			

Discussion

Our observations of four species of North Sea fishes, spawning in a few hotspots are consistent with historic spawning areas (Coull *et al.*, 1998; Gibb *et al.*, 2004; Heath *et al.*, 1994). The present observations of small areas with high egg densities reflect currently lower than maximum population sizes (ICES, 2010b), while the overall extent of spawning areas is similar to the extent when population sizes were larger than now (Brander, 1994; Daan, 1978). Neither has the hydrographic structure changed much, compared to what has been observed earlier (Otto and Zimmerman, 1990).

Hydrography and egg distribution

Compared to Otto and Zimmerman (1990) the hydrography in 2009 was remarkably similar to the figures shown in their review which were based on data from 1962. The marked difference between the two study years was the restriction of fresher water to the German Bight in 2004. This was not an effect of different sampling periods, as a comparison for the same calendar days showed. Egg densities were highest in the historic spawning areas described in Fox *et al.* (2008) and earlier literature (Brander, 1994; Daan, 1978). The main difference between 2004 and 2009 was in the Southern Bight. There, egg densities were far higher in 2009, and patchiness in all the North Sea was higher in that year. The higher patchiness in 2009 may be attributed to the ~3 weeks earlier sampling period, than in 2004. The difference in egg abundance in the Southern Bight correlates with differences in hydrography as in 2009 water below a salinity of 34 was not confined to the German Bight. Likely, inflow from rivers in France, via the English Channel, and the Netherlands was higher in that year. This water was colder too, although the difference to 2004 was not so pronounced as was seen in the salinity. Additional sampling of fish eggs was carried out in the Southern Bight, the German Bight and the eastern English Channel (Lelièvre, 2010). Here, high abundances were shown for eggs of all species in the Southern Bight, in 2006 and 2008, but in 2007 to a lesser extent (Lelièvre *et al.*, in press). In 2006 water of low salinity was not restricted to the German Bight and the interface between fresh and saline water was well offshore, which resembles the situation in 2009. In 2007 the fresher water was similarly not restricted to the German Bight but the interface was closer to shore, which is likely to have resulted in higher turbidity, which previously has been identified as an important factor for cod (Brander, 1994). From the comparison of the years we deduce that a more seaward position of the boundary between freshwater influenced areas and marine water may attract more spawning fish to the area.

Our observations on cod egg distribution are consistent with Brander (1994) who identified the western-central North Sea (2^oW-2^oE and 52.3-56^oN) as a minor contributor to the spawning of cod, and the German and Southern Bights as major contributors in alternating periods, 1948-1956 and 1958-1972 respectively. In 2004 and 2009 the distribution of cod eggs was concentrated to a few patches in the Southern Bight, while in the German Bight it was highly dispersed, similar to what Brander (1994) described. He attributed the high concentration in the central Southern Bight mainly to water transparency, in contrast to other areas where cod seemingly do not avoid turbid waters. However, higher turbidity may indicate stronger currents and winds, transporting the eggs out of the Southern Bight, which would explain the low egg density without a different spawning behaviour of cod in this area. When analysed by development stages the areas with high abundance of cod eggs contracted over time, as currents in the southern North Sea dispersed the eggs at about 5 km d^{-1} (Brander, 1994) resulting in a transport of around a 100 km from spawning to hatching, based on temperature dependent egg development (Geffen *et al.*, 2006). Much of the cod fisheries in the North Sea currently take place in the northern North Sea, and catches of mature females are also high (Fox *et al.*, 2008). Yet, while high egg densities were found between the Shetland Isles and 2^{o}E, the egg densities east of that latitude did not match with what was predicted from the catches of mature cod.

For haddock, Thompson (1928) reported that the greatest concentration of spawning fish was observed on the plateau between the Orkney-Shetland Isles and Norway in depths >100 m, with concentrations east of the Moray Firth, Buchan Deep, Farne Deep, The Gut and Fisher Bank. Saville (1959) found widespread distribution of eggs over the whole of the northern North Sea from the Scottish coast to the Norwegian Deeps, with the exception of the Moray Firth and an area around the Fladen Ground (an exception also noted by Damas, 1909). The extent of haddock eggs found by Heath *et al.* (1994) in 1992 was comparable with that of Saville’s study, although eggs were concentrated further north and west (Fig. 5). A model study by Heath and Gallego (1998) estimated high egg production from mature fish for the Moray Firth, the Scottish east coast and between the Orkney and Shetland Isles, which is well reflected in the results of the two surveys. However their model did not exhibit high abundances to the immediate East of the Shetland Isles, which were present in 2004, 2009 and past egg surveys. On the other hand, high abundances south of the Moray Firth only occurred in 2004. In earlier plankton observations Heath *et al.* (1994) found a spatial segregation of late stage cod and haddock eggs, in colder North Sea water and on the warmer outer shelf respectively, which would fit with the preferences for different zones of a frontal system for larvae of different gadoid species (Munk *et al.*, 1999). The centres of egg abundance were more stable compared to other species, in area as well as in peak abundances. Dispersal was low, while the contraction of medium abundances can be explained by mortality in the early stages and a combination of mortality and dispersal in the later stages. Similarly, mature haddock abundance in first quarter surveys was stable with little change between the 1980s and 1990s (Hedger *et al.*, 2004).

It has been suggested that whiting has two stocks in the North Sea, one east of England and one east of the Shetland Isles (Gibb *et al.*, 2004) which would be consistent with our findings. Adults of whiting are known to prefer shallow water with temperatures between 6-9^{o}C (Loots *et al.*, 2011), which is also consistent with our observations. Whiting has a long spawning period lasting from February to June with increasingly later spawning at higher latitudes (Hislop, 1984). Assuming that the spawning period was not substantially different from 2004, the lack of significant egg densities east of the Shetland Isles in 2009 may thus be explained by the earlier sampling. However, when looking at the distribution pattern of single stages in 2004, this is not supported, as the early stages are more abundant in the South, while stage IV and V are the most abundant in the North. As temperatures decreased from North to South it may lead to the notion that spawning occurred earlier in the northern spawning area. However, this hydrographic situation is not unique to that year and therefore this explanation is in contrast to the observations of Hislop (1984) . A more likely explanation is that as whiting spawns in batches over a period between 1.5 and 2 months well into late spring (Hislop, 1984) we might just be seeing the beginning of a later spawning batch in the South, while in the North the previous batch is in the later stages.

The relatively homogenous distribution of plaice eggs in the German Bight and along the Danish coast, particularly in 2004, is a good representation of this species' large spawning area in the southern North Sea and English Channel (Metcalfe, 2006). Loots *et al.* (2010a) identified also Flamborough Head, Moray Firth and Firth of Forth as suitable areas for spawning adults which exhibited some abundance in the 2004 and 2009 surveys. The decrease in area with high abundance over the course of development from stage I to stage V may be due to the typically high mortality of fish eggs (Bunn *et al.*, 2000; Mcgurk, 1986; Pepin, 1991) showing its effect primarily on the edge of the area and in later stages dispersal may be important too.

Effects of species, stage and spawning area

A consistent result in the ANOVA is that the abundances of the later stages are not significantly different from each other for any of the species. This is probably due to differences in stage durations. For cod and plaice the shortest stages are II and IV with around 2 and 2.5 days respectively, (at 6°C; Fox *et al.*, 2003; Geffen *et al.*, 2006), while stages I, III and V are on the order of 3.5 to 5.5 days in duration. Longer stage duration extends the time during which the egg could be sampled or eaten. Overall the most common stage was stage I (IA, IB combined). A significantly lower number of eggs in the other stages of similar duration may be due to either the progress of egg development, or mortality due to various causes. The absence of significant difference between stages II and V may be due to a shorter duration of stage II and thus low numbers at any given time, while at stage V numbers might be lower, due to mortality. The relation between the stages III to V was mostly the same within the separate spawning areas, only in roundfish area 2 were the abundances of stages IV and V significantly different, while the abundances of any given stage were always significantly different between at least two spawning areas. Since abundant spawning was not confined to only one area, this result suggests different sub-populations with different progress of the spawning seasons, as was previously suggested for cod (Wright *et al.*, 2006).

The results for the interaction of species and spawning areas, are likewise interesting as for cod and plaice, the German Bight clearly stands out as different from all other areas. Although in 2009 abundances were higher in the Southern Bight, the abundances in the German Bight were high in both years indicating this area as the more important one over time, which compares well with literature (Brander, 1994; Harding and Nichols, 1987; Metcalfe, 2006). As plaice apparently prefers shallow water for spawning (Harding *et al.*, 1978; this study) this large shallow area is naturally attractive.

Inferring the spawning grounds from egg distribution alone unavoidably will include a degree of unobserved drift from the spawning site, particularly when including all stages. However, mapping the distribution of single stages has not shown substantial differences in their distributions. This indicates that drift has no major influence on the inference we make, but future work may include a combination with a drift model to make identification of spawning grounds even more accurate.

Outlook and Conclusions

Spawning locations presumably reflect a long term selection for areas from which sufficient offspring survive to sustain the population. The spawning locations of the species examined in the present study appear geographically relatively stable, while for some other species such as mackerel (*Scomber scombrus*) location of spawning appears quite variable (Beare and Reid, 2002). However, the cues which adult fish use to navigate to spawning areas are poorly understood. Arnold (1994) suggested a role of selective tidal stream transport in the spawning migration of cod in the southern North Sea. Species with relatively fixed spawning locations are more likely to be affected by changes in the hydrographic environment compared with a more flexible species such as mackerel. For species with fixed spawning locations we might expect climate change to lead to gradual changes in larval and juvenile survival at certain spawning locations. This can eventually appear as a range shift in the adult population but is the result of differential survival between spawning sites rather than re-location of adult fish (Andrews *et al.*, 2006).

Changes in the distribution of several of the North Sea fishes studied here are apparent from a number of recent studies. Rindorf and Lewy (2006) as well as Perry *et al.* (2005) have attributed these changes to climate change. Both studies used data from across the North Sea and inferred that changes in distribution reflect stock level changes. Such conclusions are opposed by other studies that saw evidence for population structuring, since apparent northward shifts in stock distribution could be explained by changes in local populations (Heath *et al.*, 2008; Holmes *et al.*, 2008; Neat and Righton, 2007). Other studies argued that the actual environmental conditions are rather unimportant compared to factors such as population size and geographical attachment (Loots *et al.*, 2010b). The present study tends to support the studies by Loots *et al.* (2010b; 2011) as it indicates that the distribution of eggs is similar to the spawning distribution in these studies and previous literature. While spawning always occurred in the previously described spawning areas, the centres of abundance, at least in the southern North Sea, varied between the years. Hence, fish may have a limited choice in selecting the spawning location, depending on the hydrographic conditions within a given spawning ground and year. If the overall hydrography of the North Sea changes due to warming or increased precipitation, this might affect spawning success and subsequent recruitment to the stock.

Acknowledgements

For the coordination of the surveys, to the Planning Group on North Sea Egg Surveys (PGEGGS), ICES. Captains and crews of the participating research vessels from Denmark, France, Germany, the Netherlands, Norway, Scotland and England. All the scientific staff of the participating institutes who sampled under winter conditions, worked for tedious hours in the laboratory, or both. Stéphanie Lelièvre, Christophe Loots and Sandrine Vaz received additional financial support from the INTERREG IV A France (Channel) – England cross-border European cooperation programme, co-financed by the European Regional Development Fund as part of the CHannel integrated Approach for marine Resource Management (CHARM) Phase 3 project.

References

Andrews, J.M., Gurney, W.S.C., Heath, M.R., Gallego, A., O'Brien, C.M., Darby, C. and Tyldesley, G. (2006) Modelling the spatial demography of Atlantic cod (*Gadus morhua*) on the European continental shelf. *Can. J. Fish. Aquat. Sci.* **63**(5)**:**1027-1048.

Arnold, G.P., Walker, M.G., Emerson, L.S. and Holford, B.H. (1994) Movements of Cod (*Gadus morhua* L.) in Relation to the Tidal Streams in the Southern North Sea. *Ices. J. Mar. Sci.* **51**(2)**:**207-232.

Bakun, A. (1996) *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics.* San Diego: University of California, 323pp.-

Beare, D.J. and Reid, D.G. (2002) Investigating spatio-temporal change in spawning activity by Atlantic mackerel between 1977 and 1998 using generalized additive models. *Ices. J. Mar. Sci.* **59**(4)**:**711-724.

Brander, K.M. (1994) The Location and Timing of Cod Spawning Around the British Isles. *Ices. J. Mar. Sci.* **51**(1)**:**71-89.

Brown, J., Hill, A.E., Fernand, L. and Horsburgh, K.J. (1999) Observations of a seasonal jet-like circulation at the central North Sea cold pool margin. *Est. Coast. Shelf. Sci.* **48**(3)**:**343-355.

Bunn, N.A., Fox, C.J. and Webb, T. (2000) A literature review of studies on fish egg mortality: Implications for the estimation of spawning stock biomass by the annual egg production method. CEFAS, *111,* 37pp.

Coull, K.A., Johnstone, R. and Rogers, S.I. (1998) Fisheries sensitivity maps in British Waters. United Kingdom Offshore Operators Association (UKOOA), Aberdeen, Scotland.

Cushing, D.H. (1990) Hydrographic Containment of a spawning group of plaice in the Southern Bight of the North Sea. *Mar. Ecol. Prog. Ser.* **58**(3)**:**287-297.

Daan, N. (1978) Changes in cod stocks and cod fisheries in the North Sea. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **172:**39-57.

Daan, N. (1981) Comparison of estimates of egg production of the Southern Bight cod stock from plankton surveys and market statistics. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **178:**242-243.

Damas, D. (1909) Contribution à la biologie des gadides. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **10:**1-227.

Fox, C.J., Geffen, A.J., Blyth, R. and Nash, R.D.M. (2003) Temperature-dependent development rates of plaice (*Pleuronectes platessa* L.) eggs from the Irish Sea. *J. Plankton Res.* **25**(11)**:**1319-1329.

Fox, C.J., Taylor, M., Dickey-Collas, M., Fossum, P., Kraus, G., Rohlf, N., Munk, P., van Damme, C.J.G., Bolle, L.J., Maxwell, D.L. and Wright, P.J. (2008) Mapping the spawning grounds of North Sea cod (*Gadus morhua*) by direct and indirect means. *P. Roy. Soc. B-Biol. Sci.* **275**(1642)**:**1543-1548.

Fraser, J.H. (1968) Zooplankton sampling. *Nature* **211:**915-916.

Geffen, A.J., Fox, C.J. and Nash, R.D.M. (2006) Temperature-dependent development rates of cod *Gadus morhua* eggs. *J Fish Biol.* **69**(4)**:**1060-1080.

Gehringer, J.W. (1962) The Gulf III and other modern high-speed plankton samplers. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **153:**19-22.

Gibb, F.M., Wright, P.J., Gibb, I.M. and O'Sullivan, M. (2004) Haddock and Whiting Spawning Areas in the North Sea and Scottish West Coast. Fishery Research Services, Internal Report, *11/04,* 11+figures pp.

Golden Software (2002) Surfer. (Version 8.00) Golden, CO: Golden Software, Inc.

Golden Software (1999) Grid Operations. In: *Surfer 7 User's Guide.* Golden: Golden Software, Inc., Chap. 16:pp. 361-414.

Harding, D. and Nichols, J.H. (1987) Plankton surveys off the north-east coast of England in 1976 An introductory report and summary of the results. Directorate of Fisheries Research, *MAFF-DFR-TR-86,* 56pp.

Harding, D., Nichols, J.H. and Tungate, D.S. (1978) The spawning of plaice (*Pleuronectes platessa*) in the southern North Sea and English Channel. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **172:**102-113.

Heath, M., Rankine, P. and Cargill, L. (1994) Distribution of Cod and Haddock Eggs in the North Sea in 1992 in Relation to Oceanographic Features and Compared with Distributions in 1952-1957 (Abstract). *ICES mar. Sci. Symp.* **198:**438-439.

Heath, M.R. and Gallego, A. (1998) Bio-physical modelling of the early life stages of haddock, *Melanogrammus aeglefinus*, in the North Sea. *Fish. Oceanogr.* **7**(2)**:**110-125.

Heath, M.R., Kunzlik, P.A., Gallego, A., Holmes, S. and Wright, P.J. (2008) A model of meta-population dynamics for North Sea and West of Scotland cod - The dynamic consequences of natal fidelity. *Fish. Res.* **93**(1-2)**:**92-116.

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A. and Andrews, J. (2004) Analysis of the spatial distributions of mature cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980-1999) using generalised additive models. *Fish. Res.* **70**(1)**:**17-25.

Hislop, J.R.G. (1984) A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the North Sea. In: *Fish reproduction: strategies and tactics.* Potts, G.W. and Wooton, R.J. (eds) Oxford: Academic Press, pp. 311-330.

Höffle, H., van Damme, C.J.G., Lelièvre, S., Loots, C., Vaz, S. and Munk, P. (submitted (b)) Egg distribution of four common North Sea fishes - Hydrographic and geographic influence on distribution *Fish. Oceanogr.* 31pp.

Holmes, S.J., Wright, P.J. and Fryer, R.J. (2008) Evidence from survey data for regional variability in cod dynamics in the North Sea and West of Scotland. *Ices. J. Mar. Sci.* **65**(2)**:**206-215.

ICES (2007) Results of the spring 2004 North Sea ichthyoplankton surveys. International Council for the Exploration of the Sea, ICES Cooperative Research Report, *No. 285,* 59pp.

ICES (2008) Report of the Planning Group on North Sea Cod and Plaice Egg Survey (PGEGGS), 13-14 May 2008, Lowestoft, UK. ICES, *ICES CM 2008/LRC: 07,* pp. 17-19.

ICES (13-11-2009) ICES Dataset on Ocean Hydrography. http://www.ices.dk/ocean/

ICES (2010a) Manual for the International Bottom Trawl Surveys. International Council for the Exploration of the Sea, *Revision VIII,* 73pp.

ICES (2010b) Report of the ICES Advisory Committee 2010. *Book 6,* 309pp.

Lelièvre, S. (2010) Identification and characterisation of winter spawning ground in the English Channel and Southern North Sea. Université de Nantes 334pp.

Lelièvre, S., Vaz, S., and Fox, C. (in press) The effectiveness of the Continuous Underway Fish Egg Sampler (CUFES) in the southern North Sea compared with standard vertical plankton hauls.

Lelièvre, S., Verrez-Bagnis, V., Jerome, M. and Vaz, S. (2010) PCR-RFLP analyses of formalin-fixed fish eggs for the mapping of spawning areas in the Eastern Channel and Southern North Sea. *J. Plankton Res.* **32**(11)**:**1527-1539.

Loots, C., Vaz, S., Koubbi, P., Planque, B., Coppin, F. and Verin, Y. (2010a) Inter-annual variability of North Sea plaice spawning habitat. *J. Sea. Res.* **64**(4)**:**427-435.

Loots, C., Vaz, S., Planque, B. and Koubbi, P. (2010b) What controls the spatial distribution of the North Sea plaice spawning population? Confronting ecological hypotheses through a model selection framework. *Ices. J. Mar. Sci.* **67**(2)**:**244-257.

Loots, C., Vaz, S., Planque, B. and Koubbi, P. (2011) Understanding what controls the spawning distribution of North Sea whiting (*Merlangius merlangus*) using a multi-model approach. *Fish. Oceanogr.* **20**(1)**:**18-31.

Mcgurk, M.D. (1986) Natural Mortality of Marine Pelagic Fish Eggs and Larvae - Role of Spatial Patchiness. *Mar. Ecol. Prog. Ser.* **34**(3)**:**227-242.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J. and Zhao, Z.-C. (2007) Global Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., and Miller, H.L. (eds) Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press, Chap. 10

Metcalfe, J. (2006) Fish population structuring in the North Sea: understanding processes and mechanisms from studies of the movements of adults. *J Fish Biol.* **69:**48-65.

Millero, F.J. and Poisson, A. (1981) International One-Atmosphere Equation of State of Seawater. *Deep-Sea Res. Pt. A* **28**(6)**:**625-629.

Munk, P., Fox, C.J., Bolle, L.J., van Damme, C.J.G., Fossum, P. and Kraus, G. (2009) Spawning of North Sea fishes linked to hydrographic features. *Fish. Oceanogr.* **18**(6)**:**458-469.

Munk, P., Larsson, P.O., Danielssen, D.S. and Moksness, E. (1999) Variability in frontal zone formation and distribution of gadoid fish larvae at the shelf break in the northeastern North Sea. *Mar. Ecol. Prog. Ser.* **177:**221-233.

Munk, P. and Nielsen, J. (2005) *Eggs and Larvae of North Sea Fishes.* Frederiksberg: Biofolia, 224pp.

Munk, P. (2007) Cross-frontal variation in growth rate and prey availability of larval North Sea cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* **334:**225-235.

Nash, R.D.M., Dickey-Collas, M. and Milligan, S.P. (1998) Descriptions of the Gulf VII/PRO-NET and MAFF/Guildline unencased high-speed plankton samplers. *J. Plankton Res.* **20**(10)**:**1915-1926.

Neat, F. and Righton, D. (2007) Warm water occupancy by North Sea cod. *P. Roy. Soc. B-Biol. Sci.* **274**(1611)**:**789-798.

Nellen, V.M. and Hempel, G. (1969) Versuche zur Fängigkeit des 'Hai' und des modifizierten Gulf-V- Plankton-Samplers 'Nackthai'/comparisons of the fishing efficiency of the Gulf III sampler 'Hai' and a modfied sampler 'Nackthai'. *Ber. Deut. Wiss. Komm. Meeresf.* **20:**141-154.

Otto, L. and Zimmerman, J.T.F. (1990) Review of the Physical Oceanography of the North Sea Part 1. General Review. *Neth. J. Sea. Res.* **26**(2-4)**:**163-193.

Pepin, P. (1991) Effect of Temperature and Size on Development, Mortality, and Survival Rates of the Pelagic Early Life History Stages of Marine Fish. *Can. J. Fish. Aquat. Sci.* **48**(3)**:**503-518.

Perry, A.L., Low, P.J., Ellis, J.R. and Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science* **308**(5730)**:**1912-1915.

Pingree, R.D. and Griffiths, D.K. (1978) Tidal Fronts on Shelf Seas Around British-Isles. *J. Geophys. Res. -Oc. Atm.* **83**(NC9)**:**4615-4622.

Posgay, J. and Marak, R.R. (1980) The MARMAP bongo zooplankton samplers. *J. Northwest Atl. Fish. Sci.* **1:**91-99.

Raitt, D.F.S. (1967) Cod spawning in Scottish waters. Preliminary investigations. *ICES CM 1967/F:29,* 3pp. + 13 figures.

Rindorf, A. and Lewy, P. (2006) Warm, windy winters drive cod north and homing of spawners keeps them there. *J. Appl. Ecol.* **43**(3)**:**445-453.

Saville, A. (1959) The planktonic stages of the haddock in Scottish waters. *Mar. Res.* **3:**1-23.

Simpson, J.H., Bos, W.G., Schirmer, F., Souza, A.J., Rippeth, T.P., Jones, S.E. and Hydes, D. (1993) Periodic Stratification in the Rhine Rofi in the North Sea. *Oceanol. Acta.* **16**(1)**:**23-32.

Taylor, M.I., Fox, C., Rico, I. and Rico, C. (2002) Species-specific TaqMan probes for simultaneous identification of cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.) and whiting (*Merlangius merlangus* L.). *Mol. Ecol. Notes* **2**(4)**:**599-601.

Thompson, H.A.R.O. (1928) The haddock of the northwestern North Sea. *Cons. Perm. Internal. Explor. Met. Rapp. & Proc. Verb. Reunions* **52-1927**((3))**:**70

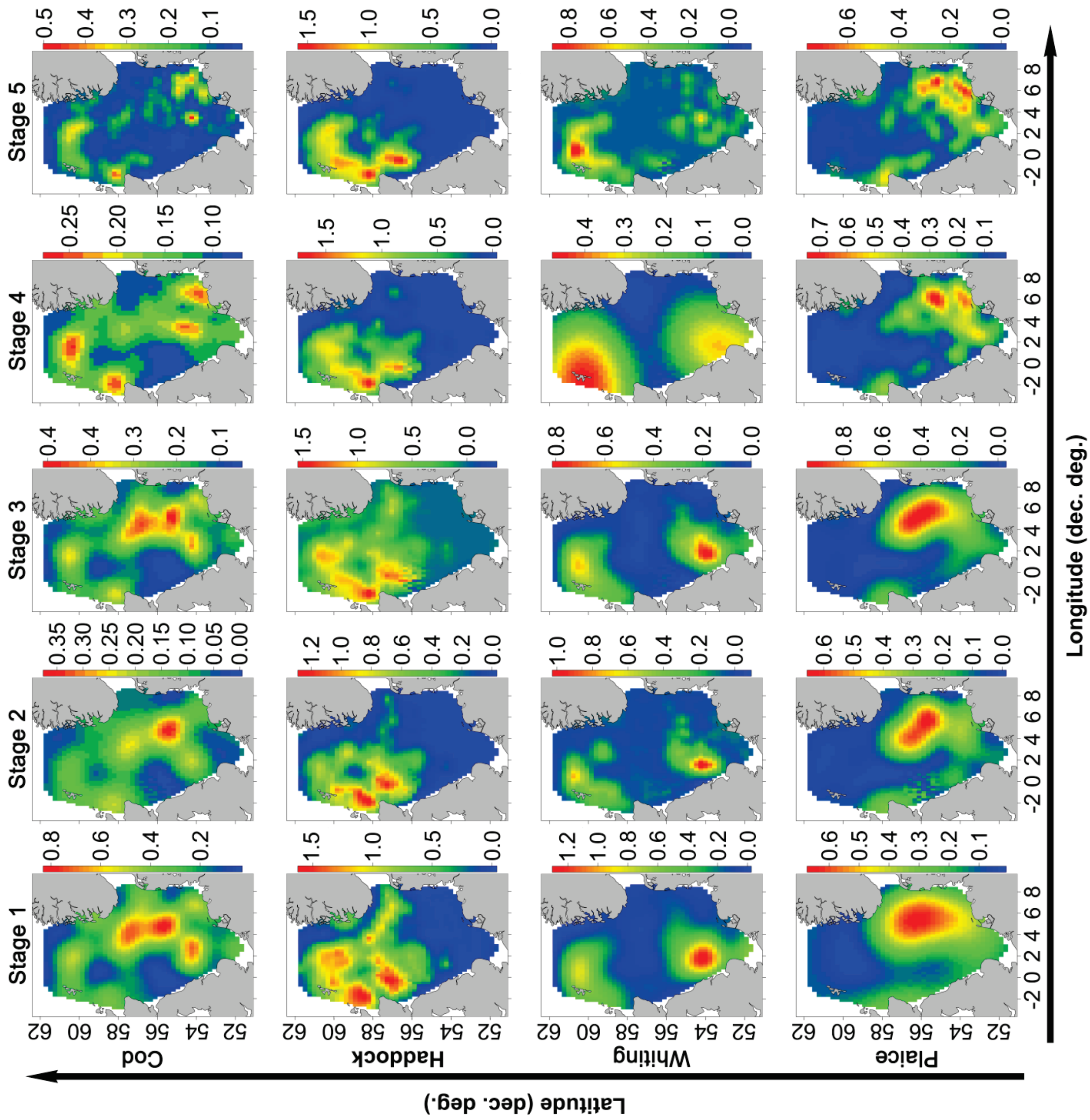
UNESCO (1968) UNESCO Report. Monograph on Oceanographic Methodology. *vol. 2,* pp. 153-159.

Webster, R. and Oliver, M.A. (2001) *Geostatistics for Environmental Scientists.* Cichester: John Wiley and Sons, 286pp.-

Wright, P.J., Neat, F.C., Gibb, F.M., Gibb, I.M. and Thordarson, H. (2006) Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *J Fish Biol.* **69:**181-199.

Supplement

Figure S1: Maps of single development stages for the eggs of all species in 2004. The egg abundances are log(N+1)-transformed and krigged on a 0.23 X 0.23 dec. deg. in R. The centres of abundance changed little in position during the development of the eggs, while they usually contracted in area. In the early stages this is likely due to mortality alone as there is a significant difference in abundance from stage to stage. In the later stages, in which overall abundance is not significantly different, this might be due to a combination of dispersal and predation.



Paper II

Running title: Hydrographic and geographic influence on fish eggs

Egg distribution of four common North Sea fishes –Hydrographic and geographic influence on distribution

HANNES HÖFFLE[1*], CINDY J. G. VAN DAMME[2], STÉPHANIE LELIÈVRE[3], CHRISTOPHE LOOTS[3], SANDRINE VAZ[3] AND PETER MUNK[1]

[1] *DTU Aqua, National Institute of Aquatic Resources, Technical University of Denmark, Kavalergården 6, DK-2920 Charlottenlund, DENMARK*

[2] *IMARES, Institute for Marine Resources and Ecosystem Studies, Haringkade 1, 1976 CP, Ijmuiden, The Netherlands*

[3] *Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), Laboratoire Ressources Halieutiques, 150 quai Gambetta, BP699, F-62321, Boulogne sur Mer, France*

Correspondence. e-mail: hhoe@aqua.dtu.dk

Abstract

North Sea fishes tend to return to specific spawning areas every year. These areas have been identified during a succession of studies, often many years apart. It remains however uncertain to which extent the environment influences the precise spawning location in any given year. Two ichthyoplankton surveys, conducted in the North Sea 2004 and 2009 allow for an examination of early stage distribution in cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and plaice (*Pleuronectes platessa*), in relation to environment and spatial dependency. In the present paper we investigate the relative influence of bottom or surface hydrography on early stage distribution with Generalized Additive Models (GAM). The selected models had high explanatory power and explained up to more than half of the variation in the data. The results show that abundance for most species could be best explained by surface conditions, while for presence/absence surface and bottom conditions explained two species, respectively. The environmental factors were more important for the presence/absence of eggs than for estimated abundances and explained more of the variation for those species which are close to their southern limit of distribution in the North Sea. These species may thus come under greater pressure if the North Sea waters become increasingly warmer.

Keywords: Fish eggs, *Gadidae*, *Pleuronectes platessa*, Hydrography, Spatial analysis, GAM

Introduction

Recent studies and predictions for the future of the North Sea (Meehl *et al.*, 2007; Perry *et al.*, 2005) have risen concerns whether the fish are able to adapt to altered conditions and change their spawning strategies or if spawning and offspring survival will be severely influenced. To address this question of adaptability, we need to know more about the determining factors behind use of spawning areas by these fishes. Cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and plaice (*Pleuronectes platessa*) are commercially important and heavily exploited species in the North Sea. Although knowledge about spawning patterns is essential for a further understanding of the early life history and the subsequent recruitment to the fish stocks, targeted studies on the spawning distribution of any of these species are relatively few and infrequent (e.g. Daan, 1981; Gibb *et al.*, 2004; Harding *et al.*, 1978). When such studies, often decades apart, are compared, they show spawning areas with some degree of variation, but generally high stability in time. Fronts are important in the spawning season for many species which is late winter/early spring (Munk and Nielsen, 2005) and are mostly salinity fronts, based on the interaction between runoff from land and the oceanic water from the Atlantic (Simpson *et al.*, 1993). Since the precipitation in Western Europe, and thus the runoff into the North Sea, is predicted to change (Meehl *et al.*, 2007), the position of these fronts is likely to change, with potential effects on spawning and the survival of offspring from affected areas. The prospect of conditions outside the observed range, calls for investigation on how the distribution of fish eggs is influenced by their environment.

Modelling the distribution of populations has made great progress in recent years. Earlier studies (e.g. Planque *et al.*, 2007) used only the environmental conditions to explain the distribution of a population, ignoring the population dynamics and demography. This approach is appropriate for modelling the niche of a species. However, for specific population this approach entails the risk to ignore internal dynamics of the population and thus create poorly defined models (Loots *et al.*, 2010b). As a remedy, Planque *et al.* (2011) suggested a group of hypotheses, external (geographic attachment, environmental conditions) and internal (e.g. demographic structure, spatial dependency) to the population in question, which should be included in modelling the distribution of a specific fish population. Fish eggs are not directly influenced by some of the internal hypothesis, as they cannot exhibit different behaviours according to development stage (e.g. Chen *et al.*, 1997). However, higher spawning stock biomass is likely to increase patch size and density. Spatial dependency, inherent to all population distributions has to be taken into account. Pelagic fish eggs are often positively or neutrally buoyant and aggregate in the water column, often close to the surface (Coombs *et al.*, 1990; Fritsch, 2005), while bottom hydrography has been successfully used to describe the spawning distribution of several groundfish species (Loots *et al.*, 2010b; Loots *et al.*, 2011). Therefore pelagic fish eggs are likely affected by bottom hydrography through the parent population and directly by surface hydrography and both have to be considered, when modelling the distribution.

A targeted international survey in 2004 addressed the extent of current spawning areas in the North Sea and potential linkages to frontal hydrography. Fox *et al.* (2008) found that all except one of the previously identified spawning areas for cod are still active. Munk *et al.* (2009) found that spawning mostly occurred near fronts, while the peak egg abundances where at the fronts themselves. These findings are important in relation to climate change. Following on the 2004 survey, a second survey in 2009 provided an additional coverage of the North Sea and allowed the examination of fish egg distribution in greater detail. A sibling study (Höffle *et al.*, submitted) indicated that the basic hydrographic structure of the North Sea and the distribution of fish eggs exhibit little variation on large temporal and spatial scales. Here we examine the hypothesis that for all species the hydrographic conditions have an overarching influence on where eggs are present and how abundant they are. To do so we statistically investigate the linkages between observed distribution, hydrography and the interdependence between locations of spawning.

Materials and Methods

Survey design and field sampling

Sampling was carried out across the North Sea (Fig. 1) by five participating countries during dedicated surveys or during the annual International Bottom Trawl Survey for the first quarter (IBTS 1Q). Periods of sampling were from 16th February to 23rd of March 2004, and from 17th of January to 6th of March 2009 (Table 1).

Table 1: Survey cruises in this study. For the BONGO nets only the mesh size for the samples used in the analysis is given.
Abbreviations: add. IBTS = Additional IBTS-Sampling, IHLS = International Herring Larvae Surveys, PLACES = Plaice and Cod Egg Surveys, PCEGGS = Planning Group on North Sea Cod and Plaice Egg Surveys (reproduced from: Höffle *et al.*, submitted)

Year	Country	Survey	Ship	Start Date	End Date	Gear	Mesh (µm)	Nos. Hauls
2004	NL	PLACES	Tridens II	1.3.04	4.3.04	Gulf VII	270	41
	DE	PLACES	Heinke	16.2.04	23.2.04	BONGO	500	40
	UK	PLACES	Corystes	18.2.04	8.3.04	Gulf VII	270	134
	DK	PLACES	Dana	25.2.04	6.3.04	BONGO	330	92
	NO	PLACES	H. Mosby	8.3.04	23.3.04	Gulf III	330	86
2009	SC	PGEGGS	Scotia	20.2.09	6.3.09	BONGO	350	53
	FR	add. IBTS	Thalassa	17.1.09	13.2.09	WP2	500	103
	NO	add. IBTS	G. O. Sars	8.2.09	21.2.09	Gulf VII	280	59
	NL	IHLS	Tridens II	19.1.09	22.1.09	Gulf VII	280	83
	DK	add. IBTS	Dana	31.1.09	17.2.09	BONGO	330	68

The samples were taken with Gulf III (Gehringer, 1962; Nellen and Hempel, 1969) and VII (Nash et al., 1998), BONGO (Posgay and Marak, 1980) and WP2 (Fraser, 1968; UNESCO, 1968) nets, covering the entire North Sea from 51.5°N to 62°N. Nets were deployed in either vertical hauls (WP2) or in double oblique hauls (all other nets), down to five metres above sea bottom or a maximum of 100 m depth. In shallow water, multiple double oblique hauls were carried out (ICES, 2008) to ensure the minimum deployment time of 10 minutes. To determine cod-like eggs to species level, single eggs without oil globules and diameters of 1.1-1.75 mm (Fox et al., 2008) or 0.97 – 1.89 mm (Lelièvre et al., 2010) were fixed for later genetic analysis, either in 96% ethanol (Fox et al., 2008; Taylor et al., 2002) or in buffered 0.864% formalin solution (Lelièvre et al., 2010).

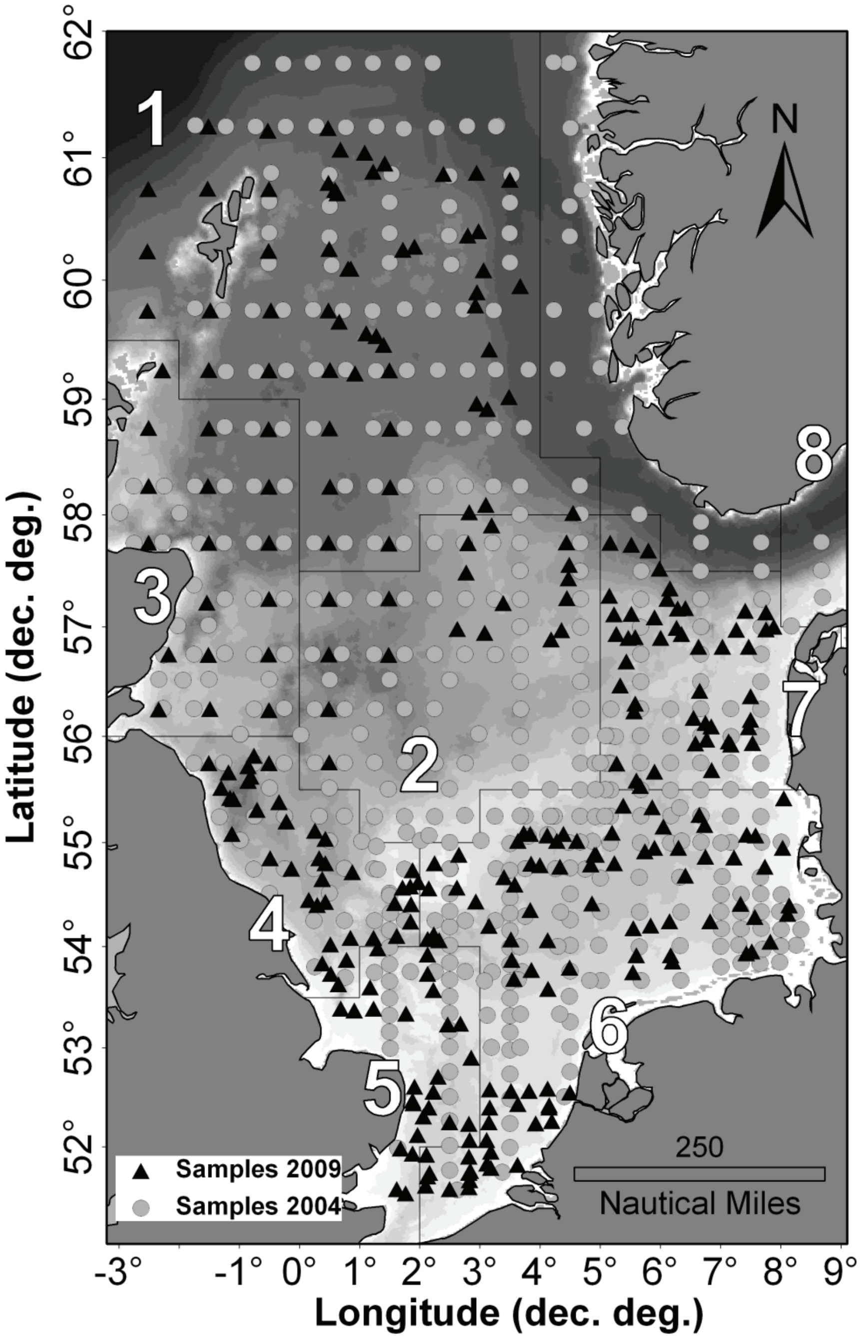


Figure 1: Sampling positions, in 2004 (grey circles) and in 2009 (black triangles). The underlying contour map shows the topography of the North Sea, in 10 m steps down to a 100 m and increasing steps to greater depths. Lines delineate the ICES roundfish areas, numbered counter clockwise 1 to 8.

Egg and larvae identification

Subsamples of at least a 100 eggs in the desired size range (>1.16 mm; Russel, 1976) were staged and visually identified to the lowest possible taxonomic level (Ryland *et al.*, 1975; Thompson and Riley, 1981). The preserved eggs were identified either with TaqMan probes (Fox *et al.*, 2008) or cytochrome *b* PCR – RFLP (Lelièvre *et al.*, 2010). Accuracy of TaqMan probes is >98% for cod, haddock and whiting (Taylor *et al.*, 2002) while compared to visual identification the cytochrome *b* PCR-RFLP was 98% accurate for cod and 71% accurate for whiting (Lelièvre *et al.*, 2010). The identified gadoid eggs were assigned to each species according to the proportion obtained from genetic analyses, for stations where this was not possible the proportion in 2004 was derived from a multinomial Generalized Additive Model (GAM) over the whole survey area (Fox *et al.*, 2008) and in 2009 from the average proportion for the other stations in the same ICES square. Density of fish eggs was calculated for each sample in numbers per m^2 as follows:

$$D = \frac{n \times f \times d_s}{V} \qquad (1)$$

where D is the density, n the egg count, f the raising factor, d_s the sampled Depth and V the sampled volume. For presence/absence the numbers were binary transformed to 0 and 1, respectively.

Geostatistics

Hydrographic data were obtained from CTD hauls during the survey and augmented with data from the ICES oceanographic data base (ICES 2009). Data sets containing erroneous pressure measurement, temperatures (<0°C or >11°C) and salinities (<20 or >37) were excluded from further analysis, while the retained values were used to calculate density as σ_t (kg m^{-3}-1000) according to UNESCO standards (Millero and Poisson, 1981). For each hydrographic variable at three depths (5 m, 20 m and bottom), an experimental variogram was calculated in Surfer 8 (Golden Software, 2002), based on the equation (Webster and Oliver, 2001):

$$\gamma(\mathrm{h}) = \frac{1}{2 \times \mathrm{n(h)}} \times \sum [\mathrm{z(x+h)} - \mathrm{z(x)}]^2 \tag{2}$$

Where *n(h)* is the number of pairs of observation for the distance between measurements *h, z(x)* is the observed value for the respective hydrographic variable at a given location *x* and *γ(h)* is the resulting experimental variogram. A theoretical variogram $\gamma' = F_{(\gamma)}$ was fit to the data based on a linear model with least square regression. Using that theoretical variogram the hydrographic data was interpolated on a regular grid of 0.25 by 0.25 decimal degrees (dec. deg.) with ordinary kriging. The interpolated density was used to calculate the horizontal density gradient in g m^{-3} per nautical mile (NM^{-1}, 1.852 km^{-1}) with the formula (Golden Software, 1999):

$$\|\vec{g}\| = \sqrt{\left(\frac{Z_E - Z_W}{2\Delta x}\right)^2 + \left(\frac{Z_N - Z_S}{2\Delta y}\right)^2} \tag{3}$$

Where $\vec{g}$ is the density gradient, Z_E and Z_W are adjacent grid points in East-West direction, Z_N and Z_S are adjacent grid points in North-South direction, and Δx and Δy are the distances in longitudinal and latitudinal direction, respectively.

Modelling the spatial dependency

Spatial dependency in the biological data was modelled in R (R Development Core Team, 2008, packages referenced in the appendix). We took the approach of Principal Coordinates of Neighbour Matrices (PCNM), adding the additional benefit of estimating the average patch size for each species. The procedure is described in detail in Borcard & Legendre (2002) and Blanchet *et al.* (2008). We took the code for the oribatid mite example, given in Borcard *et al.* (2011), as a template which was modified to suit our data. Similar to Loots *et al.* (2010b) we set the threshold p-value to a low 0.002 to avoid building too complex spatial models. The spatial scale was then determined by computing a Gaussian variogram model to determine the range of the variogram for the spatial scale of each PCNM (Bellier *et al.*, 2007). Plotting the eigenvalues of the selected PCNMs against their range (Fig. 2) we then subdivided them into submodels for a broad, medium, fine and very fine scale.

Selection of explanatory variables

In order to examine the hydrographic parameters for correlation throughout the water column, the values extracted for 5 m, 20 m and bottom depth were plotted on pair plots and the variance inflation factors (VIF) calculated. Temperature (^{o}C) was included from the measurements at 5 m depth. The values for 20 m depth were well correlated (R^2=1) with the surface, allowing the use of salinities and density gradients (g m^{-3} NM^{-1}) from this stratum to substitute for the surface values, as the conductivity measurements at 20 m were more reliable. Collinearity between surface and bottom measurements was less strong than between surface and 20 m. Therefore the 20m (surface control model) and bottom (bottom control model) variables were applied to the otherwise same GAM-models. The collinearity between temperature, salinity and density gradient was milder, with VIF values between the critical values given by Zuur (2009) and Borcard (2011). As the smoothing splines in the GAM-models did not exhibit any substantial changes, once one of these covariates was removed, we decided to keep all of them.

Bottom depth was included as it has been shown to exert a strong influence on the spawning distribution of plaice and whiting (Loots *et al.*, 2010b; 2011). The day of the year (henceforth ‘Year Day’) was included, since other than with long time series the variation in sampling date could not be neglected. The year was included to capture several, not individually measured factors like different sampling gears and survey designs and variations in the parent population. At last, to examine the spatial dependency, sub-models for very fine, fine, medium and broad scales were included.

GAM Models

GAM models were constructed in R (R Development Core Team, 2008, packages referenced in the appendix) for presence/absence data, using a binomial model with a logit link and a Gaussian model with an identity link for the log-transformed non-zero abundances, following the general form (Hastie and Tibshirani, 1990; Loots *et al.*, 2010a):

$$g(E[Y]) = \beta_0 + f_1X_1 + f_2X_2, \ldots, +f_nX_n = \beta_0 + \sum_{i=1}^{n} f_iX_i \qquad (4)$$

The link function is $g()$, Y is the response, β_0 is the intercept, $f_{1\text{-}n}$ the smoothing functions and $X_{1\text{-}n}$ the explanatory variables. The approach of modelling for abundances and presence/absence apart should allow to cope with zero inflated, log-normal distributions (Loots *et al.*, 2011). GAMs were initially constructed with inclusion of either surface or bottom hydrography. The choice of the best fitting GAM model within either the surface control model or the bottom control model was based on Generalized Cross Validation (GCV) or Un-Biased Risk Estimator (UBRE) scores (both: Wood, 2006) for abundance and presence/absence, respectively. Terms were removed from the model based on the degree of freedom, the presence of zero in the confidence interval and the rising GCV or UBRE score (Wood, 2001). Variables with estimated degrees of freedom close to 1 were retained as linear terms if they still contributed to the explanatory power of the model or if the scores increased to a large extent if they were dropped. The choice between the two optional control models depended on the Akaike Information Criterion (AIC), following the equation (Akaike, 1974; Loots *et al.*, 2010b):

$$AIC = -2 \times logL + 2 \times p \qquad (5)$$

The final GAM model was validated for normality of residuals and patterns in the residuals and the spread and no such patterns were found. Post hoc the amount of variation purely explained by each covariate was extracted by variation partitioning with RDA-adjusted R^2 (Peres-Neto *et al.*, 2006). As this method only allows four explanatory matrices the environmental and temporal variables were combined, as well as the fine and very fine scale spatial dependency.

Results

Egg distribution and habitat

The hydrography in 2004 and in 2009 was characterized by a pool of relatively warm (>7°C) and saline (>34.4) water in the centre of the North Sea and colder, fresher water along the eastern margins. The position of the boundary between oceanic and coastal water was further offshore in 2009 than in 2004 while density gradients were steeper in the northern North Sea and shallower in the German and Southern Bights (for details see: Höffle *et al.*, submitted; Munk *et al.*, 2009).

Overall, centres of egg abundance were found in the German and Southern Bights and around the Orkney and Shetland Isles. The majority of eggs was found in temperatures of 5.5-8.5°C in 2004 and in 4-6°C in 2009. The peak abundances occurred in both years in salinities between 34 and 36 and at density gradients between 0.5 and 1.5 g m^{-3} NM^{-1}. Species specific peaks were not necessarily in these ranges. All gadoids exhibited high abundances east of the Shetland Isles. While haddock seldom occurred south of 56°N, cod and whiting had southern centres of abundance. Cod was abundant in the German Bight in 2004 and the Southern Bight in 2009 and whiting between England and the Dogger Bank. Plaice also had two centres, the German Bight in the South and the Moray Firth in the North.

Spatial structuring

The threshold for truncating the distance matrix was 0.52 dec. deg. Of the PCNMs, 404 were found to have positive eigenvalues. Of these spatial structures 8 were significant for cod, 12 each for whiting and plaice and 15 for haddock. When plotting the eigenvalues against the variogram range of each PCNM, four distinct groups were discernible (Figs 2, 3), on ranges of 0-22 NM (very fine scale), 22-32 NM (fine scale), 32-49 NM (medium scale) and above 49 NM (broad scale).

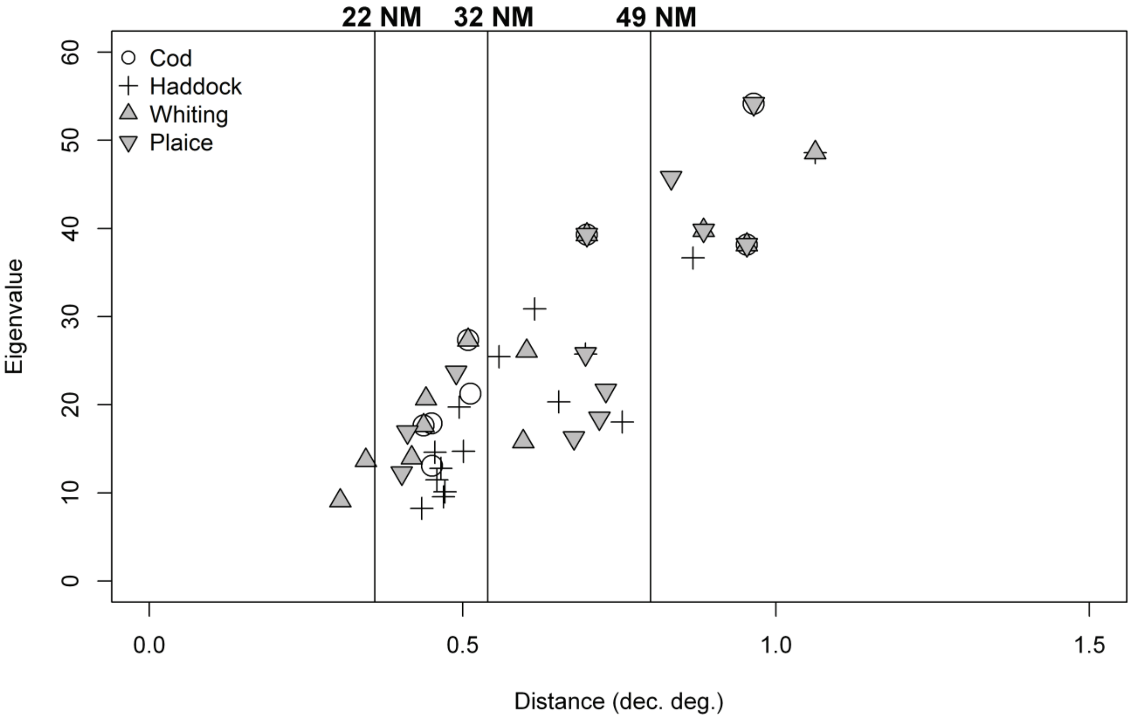


Figure 2: Range in decimal degrees of spatial sub-models for the eggs of cod, haddock, whiting and plaice on very fine (0-22 NM), fine (22-32 NM), medium (32-49 NM), and broad (>49 NM) scales. The solid lines define the thresholds for the spatial sub-models of the eggs. The boundaries between scales are denoted in nautical miles on the top axis. Eigenvalues are non-dimensional and proportional to Moran's I.

GAM - fitting

The best fitting model for the abundance of most species in the study was the surface control model with only haddock having a better fit with the bottom control model (Table 2). For the presence/absence cod and plaice had a better fit with the bottom control, while haddock and whiting were best explained by the surface control model. Spatial structures were retained on all scales, except for the presence/absence of cod, where all PCNMs on the medium scale were dropped during the backfitting process. Many PCNMs had degrees of freedom close to 1 but otherwise did not fulfil the criteria for dropping and were included as linear terms. In the abundance models no hydrographic terms were dropped or linearized, except the density gradient for plaice. The density gradient was also dropped from the presence/absence models for cod and whiting. The year was retained, except for the presence/absence of cod and in both models for plaice. The relation to the spatial variables took various forms (Figs 4, 5 and supplement figures), while for the environmental variables and the year day they were more or less s-shaped (see figure captions and supplement for details). Confidence bands widened at the ends of the covariates range because of the low number of observations. The explained deviation (Table 2) for the abundance was between 51.8% (cod) and 80.3% (haddock) and for presence/absence between 61% and 72.9%.

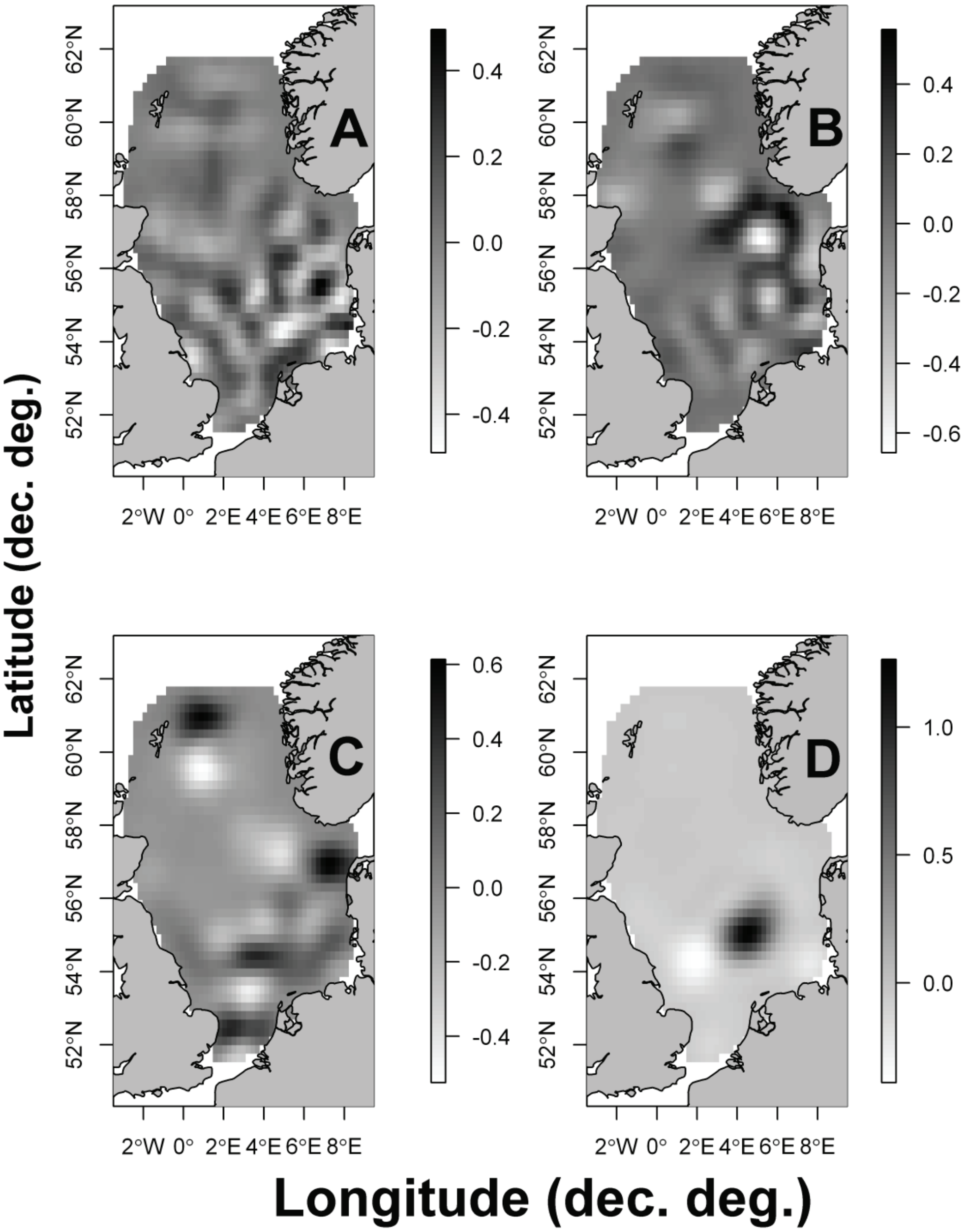


Figure 3: Representative spatial sub-models for the aggregation of fish eggs on very fine (A), fine (B), medium (C) and broad scales (D). Units are non-dimensional. Each range is subdivided into 100 intervals, darker shades represent a higher degree of aggregation.

Table 2: Results of GAM models fit to the abundance and presence/absence of fish eggs. Smooth terms are in parenthesis with prefix ‘s’, categorical terms have the prefix ‘factor’ and linear terms have no prefix or parenthesis.

Abbreviations: yr. = year, very f.sc. = very fine scale, f.sc. = fine scale, m.sc. = medium scale, b.sc. = broad scale, b.d. = bottom depth, j.d. = year day, s.t. = surface temperature, b.t. = bottom temperature, s.s. = surface salinity, b.s. = bottom salinity, s.σ_t. = surface density gradient, b.σ_t. = bottom density gradient

Gaussian models for non zero abundance

Species	Model Formula	exp. Dev.	AIC
Cod	s(f.sc.) + f.sc. + s(m.sc.) + s(b.sc.) + s(b.d.) + s(j.d.) + s(s.t.) + s(s.s.) + s(s.σ_t)	51.80%	1123.6
Haddock	factor(yr.) + s(f.sc.) + f.sc. + s(m.sc.) + s(b.sc.) + s(b.d.) + s(j.d.) + s(b.t.) + s(b.s.) + s(b.σ_t)	80.30%	632.6
Whiting	factor(yr.) + s(very f.sc.) + s(f.sc.) + f.sc. + s(m.sc.) + m.sc. + s(b.sc.) + s(b.d.) + s(j.d.) + s(s.t.) + s(s.s.) + (s.σ_t)	69.10%	1006.8
Plaice	s(f.sc.) + s(m.sc.) + m.sc. + s(b.sc.) + b.sc. + s(b.d.) + s(j.d.) + s(s.t.) + s(s.s.) + s.σ_t	57.50%	1586.4

Binomial models for presence/absence

Species	Model Formula	exp. Dev.	AIC
Cod	factor(yr.) + s(f.sc.) + f.sc. + s(b.sc.) + s(b.d.) + s(j.d.) + s(b.t.) + s(b.s.)	61.00%	444.4
Haddock	factor(yr.) + s(f.sc.) + f.sc. + s(m.sc.) + m.sc. + s(b.sc.) + s(b.d.) + s(j.d.) + s(s.t.) + s(s.s.) + (s.σ_t)	72.90%	351.2
Whiting	factor(yr.) + very f.sc. + s(f.sc.) + f.sc. + s(m.sc.) + m.sc. + s(b.sc.) + s(b.d.) + s(j.d.) + s(s.t.) + s(s.s.)	62.80%	449.6
Plaice	s(f.sc.) + s(m.sc.) + m.sc. + s(b.sc.) + s(b.d.) + s(j.d.) + s(b.t.) + s(b.s.) + s(b.σ_t)	69.10%	582.1

Variance partitioning showed that the covariates in the final GAMs explained between 23% (cod) and 55.6% (haddock) of the variation for the abundance (Table 3) while the percentages were 17% (plaice) to 47.9% (haddock) for the presence/absence. In both cases the environmental-temporal covariates explained more of the variation than the spatial covariates on any single scale. However, they often contained a large shared component, showing that these covariates were themselves spatially structured. All unique contributions were significant, except the fine scale structures for the presence/absence of plaice which was slightly not significant (p=0.06).

Table 3: Explained variation of the groups of explanatory variables. The group 'Environment' also includes the year (recoded to numerical variables), and the year day. The very fine scale spatial structures are included in the fine scale. Shared is the contribution of each variable including interactions with other variables, pure is the contribution of each variable alone.

Abundance	**Cod**		**Haddock**		**Whiting**		**Plaice**	
	Shared	**Pure**	**Shared**	**Pure**	**Shared**	**Pure**	**Shared**	**Pure**
Fine scale	7.0%	4.6%	9.4%	5.9%	6.2%	3.1%	5.6%	3.9%
Medium scale	2.6%	2.2%	30.6%	14.5%	6.7%	5.0%	10.6%	9.2%
Broad scale	9.8%	4.9%	12.3%	8.3%	27.8%	18.6%	19.6%	6.7%
Environment	12.7%	6.8%	37.3%	20.2%	12.3%	4.4%	18.5%	6.7%

Presence/Absence	**Cod**		**Haddock**		**Whiting**		**Plaice**	
	Shared	**Pure**	**Shared**	**Pure**	**Shared**	**Pure**	**Shared**	**Pure**
Fine scale	2.3%	1.0%	2.3%	0.6%	1.3%	0.5%	0.4%	0.4%
Medium scale	-	-	6.2%	0.8%	2.7%	2.6%	1.5%	1.4%
Broad scale	1.1%	1.0%	3.7%	2.5%	3.6%	3.4%	8.0%	2.7%
Environment	21.8%	20.1%	44.4%	37.3%	34.7%	34.0%	13.8%	8.6%

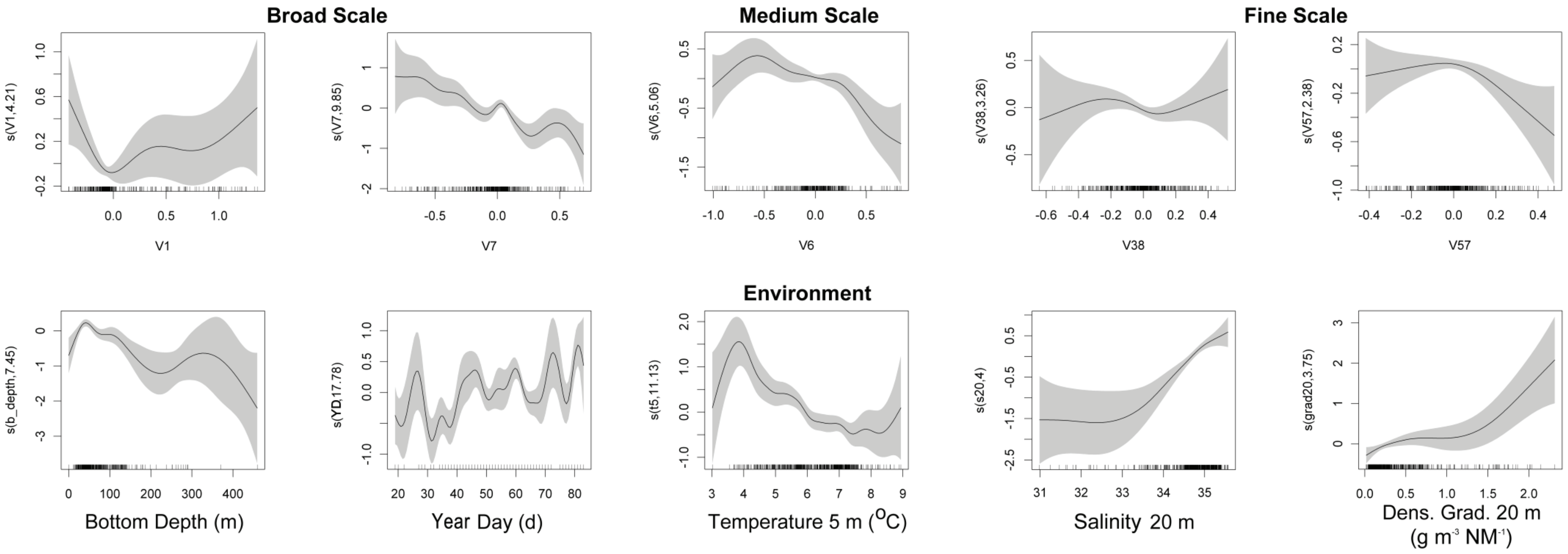


Figure 4: Smooth plots for the best fitting GAM model for the abundance of cod. Categorical and linear variables are not shown. The solid lines depict the smoothed values, the shaded area depicts the 95% confidence interval. Salinity and density gradient show a tendency to an optimum in the higher range of the covariate, while the relation to bottom depth and the spatial sub-models V6 and V57 was more or less bell shaped, exhibiting an optimal window. Surface temperature hinted to an optimum in the lower range.

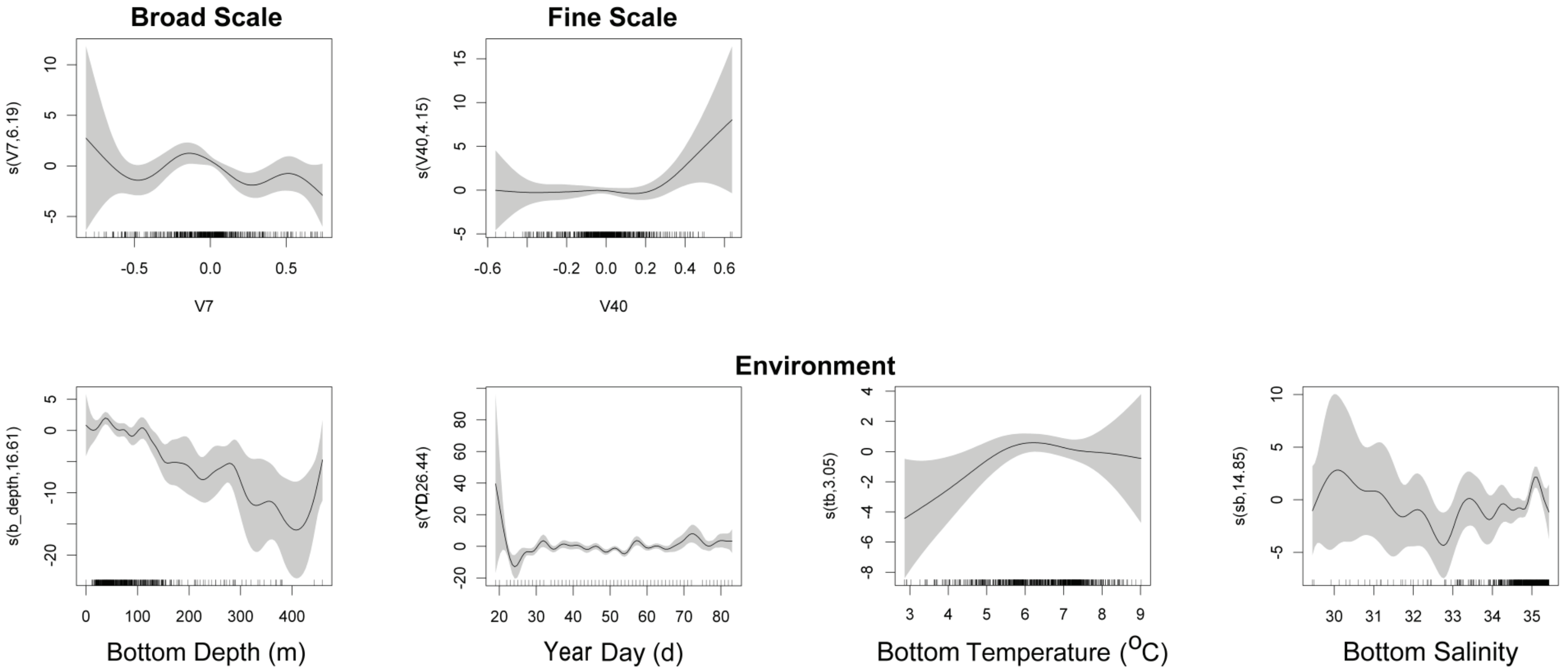


Figure 5: Smooth plots for the best fitting GAM model for the presence/absence of cod. Categorical and linear variables are not shown. The solid lines depict the smoothed values, the shaded area depicts the 95% confidence interval. The remaining spatial submodels displayed opposite shapes, V7 for the broad range was wave shaped with local optima, while V40 for the fine scale exhibited a rise towards higher values. Bottom depth showed a decline with increasing depth. Bottom temperature came closest to a bell shape, showing that other than in the abundance the optimal window is at medium temperatures.

Discussion

Our observations show that fish eggs can be found almost everywhere in the ‘potential’ spawning area, where hydrography appears suitable for spawning (Planque *et al.*, 2007). As pelagic fish eggs are dispersed in the upper water column (Coombs *et al.*, 1990; Fritsch, 2005), the abundance and to a lesser extent the presence/absence information were usually better explained with hydrographic data from the surface. The explanatory power of the GAM-models was additionally improved, by including spatial dependency, particularly on medium and broad scales, where it explained a large part of the variation.

Relation of egg distribution to physical variables

Cod eggs were more abundant in the lower temperature range (ca. 4°C), hence, are generally within the optimal range of 2-10°C determined by Laurence and Rogers (1976). These authors also defined a salinity range of 28-36 for cod, which covered the salinities measured in the present study. For haddock Laurence and Rogers (1976) determined ranges of 4-10°C and salinities of 30-36. The higher salinity range of haddock, compared to cod, is apparent in the relationship of presence/absence to salinity at 20 m as their probability of occurrence increases at salinities above 34. Cod eggs occurred in water much shallower than a 100 m, while haddock eggs were most commonly found and were most abundant at bottom depths of ca. 100 m. Similarly earlier studies (e.g. Munk *et al.*, 2002) have found cod larvae primarily in shallow water, while haddock eggs have been reported for bottom depths >100 m (Thompson, 1928). While cod eggs were more abundant at high density gradients, haddock abundance declined at gradient >0.6 g m^{-3} NM^{-1}. Munk *et al.* (1999) similarly observed a distribution of haddock larvae offshore of a front, while cod larvae tended to be directly at or slightly inshore of a frontal system.

The probability to find whiting eggs was higher in the upper temperature range, while abundance was above average at ca. 4°C and at >7°C. These results would fit with the apparent preferred range of the adults (Loots *et al.*, 2011) and in the optimal range of egg survival determined by Povoa *et al.* (2011). Abundance and presence/absence also peaked at depths <100 m, likewise the preferred depth range of the adults (Loots *et al.*, 2011). Like for cod, abundance and presence/absence were deviating above average at higher density gradients, indicating that in this study whiting eggs were more common at central parts of the fronts, in contrast to other studies where whiting larvae were found inshore of a frontal system (Munk *et al.*, 1999).

Like cod and whiting, plaice egg abundance was above average in shallow water, which is consistent with observations of frequent spawning in shallow areas of the North Sea (Simpson, 1959). In our study egg abundance was above average at 4-6°C, falling into the established temperature range for plaice egg survival of 2-8°C (Wegner *et al.*, 2003). However, the probability of occurrence peaked at 7-9°C. This might be due to samples with low abundances commonly occurring in the warmer water away from the coasts (c.f. Fig. 4, Höffle *et al.*, submitted). While presence/absence did not deviate much from the average in relation to bottom salinity, the abundance was lower than average when salinities at 20 m were above or below 35. Similarly, high salinity in the Southern Bight might offer optimal conditions for plaice eggs (Cushing, 1990). The linear relationship between egg abundance and density gradient, had a shallow slope (k=0.039), while the probability of occurrence was around average below gradients of 2 g m^{-3} NM^{-1} and then started to deviate above average.

Explanatory power for variation in the data

For the abundance, when combined on all scales, the spatial dependency had a greater pure contribution to the explained variation than the environment. This was not the case for the presence/absence of fish eggs. Like suggested in earlier studies (Loots *et al.*, 2010b; Loots *et al.*, 2011; Planque *et al.*, 2011) this may indicate that the environmental variables are more important for defining the boundaries of a populations habitat, analogous to a species distribution model, while the abundance in any given place within this area depends on factors such as demographic structure or habitat selection of the parent population. The broad scale explained more of the variation in presence/absence than the spatial dependency on the other scales. For the variation in abundance, the proportion between broad and medium scale was species specific.

For species that are well within their environmental range, processes other than hydrography may be more influential, which was shown for plaice (Loots *et al.*, 2010b).

Conversely for populations on the edge of their range, changes in the environment might have huge impact. Due to its environmental preferences when mature, haddock is restricted to the northern North Sea (Hedger *et al.*, 2004), which might be the background for the observed high contribution of the environment for the explained variation, in the shared as well as in the pure component. The North Sea cod stock is one of the more southern stocks within the species' range (Drinkwater, 2005). As such it exhibited strong contributions of the environment to the explained variation of presence/absence, but much less for the abundance. Other than haddock, cod is not restricted to one part of the North Sea and therefore the environmental influence might not be as strong as for haddock. There is also a strong influence of the environment on the presence/absence of whiting. For this species the sampling was done in the very early phase of the spawning period, and we cannot exclude that this has affected the possibilities to find its eggs.

As the environment has a large shared component with the spatial dependency this may also explain why in some GAM models the data is best described by the bottom control model, as the environment might also have an effect through the spatial structures and thus result in a better model fit. This might also be in accordance with the demersal habits of the adults.

Model fitting alone, based on AIC can still be influenced by spatial autocorrelation even when it was accounted for by the PCNM analysis. Predicting the distribution of another, independent data set was recommended as more appropriate for model evaluation (Planque *et al.*, 2011), as long as the covariates are not outside the observed range. However, splitting two years of data would entail the loss of too much variation, and splitting both of them would still cause problems with autocorrelation. Therefore, we decided against this procedure, but the data produced by future surveys can be used for validation.

Conclusion

Our results indicate that the effect of long term changes in environmental conditions of the North Sea, which is predicted to become warmer and fresher (Meehl *et al.*, 2007), might differ among the common species in the area. While increasing temperature would generally increase the probability of occurrence and decrease abundances, other effects are indicated for cod and whiting. Decreasing salinity would generally be of less importance, with noticeable effects only on plaice and whiting. Future studies might integrate hydrographic information already during the field survey. Our observations of a better prediction of egg distribution from hydrographic data measured at the surface, point to the feasibility of using satellite derived physical surface information, particularly sea surface temperature, to guide field sampling and the subsequent analysis of point estimates of egg distribution.

Acknowledgements

For the coordination of the surveys, to the Planning Group on North Sea Egg Surveys (PGEGGS), ICES. Captains and crews of the participating research vessels from Denmark, France, Germany, the Netherlands, Norway, Scotland and England. All the scientific staff of the participating institutes who sampled under winter conditions, worked for tedious hours in the laboratory, or both. Stéphanie Lelièvre, Christophe Loots and Sandrine Vaz received additional financial support from the INTERREG IV A France (Channel) – England cross-border European cooperation programme, co-financed by the European Regional Development Fund as part of the CHannel integrated Approach for marine Resource Management (CHARM) Phase 3 project.

References

Akaike, H. (1974) A New Look at the Statistical Model Identification. *Ieee T. Automat. Contr.* **AC19**(6)**:**716-723.

Bellier, E., Monestiez, P., Durbec, J.P. and Candau, J.N. (2007) Identifying spatial relationships at multiple scales: principal coordinates of neighbour matrices (PCNM) and geostatistical approaches. *Ecography* **30**(3)**:**385-399.

Blanchet, F.G., Legendre, P. and Borcard, D. (2008) Forward selection of explanatory variables. *Ecology* **89**(9)**:**2623-2632.

Borcard, D., Gillet, F. and Legendre, P. (2011) *Numerical Ecology with R. Use R!* Gentleman, R., Hornik, K., and Parmigiani, G. New York: Springer, 249pp.

Borcard, D. and Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Model.* **153**(1-2)**:**51-68.

Chen, Y., Liggins, G.W., Graham, K.J. and Kennelly, S.J. (1997) Modelling the length-dependent offshore distribution of redfish, *Centroberyx affinis*. *Fish. Res.* **29**(1)**:**39-54.

Coombs, S.H., Nichols, J.H. and Fosh, C.A. (1990) Plaice Eggs (*Pleuronectes platessa* L.) in the southern North Sea: abundance, spawning area, vertical distribution and buoyancy. *J. Conseil.* **47**(2)**:**133-139.

Cushing, D.H. (1990) Hydrographic Containment of a spawning group of plaice in the Southern Bight of the North Sea. *Mar. Ecol. Prog. Ser.* **58**(3)**:**287-297.

Daan, N. (1981) Comparison of estimates of egg production of the Southern Bight cod stock from plankton surveys and market statistics. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **178:**242-243.

Drinkwater, K.F. (2005) The response of Atlantic cod (*Gadus morhua*) to future climate change. *Ices. J. Mar. Sci.* **62**(7)**:**1327-1337.

Fox, C.J., Taylor, M., Dickey-Collas, M., Fossum, P., Kraus, G., Rohlf, N., Munk, P., van Damme, C.J.G., Bolle, L.J., Maxwell, D.L. and Wright, P.J. (2008) Mapping the spawning grounds of North Sea cod (*Gadus morhua*) by direct and indirect means. *P. Roy. Soc. B-Biol. Sci.* **275**(1642)**:**1543-1548.

Fritsch, M. (2005) Traits biologiques et exploitation du bar commun *Dicentrarchus labrax* (L.) dans le pêcheries françaises de la Manche et du Golfe de Gascogne. Mémoire de thèse. Ifremer 314pp.

Gibb, F.M., Wright, P.J., Gibb, I.M. and O'Sullivan, M. (2004) Haddock and Whiting Spawning Areas in the North Sea and Scottish West Coast. Fishery Research Services, Internal Report, *11/04,* 11+figures pp.

Golden Software (2002) Surfer. (Version 8.00) Golden, CO: Golden Software, Inc.

Golden Software (1999) Grid Operations. In: *Surfer 7 User's Guide.* Golden: Golden Software, Inc., Chap. 16:pp. 361-414.

Harding, D., Nichols, J.H. and Tungate, D.S. (1978) The spawning of plaice (*Pleuronectes platessa*) in the southern North Sea and English Channel. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **172:**102-113.

Hastie, T.J. and Tibshirani, R.J. (1990) *Generalized Additive Models.* New York: Chapman and Hall, 333pp.-

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A. and Andrews, J. (2004) Analysis of the spatial distributions of mature cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980-1999) using generalised additive models. *Fish. Res.* **70**(1)**:**17-25.

Höffle, H., Fox, C., Loots, C., Nash, R.D.M., Vaz, S., Wright, P. and Munk, P. (submitted (a)) Egg distribution of four common North Sea fishes - Local variation in spawning area usage *Fish. Oceanogr.* 28pp.

ICES (13-11-2009) ICES Dataset on Ocean Hydrography. http://www.ices.dk/ocean/

Laurence, G.C. and Rogers, C.A. (1976) Effects of Temperature and Salinity on Comparative Embryo Development and Mortality of Atlantic Cod (*Gadus morhua* L.) and Haddock (*Melanogrammus aeglefinus* L.). *J. Conseil.* **36**(3)**:**220-228.

Lelièvre, S., Verrez-Bagnis, V., Jerome, M. and Vaz, S. (2010) PCR-RFLP analyses of formalin-fixed fish eggs for the mapping of spawning areas in the Eastern Channel and Southern North Sea. *J. Plankton Res.* **32**(11)**:**1527-1539.

Loots, C., Vaz, S., Koubbi, P., Planque, B., Coppin, F. and Verin, Y. (2010a) Inter-annual variability of North Sea plaice spawning habitat. *J. Sea. Res.* **64**(4)**:**427-435.

Loots, C., Vaz, S., Planque, B. and Koubbi, P. (2011) Understanding what controls the spawning distribution of North Sea whiting (*Merlangius merlangus*) using a multi-model approach. *Fish. Oceanogr.* **20**(1)**:**18-31.

Loots, C., Vaz, S., Planque, B. and Koubbi, P. (2010b) What controls the spatial distribution of the North Sea plaice spawning population? Confronting ecological hypotheses through a model selection framework. *Ices. J. Mar. Sci.* **67**(2)**:**244-257.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J. and Zhao, Z.-C. (2007) Global Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., and Miller, H.L. (eds) Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press, Chap. 10

Millero, F.J. and Poisson, A. (1981) International One-Atmosphere Equation of State of Seawater. *Deep-Sea Res. Pt. A* **28**(6)**:**625-629.

Munk, P., Fox, C.J., Bolle, L.J., van Damme, C.J.G., Fossum, P. and Kraus, G. (2009) Spawning of North Sea fishes linked to hydrographic features. *Fish. Oceanogr.* **18**(6)**:**458-469.

Munk, P., Larsson, P.O., Danielssen, D.S. and Moksness, E. (1999) Variability in frontal zone formation and distribution of gadoid fish larvae at the shelf break in the northeastern North Sea. *Mar. Ecol. Prog. Ser.* **177:**221-233.

Munk, P. and Nielsen, J. (2005) *Eggs and Larvae of North Sea Fishes.* Frederiksberg: Biofolia, 224pp.

Munk, P., Wright, P.J. and Pihl, N.J. (2002) Distribution of the early larval stages of cod, plaice and lesser sandeel across haline fronts in the North Sea. *Estuar. Coast. Shelf. S.* **55**(1)**:**139-149.

Peres-Neto, P.R., Legendre, P., Dray, S. and Borcard, D. (2006) Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology* **87**(10)**:**2614-2625.

Perry, A.L., Low, P.J., Ellis, J.R. and Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science* **308**(5730)**:**1912-1915.

Planque, B., Loots, C., Petitgas, P., Lindstrom, U. and Vaz, S. (2011) Understanding what controls the spatial distribution of fish populations using a multi-model approach. *Fish. Oceanogr.* **20**(1)**:**1-17.

Planque, B., Bellier, E. and Lazure, P. (2007) Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. *Fish. Oceanogr.* **16**(1)**:**16-30.

Povoa, I., Davie, A., Treasurer, J. and Migaud, H. (2011) Broodstock spawning and larviculture of whiting (*Merlangius merlangus* L.) reared in captivity. *Aquac. Res.* **42**(3)**:**386-398.

R Development Core Team (2008) R: A language and environment for statistical computing. (Version 2.14.0) Vienna, Austria: R Foundation for Statistical Computing, http://www.R-project.org

Russel, F.S. (1976) *The Eggs and Planktonic Stages of British Marine Fishes.* London: Academic Press, 524 pages.

Ryland, J.S., Nichols, J.H. and Sykes, A.M. (1975) Effect of Temperature on Embryonic-Development of Plaice, *Pleuronectes platessa* L. (Teleostei). *J Exp. Mar. Biol. Ecol.* **18**(2)**:**121-137.

Simpson, A.C. (1959) The spawning of the plaice in the North Sea. *Fish. Inv. ser. 2, Sea Fisher.* **22**(7)**:**1-111.

Simpson, J.H., Bos, W.G., Schirmer, F., Souza, A.J., Rippeth, T.P., Jones, S.E. and Hydes, D. (1993) Periodic Stratification in the Rhine Rofi in the North Sea. *Oceanol. Acta.* **16**(1)**:**23-32.

Taylor, M.I., Fox, C., Rico, I. and Rico, C. (2002) Species-specific TaqMan probes for simultaneous identification of (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.) and whiting (*Merlangius merlangus* L.). *Mol. Ecol. Notes* **2**(4)**:**599-601.

Thompson, B.M. and Riley, J.D. (1981) Egg and larval development studies in the North Sea cod (*Gadus morhua* L.). *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **178:**553-559.

Thompson, H.A.R.O. (1928) The haddock of the northwestern North Sea. *Cons. Perm. Internal. Explor. Met. Rapp. & Proc. Verb. Reunions* **52-1927**((3))**:**70

Webster, R. and Oliver, M.A. (2001) *Geostatistics for Environmental Scientists.* Cichester: John Wiley and Sons, 286pp.-

Wegner, G., Damm, U. and Purps, M. (2003) Physical influences on the stock dynamics of plaice and sole in the North Sea. *Sci. Mar.* **67:**219-234.

Wood, S.N. (2001) mgcv: GAMs and generalized ridge regression for R. *R News* **1:**20-25.

Wood, S.N. (2006) *Generalized Additive Models: An Introduction with R.* London: Chapman & Hall, 410pp.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. and Smith, G.M. (2009) *Mixed Effects Models and Extension in Ecology with R. Statistics for Biology and Health.* Gail, M., Krickeberg, K., Samet, J.M., Tsiatis, A., and Wong, W. New York: Springer Science and Business Media, 574pp.-

Appendix

Table A1: R-packages und purpose they were used for. The table contains only the packages for specific purposes which are not included in the basic installation of R.

Title	Application	Reference
PCNM	Calculation of Principle Coordinates of Neighbour Matrices	(Legendre et al., 2010)
packfor	Forward selection of PCNMs within the prescribed p-value	(Dray et al., 2009)
car	Power transformation	(Fox and Weisberg, 2011)
AED	Calculation of Variance Inflation Factors (VIF)	(Zuur, 2009)
mgcv	GAM fitting	(Wood, 2001)
vegan	Functions rda() and varpart() for variation partitioning	(Oksanen et al., 2011)

References

Dray, S., with contributions of Legendre, P. and Blanchet, G. (2009) packfor: Forward Selection with permutation (Canoco p. 46). (R package version 0.0-7/r58) , http://R-Forge.R-project.org/projects/sedar/

Fox, J. and Weisberg, S. (2011) An {R}Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage.: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Legendre, P., Borcard, D., Blanchet, G. and Dray, S. (2010) PCNM: PCNM spatial eigenfunction and principal coordinate analyses. (R package version 2.1/r82) , http://R-Forge.R-project.org/projects/sedar/

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. and Wagner, H. (2011) vegan: Community Ecology Package. (R package version 1.17-10) , http://CRAN.R-project.org/package=vegan

Wood, S.N. (2001) mgcv: GAMs and generalized ridge regression for R. *R News* **1:**20-25.

Zuur, A.F. (2009) AED: Data files used in Mixed effects models and extensions in ecology with R. http://www.highstat.com/book2.htm

Supplement

The figures in this supplement depict smooth splines of the Generalized Additive Models (GAMs) for the abundance and presence/absence of all species except cod. The figures for cod can be found as figures 4 and 5 in the paper. In all figures the solid line depicts the smoothed values, the shaded area the 95% confidence interval. Categorical and linear terms are not depicted.

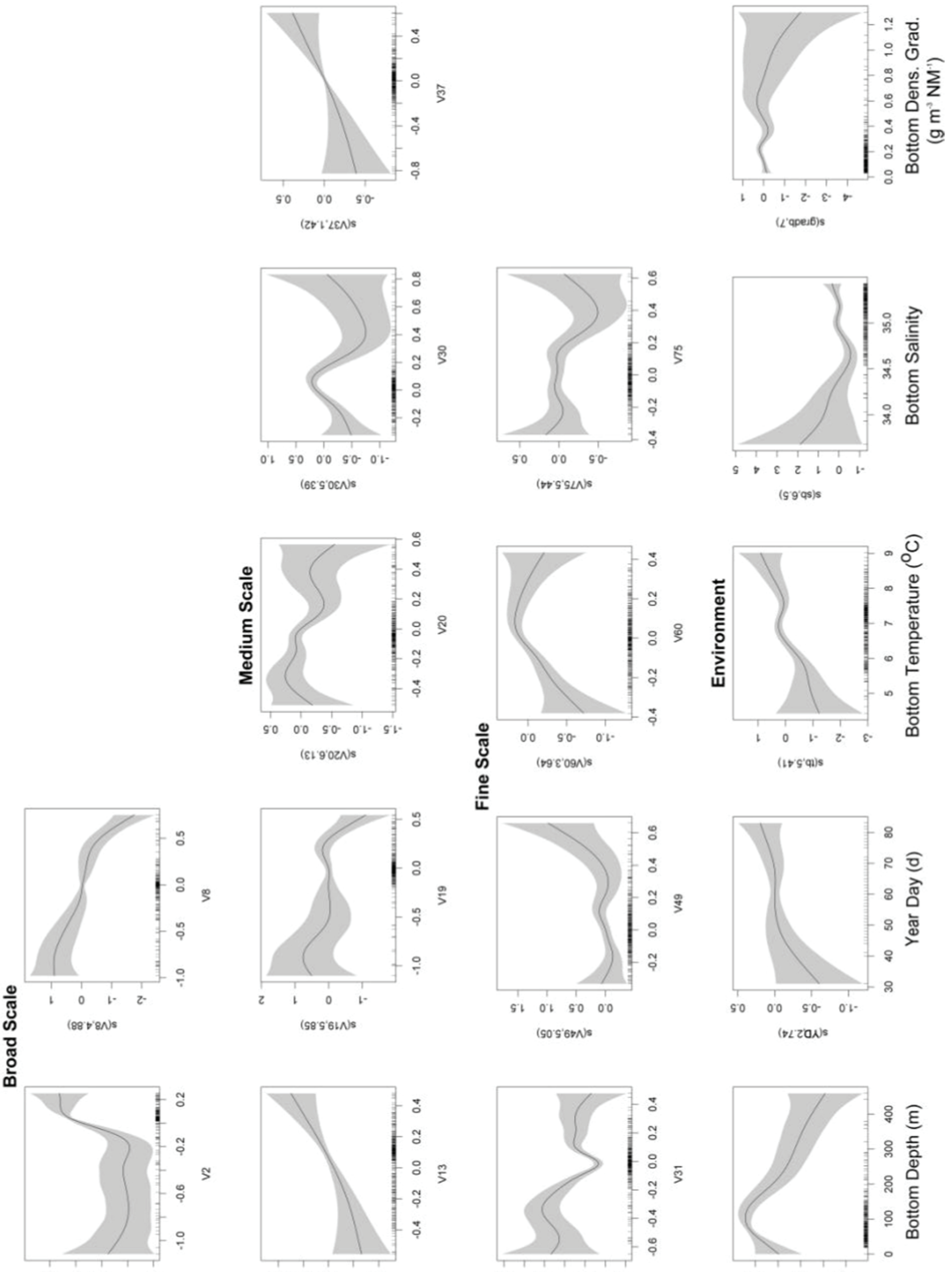


Figure S1: Smooth plots for the best fitting Gaussian GAM model for the abundance of haddock. The relation to the spatial sub-models was mostly trough or bell shaped with a few splines being almost linear, showing decreasing deviance on broad scale and increasing deviance on medium scale. The relation to year day and bottom temperature exhibited a steady rise in deviance while for bottom depth and the density gradient on the bottom it was peaking in the lower range and then steadily falling.

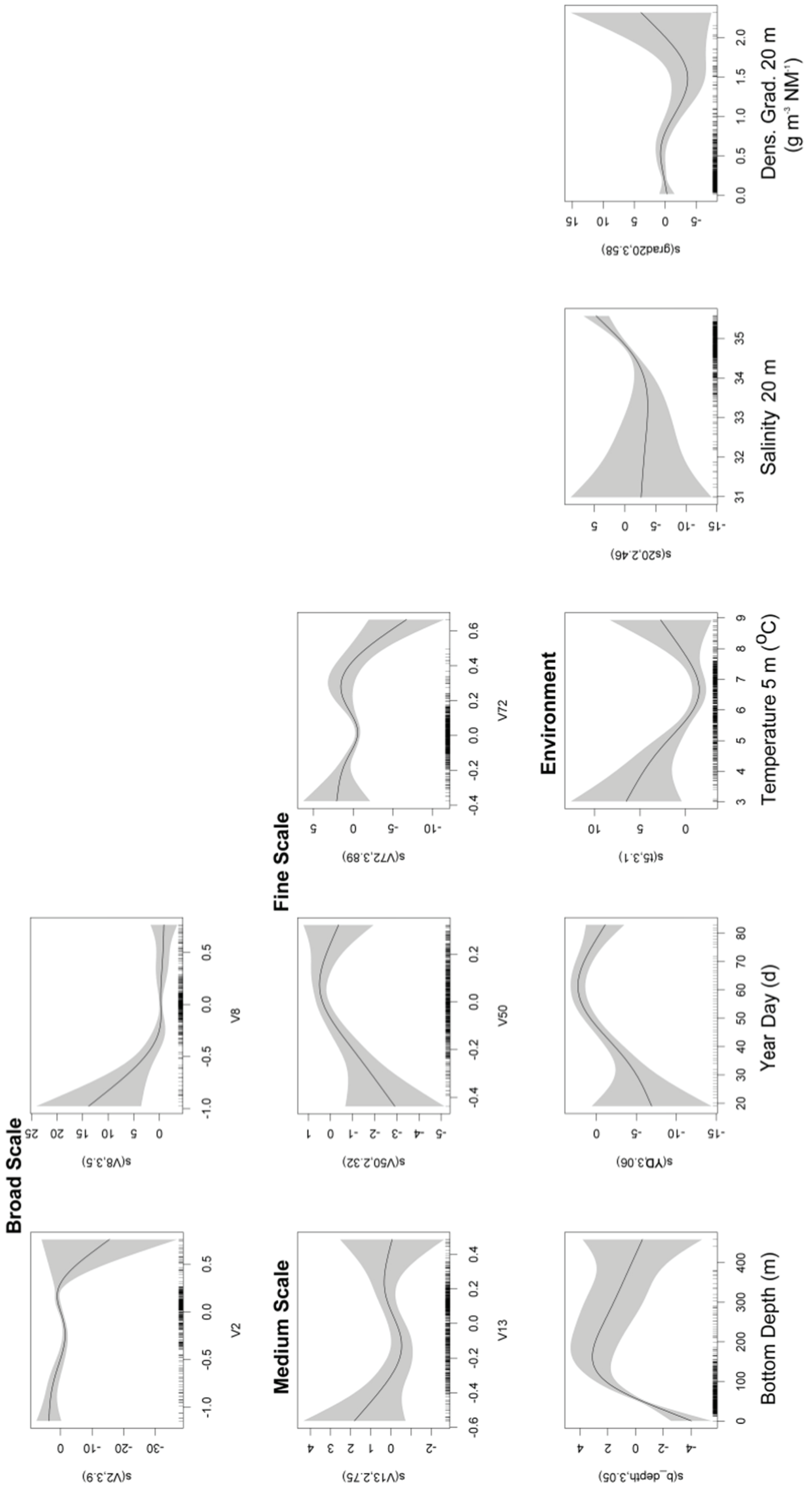


Figure S2: Smooth plots for the best fitting binomial model for the presence/absence of haddock. The overall trend in the relation to the spatial sub-models was a decrease in deviance with increasing values in the eigenvector. Only V50 on the fine scale deviated in being bell-shaped and having an optimum around zero. The relation to the environmental variables was similar to the abundance. However, the relation to the density gradient exhibited an increase in deviance at high values and the relation to the temperature was trough shaped instead of having a tendency to increase.

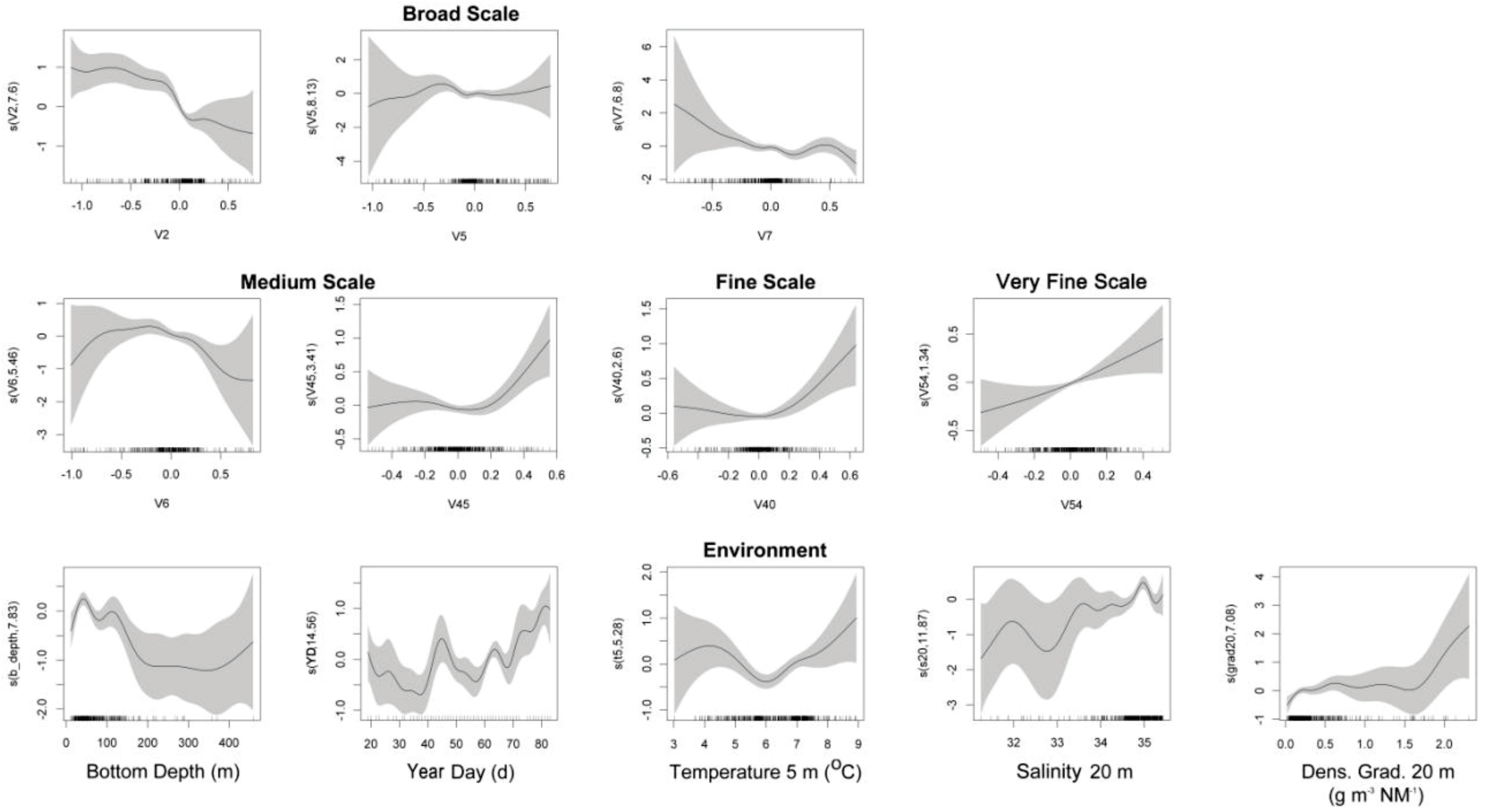


Figure S3: Smooth plots for the best fitting Gaussian GAM model for the abundance of whiting. The deviance on broad scale decreased or was stable close to zero with increasing values for the spatial sub-model. On medium, fine and very fine scale it was increasing, in case of the very fine scale almost linear. Only V6 on the medium scale was stable around zero for most of the range and decreasing towards either extreme. The optimum for the relation the bottom depth was at less than 100 m while the deviance was generally increasing towards later dates or higher temperatures and density gradients.

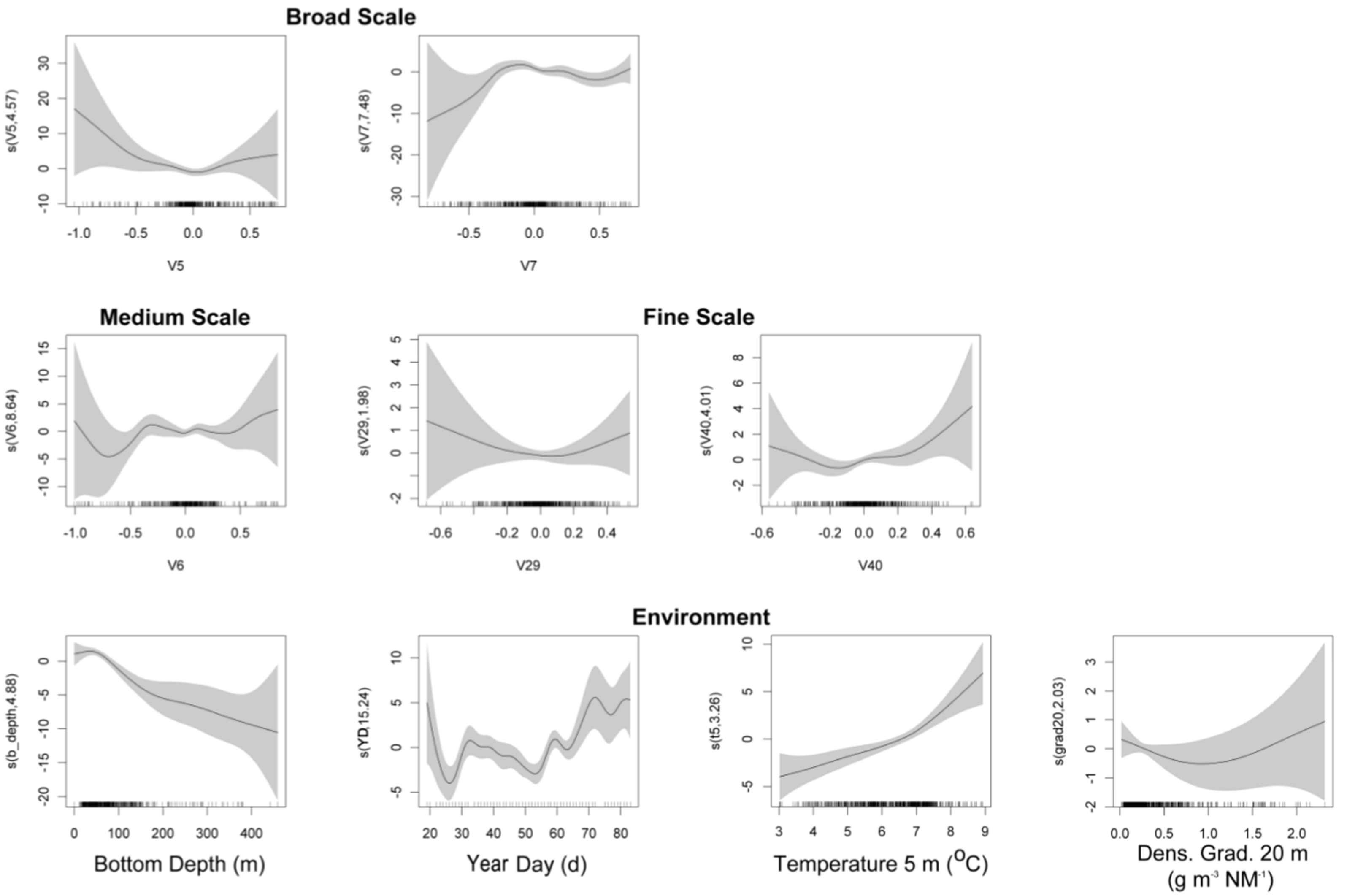


Figure S4: Smooth plots for the best fitting binomial GAM model for the presence/absence of whiting. The smooth splines for most of the spatial sub-models had the shape of a shallow trough, except on the medium scale were it did only deviate from zero at the extremes of the range and for V7 on the broad scale where it was also deviating only at the extreme of the negative range. The deviance decreased in the relation to bottom depth and increased for the year day and the density gradient.

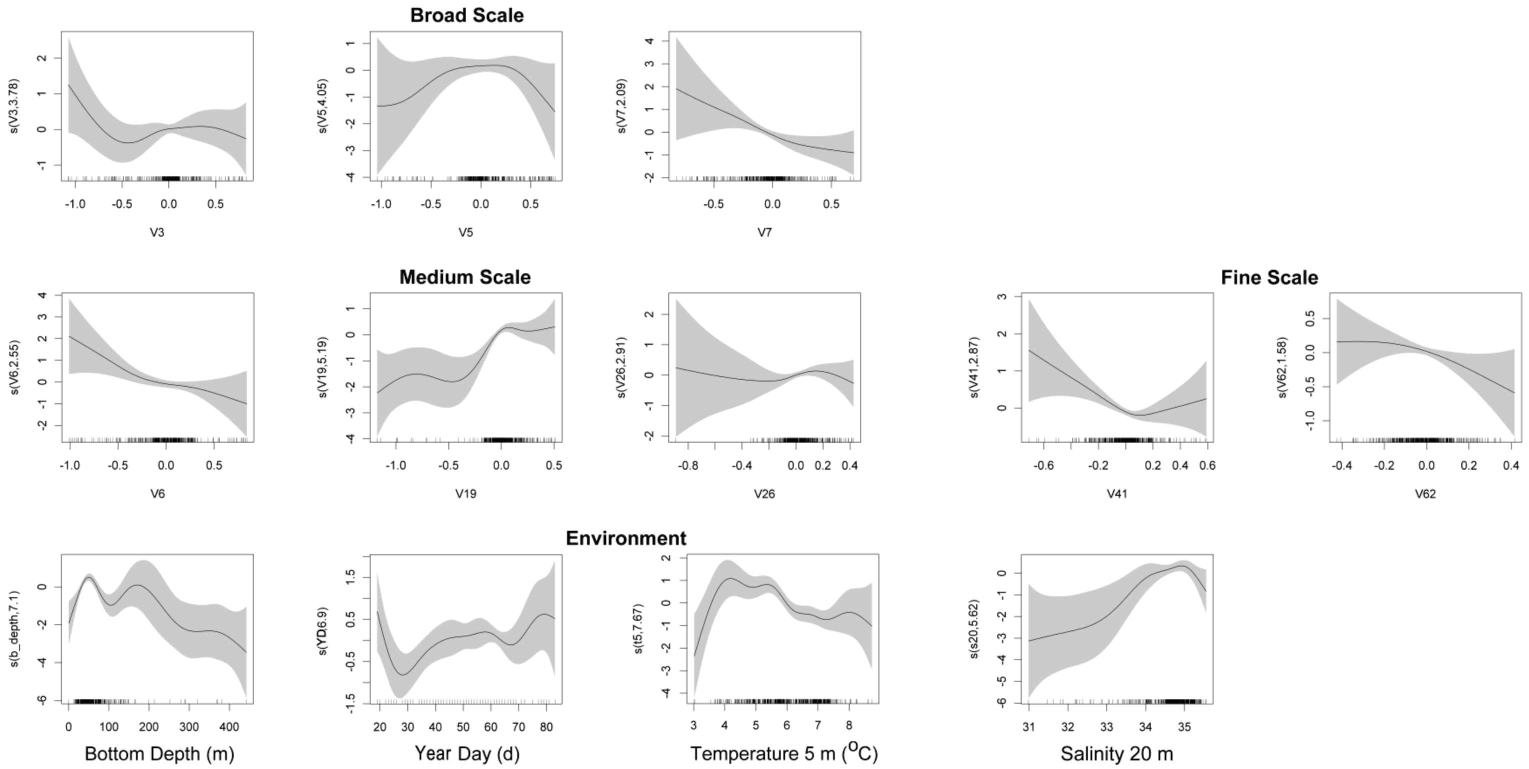


Figure S5: Smooth plots for the best fitting Gaussian GAM model for the abundance of plaice. The deviance in relation to the spatial sub-models was mostly decreasing, except for the sub-models V5 on broad scale and V19 on medium scale, where it was bell shaped and increasing, respectively. For the bottom depth, the deviance peaked at shallow depths and then decreased with a second smaller peak at depths deeper than 100 m. The deviance dropped between day 20 and 30 and then increased towards later dates, while it was steadily rising until a salinity of 35 and decreasing thereafter.

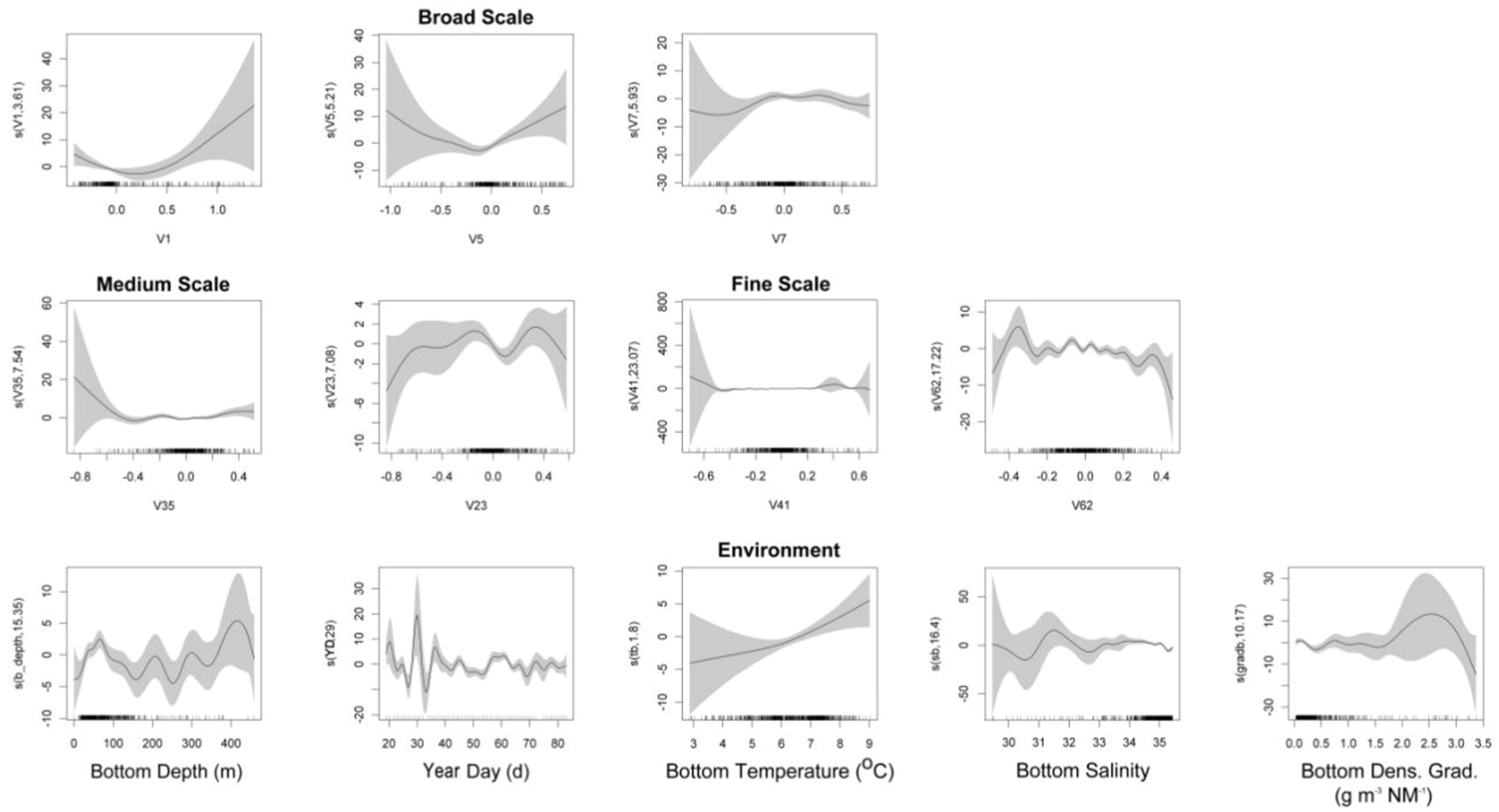


Figure S6: Smooth plots for the best fitting binomial model for the presence/absence of plaice. The deviance for most of spatial sub-models was relatively stable around zero. For the broad scale it also exhibited the form of a shallow trough, with the highest deviances at the extremes of the range. Similarly the deviance oscillated around zero for bottom depth and Year Day. For the temperature it was steadily rising with higher temperatures, while the density gradient was stable around zero for the most part of the range and then developed a bell shape above 2 g m^{-3} NM^{-1}.

Paper III

Differences in vertical distribution of larval fishes in relation to hydrography and prey

HANNES HÖFFLE[1*], RICHARD D. M. NASH[2], TONE FALKENHAUG[3] & PETER MUNK[1]

[1] *DTU Aqua, National Institute of Aquatic Resources, Technical University of Denmark, Kavalergården 6, DK-2920 Charlottenlund, Denmark. pm@aqua.dtu.dk*
[2] *Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway. richard.nash@imr.no*

[3] *Institute of Marine Research, Flødevigen, 4817 His, Norway. Tone.Falkenhaug@imr.no*

**Correspondence.* E-mail: hhoe@aqua.dtu.dk

Running head: Vertical distribution of fish larvae in the North Sea.

Abstract

As part of the plankton, fish larvae have little influence on their overall horizontal movements, while they are obviously able to control their vertical position in the water column. However, the vertical distribution is quite variable. While some factors, such as prey and light have an apparent influence on vertical distributions, the effects of other factors are more ambiguous. Notably, distributional differences between fish larval species are poorly understood. During a survey in the northern North Sea, information on the vertical distribution of a range of larval species was assembled, and a comparative analysis between species was carried out. The vertical distributions of the ten different species showed similarities but also notable differences. During the day the different species aggregated in either the upper or the middle of the water column, while they increased in abundance at shallower depths during the night. Others were distributed in greater depths during all light conditions. Hence, while there were some differences in migratory behaviour, the different larval species generally remained at the same relative position compared to the other species of the larval community.

Keywords: Fish larvae, Gadidae, Flatfish, Vertical distribution, North Sea

Introduction

Compared to current speeds the swimming ability of fish larvae is of minor importance, limiting their capability to influence their location in the horizontal plain. However, on the vertical axis larval swimming has far greater importance, influencing also horizontal transport, as current speed and direction can change with depth (Fortier & Leggett 1983; Sclafani et al. 1993).Vertical distribution patterns of fish larvae can be roughly classified into three broad categories: i) type I migrations as upward movement at the beginning of night and downward movement at the beginning of day; ii) type II as the opposite (Neilson & Perry 1990) and a pattern of aggregation during the day and dispersal throughout the night (Gray 1998; Leis 1991; Olivar & Sabatés 1997). Exogenous factors that influence the observed patterns are, among others, light, prey and predator distribution, as well as effects of temperature and salinity.

Species and congeners often exhibit similar distribution patterns, regardless of the prevailing environmental conditions (Olivar & Sabatés 1997; Röpke 1993; Southward & Barrett 1983). Characteristically distinct fish larval assemblages can be found in different depth strata (Gray & Kingsford 2003; Olivar & Sabatés 1997). However, taxonomy interacts with development. Many species exhibit different vertical behaviours at different stages(c. f. Table 1; Neilson & Perry 1990). In the larval stage, size and consequently swimming ability are important for determining vertical distribution. Lough & Potter (1993) observed the initiation of vertical migration in cod (*Gadus morhua* Linnaeus, 1758) and haddock (*Melanogrammus aeglefinus* Linnaeus, 1758) at standard lengths (SL) of 6-8 mm, and a firmly established type I migration at lengths greater than 9 mm SL. Smaller larvae and particularly those in poor condition may be more strongly influenced by buoyancy (Sclafani et al. 1993). However, even in their earliest stages, larvae will migrate if unfavourable conditions make it necessary (Grønkjær & Wieland 1997). The influence in hydrography, in particular the position of the thermocline, is more unclear. Some studies found a connection between larval distributions and the thermocline for certain taxa (Olivar & Sabatés 1997) and/or size classes (Lough et al. 1996; Lough & Potter 1993), while others found the same distributional patterns, both of single taxa and larval assemblages, irrespective of water column stratification (Gray 1998; Gray & Kingsford 2003). Gray and Kingsford (2003) attributed their failure to find a relationship between distributions and the thermocline, to a combination of the gradual and ephemeral character of thermoclines in their study region and the lag-phase between the occurrence of hydrographic cues and the larvae's reaction.

The influence of prey and predator distributions was pointed out by Pearre (1973) who, based on his studies of *Sagitta elegans* (Verrill, 1873), introduced the hunger-satiation hypothesis. In this case vertical movements were related to the concurrent needs of feeding in the upper water column and hiding from visual predators at greater depths. The hypothesis was later applied to other planktonic organisms, including fish larvae (Pearre 2003). Visually hunting fish larvae can follow different strategies to satisfy these needs. They may rise at night, together with their zooplankton prey or may stay deeper and feed on vertically migrating prey (Lovetskaya 1953). Neilson and Perry (1990) suggested a feeding/avoidance window at dusk and dawn, when light conditions are sufficient for feeding but predators may still be at greater depths. The influence of light depends on the species. Some seem to seek a certain isolume, which primarily governs their vertical distribution (Woodhead 1966). This has been suggested as the background for aggregations during the day and diffuse distribution during the night while the primary cue would then be missing (Leis 1991). However, the effect of light is species specific as has been shown in concurrent studies (Catalán et al. 2011; Vollset et al. , submitted), for example some species are shown to be adapted to low illumination (e.g. Downing & Litvak 2001; Huse 1994; Yoon et al. 2010).

One factor alone rarely determines the vertical distribution of fish larvae throughout a diel cycle. While prey abundance was one controlling factor for mesopelagic larvae in the Arabian Sea (Röpke 1993) and *Sardinella aurita* (Valenciennes, 1847) in the northwestern Mediterranean Sea (Sabatés et al. 2008), they were also limited by hydrography. The mesopelagic species by a warm mixed layer above, and *S. aurita* likely by the ca. 15°C cool water below the pycnocline. Likewise, food availability, the relationship between illumination and prey abundance, has given good correlations with the distribution of Baltic cod larvae (Grønkjær & Wieland 1997). Statistical models for the vertical distribution of different taxa have shown the influence of several interacting factors (Hernandez et al. 2009) as well as highest predictive power when including only a single factor (Huebert et al. 2010).

Hydrographic features have a strong influence on horizontal distribution and drift of fish larvae. Several studies have shown that fish larvae are aggregated in or near fronts (Kiørboe et al. 1988; Munk et al. 2002; Sabatés 1990), often with species specific positions relative to the frontal zone (Munk , submitted). The vertical distribution of larvae will, however, also influence their horizontal transport, while different currents at different depths might lead to a retention within or a displacement out of an area (Fortier & Leggett 1983; Fortier & Leggett 1982; Govoni & Pietrafesa 1994).

With the apparent species differences in vertical distributions and migrations, a comparative approach might elucidate the factors which are of prime importance. Few studies have analysed the distributional patterns of a wider range of species in a comparative way. Such an opportunity was available in the northern North Sea in 2010. Here we sampled in areas where several fish species spawn in spring, and we were able to describe both the major horizontal distributional patterns from transects of stations, and the vertical patterns by vertical stratified sampling over an 18 hours period. In this contribution we focus on the distributional patterns of larval fish in relation to hydrography and prey distribution, and on the persistency in the relative distributional differences among species.

Materials and Methods

Field sampling

Sampling was undertaken on the R/V G.O. Sars (IMR, Bergen, Norway), between 25th April and 5th of May 2010, during a survey covering transects at 59.3 and 60.75°N (Figure 1). Five additional stations were sampled with GULF VII and MOCNESS over the course of 18 hours in a 5 x 5 nautical miles (NM) sized area (henceforth 18h-station) east of the Shetland islands.

Depth integrated samples were taken in double oblique hauls with a 76 cm diameter GULF VII high speed sampler (Nash et al. 1998), down to about 100 m depth. The sampler was equipped with a mechanical flow meter (General Oceanics, USA) in the mouth of the nosecone. A SCANMAR depth sensor was attached to the sampler and provided both depth and temperature measurements. For depth discrete sampling a MOCNESS (Wiebe et al. 1985) with a 1 m^2 opening and 4 nets (180 µm mesh) was deployed to ca. 100 m and then hauled to the surface, sampling the water column in strata with nets opening at about 100, 75, 40 and 20 m. Flow meters and a CTD were attached to the MOCNESS and the filtered volume (m^3) estimated for each stratum. Larvae were sorted on board G.O. Sars and were preserved in borax buffered 4% formaldehyde. Zooplankton was split in two fractions before preservation, using a Motoda splitting device. One half was preserved for identification and enumeration whilst the other half was size fractioned into <1000 µm, 1000-2000 µm and >2000 µm. Each size fraction was dried at 60°C to constant weight in order to obtain dry weights, which were converted to milligrams per m^3 (mg m^{-3}) based on the volume of water filtered.

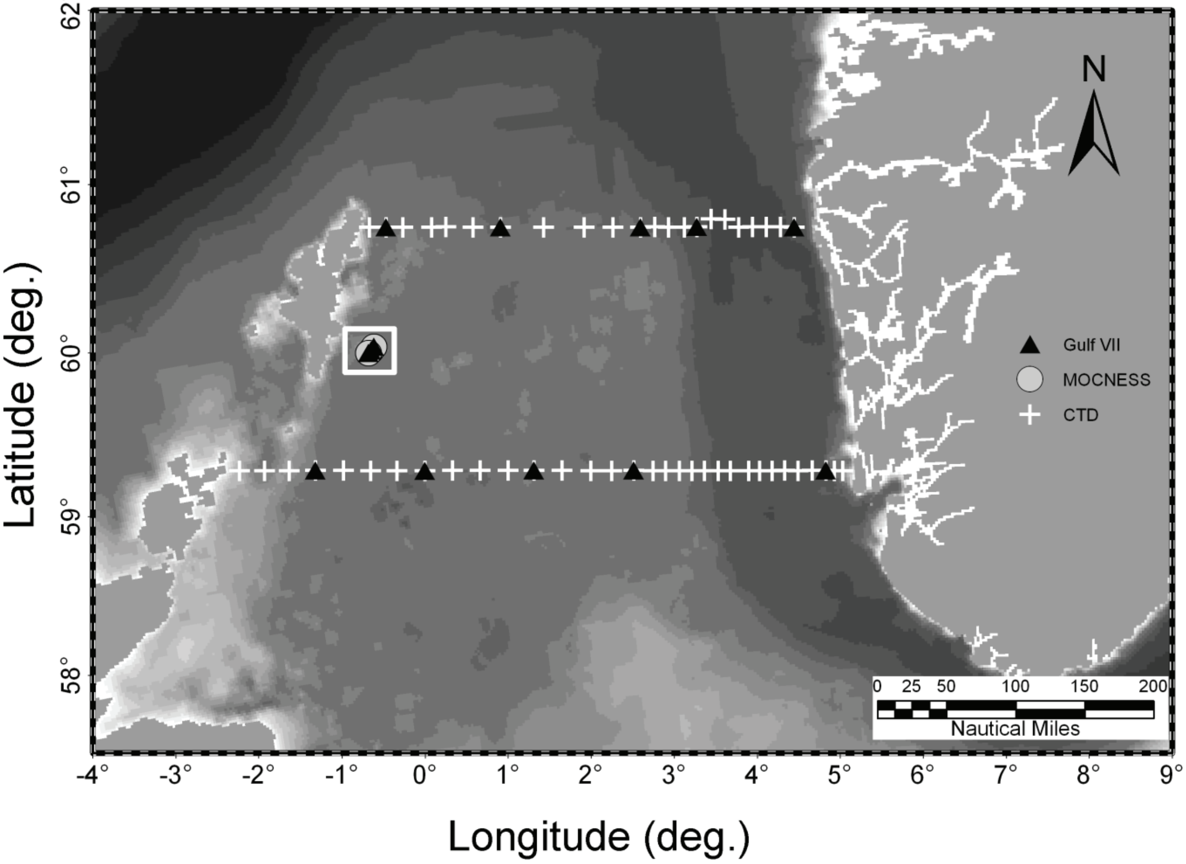


Figure 1: CTD, GULF VII and MOCNESS stations sampled during the survey. The aggregation of samples in the white rectangle represents the 18 hours station, containing 5 hauls with each gear in a 5 x 5 NM square.

Laboratory procedures

The preserved larvae were cleaned from formalin under running water for 10-15 minutes. All larvae were then identified to the lowest taxonomic level, using either Russell (1976), Schmidt (1906) or Munk & Nielsen (2005) as keys. Standard length (SL; tip of the snout to the end of the notochord) was measured to the nearest 0.1 mm with an ocular micrometer. To correct for shrinking, live SL was calculated with the equation by Bolz and Lough (1984), after correcting for formalin shrinkage (Theilacker 1980).

Data treatment and analysis

Water density was calculated according to UN standards (Millero & Poisson 1981) from temperature and salinity measured during the transects. The vertical profiles of calculated densities were interpolated on a regular grid (0.5° x 5 m) with ordinary kriging in Surfer 8 (Golden Software 2002), while contour plots were constructed in Sigmaplot 12 (Systat Software Inc. 2011). The vertical profiles for the five hauls at the 18h-station are given as line graphs.

For each species in the depth integrated hauls, the catch was converted to no. m^{-2} by dividing by the filtered volume and multiplying by the maximum sampler depth. Catch of larvae in the depth discrete hauls was converted to no. m^{-3} by dividing by the filtered volume in a given stratum and these values were used in calculation of the depth of the centre of abundance (Z_{cm}) from

$$Z_{cm} = \frac{\sum D_j \times WD_j \times A_j}{\sum WD_j \times A_j} \qquad (1)$$

Where D_j is the sampled depth, WD_j the width of the individual stratum, A_j is the abundance of the larvae and j expresses the range of sampling depths.

Only larvae data for which the maximal abundance in a given stratum reached above 2 per 100 m^3 were used, as was the abundance of Zooplankton <1000 µm. The station sampled at 06:20 UTC was excluded from calculations for day distributions and Z_{cm}, as it was the first sample after sunrise and considered to be biased by the night distribution. Abundances per stratum were compared visually between species and between day and night. Similarly Z_{cm} was compared among species for day, dusk and night as well as the relationship of species to the hydrography in the transects.

The depth of the centre of abundance was tested for significant differences between species, using one-factorial ANOVA for all species together and for Gadidae and flatfish apart. Data were tested beforehand with a Shapiro-Wilks and Levene’s test and were found to fulfil the requirements for normality and homogeneity of variance. Post hoc Tukey’s HSD was applied to discern between which species significant differences occurred.

Results

Hydrography

Along both transects we observed a cool (<7°C), low saline (<34) surface layer over the Norwegian trench, extending to ca. 50 m depth (Figure 2), representing the Norwegian Coastal Current (NCC). Coldest temperatures occurred at ca. 30 m, while lowest salinities and densities were at about 10 m depth (Figure 2a, b). Beneath the NCC water the temperature increased down to 200-300 m, while at greater depths temperatures fell below 7°C. On the shallow plateau, between 1°W and 3°E, temperature changed markedly with depth, while salinity was almost homogenous throughout the water column, except for the eastern margins. In the southern transect a thermocline at about 50 m was separating water of >7°C from cooler water below. In the northern transect the warmer water reached down to a 100 m and the thermocline was less strong. On the western margins of the southern transect water temperature increased rapidly between 0.5°W and 1°W. Similarly, salinity decreased from about 1.7°W westwards and together with temperature formed a frontal structure. In the North, temperature increased more gradually, while salinity did not change. Overall the highest temperatures were measured at >8°C on the western margins.

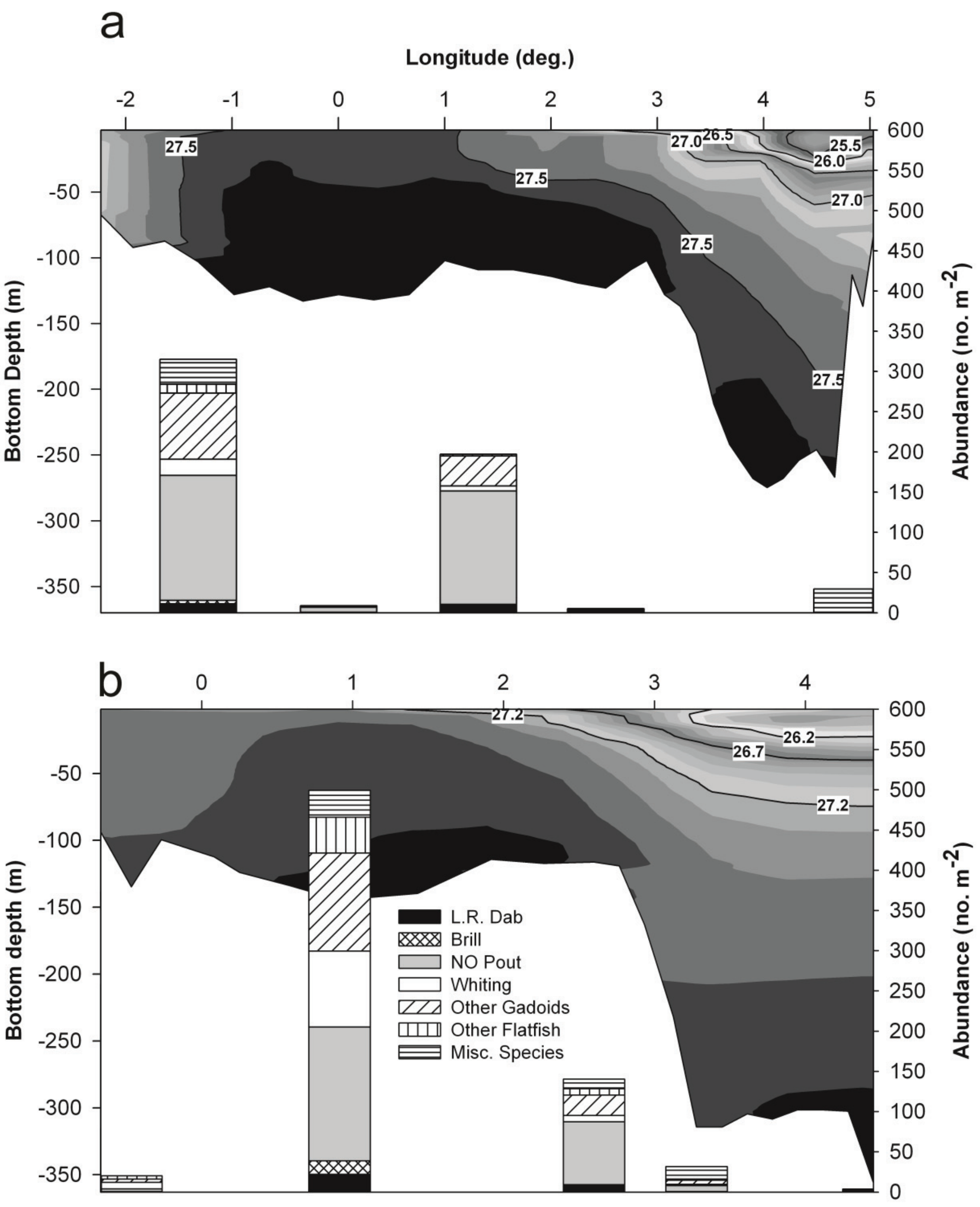


Figure 2: Profiles of water density (0.5 kg m^{-3} contours) and abundance of fish larvae along the transects at 59.3°N (panel a) and 60.75°N (panel b). Only the most common species are given, while gadoids other than Norway pout and whiting, and flatfish other than long rough dab and brill are combined. Miscellaneous species comprises *Clupeidae*, *Argentiniade*, *Ammodytidae*, *Lotidae* and *Gobidae* which did not commonly occur.

The hydrography at the 18h-station exhibited little variability in time or depth (Figure 3). Salinity was relatively high and stable, only changing from 35.32 to 35.33 in the sampled water column of 120 m. The temperature likewise varied little, it was about 8°C to 50 m and then declined continuously to 7.6°C Fluorescence peaked at 0.12 µg L^{-1}, but estimates varied during the period of investigation.

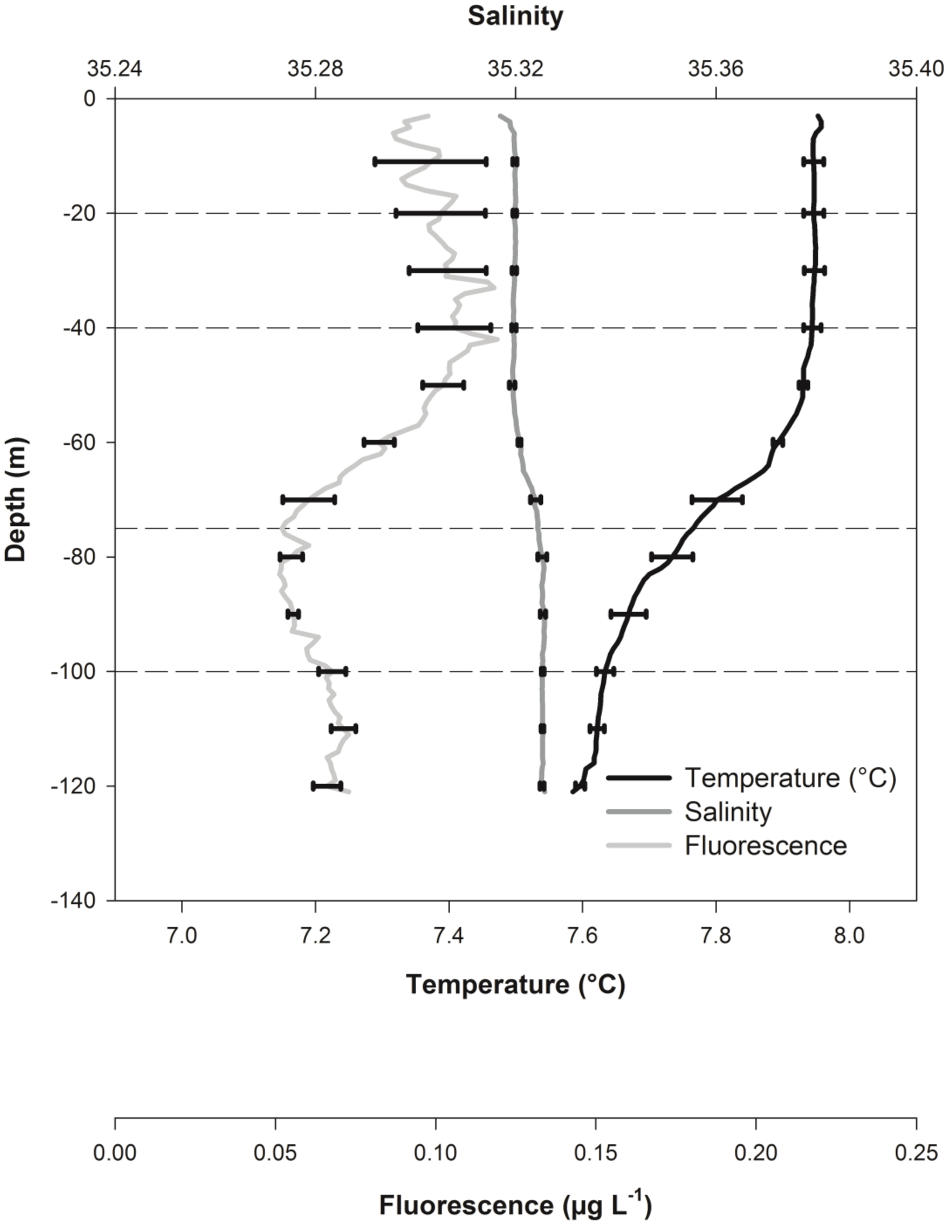


Figure 3: Temperature, salinity and fluorescence at the 18h-station, averaged over all 5 hauls. The broken lines depict the boundaries between the sampled depth strata in depth discrete hauls. Most changes in hydrography and fluorescence occurred between 50 and 80 m, mainly in the stratum between 40 and 75 m. Error bars are only show for every ten metres of depth.

Horizontal distribution - transects

During the survey, a total of 2030 fish larvae of 27 species in 9 families were identified (Tables 1, S1). Overall and similar to temperature and salinity, species richness and abundance of fish larvae increased from East to West. Abundances in the area of the Norwegian trench were mostly <30 m^{-2} (Figures 2a, b). In this area there were no flatfish, and there were only gadoid larvae close to the western slope of the trench. Over the shallow plateau abundances were mostly low (<10 m^{-2}), however long rough dab (*Hippoglossoides platessoides* Fabricius, 1780) and Norway pout (*Trisopterus esmarkii* Nilsson, 1855) occurred at abundances of ca. 200 and 300 m^{-2}, respectively. Both the stations with these high abundances were at the boundary of salinities between 35 and 35.2, where also sharp changes in σ_t and high concentrations of zooplankton 180 - 1000 µm (70 mg m^{-3} and 50 mg m^{-3}) were observed. Along the northern transect larval abundance and species diversity increased from the western slope of the Norwegian trench westward to ca. 1°E, up to a maximum abundance of 500 m^{-2} (Figure 2b). At the same station the highest concentrations of zooplankton <1000 µm, 200 mg m^{-3}, was observed. In both transects the dominant species was Norway pout, followed by whiting (*Merlangius merlangus* Linnaeus, 1758). Flatfish of the families *Pleuronectidae* and *Scophthalmidae* were more abundant and species rich in the northern transect than at the southern. Notably *Ammodytidae* of 3 species were limited to the southern transect with only lesser sandeel (*Ammodytes marinus* Raitt, 1934) at >10 m^{-2}. Ling (*Molva molva* Linnaeus, 1758) was found in high abundance, (33.3 m^{-2}), at one station of the northern transect, but did not occur elsewhere (Table S1a).

At the single location between the two transects whiting was almost twice as abundant as Norway pout, while other gadoids were much less abundant (<20 m^{-2}) than either of these. Blue ling (*Molva dipterygia* Pennant, 1784) and northern rockling (*Ciliata septentrionalis* Collett*, 1875*) were found in abundances over 20 m^{-2}. Flatfish were similarly species rich and abundant as in the northern transect. Long rough dab and brill (*Scolphthalmus rhombus* Linnaeus, 1758) were most abundant, with 25.2 m^{-2} and 18.6 m^{-2}, respectively. *Clupeidae*, *Argentinidae* and *Gobiidae* occurred sporadically along the transects as well as the 18h-station, in some hauls in high numbers (Table 1).

Table 1: Average abundances and standard lengths (±1 SE) for all fish species identified. Numbers are based on depth integrated GULF VII hauls during transects and the 18h-station. Species which are marked with asterisks have only been found in MOCNESS hauls and the numbers are based on these hauls. The column transect indicates during which transects a species was found. The abundances and standard lengths for the individual transects are given in the supplement (Table S1).

Abbreviations: S=Southern transect, N=Northern transect, 18h=18h-station

	Taxon		**Abundance**			**Std. Lenght**		
Family	**Species**	**Transect**	**(no. m^{-2})**			**(mm)**		
Ammodytidae	*Ammodytes marinus*	S	15.5	±	0.0	16.2	±	0.0
	*Hyperoplus immaculatus**	18h	1.0	±	0.0	11.9	±	0
	Hyperoplus lanceolatus	S, 18h	3.3	±	1.3	23.6	±	13.1
	Unidentified	S	1.2	±	1.0	17.5	±	16.8
Argentinidae	*Argentina sphyraena*	S, 18h	20.4	±	12.9	9.9	±	1.3
Clupeidae	*Clupea harengus*	N, S, 18h	9.5	±	3.6	17.4	±	1.4
Gadidae	*Gadus morhua*	S, 18h	7.1	±	3.8	9.3	±	4.3
	Melanogrammus aeglefinus	N, S, 18h	7.8	±	2.2	8.1	±	2.7
	Merlangius merlangus	N, S, 18h	81.8	±	34.2	6.7	±	1.0
	Pollachius pollachius	N, S, 18h	8.2	±	3.6	8.5	±	1.5
	Pollachius virens	N, S, 18h	13.2	±	2.9	8.1	±	2.4
	Trisopterus esmarkii	N, S, 18h	74.4	±	20.1	8.5	±	2.0
	Trisopterus minutus	N, S, 18h	11.8	±	3.9	6.8	±	1.6
	Unidentified	N, S, 18h	12.2	±	3.2	6.2	±	1.6
Gobiidae	*Gobius niger*	18h	4.1	±	0.0	5.5	±	0.0
	Gobiusculus flavescens	N, 18h	17.3	±	0.6	6.9	±	0.1
	*Unidentified**	18h	0.9	±	0.0	2.7	±	0.0
Lotidae	*Ciliata mustela*	S	4.4	±	0.0	5.1	±	0.0
	Ciliata septentrionalis	N, 18h	20.2	±	9.0	5.7	±	0.5
	Molva dipterygia	N, 18h	20.7	±	15.1	7.2	±	1.0
	Molva molva	N, 18h	23.0	±	10.3	6.1	±	1.2
Pleuronectidae	*Glyptocephalus cynoglossus*	N, 18h	7.2	±	2.6	7.7	±	1.8
	Hippoglossoides platessoides	N, S, 18h	15.4	±	6.6	9.4	±	2.2
	Limanda limanda	N, S, 18h	8.2	±	2.5	7.3	±	2.9
	*Platichthys flesus**	18h	2.0	±	0.0	3.5	±	0
	Pleuronectes platessa	N, 18h	7.6	±	3.5	8.3	±	2.9
	Unidentified	N, 18h	2.5	±	0.7	6.5	±	1.6
Scophthalmidae	*Lepidorhombus whiffiagonis*	N	5.5	±	0.0	10.6	±	0.0
	Phrynorhombus norvegicus	N	1.1	±	0.3	9.2	±	2.0
	Scophthalmus rhombus	N, S, 18h	14.4	±	6.0	4.6	±	0.7
Triglidae	*Eutrigla gurnardus**	18h	1.2	±	0.2	6.3	±	0.3

Vertical distribution – 18 hours station

In the MOCNESS hauls, the zooplankton <1000 µm exhibited only minor changes in vertical distribution during the period. Coinciding with fluorescence, the two topmost strata held the highest abundances, slightly more than 30% (Figures 4 and 5).

The relative abundance of larvae in each stratum was plotted as % of the total abundance for day and night apart. Z_{cm} was calculated and plotted for day, dusk, night and for single samples. The vertical distribution of ten species, seven gadoids and three flatfish, was used. One group of gadoid larvae, constituted by cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting and pollock (*Pollachius pollachius* Linnaeus, 1758), were distributed in the upper water column (0 – 40 m) during day and night. Cod (62%) and haddock (52%) were most abundant at 0 – 20 m during the day and at 20 – 40 m at night, with 100% and 69% respectively (Figures 4a, b). For whiting (Figure 4c) and pollock (Figure 4d) the change between these strata was reversed, as their abundance increased by 32 and 38 percent points at 0 – 20 m during the night. While cod was never found below 40 m depth, the other species occurred in the deeper strata and ascended to shallower depths at night, Z_{cm} decreased accordingly (Figure 6a).

Saithe (*Pollachius virens* Linnaeus, 1758) and the two *Trisopterus* species (Figures 4e, g) were distributed in the strata below 40 m during the day. During the night saithe and poor cod (*Trisopterus minutus* Linnaeus, 1758) were most common in the upper water column, while 53% of Norway pout larvae remained at 75 – 100 m depth.

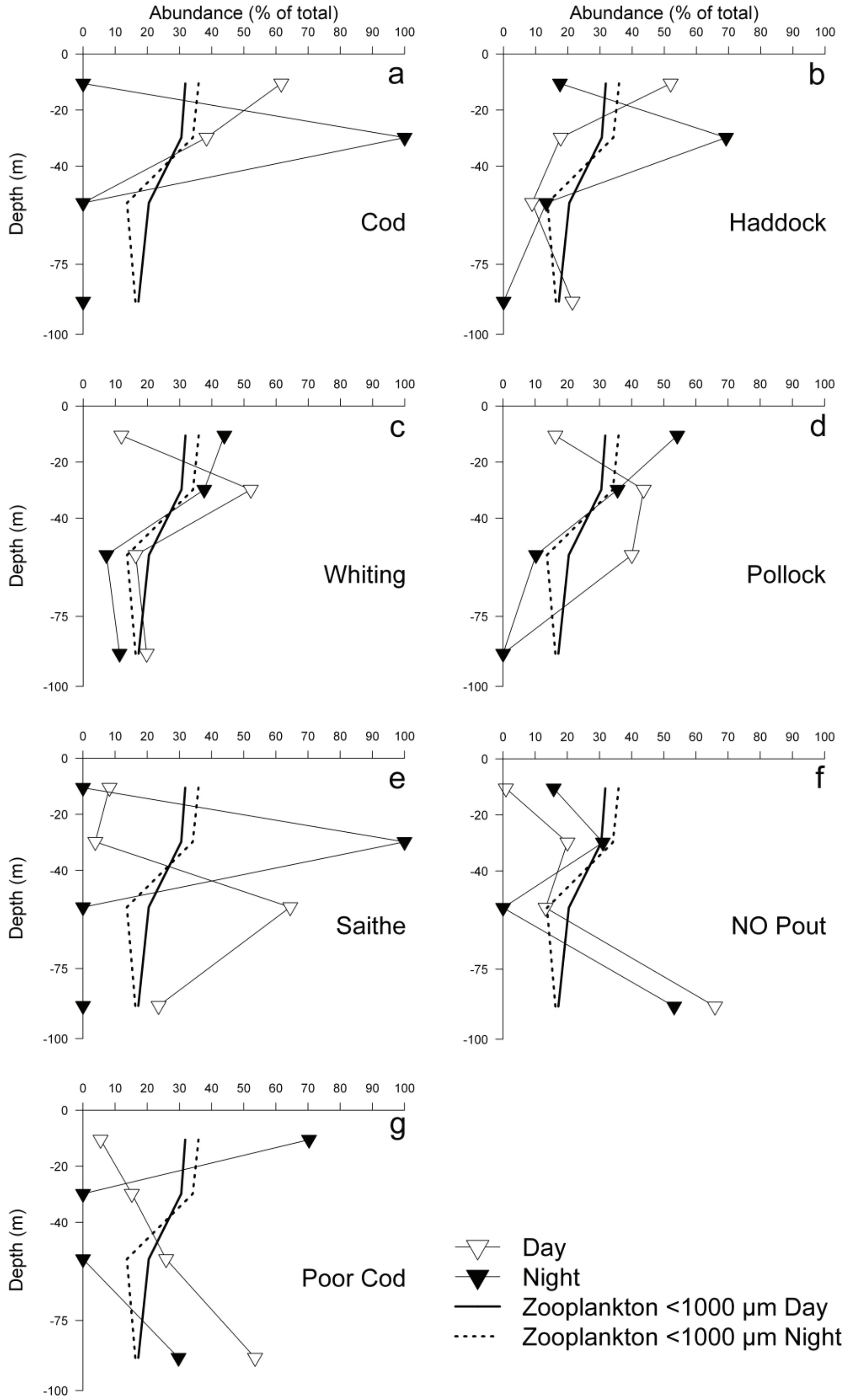


Figure 4: Vertical distribution of gadoid fish larvae and zooplankton biomass (dw) <1000 µm, during day and night in % of total abundance or biomass. The y-axis depicts the boundaries between sampled strata.

In daylight all three flatfish species, witch (*Glyptocephalus cynoglossus* Linnaeus, 1758), brill and long rough dab were most abundant at 40 – 75 m depth (Figure 5), varying between 45% for witch and 57% for brill. During the night, witch and long rough dab were most abundant in the upper water column, peaking with 47% at 0 – 20 m and 77% at 20 – 40 m, respectively. Brill remained most abundant at 40 – 75 m depth.

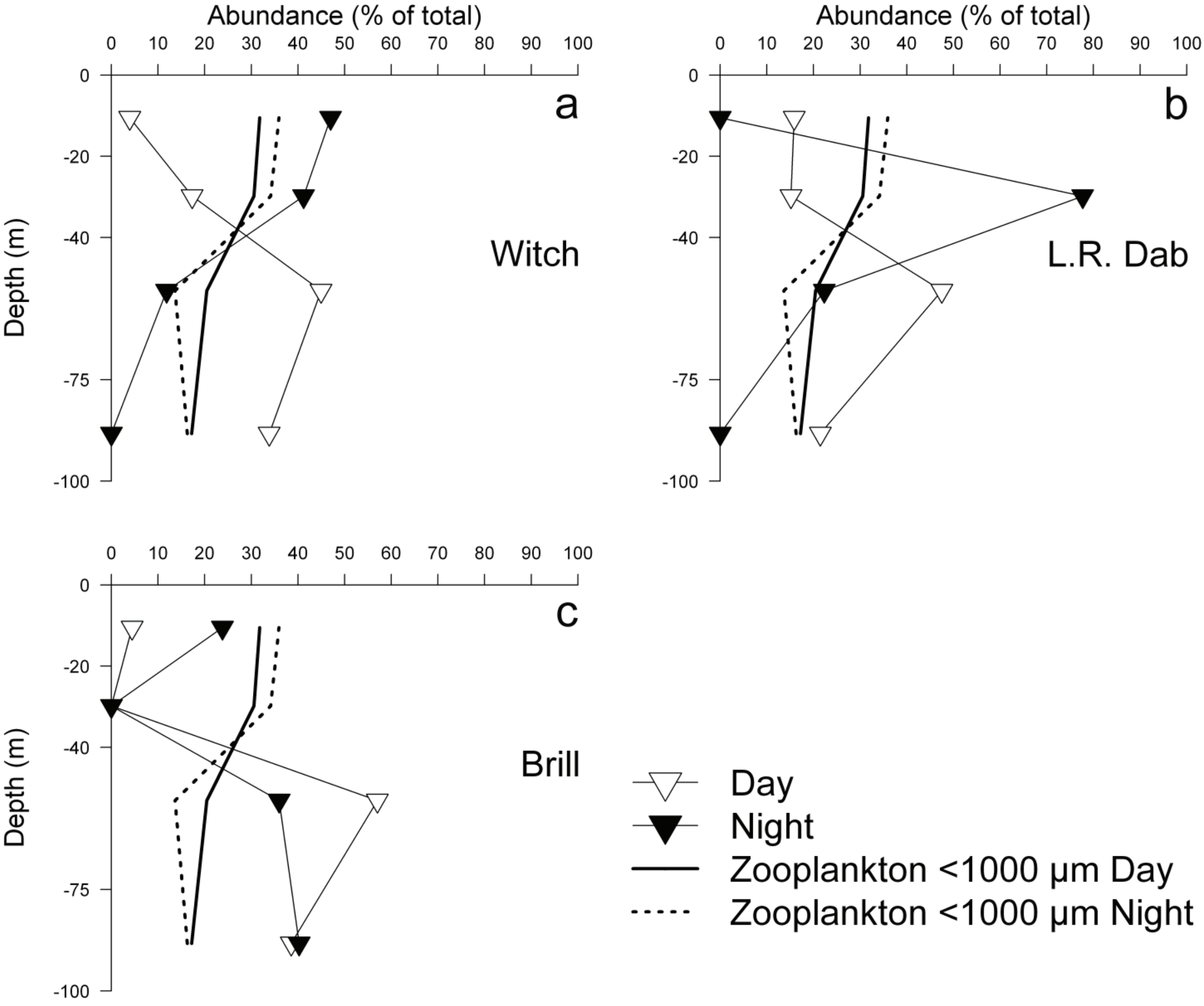


Figure 5: Vertical distribution of flatfish larvae and zooplankton biomass (dw) <1000 µm, during day and night in % of total abundance or biomass. The y-axis depicts the boundaries between sampled strata.

Differences between depth of the centre of mass of larval species were only significant within a single family, *Gadidae* (F_6=2.5; p=0.047), but not for the group of flatfish (F_2=0.2; p=0.82) or in an analysis of all species together (F_9=1.8; p=0.1). The pattern in change of Z_{cm}, between different light conditions was similar for most species (Figures 6a, b). Except for cod, Norway pout and brill Z_{cm} decreased at night. While cod was found at greater depth during the night, Norway pout and brill already ascended between day and dusk.

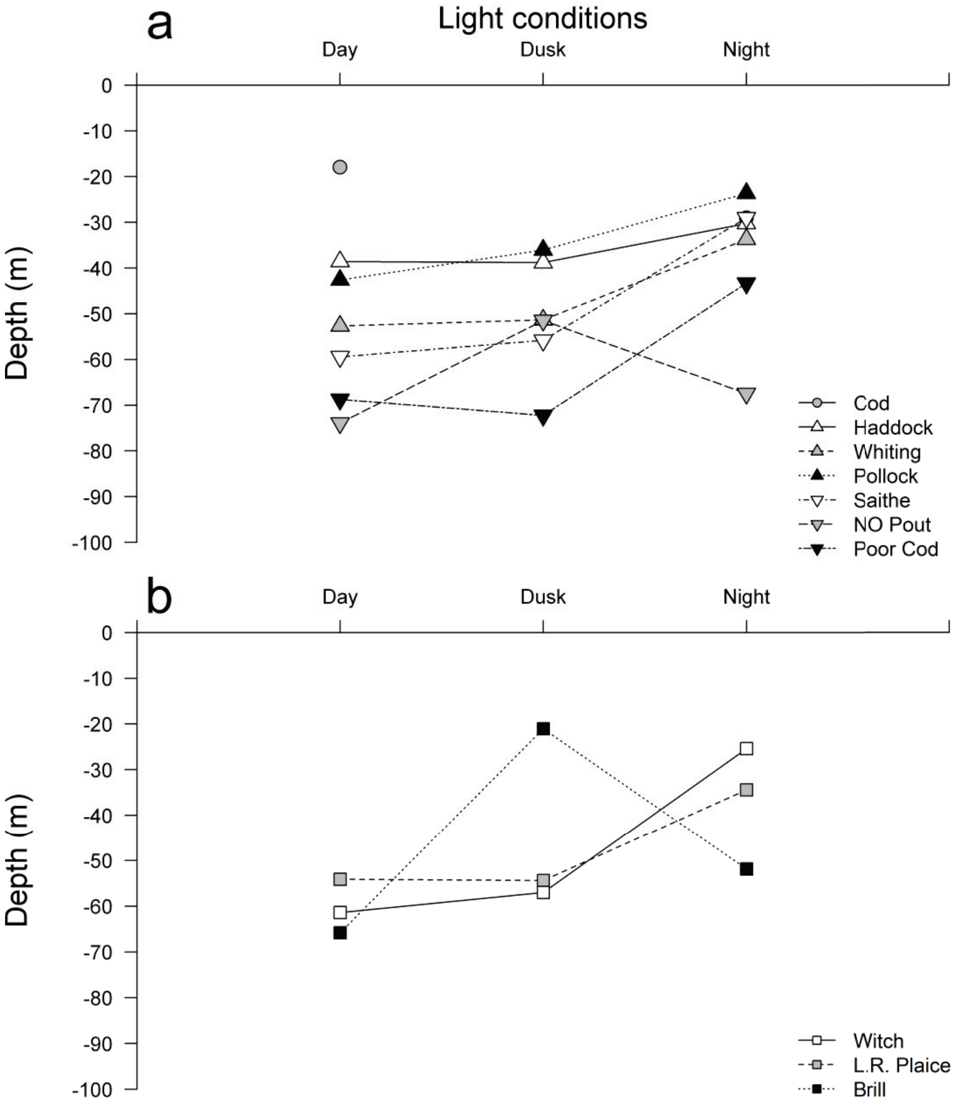


Figure 6: Depth of the centre of mass for gadoid (a) and flatfish larvae (b) during three different light environments. Due to the long days at this time of the year, there was only one station at dusk (21:52 UTC) and night (23:56 UTC), while three stations were in daylight (19:14 UTC, 06:20 UTC and 08:22 UTC).

Discussion

Our study provides evidence for type I vertical migrations in the species examined, except for cod (*Gadus morhua*). However, in time, the migration patterns were not completely consistent, as Norway pout (*Trisopterus esmarkii*) and Brill (*Scophthalmus rhombus*) ascended earlier and pollock (*Pollachius pollachius*) continued to rise until the early morning. With the exception of the two *Trisopterus* species the centre of abundance of all species was within the 20-40 m stratum either at dusk or during the night. In contrast to previous studies (Gray 1996; Olivar & Sabatés 1997) we observed distinct assemblages in the upper and lower water column only during the day.

Our hydrographic observations are in accordance with findings described for the Feie-Shetland section, reported by Hackett (1981). Hydrographic fronts were apparent at the western and eastern margins of the transects. Larval abundances and concentrations of zooplankton <1000 µm were highest in vicinity of these fronts which might imply that the frontal processes aggregate the zoo- and ichthyoplankton (Olson et al. 1994; Olson & Backus 1985). Larval drift and dispersion from spawning grounds around the Shetland Isles are indicated by the general decline in larval abundance and diversity in parallel with an increase in larval mean lengths from these areas towards the East. Similar patterns have been suggested for Norway pout in other studies (Lambert et al. 2009; Nash et al. , submitted).

In accordance with such an east-west size gradient, the smallest average standard lengths were measured at the westerly positioned 18h-station. Cod and haddock (*Melanogrammus aeglefinus*) larvae were in the 6 – 8 mm size range in which Lough & Potter (1993) have observed the first appearance of vertical migrations. The lack of cod larvae below 40 m is in accordance with other observation of early cod larvae confined to the waters above the thermocline (Grønkjær et al. 1997; Grønkjær & Wieland 1997; Huwer et al. 2011; Lough & Potter 1993). Our observations of Type II distributions in cod larvae are described earlier for both the Atlantic and the Pacific cod (*Gadus macrocephalus* Tilesius, 1810) (Boehlert et al. 1985; Munk , submitted). The depth distributions found for haddock, whiting, pollock, Norway pout, witch (*Glyptocephalus cynoglossus*) and long rough dab (*Hippoglossoides platessoides*) was similar to the findings of Economou (1987). Saithe exhibited less variation in Z_{cm} in earlier studies (Munk , submitted). Poor cod (*Trisopterus minutus*) was found shallower than in the present study (Olivar & Sabatés 1997). During the day Frank et al. (1992) found a shallower distribution of witch and long rough dab than in this study, however bottom depth in their study was at 45 m, which may have constricted the depth distribution. The distribution of brill appears not to be described in the literature. In many ways it resembled the distribution of Norway pout, concerning the particularly deep Z_{cm} and the timing of the ascent. However the extent of the vertical migration was greater, covering 43 m.

Thermoclines have been described to lead either to larval aggregation (Lough & Potter 1993; Sabatés et al. 2008) or serve as a boundary for their migrations (Olivar & Sabatés 1997; Röpke 1993). Other studies found no apparent influence of thermoclines on larval vertical distribution and migration patterns (Conway et al. 1997; Gray & Kingsford 2003). The weak stratification and gradual thermocline we observed at the 18-hours station is similar to conditions in the studies of Gray & Kingsford (2003) and this might be the cause of the apparent weak influence of the thermocline in both studies.

The aggregation in the 20 - 40 m stratum during the night suggests support for the hypotheses that a starving population would ascend just far enough to find sufficient food (Pearre 2003). Zooplankton of <1000 µm size were higher concentrated in the top 40 m than below, ca. 46 mg m^{-3} compared to <=30 mg m^{-3}. Particularly high concentrations of zooplankton <1000 µm, 57 mg m^{-3} and 87 mg m^{-3} respectively, in the upper water column during dusk and the early morning may have attracted brill and pollock at these times. However, zooplankton concentration in deeper strata should have been sufficient to fulfil food requirements (equation from Economou 1987; based on: Jones 1973; Laurence 1985), as was the case for average sized Norway pout, for which the shallowest Z_{cm} was at 51 m. The deepest Z_{cm} observed after the apparent feeding period, could be due to resting in deeper, cooler water to save energy (Brett 1971) or less buoyancy due to a full stomach (Sclafani et al. 1993).

In conclusion, whilst the general observation that most of the larvae occur at depths with high concentrations of zooplankton suggests a strong influence from the distribution of potential prey, the general vertical displacement of the mean depth of larval species indicates that other environmental factors might set a species-specific ‘background-depth’ of distribution. Therefore the physical water column structure might be the key factor determining the distribution rather than the prey distributions. As suggested by Sclafani (1993), the neutral buoyancy of fish larvae is influenced by their condition. Farther developed or better fed larvae, may be deeper in the water column, due to higher specific weight. As the species differ in the proportion of tissue types, the depth of neutral buoyancy may be different even when the larvae are in the same condition. We find that the comparative approach used in the present study has the potential for new insight into the drivers behind vertical distribution patterns, and we suggest that further comparative community studies are undertaken.

Acknowledgements

The authors are grateful to the crew of the RV G.O. Sars (IMR, Norway) for undertaking the sampling and members of the IMR Plankton group for assistance with all aspects of the sampling at sea. The authors acknowledge Laura Rey at IMR, Bergen for her expertise in identifying fish larvae and all the other staff in the institute, for the support they provide to guest scientists. The basic support for this sampling programme was provided by the IMR North Sea programme.

References

Boehlert GW, Gadomski DM, Mundy BC. 1985. Vertical distribution of ichthyoplankton off the Oregon coast in Spring and Summer months. Fishery Bulletin (Washington D C). 83:611-621.

Bolz GR, Lough RG. 1984. Growth of Larval Atlantic Cod, *Gadus morhua*, and Haddock, *Melanogrammus aeglefinus*, on Georges Bank Spring, 1981. Fishery Bulletin (Washington D C). 81:827-836.

Brett JR. 1971. Energetic Responses of Salmon to Temperature - Study of Some Thermal Relations in Physiology and Freshwater Ecology of Sockeye Salmon (*Oncorhynchus nerka*). American Zoologist. 11:99-113.

Catalán I, Vollset K, Morales-Nin B, Folkvord A. 2011. The effect of temperature gradients and stomach fullness on the vertical distribution of larval herring in experimental columns. Journal of Experimental Marine Biology and Ecology. 404:26-32.

Conway DVP, Coombs SH, Smith C. 1997. Vertical distribution of fish eggs and larvae in the Irish Sea and southern North Sea. Ices Journal of Marine Science. 54:136-147.

Downing G, Litvak MK. 2001. The effect of light intensity and spectrum on the incidence of first feeding by larval haddock. Journal of Fish Biology. 59:1566-1578.

Economou AN. 1987. Ecology of survival in some gadoid Larvae of the Northern North Sea. Env. Biol. Fish. 19:241-260.

Fortier L, Leggett WC. 1982. Fickian Transport and the Dispersal of Fish Larvae in Estuaries. Can. J. Fish. Aquat. Sci. 39:1150-1163.

Fortier L, Leggett WC. 1983. Vertical Migrations and Transport of Larval Fish in a Partially Mixed Estuary. Can. J. Fish. Aquat. Sci. 40:1543-1555.

Frank KT, Loder JW, Carscadden JE, Leggett WC, Taggart CT. 1992. Larval Flatfish Distributions and Drift on the Southern Grand Bank. Can. J. Fish. Aquat. Sci. 49:467-483.

Golden Software. 2002. Surfer. Version 8.00. Golden, CO: Golden Software, Inc. Computer Programe.

Govoni JJ, Pietrafesa LJ. 1994. Eulerian views of layered water currents, vertical distribution of some larval fishes, and inferred advective transport over the continental shelf off North Carolina, USA, in winter. Fisheries Oceanography. 3:120-132.

Gray CA. 1996. Do thermoclines explain the vertical distributions of larval fishes in the dynamic coastal waters of south-eastern Australia? Marine and Freshwater Research. 47:183-190.

Gray CA. 1998. Diel changes in vertical distributions of larval fishes in unstratified coastal waters off southeastern Australia. Journal of Plankton Research. 20:1539-1552.

Gray CA, Kingsford MJ. 2003. Variability in thermocline depth and strength, and relationships with vertical distributions of fish larvae and mesozooplankton in dynamic coastal waters. Marine Ecology Progress Series. 247:211-224.

Grønkjær P, Clemmesen C, St.John M. 1997. Nutritional condition and vertical distribution of Baltic cod larvae. Journal of Fish Biology. 51:91-352.

Grønkjær P, Wieland K. 1997. Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. Marine Ecology Progress Series. 154:91-105.

Hackett B. 1981. The Feie-Shetland section: a hydrographic atlas. Report No. 3/81. 20 pp and figs.

Hernandez FJ, Hare JA, Fey DP. 2009. Evaluating diel, ontogenetic and environmental effects on larval fish vertical distribution using Generalized Additive Models for Location, Scale and Shape. Fisheries Oceanography. 18:224-236.

Huebert KB, Sponaugle S, Cowen RK. 2010. Predicting the vertical distributions of reef fish larvae in the Straits of Florida from environmental factors. Can. J. Fish. Aquat. Sci. 67:1755-1767.

Huse I. 1994. Feeding at different illumination levels in larvae of three marine teleost species: Cod, *Gadus morhua* L., plaice, *Pleuronectes platessa* L., and turbot, *Scophthalmus maximus* (L.). Aquaculture and Fisheries Management. 25:687-695.

Huwer B, Clemmesen C, Gronkjaer P, Koster FW. 2011. Vertical distribution and growth performance of Baltic cod larvae - Field evidence for starvation-induced recruitment regulation during the larval stage? Prog. Oceanogr. 91:382-396.

Jones R. 1973. Density dependent regulation of the numbers of cod and haddock. Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer. 164:156-173.

Kiørboe T, Munk P, Richardson K, Christensen V, Paulsen H. 1988. Plankton Dynamics and Larval Herring Growth, Drift and Survival in A Frontal Area. Marine Ecology Progress Series. 44:205-219.

Lambert G, Nielsen J, Larsen LI, Sparholt H. 2009. Maturity and growth population dynamics of Norway pout (*Trisopterus esmarkii*) in the North Sea, Skagerrak, and Kattegat. Ices Journal of Marine Science. 66:1899-1914.

Laurence GC. 1985. A report on the development of stochastic models of food limited growth and survival of cod and haddock larvae on Georges Bank. NOAA Technical Memorandum, Report No. NMFS-F/NEC-36. p 83-150.

Leis JM. 1991. Vertical distribution of Fish Larvae in the Great Barrier Reef Lagoon, Australia. Marine Biology. 109:157-166.

Lough RG, Caldarone EM, Rotunno TK, Broughton EA, Burns BR, Buckley LJ. 1996. Vertical distribution of cod and haddock eggs and larvae, feeding and condition in stratified and mixed waters on southern Georges Bank, May 1992. Deep-Sea Research Part Ii-Topical Studies in Oceanography. 43:1875-1904.

Lough RG, Potter DC. 1993. Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. Fishery Bulletin. 91:281-303.

Lovetskaya AA. 1953. Distribution and behavior of the Caspian Sea sprat. Fisheries Industry. 12:29-35.

Millero FJ, Poisson A. 1981. International One-Atmosphere Equation of State of Seawater. Deep-Sea Research Part A-Oceanographic Research Papers. 28:625-629.

Munk P. submitted. Physics and fish larvae - linkages across a frontal zone at the Norwegian Trench.

Munk P, Nielsen J. 2005. Eggs and Larvae of North Sea Fishes. Frederiksberg: Biofolia. 224pp.

Munk P, Wright PJ, Pihl NJ. 2002. Distribution of the early larval stages of cod, plaice and lesser sandeel across haline fronts in the North Sea. Estuar. Coast. Shelf. S. 55:139-149.

Nash RDM, Dickey-Collas M, Milligan SP. 1998. Descriptions of the Gulf VII/PRO-NET and MAFF/Guildline unencased high-speed plankton samplers. Journal of Plankton Research. 20:1915-1926.

Nash RDM, Wright P, Matejusova I, Dimetrov S, O'Sullivan M, Augley J, Höffle H. submitted. Spawning location of Norway pout (*Trisopterus esmarkii* Nilsson) in the North Sea. Ices Journal of Marine Science.

Neilson JD, Perry RI. 1990. Diel Vertical Migrations of Marine Fishes - An Obligate Or Facultative Process. Adv. Mar. Biol. 26:115-168.

Olivar MP, Sabatés A. 1997. Vertical distribution of fish larvae in the north-west Mediterranean Sea in spring. Marine Biology. 129:289-300.

Olson DB, Backus RH. 1985. The Concentrating of Organisms at Fronts: A cold-water Fish and a warm-core Gulf Stream ring. Journal of Marine Research. 43:113-137.

Olson DB, Hitchcock GL, Manano A, Ashjian CJ, Peng G, Nero RW, Podesta GP. 1994. Life on the edge: marine life and fronts. Oceanography. 7:52-60.

Pearre S. 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. Biological Reviews. 78:1-79.

Pearre S. 1973. Vertical Migration and Feeding in *Sagitta elegans* Verrill. Ecology. 54:300-314.

Röpke A. 1993. Do larvae of mesopelagic fishes in the Arabian Sea adjust their vertical distribution to physical and biological gradients? Marine Ecology Progress Series. 101:223-235.

Russel FS. 1976. The Eggs and Planktonic Stages of British Marine Fishes. London: Academic Press. 524 pages.

Sabatés A. 1990. Changes in the Heterogeneity of Mesoscale Distribution Patterns of Larval Fish Associated with A Shallow Coastal Haline Front. Estuarine, Coastal and Shelf Science. 30:131-140.

Sabatés A, Zaragoza N, Grau C, Salat J. 2008. Vertical distribution of early developmental stages in two coexisting clupeoid species, *Sardinella aurita* and *Engraulis encrasicolus*. Marine Ecology Progress Series. 364:169-180.

Schmidt J. 1906. The pelagic post-larval stages of the Atlantic species of Gadus Part I. Bianco Lunos Bogtrykkeri, Report No. Bind I Nr. 4.

Sclafani M, Taggart CT, Thompson KR. 1993. Condition, Buoyancy and the Distribution of Larval Fish - Implications for Vertical Migration and Retention. Journal of Plankton Research. 15:413-435.

Southward AJ, Barrett RL. 1983. Observations on the Vertical distribution of zooplankton, Including post-larval teleosts, off Plymouth in the presence of a thermocline and a chlorophyll dense layer. Journal of Plankton Research. 5:599-618.

Systat Software Inc. 2011. SigmaPlot for Windows. Version 12.0.

Theilacker GH. 1980. Changes in Body Measurements of Larval Northern Anchovy, *Engraulis mordax*, and Other Fishes Due to Handling and Preservation. Fishery Bulletin. 78:685-692.

Vollset KW, Catalan I, Fiksen O, Folkvord A. submitted. State dependend behaviour of larval cod according to temperature and light gradients in experimental columns.

Wiebe PH, Morton AW, Bradley AM, Backus RH, Craddock JE, Barber V, Cowles TJ, Flierl GR. 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Marine Biology. 87:313-323.

Woodhead PMJ. 1966. The behaviour of fish in relation to light in the sea. Oceanography and Marine Biology Annual Review. 4:337-403.

Yoon HS, Hwang JH, Choi SD. 2010. Effect of light intensity on first feeding of the chub mackerel *Scomber japonicus* larvae. Animal Cells and Systems. 14:125-128.

Supplement:

Table S1: Average abundances and standard lengths (±1 SE) for all species identified in the northern transect (a), the southern transect (b) and at the 18h-station (c). Numbers are based on depth integrated GULF VII, except for species which were only found in MOCNESS hauls. These species are denoted with asterisks.

a

	Taxon		**Abundance**			**Std. Lenght**		
Transect	**Family**	**Species**	**(no. m^{-2})**			**(mm)**		
60.75°N	Clupeidae	*Clupea harengus*	8.7	±	2.5	18.2	±	0.2
	Gadidae	*Melanogrammus aeglefinus*	6.9	±	4.2	8.9	±	1.2
		Merlangius merlangus	28.0	±	22.2	7.7	±	0.3
		Pollachius pollachius	3.8	±	0.9	8.4	±	0.2
		Pollachius virens	14.1	±	7.1	9.2	±	0.5
		Trisopterus esmarkii	64.2	±	38.1	8.5	±	0.5
		Trisopterus minutus	17.5	±	15.8	8.7	±	0.3
		Unidentified	7.4	±	1.9	6.1	±	0.5
	Gobiidae	*Gobiusculus flavescens*	16.6	±	0.0	6.9	±	0.0
	Lotidae	*Ciliata septentrionalis*	6.0	±	5.1	5.5	±	0.3
		Molva dipterygia	5.5	±	0.0	6.5	±	0.0
		Molva molva	33.3	±	0.0	5.2	±	0.0
	Pleuronectidae	*Glyptocephalus cynoglossus*	6.2	±	4.9	9.5	±	0.4
		Hippoglossoides platessoides	15.1	±	7.1	8.5	±	0.3
		Limanda limanda	7.8	±	4.5	7.3	±	1.7
		Pleuronectes platessa	11.1	±	0.0	6.3	±	0.0
		Unidentified	1.7	±	0.9	7.8	±	0.4
	Scophthalmidae	*Lepidorhombus whiffiagonis*	5.5	±	0.0	10.6	±	0.0
		Phrynorhombus norvegicus	1.1	±	0.3	9.2	±	0.7
		Scophthalmus rhombus	9.0	±	7.7	5.3	±	0.5

b

	Taxon		**Abundance**			**Std. Lenght**		
Transect	**Family**	**Species**	**(no. m^{-2})**			**(mm)**		
59.3°N	Ammodytidae	*Ammodytes marinus*	15.5	±	0.0	16.2	±	0.0
		Hyperoplus lanceolatus	3.0	±	1.9	18.1	±	5.3
		Unidentified	1.2	±	1.0	17.5	±	3.7
	Argentinidae	*Argentina sphyraena*	2.2	±	0.0	10.0	±	0.0
	Clupeidae	*Clupea harengus*	14.6	±	13.8	17.3	±	26.3

b (continued)

	Taxon		Abundance	Std. Lenght
Transect	**Family**	**Species**	**(no. m^{-2})**	**(mm)**
59.3°N	Gadidae	*Gadus morhua*	7.4 ± 5.3	10.5 ± 3.5
		Melanogrammus aeglefinus	12.7 ± 5.6	10.1 ± 5.0
		Merlangius merlangus	13.1 ± 6.9	5.8 ± 8.2
		Pollachius pollachius	5.2 ± 3.1	9.7 ± 6.7
		Pollachius virens	6.6 ± 4.5	10.1 ± 10.5
		Trisopterus esmarkii	76.1 ± 41.7	10.2 ± 5.0
		Trisopterus minutus	11.0 ± 6.8	6.4 ± 7.9
		Unidentified	5.5 ± 3.4	9.2 ± 0.0
	Lotidae	*Ciliata mustela*	4.4 ± 0.0	5.1 ± 0.0
	Pleuronectidae	*Hippoglossoides platessoides*	5.7 ± 2.9	11.1 ± 6.3
		Limanda limanda	6.6 ± 4.5	7.6 ± 10.9
	Scophthalmidae	*Scophthalmus rhombus*	4.4 ± 0.0	3.8 ± 0.0

c

	Taxon		Abundance	Std. Lenght
Transect	**Family**	**Species**	**(no. m^{-2})**	**(mm)**
18h-Station	Ammodytidae	*Hyperoplus immaculatus**	1.0 ± 0.0	11.9 ± 0
		Hyperoplus lanceolatus	4.1 ± 0.0	40.0 ± 0.0
	Argentinidae	*Argentina sphyraena*	25.0 ± 15.6	9.9 ± 0.5
	Clupeidae	*Clupea harengus*	2.5 ± 0.0	14.9 ± 0.0
	Gadidae	*Gadus morhua*	6.4 ± 0.0	5.8 ± 0.0
		Melanogrammus aeglefinus	4.5 ± 0.8	6.3 ± 0.6
		Merlangius merlangus	152.3 ± 61.9	6.2 ± 0.2
		Pollachius pollachius	15.7 ± 10.0	7.4 ± 0.6
		Pollachius virens	15.3 ± 3.8	6.7 ± 0.9
		Trisopterus esmarkii	81.2 ± 34.7	7.2 ± 0.1
		Trisopterus minutus	9.3 ± 3.6	5.9 ± 0.6
		Unidentified	18.0 ± 4.9	5.3 ± 0.2
	Gobiidae	*Gobius niger*	4.1 ± 0.0	5.5 ± 0.0
		Gobiusculus flavescens	17.9 ± 0.0	6.8 ± 0.0
		*Unidentified**	0.9 ± 0.0	2.7 ± 0.0
	Lotidae	*Ciliata septentrionalis*	29.7 ± 12.1	5.7 ± 0.2
		Molva dipterygia	35.8 ± 0.0	7.9 ± 0.0
		Molva molva	12.7 ± 0.0	6.9 ± 0.0
	Pleuronectidae	*Glyptocephalus cynoglossus*	7.7 ± 3.5	6.9 ± 0.5
		Hippoglossoides platessoides	25.2 ± 15.6	8.2 ± 0.7
		Limanda limanda	12.5 ± 0.0	6.8 ± 0.0
		*Platichthys flesus**	2.0 ± 0.0	3.5 ± 0.0
		Pleuronectes platessa	4.1 ± 0.0	10.4 ± 0.0
		Unidentified	3.3 ± 0.8	5.3 ± 0.2
	Scophthalmidae	*Scophthalmus rhombus*	18.6 ± 9.1	4.5 ± 0.2

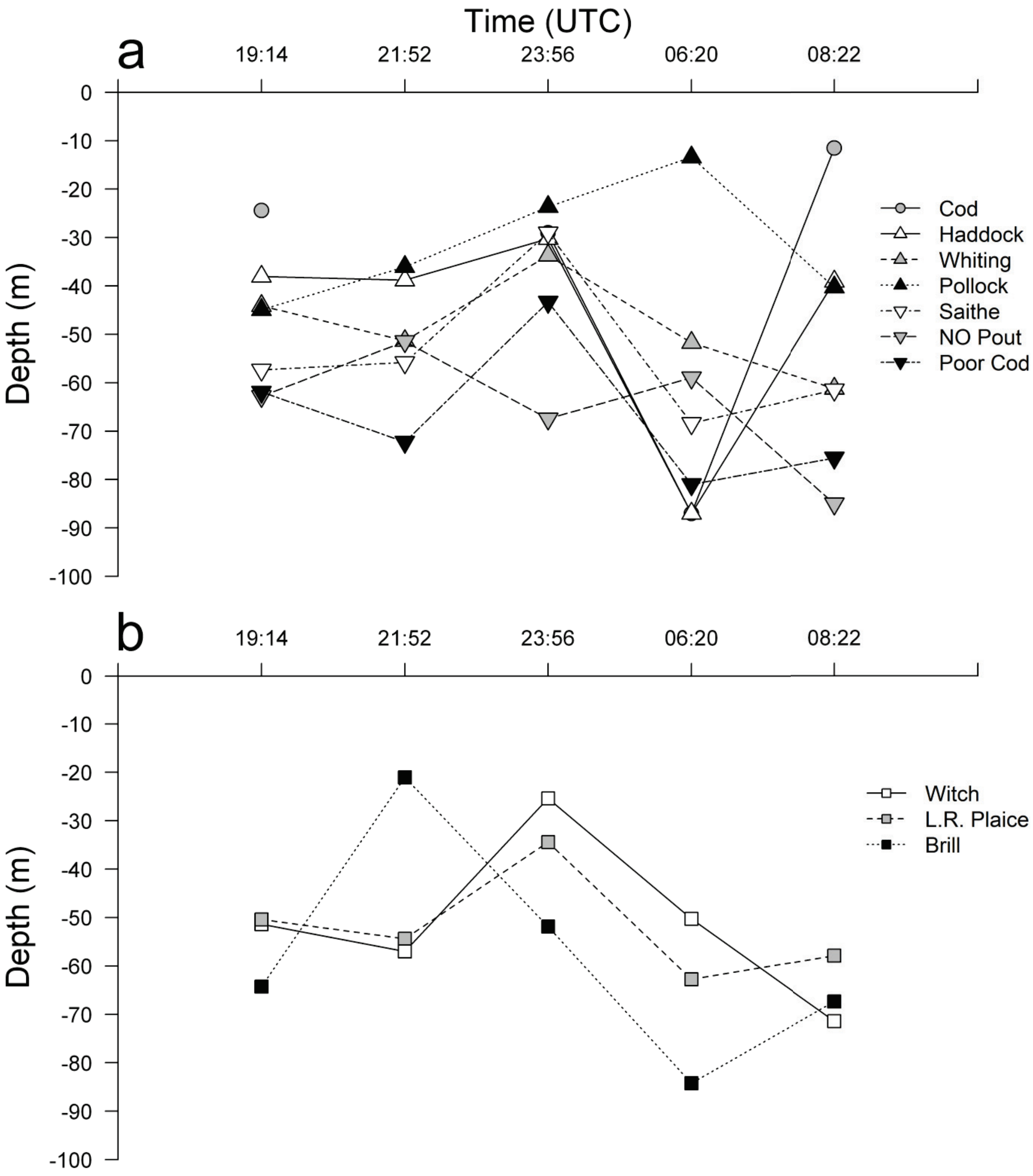


Figure S1: Depth of mass for gadoid (a) and flatfish larvae (b) for individual samples taken at the 18h-station. Daylight stations were at 19:14 UTC, 06:20 UTC and 08:22 UTC, the station at 21:52 UTC was during dusk and the station at 23:56 UTC in the night.

Paper IV

Distribution of juvenile cod settlement sites in the North Sea during the period 1991 to 2010

HANNES HÖFFLE[1*] AND PETER MUNK[1]

[1]*DTU Aqua, National Institute of Aquatic Resources, Technical University of Denmark, Kavalergården 6, DK-2920 Charlottenlund, DENMARK*

**Correspondence.* E-mail: hhoe@aqua.dtu.dk

Abstract

Settlement to the sea bottom is a crucial event in the early life of demersal fishes. In the North Sea juvenile cod (*Gadus morhua*) settles at traditional nursery grounds on offshore banks or in shallow coastal areas. The conditions in these areas are determined by temporally invariable factors like bottom depth and dynamic factors like hydrography and by extension climatic variability. In the present study we examined the distribution of juvenile North Sea cod from a 20 year period, 1991 to 2010 with the aim of estimating the relative influence of environmental factors on juvenile cod settlement. Samples of juveniles and hydrographic information were available from the International Bottom Trawl Survey (IBTS) in the third quarter of the year. During the investigated period the observed bottom temperature and salinity showed marked frontal phenomena across the central and in the northwestern North Sea, structures that persisted during the two decades. While the abundance of juveniles generally declined over the years, the nursery grounds in the Skagerrak/Kattegat became relatively more important. Their potential habitat was modelled using Generalized Additive Models (GAMs) on presence/absence information of juvenile cod. This showed temperature, salinity, bottom depth and geographic position as the core variables for describing their habitat. A model fit to five year periods gave an explained deviation up to 51% and a good agreement between predicted and observed distributions for the following five year period. When using model fit to a longer 10-year period the predictions were however poor; apparently this

model fit did not fully capture the declining occurrence of juvenile cod in the central North Sea seen during the 2000s. Hence, habitat modelling is useful for analysis and description of juvenile North Sea cod distributions on the shorter time scale, while understanding of long-term decadal changes necessitates incorporation of population dynamics of the stocks.

Introduction

During the early juvenile stage cod (*Gadus morhua*) changes habitat from the planktonic/pelagic of the larval life to the demersal of the adults. This change might influence survival as mortalities during this stage have been reported to reach the levels seen in earlier stages (Serchuck *et al.*, 1994; Sissenwine, 1984). However, the absence of a check on the otoliths during this period, which would mark drastic changes in condition (Bolz and Lough, 1988), as well as the prolonged presence of the planktonic copepods in stomachs of settled young cod (Hüssy *et al.*, 1997; Pinnegar and Stafford, 2007) indicate a gradual change in their choice of habitat.

The demersal life of the settled juveniles is influenced by the type of substrate at the settling site, different types of substrate entail different post-settlement mortality rates (Juanes, 2007), and a more complex relief such as on gravel or in seagrass beds may promote survival by providing more refuge from predators. (Gotceitas *et al.*, 1997; Lough, 2010; Lough *et al.*, 1989), Juvenile cod might start to seek a suitable area for settlement already at sizes of 35 mm (Andrews *et al.*, 2006; Heath *et al.*, 2008) and the location of settlement would partially be determined by active swimming and partially by passive transport.

The influence of currents on the drift of larvae/juveniles to the settling sites has led to concerns about the effect of climate change on the distribution of settling juvenile fish. Rindorf & Lewy (2006) proposed a climate related northward shift in the centre of abundance of juvenile 1-group North Sea cod. They suggested that a series of warm winters, with predominant winds from the south has led to a shift of settling juveniles towards the north, which would subsequently spawn in these areas due to homing behaviour. However, using a higher resolution for the population structure the observed shift of the population centre can be explained by changes in local sub-populations alone (Holmes *et al.*, 2008; Righton *et al.*, 2007). Likewise, while homing might be important in some cases the separation of some sub-populations in the North Sea can be explained by their distance and the effects of oceanography alone (Heath *et al.*, 2008). Distances between spawning areas and settling sites can be substantial, for example settling sites in the southern North Sea may receive settling juveniles from across the North Sea (Heath *et al.*, 2008). Similarly, the Skagerrak receives a considerable percentage of settling juveniles through influx from the North Sea (Stenseth *et al.*, 2006).

The distributional patterns of juvenile cod in the North Sea were surveyed during the International 0-group Gadoid Survey (IOGS), conducted in June from 1969 to 1980. During these surveys aggregations of pelagic 0-group cod, ranging in mean lengths from 3 to 5 cm (Riley and Parnell, 1984), were found off the Danish west coast, east of Shetland and of the Firth of Forth (Holden, 1981). The lower end of the size range for demersal 0-group cod was found to be 6 cm (Riley and Parnell, 1984).

Additional information on distribution of juvenile cod has become available from the onset of the third quarter surveys in 1991 during an International Bottom Trawl Survey programme coordinated by ICES. While the IOGS were dedicated to the catch of pelagic juveniles, the IBTS is not targeting fish in the size range of the early pelagic juveniles. As the name of the program indicates, the gear is a bottom trawl (GOV) designed for catching larger juveniles and adults; hence the catch of small juveniles is mainly due to the small-meshes in the cod-end part of the trawl. While catches are highly variable, 0-group cod were quite frequently caught. From the available time series 1991-2010 of 5658 hauls, 1260 of these contained some 0-group cod. Hence, due to the large spatial and temporal coverage this survey series contains valuable information, and in the present study we will use the observations for two purposes: 1) to describe the general distribution of settlements sites and changes herein during the 20 year period and 2) to elucidate potential environmental influence on distributional patterns of settling sites from general additive models of presence/absence information.

Materials and Methods

Field sampling and data treatment

Since 1991 the International Bottom Trawl Survey (IBTS) is conducted in the 1st and 3rd quarter of each year, and between 1991 and 1996 also quarters two and four were surveyed. Each ICES rectangle (1° longitude x 0.5° latitude) is fished twice per survey with a GOV-trawl which is a bottom trawl but with a height of about 4.5 m (GOV = Grande Ouverture Verticale). Duration of hauls is standard 30 minutes each (ICES, 2010a). Catches are sorted, identified to species level, measured and aged aboard ship and the data stored in the DATRAS data base (ICES, 2012a). For the present study, data was extracted from DATRAS and the ICES oceanographic data bases (ICES, 2012b), covering a geographic area from 3°W to 12°E and 51 – 62°N, including the North Sea proper, the Skagerrak and the Kattegat. Fishing data was extracted as Catch Per Unit Effort (CPUE, Nos. h^{-1}) for each haul and for each statistical rectangle for the periods 1991-1996 (all quarters) and 1991-2010 (3rd quarter).

Temperature and salinity data was extracted for the 3rd quarter only. CTD casts with missing data, in river mouths and fjords were removed and the remainder used in two ways. Firstly neighbouring CTD casts and GOV hauls were determined by calculating the great circle distance between fishing hauls and the CTD casts in R (package sp; Bivand *et al.*, 2008). Only fishing hauls were considered for statistical analysis, where the nearest CTD station was no more than 10 nautical miles (NM) away and no more than 7 days earlier or later, reducing the number of stations available for statistical analysis from 5658 to 2830.

Secondly an experimental variogram was calculated for each year’s bottom temperature and bottom salinity and a theoretical variogram of spherical type was selected by eye-fitting and least square regression. The average bottom temperature and salinity were interpolated by kriging on a regular grid of 0.15 by 0.15 degrees.

Mean CPUE for 0-group cod by statistical rectangle was calculated for five year periods, log(n+1) transformed and plotted in R (R Development Core Team, 2008) for all quarters from 1991-1995 and for the 3rd quarter for the reminder of the years. All fish caught in the GOV-trawl were considered as associated to the bottom and therefore settled. Since the GOV-trawl has relatively large mesh sizes, (200-50 mm vs. 150-12 mm; Holden, 1981; ICES, 2010a) the CPUE was not considered reliable enough for quantitative statistical analysis. Therefore CPUE per haul was binary transformed to 1 for values >0 and 0 for hauls without catch of 0-group cod. Similarly to the information on hydrography the presence/absence of juveniles for each year was interpolated by kriging on a regular grid (0.5 x 0.5 degrees) and the mean probability of occurrence of 0-group cod was calculated for periods of five and ten years.

The potential habitat of settled juvenile cod was fitted to the data in the periods 1991-1995, 2001-2005 and 1991-2000 using Generalized Additive Models (GAMs). Of the 2830 available stations, 813 stations fell in the period 1991-1995 and 744 in the period 2001-2005. For the ten year period 1991-2000 the number of stations was 1352. GAM models were based on the general form (after Wood, 2006):

$$g(\mu_i) = \beta_0 + f_1(x_{1i}) + f_2(x_{2i}) + \cdots + f_n(x_{ni}) \tag{1}$$

where g is a known monotonic link function, $\mu i \equiv E(y_i)$ is determined by the explanatory variables x_{1i} to x_{ni}, f_j are smooth functions for these covariates and β_0 is a vector of parameters to be estimated. For the presence/absence data in this model g was a logit link and the exponential family distribution y_i was binomial. Covariates for the model were chosen upon a review of the existing literature, and could be distinguished into temporally stable variables (e.g. bottom depth) and such that are variable in time, like temperature and salinity. Geographic location was included as an isotropic bivariate term, as this may be more meaningful than summing up longitude and latitude as single terms (Wood and Augustin, 2002). As it influences the availability of prey and refuge, the substrate type may be an important factor for the distribution of 0-group cod (Lough, 2010). Hence, six categories of substrate, namely coarse sediment, mixed sediment, sand to muddy sand, mud to sandy mud, till, rock and other hard substrates (EUSeaMap, 2011) were introduced into the model. Bottom depth was included as 0-group cod was shown to be particularly abundant in shallow water (Riley and Parnell, 1984). The depth was extracted from a 1 NM grid (Weiergang, 1995) and the slope calculated from the same grid in ArcMap (ESRI, 2010) with the formula:

$$\Theta = \tan^{-1}\left\{\sqrt{\left[\left(\frac{dz}{dx}\right)^2 + \left(\frac{dz}{dy}\right)^2\right]}\right\} \times \frac{180}{\pi} \tag{2}$$

where Θ is the slope in degrees, dx the distance in longitudinal direction, dy the distance in latitudinal direction and dz is the change in elevation. The constant converts the result from radians to degrees.

Slope was included, since the shelf break and the margins of offshore banks are focal points for the occurrence of tidal fronts, which promote the production of food (Otto *et al.*, 1990). Since we were interested in the influence of time variable factors on the distribution of settled juvenile cod, we included the bottom temperature and bottom salinity as single terms and their tensor product to characterize the water mass on the whole. Although it is not part of the abiotic environment, the presence/absence of 2-group cod was included, because at this age cod starts to feed on smaller gadoids, including younger conspecifics, while the 2-group is at least seasonally in the same area as the settled 0-group cod (Riley and Parnell, 1984) and appears not to avoid shallow and low saline areas like the older and more cannibalistic individuals.

Using only environmental data to model the habitat of a species entails the risk that their importance is overestimated (Loots *et al.*, 2010), resulting in overly complex models as none of the environmental variables is excluded. In the context of constructing the ‘potential habitat’, the modelling effort is restricted to the species response to its environment, therefore spatial dependency which would depend on the distribution of aggregations was left out of consideration (Planque *et al.*, 2011). Forward fitting, i.e. starting out with single variables and then increasing the complexity of the model while carefully comparing the performance of the different models (as in Planque *et al.*, 2007) can help to keep the number of covariates as low as possible. In the present study the model performance was evaluated by %-explained deviation, Un-Biased Risk Estimator (UBRE) and Akaike Information Criterion (AIC). In case two models were too similar to decide based on these indices we compared them in ANOVA using a Chi-square test.

To validate the fitted GAM models, the probability of occurrence for settled 0-group cod was predicted for the following five or ten year period. The number of stations to be predicted was 539 for 1996-2000, 734 for 2006-2010 and 1478 for 2000-2010. The predictions were interpolated on the same spatial grid as the observations and were evaluated graphically by comparing the interpolated surfaces for observation and model as well as with a Taylor diagram, with standard deviation, Root Mean Square Error (RMSE) and Spearman correlation coefficient ($r_{S)}$ as similarity indices.

Results

Hydrography

The bottom temperature showed the same general picture for the investigated five-year periods (Fig. 1). The dominant feature is the bottom front extending through the southern part of Skagerrak and then crossing the North Sea towards the Yorkshire coast south of Flamborough Head. The influence of the shallow Dogger Bank is obvious while the isotherms follow the bank around most of its circumference, and from the Yorkshire coast the front extends north and encircles the Shetland Isles. Off the front, in the northeastern and central North Sea, the bottom temperatures is 7-8°C, while temperatures in more shallow areas might reach 18°C . Neither the bottom salinity differed much between the five-year periods (Fig. 2). Water of Atlantic origin (>35) extends into the North Sea, reaching to latitude 56-57°N, and the central areas are influenced by this water and of relatively high salinity (>34.7). In shallow coastal areas the river runoff strongly influences the salinity patterns, and a salinity related front is apparent along the coasts of Netherlands, Germany and Denmark.

Abundance of 0-group cod

The catches of cod juveniles during the four quarters of the year illustrate the progression of cod settling and respective distribution of juveniles of a given year class during its first year of life (Fig. 5). The earliest settled juvenile cod were found in the 2nd quarter (Fig. 5a), primarily in the area of the Great Fisher Bank and off Jutland, while none were found in the rest of the North Sea. In these catches the juveniles were in the interval 3-7 cm (Fig. 3).

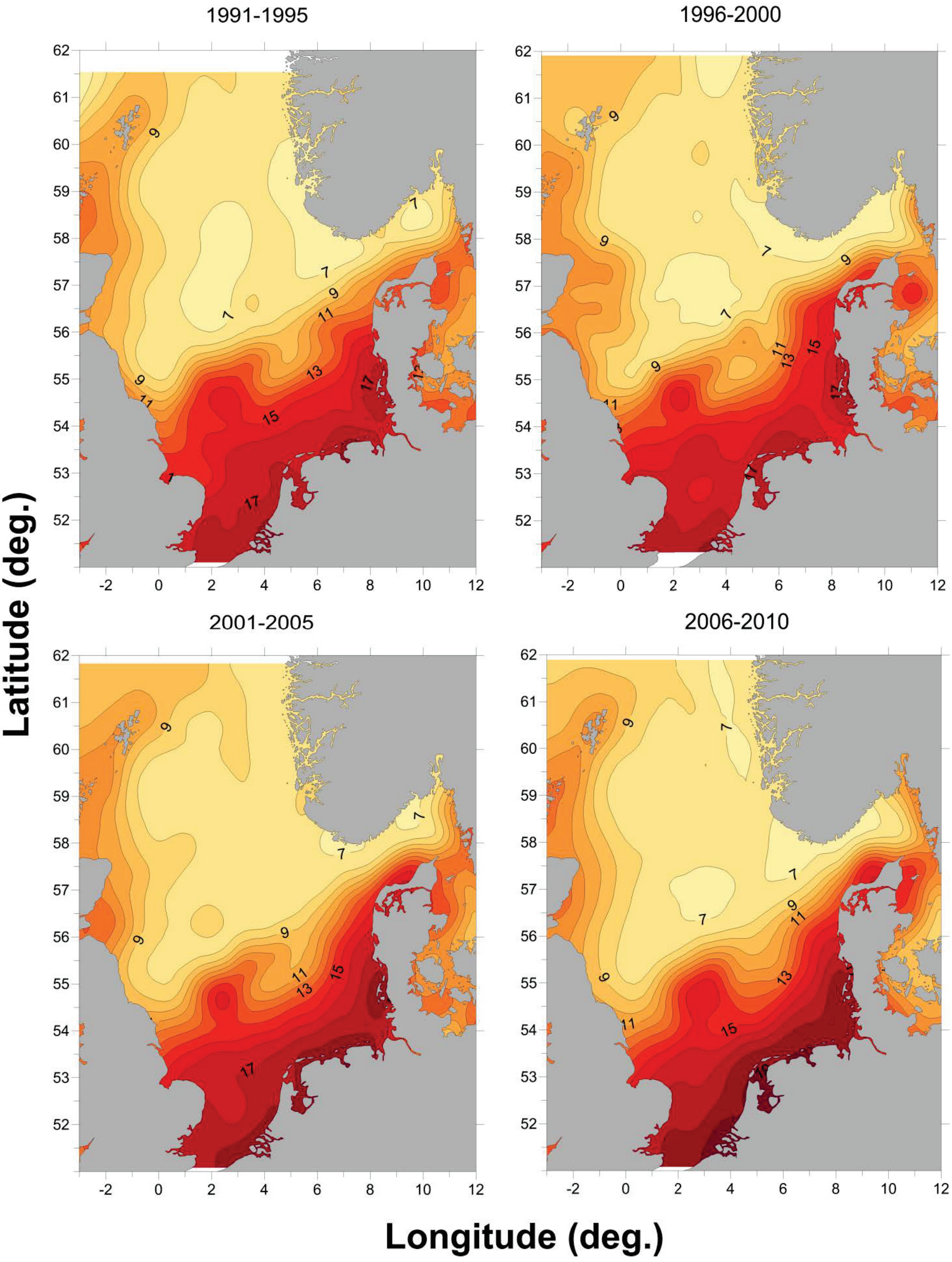


Figure 1: Mean bottom temperature (°C) in the 3rd quarter for periods of five years.

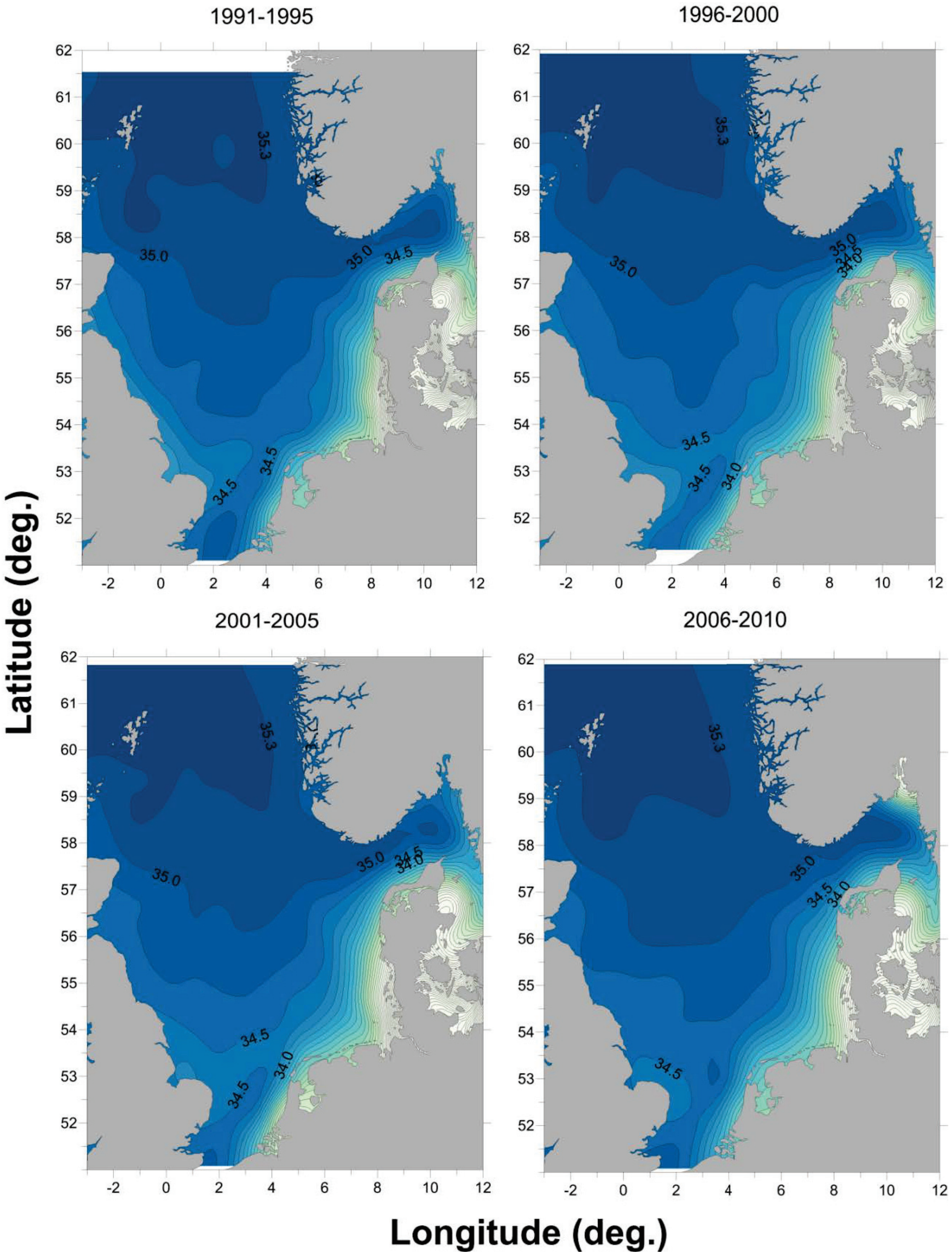


Figure 2: Mean bottom salinity in the 3rd quarter for periods of five years. The southern North Sea was mostly covered with bottom water of salinities >=34.5, salinities >=35 were found as far south as 56°N.

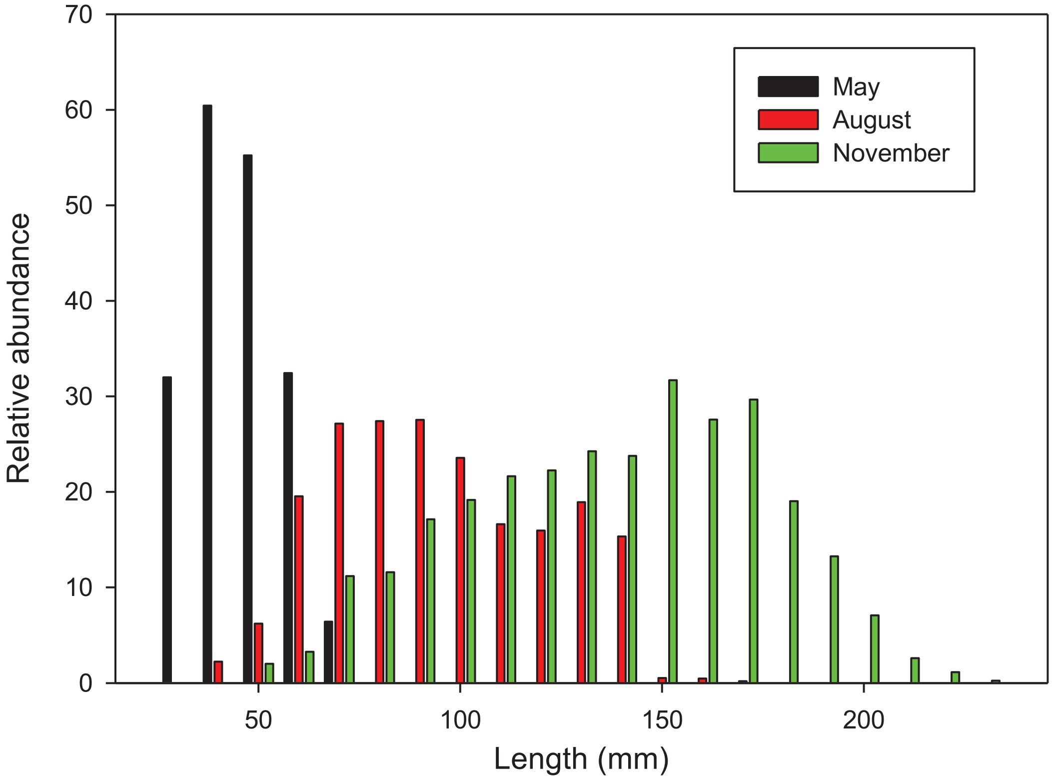


Figure 3: Relative abundance of 0-group cod per length class (mm) in GOV trawls during surveys in 1991-1996. Quarter 2 surveys were carried out in May, quarter 3 surveys in August and quarter 4 surveys in November.

In the 3rd quarter (Fig. 5b) aggregations of 0-group cod in the size range 5-14 cm in the Skagerrak, the German Bight and at the Fisher Banks, while in the 4th quarter sizes have reached 6-21 cm and abundances were more broadly distributed between the Great Fisher Bank, the Skagerrak and the German Bight (Fig. 5c). In the first quarter of the following years, 1-group cod was similarly distributed as 0-group cod in the 4th quarter, but at generally lower abundances (Fig. 5d). Only in the Skagerrak and the Kattegat abundances were of similar magnitude as in the 4th quarter, and on the western margin of the North Sea the abundances off Flamborough were higher than those of 0-group cod in the 4th quarter. On the whole, catch per unit effort declined during the period (Fig. 4). While a few years in the 1990s yielded CPUE >100 h^{-1}, in the 2000s only one year exceeded a

CPUE of 30 h^{-1}. From 2007 on CPUE was constantly declining to 0.8 h^{-1} in 2010. Similarly, the maximum CPUE fell from 2320 h^{-1} in 1991-1995 to 137 h^{-1} in 2006-2010.

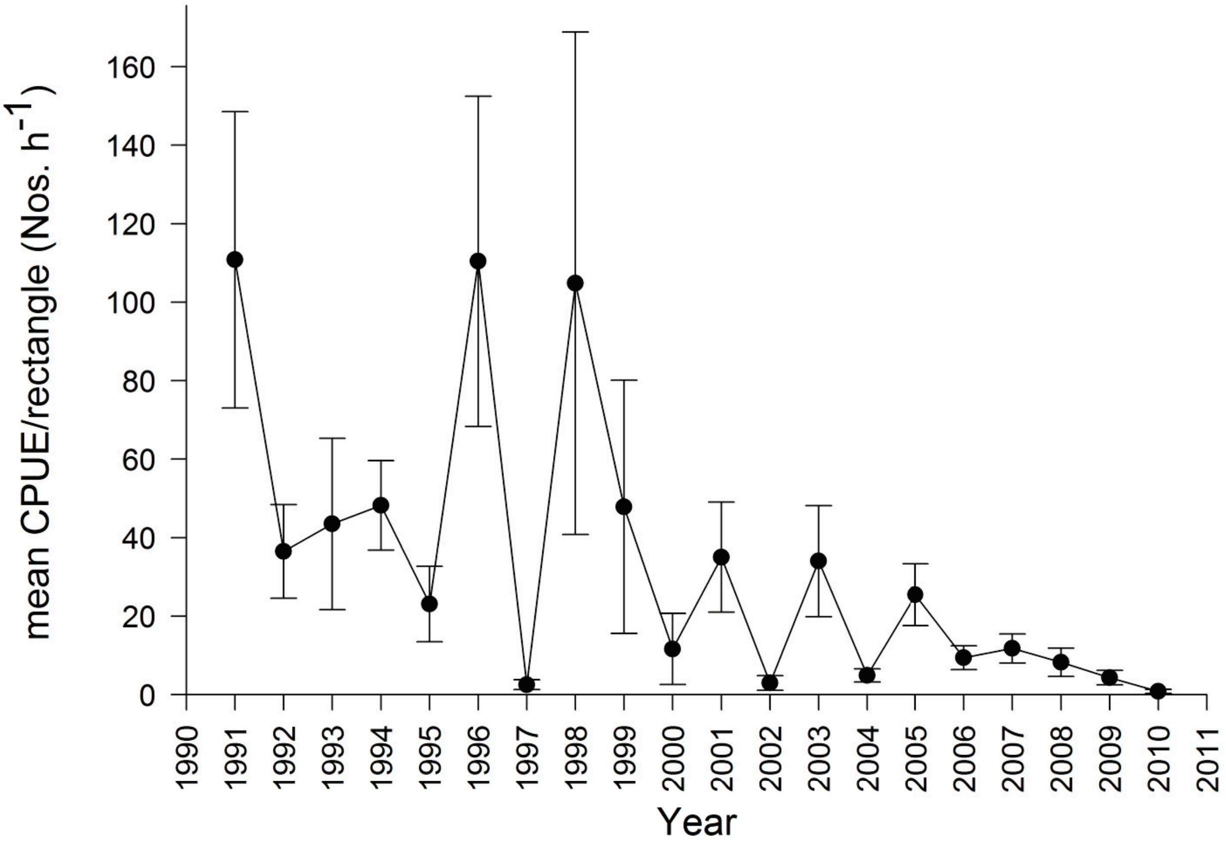


Figure 4: Mean catch per unit effort per ICES rectangle (Nos. $h^{-1}\pm 1$SE) of 0-group cod, for the 3rd quarter of each year from 1991 to 2010. In most years after 2000 the abundance was significantly lower than in the previous decade.

The distribution in the third quarter exhibited substantial change in the 20 year covered by the study (Fig. 6). While in 1991-1995 aggregations of 0-group cod occurred in the Skagerrak, the German Bight and at the Fisher Banks (Fig. 6a) offshore abundances declined in the following five years (Fig. 6b). Further, the centre of abundance in the German Bight shifted northwards along the Danish west coast. A noticeable decrease in the Skagerrak/Kattegat area occurred in 2006-2010. In that period, highest abundances in the North Sea proper were observed at the Little Fisher Bank and in the Southern bight.

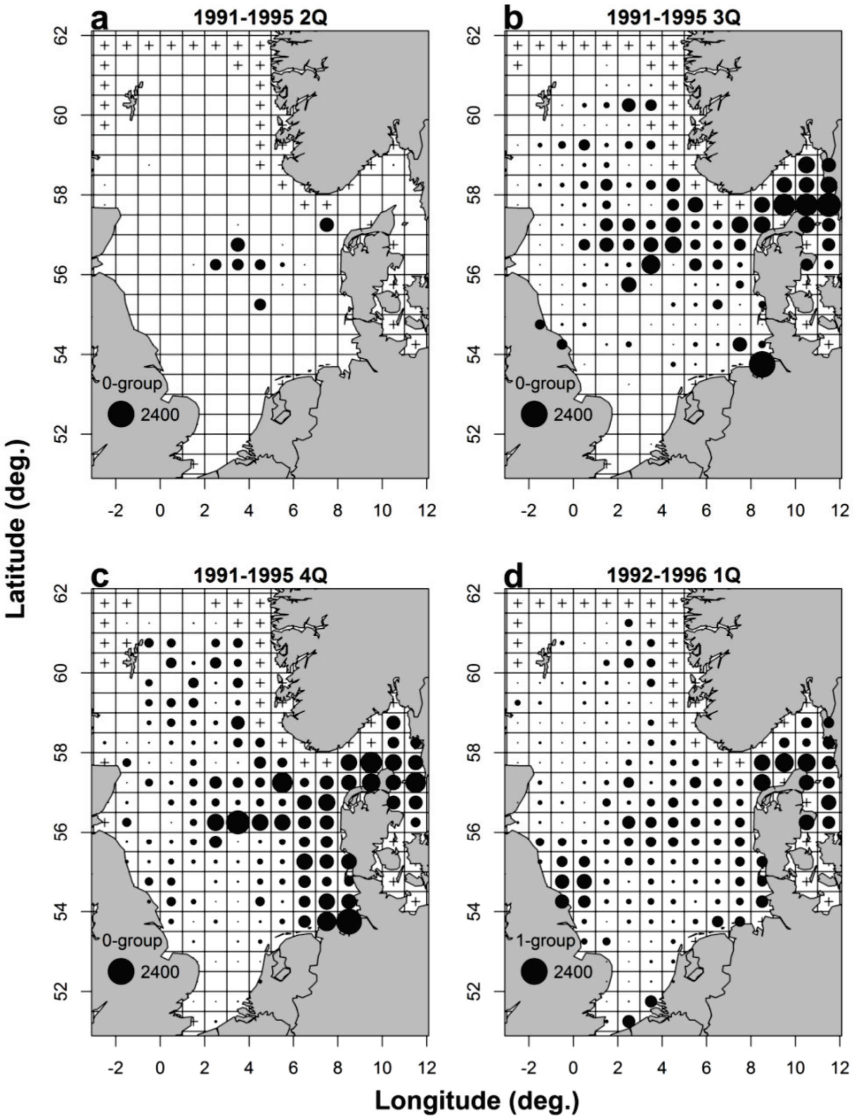


Figure 5: Catch per unit effort per ICES rectangle (log(Nos. h^{-1}+1)) for each quarter, averaged over the period 1991 to 1995 and for the 1st quarter 1992 to 1996. The maps for quarters 2-4 depict the distribution of 0-group cod, while the map for the 1st quarter depicts the distribution of 1-group cod. The reference dot in each panel depicts the next higher multiple of 100 to the peak CPUE over the whole period. Rectangles not sampled are marked with a cross.

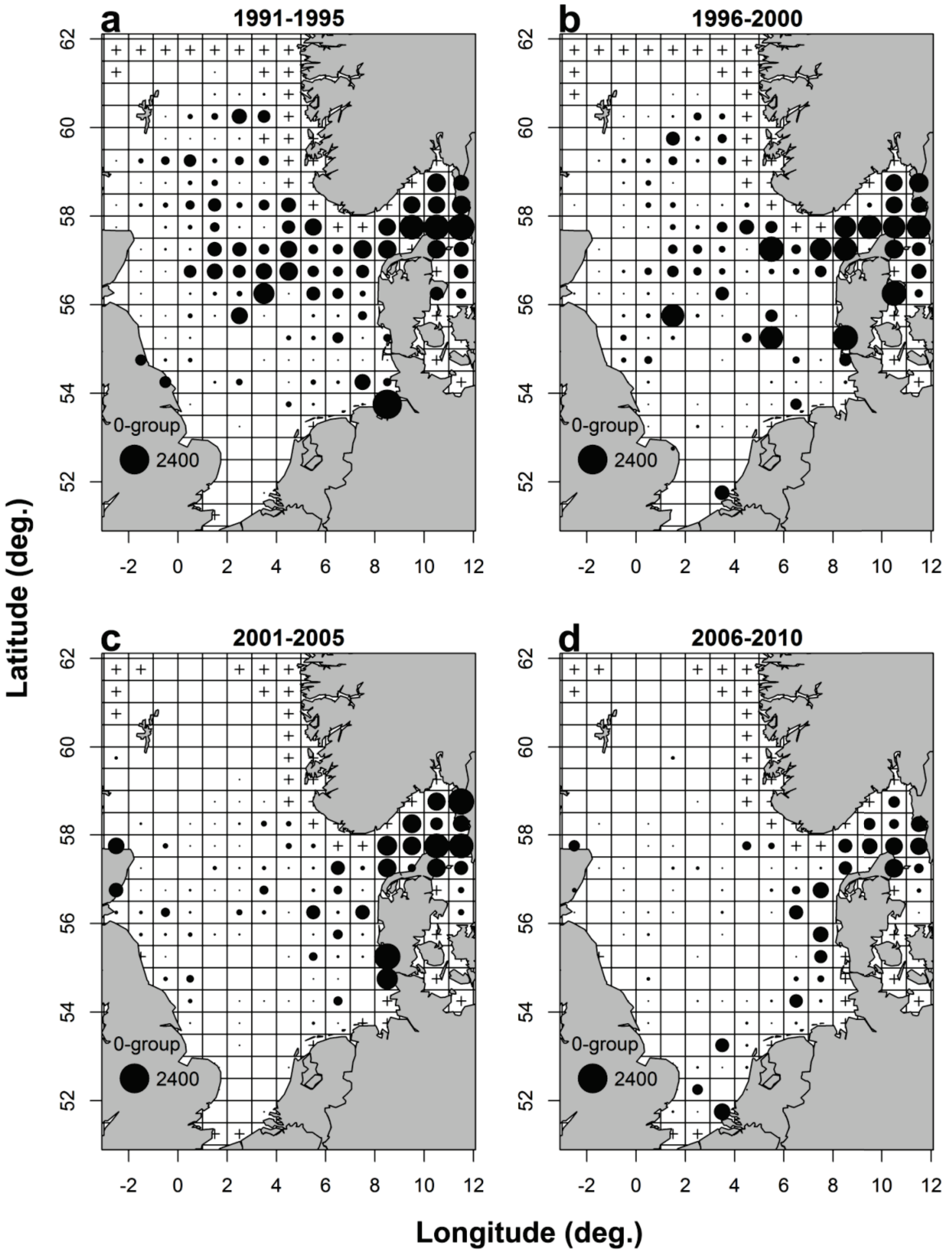


Figure 6: Mean catch per unit effort per ICES rectangle (log (Nos. h^{-1}+1)) of 0-group cod, in the 3rd quarter, for five year periods. The reference dot in each panel depicts the next higher multiple of 100 to the peak CPUE over the whole 20 years. Rectangles not sampled are marked with a cross.

Model fitting and validation

The model fit of presence/absence data showed that the dominant covariates in the best fitting models were geographical position and bottom depth as persistent covariates, and the presence/absence of 2-group cod, temperature, salinity and their interaction as non-persistent covariates. They occurred in all GAMs fitted to the periods 1991-1995 and 2001-2005 as well as in that fitted to the ten year period 1991-2000 (Table 1). When testing the single hydrographic variables, salinity was usually explaining most of the deviation, between 3.8% for 1991-2000 and 9.9% for 2001-2005. Density (kg m^{-3}-1000) was only used when fitting single variables, as it explained less than either salinity or temperature and the tensor product of the two was a superior descriptor of the water mass. Overall, the single variable which explained most of the deviation was the bivariate term for the geographic location. It also contributed most to the explained deviation in multivariate models. The best fitting model for the periods 1991-1995 (Fig. 7) and 2001-20010 (Fig. 9) contained the same covariates (Table 1). The model for 2001-2005 (Fig. 8) additionally included the slope. AIC and UBRE-scores kept on decreasing when adding further variables, but the explained deviation increased only marginally. When comparing the models in ANOVA there were no significant differences between the selected model and models including more variables. For the period 2001-2005 the difference between the model including the slope and the previous model was only near significant ($p=0.059$). However, the residual deviance was reduced by 3.3 at almost no cost in degrees of freedom (0.9). Therefore this model was chosen over the simpler model. The best fitting model explained 36.2% of the explained deviation for the ten year period. For the first five year period, 1991-1995, the fit was marginally better, at 38.8%, while for the period 2001-2005 the explained deviation was at 51.3% and generally model fit with any combination of variables was better than the fit of the corresponding models in the other periods.

Table 1: GAM fits for single variables and multiple predictor models. Explained deviation, UBRE score and AIC are given for each variable and each model. The highlighted models are those used for predicting the following period of five or ten years. Models with higher numbers of covariates were not significantly different from the selected model, when conducting a Chi-square test.

Abbreviations: b.t.=bottom temperature, b.s.=bottom salinity, b.σ_t. = bottom density, Lon = longitude, Lat = latitude, b.d. = bottom depth, S = Slope, p.a.2 = presence/absence of 2-group cod, Sed. = sediment type

Period	Step	Covariates	exp. Dev.	UBRE	AIC
1991-2000	-	s(b.t.)	2.29%	0.243	1680
	-	s(b.s.)	3.78%	0.227	1659
	-	s(b.σ_t.)	1.66%	0.254	1695
	-	s(Lon, Lat)	29.90%	-0.078	1247
	-	s(b.d.)	3.81%	0.219	1648
	-	s(S)	9.46%	0.155	1561
	-	as.factor(p.a.2)	5.75%	0.191	1611
	-	as.factor(Sed.)	9.13%	0.154	1561
	1	s(b.t.) + s(b.s.)	8.30%	0.094	1592
	2	te(b.t., b.s.) + s(b.t.) + s(b.s.)	12.10%	0.153	1559
	3	s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s.	32.70%	-0.108	1206
	4	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s.	33.60%	-0.117	1194
	5	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s. + s(b.d.)	36.20%	-0.149	1151
	6	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s. + s(b.d.) + s(S)	36.20%	-0.147	1153
	7	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s. + te(b.d., S) + s(b.d.) + s(S)	36.80%	-0.149	1150
	8	as.factor(p.a.2) + as.factor(Sed.) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s. + te(b.d., S) + s(b.d.) + s(S)	37.10%	-0.147	1153

Period	Step	Covariates	exp. Dev.	UBRE	AIC
1991-1995	-	s(b.t.)	4.97%	0.194	971
	-	s(b.s.)	4.58%	0.202	978
	-	s(b.σ_t.)	4.17%	0.211	984
	-	s(Lon, Lat)	33.00%	-0.098	733
	-	s(b.d.)	6.92%	0.162	945
	-	s(S)	9.24%	0.145	931
	-	as.factor(p.a.2)	5.44%	0.176	956
	-	as.factor(Sed.)	9.34%	0.137	925
	1	s(b.t.) + s(b.s.)	11.10%	0.137	924
	2	te(b.t., b.s.) + s(b.t.) + s(b.s.)	13.10%	0.131	919
	3	s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s.	36.00%	-0.115	719
	4	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s.	36.50%	-0.120	716
	5	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s. + s(b.d.)	38.80%	-0.145	695
	6	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s. + s(b.d.) + s(S)	38.90%	-0.143	697
	7	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s. + te(b.d., S) + s(b.d.) + s(S)	38.90%	-0.142	698
	8	as.factor(p.a.2) + as.factor(Sed.) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + b.s. + te(b.d., S) + s(b.d.) + s(S)	39.50%	-0.137	702
2001-2005	-	s(b.t.)	5.57%	-0.177	612
	-	s(b.s.)	9.93%	-0.216	584
	-	s(b.σ_t.)	7.99%	-0.201	594
	-	s(Lon, Lat)	38.20%	-0.419	432
	-	s(b.d.)	4.69%	-0.175	614
	-	s(S)	5.04%	-0.182	609
	-	as.factor(p.a.2)	1.48%	-0.155	628
	-	as.factor(Sed.)	7.50%	-0.196	598
	1	s(b.t.) + s(b.s.)	12.60%	-0.224	577
	2	te(b.t., b.s.) + s(b.t.) + s(b.s.)	17.00%	-0.244	562
	3	s(Lon, Lat) + te(b.t., b.s.) + b.t. + s(b.s.)	46.60%	-0.469	395
	4	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + s(b.s.)	48.90%	-0.484	384
	5	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + s(b.s.) + s(b.d.)	50.80%	-0.490	380
	6	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + s(b.s.) + s(b.d.) + s(S)	51.30%	-0.492	378
	7	as.factor(p.a.2) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + s(b.s.) + te(b.d., S) + s(b.d.) + s(S)	50.80%	-0.493	377
	8	as.factor(p.a.2) + as.factor(Sed.) + s(Lon, Lat) + te(b.t., b.s.) + b.t. + s(b.s.) + te(b.d., S) + s(b.d.) + s(S)	51.50%	-0.486	382

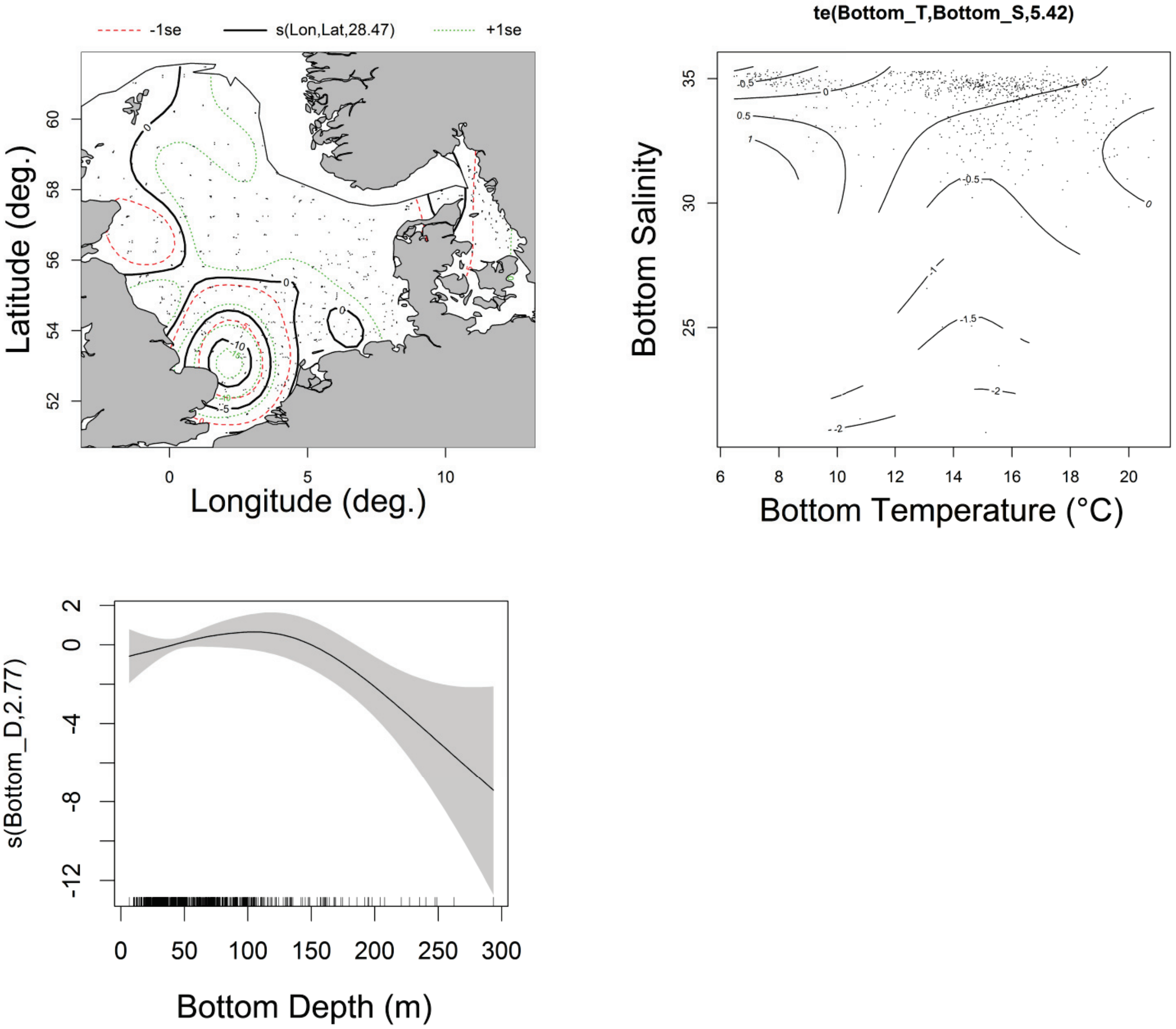


Figure 7: Smooth plots for the selected GAM-model for the period 1991-1995. Categorical (presence/absence 2-group cod) and linear terms (bottom temperature, bottom salinity) are not depicted. Longitude and latitude were used in the model as bivariate term, while the interaction of temperature and salinity was included as tensor product. Since it is the product of two linear terms, the 95% confidence interval cannot be depicted in this case.

Relationships to single covariates were similar in shape, regardless of the period. The peak deviation in the relationship to bottom depth was at ca. 100 m and declined rapidly at greater bottom depths. Similarly the relationships to bottom salinity and slope peaked in the lower third of either covariate’s range. The relationship to bottom temperature (not depicted) was linear and weakly positively correlated. Settled 0-group cod tended to co-occur with 2-group (not depicted).

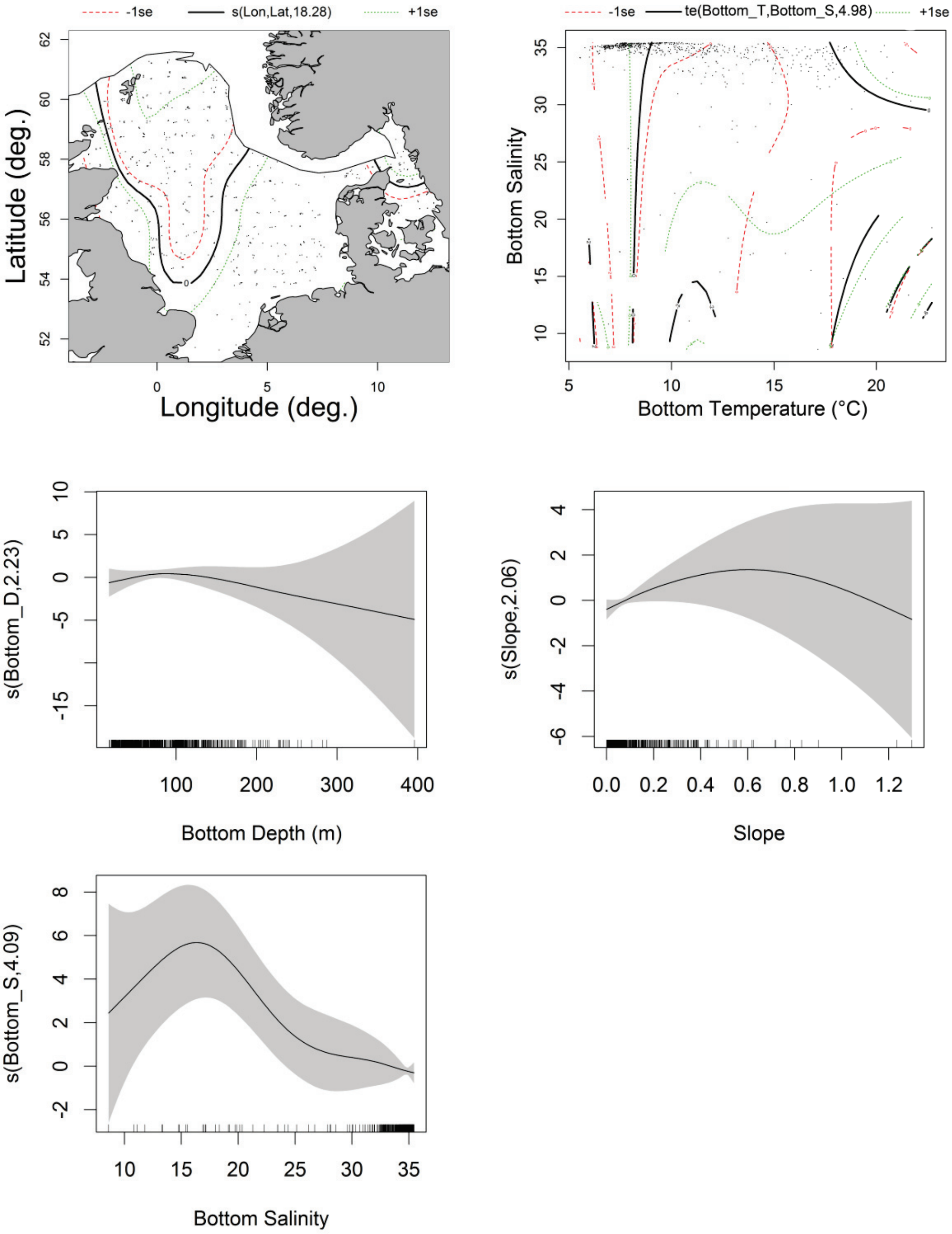


Figure 8: Smooth plots for the selected GAM-model for the period 2001-2005. Categorical (presence/absence 2-group cod) and linear terms (bottom temperature) are not depicted. Longitude and latitude were used in the model as bivariate term, while the interaction of temperature and salinity was included as tensor product.

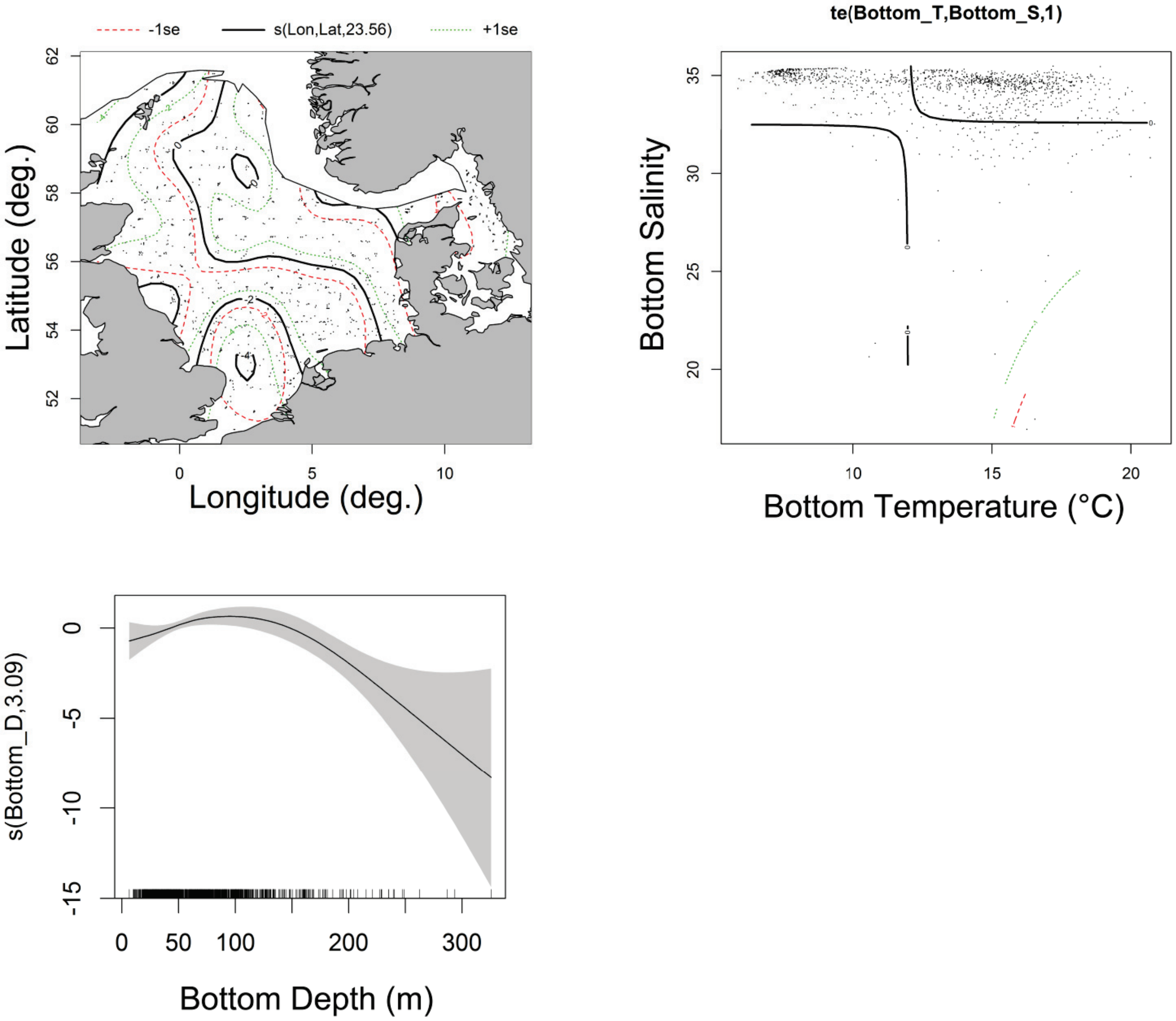


Figure 9: Smooth plots for the selected GAM-model for the period 1991-2000. Categorical (presence/absence 2-group cod) and linear terms (bottom temperature, bottom salinity) are not depicted. As the temperature and salinity interaction is the tensor product of two linear terms, the 95% confidence interval is not depicted. Longitude and latitude are included as a bivariate term.

Model predictions for the two five year periods were closely correlated with the observations ($r_s > 0.9$), while the prediction for 2001-2010 was less well correlated, but the r_s was still above 0.8 (Figure 10).

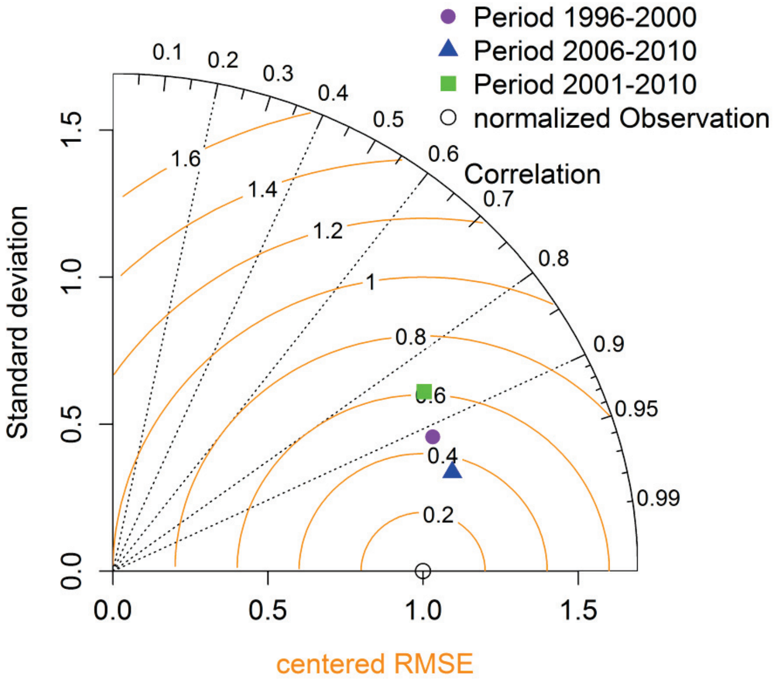


Figure 10: Taylor diagram, comparing the probability of occurrence predicted from the selected GAM models with the observations in 1996-2000, 2006-2010 and 2001-2010. Standard deviation for the observed values was normalized to 1 and the Root Mean Square Error (RMSE) normalized to 0. Standard deviation of the predictions is depicted on the y-axis, while the radii of the circle represent the correlation. The RMSE is plotted on the concentric circles around the normalized standard deviation of the observations. Only the segment of the diagram which depicts the positive correlations is shown.

The interpolated predictions showed that the prediction for the ten year period could not fully capture the decline in area of presence of 0-group cod in the central and north-western North Sea during the 2000s, as these areas exhibited medium probabilities of occurrence in the 1990s (Figure 11). The prediction of 2006-2010 from the model fitted to 2001-2005 fared better in that respect, although the decline in the central North Sea was still underestimated. Generally the predictions for both, the five and the ten year period in the 2000s exhibited some extent of overestimation, while the prediction for the second half of the 1990s exhibited a tendency of underestimating the observed probabilities.

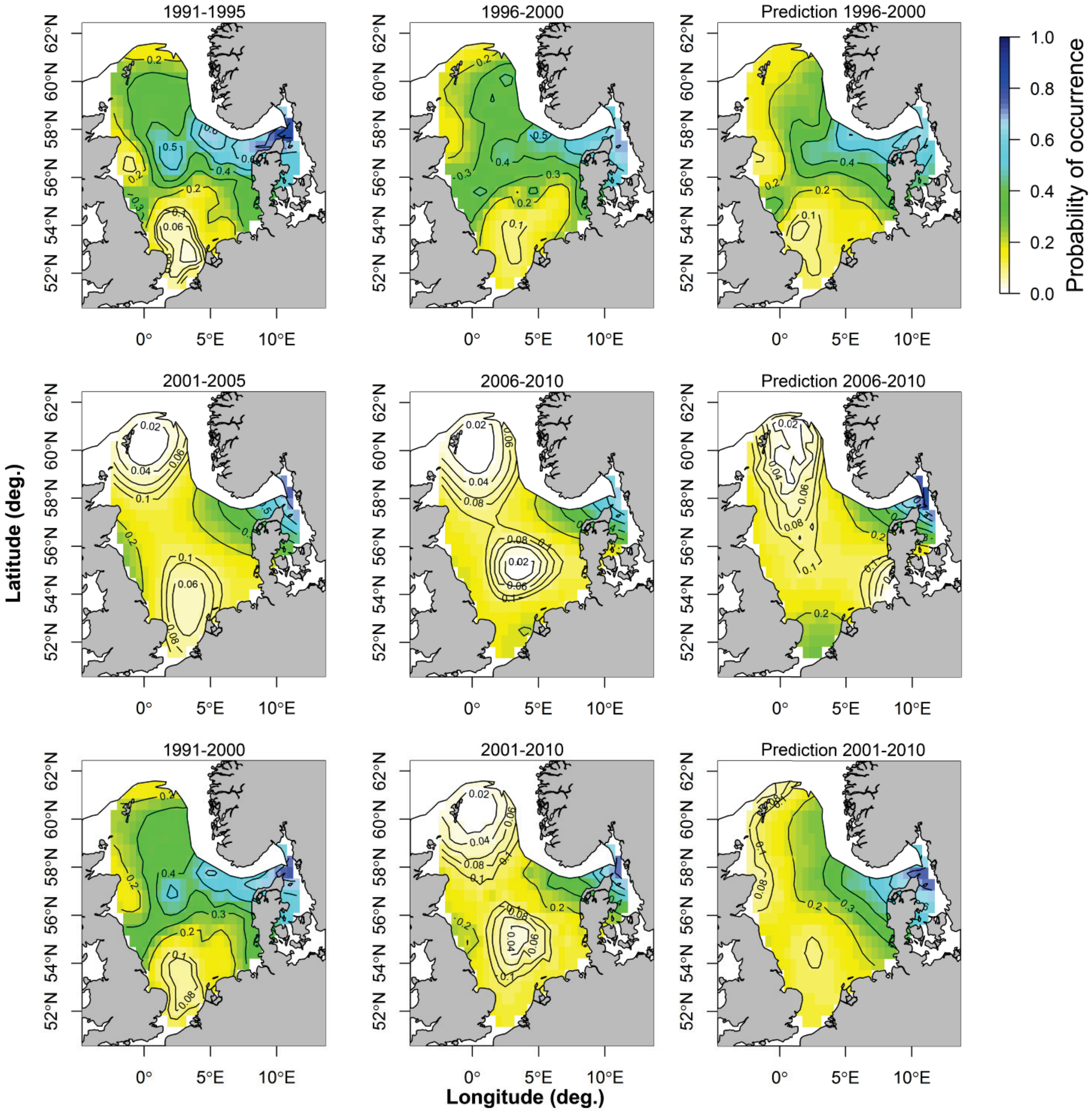


Figure 11: Interpolated probabilities of the occurrence of 0-group cod. The left column shows the probability for the periods GAMs were fitted to, the middle column shows the periods for which predictions were made and the right column shows the predictions. Areas deeper than 200 m are masked, since the number of observations at these bottom depths was too low for a sensible interpolation. Predictions for the five year periods were accurate, while the prediction for ten years could not fully capture the observed decline in the centre of the North Sea.

Discussion

The observations of the hydrographic patterns in the North Sea during the 20-year period are in accordance with general interpretation of the summer/autumn situation. Pingree and Griffiths (1978) noted the remarkable frontal structures in the North Sea and were able to predict patterns from a model which included bottom topography, position of the thermocline and the tidal mixing forces. Their findings have been confirmed during series of later studies (e.g. Otto *et al.*, 1990) and it is apparent that the so-called tidal mixing fronts exert strong influence on hydrographical and ecological patterns in the North Sea. Beside the temperature related tidal mixing fronts, the change of salinity towards the coastal freshwater influences currents and contributes to hydrographic variability in the North Sea. As apparent from our observations the fresher water masses are mixed into more offshore water masses, and the temperature and salinity based fronts merge to a complex frontal system in the southeastern areas (Simpson, 1997).

Indication of settling areas

While the GOV is unlikely to allow for quantitative estimation of the abundance of smaller settling cod, comparison to catches during the neighbouring quarters 2 and 4 indicates that the 3rd quarter catches are useable for identifying areas of high abundances and for a statistical analysis based on presence/absence. During the preceding quarter 2 the GOV was able to catch cod juveniles as small as 3 cm, hence sizes were below the smallest from the 3rd quarter and substantially smaller than the mean size during this quarter (9.5 cm). Distributional patterns in quarter 4, available from the period 1991-95, were by and large comparable to the patterns apparent in the 3rd quarter. The only major discrepancy was the relative abundance in the German Bight which was obviously higher during the 4th quarter, possibly because of delayed settling.

Model fit and relation to the environment

Overall, models fitted to the 5-year periods were explaining more of the deviation and predictions based on these models had a higher correlation with the observed data than models fitted and predicted for the 10-year periods. Likely, this is related to the higher importance of hydrographic variables in these shorter periods, as indicated by the higher percentage of deviation which was explained by these variables alone, particularly in the period 2001-2005.

The strong relationship to geographic position is consistent with the temporal stability of spawning distribution (e.g. Brander, 1994; Daan, 1978; Fox *et al.*, 2008) as well as the general circulation pattern in the North Sea (Otto and Zimmerman, 1990) on a broad scale, while within spawning grounds the centre of abundance of the egg population can be variable (Höffle *et al.*, submitted). During the pelagic phase the effects of spawning location and currents are then modified by food availability and temperature through their influence on growth until settlement size (Heath *et al.*, 2008).

The relationship between presence/absence and bottom depth was the most stable over time, mainly driven by the high occurrence of 0-group cod in the Skagerrak along the slopes of the Norwegian Trench. A steep decrease in occurrence beyond the 200 m line is not surprising for a shelf dwelling species and the line is often taken as cutoff for successful settlement in modelling studies (Andrews *et al.*, 2006; Heath *et al.*, 2008). Many studies have shown settled 0-group cod distributed in very shallow, coastal water (e.g. Kamenos *et al.*, 2004; Methven and Schneider, 1998; Riley and Parnell, 1984), which is not sampled in the IBTS survey (Chen *et al.*, 2005). Therefore it cannot be excluded that including coastal samples would cause a shift of the peak deviation towards shallower water. The high number of occurrences along the slope of the Norwegian trench may also have driven the relationship to the slope as a covariate in 2001-2005.

Björnsson and Steinarsson (2002) have calculated that the optimal growth temperature for juvenile cod of 50 g weight is 14.3°C, which is about the same temperature where the deviation from the mean was zero. In this life stage energy conservation appears not to be prioritized compared to enhanced growth. It has been hypothesized that lower salinity has advantages for development too, as it may lower the cost of osmoregulation (Riley and Parnell, 1984) and exposure to low salinities does at least not have adverse effects (Magill and Sayer, 2004). However, the main benefit of a coastal habitat seems to be that because an increased preference for higher salinities during growth of cod (Riley and Parnell, 1984), age-groups might be separated and hence cannibalism reduced.

Presence/absence of the 2-group apparently had no negative effect on the occurrence of 0-group cod, which is consistent with the findings of Riley and Parnell (1984), who found 2-group beginning to feed on younger gadoids, but only at a low rate. When exposed to later age classes under experimental conditions, 0-group cod has shown avoidance of 1+-group and 2+-group individuals ((Fraser *et al.*, 1996; Laurel and Brown, 2006) but no avoidance of the 1+-group when an age 3+ fish was added (Fraser *et al.*, 1996), The authors concluded that some habitat segregation should be expected between age 0 and age 1+ cod. This may also have been the case in our study between the 0-group and the 2-group cod, but likely at smaller spatial scales than that of our study.

Several studies emphasize the sediment type as an important factor for the survival of settled 0-group cod (e.g. Lindholm *et al.*, 1999; 2001) and the lack of improvement in the model performance when including this variable may be surprising. However, cod would settle onto any available substrate (Juanes, 2007), while differences in abundance and occurrence would develop over time with different mortality rates (Lindholm *et al.*, 1999; Lough, 2010). Such differences may not yet have been established in the early demersal phase, sampled during the IBTS 3rd quarter cruise.

Decadal variability

In the 1980s the cod stock was at a high level. The ‘gadoid outburst’ (Cushing, 1984) was ended in the 1990s and except for a few years in the mid-1990s the spawning stock biomass has been in constant decline until a historic low in 2006 (ICES, 2010b) and a subsequent slow recovery. While the decline is to some extent reflected in the present series of 0-group catches, the recovery phase is not. The catch in 2010 is among the lowest during the period. Model predictions for the period 2001-2010 based on the GAM fitted to 1991-2000 were only partially capable of capturing the decline of 0-group cod in the western and central North Sea. Similarly the less pronounced decline in the Skagerrak during the second half of the 2000s was not fully captured by the predictions made from the model for 2001-2005. Apparently the magnitudes of observed changes were not related to the parameters of the model. To explain the decline, other factors have to be taken into account. A general displacement of the population to the North, like suggested by Rindorf and Lewy (2006) seems rather unlikely however, as there was also a strong decline in the northern North Sea. It may be more related to the reduced stock sizes in some areas, like at the Viking Bank and the Dogger Bank, and the generally declining trend in recruitment for the North Sea population (Holmes *et al.*, 2008).

The mean annual surface temperature of the North Sea may rise from ca. 10.3°C (1990-1999) to 11.5°C during the first half of the 21st century (Clark *et al.*, 2003; IPCC (Intergovernmental Panel on Climate Change), 2000). In addition, precipitation over western Europe is predicted to increase (Meehl *et al.*, 2007), with subsequent increase in river runoff. North Sea cod is already close to the warm temperature limit of the species range (Rätz and Lloret, 2003), which makes it vulnerable if temperature rises too high. The influence of increased precipitation on settling 0-group cod depends on the magnitude of precipitation across seasons. If the increase is restricted to winter, increased meltwater runoff would influence the location of salinity fronts and thereby it might affect aggregation of eggs and larvae (c.f. Höffle *et al.*, 2012, submitted). On the other hand increased river runoff in summer and autumn might positively influence the low salinity refuge of 0-group cod (Riley and Parnell, 1984). Hence, climate related factors might affect the early life of cod in a complex way during different phases of the first year of life. The present habitat modelling focused on the settling phase affords important information for evaluation of the relative importance of different variables. It was able to supply good predictions on a sub-decadal time scale, but apparently for more long-term predictions the population dynamics of the North Sea sub-stocks must be taken into account.

Acknowledgements

We acknowledge ICES for providing the data and all those involved in the surveys.

References

Andrews, J.M., Gurney, W.S.C., Heath, M.R., Gallego, A., O'Brien, C.M., Darby, C. and Tyldesley, G. (2006) Modelling the spatial demography of Atlantic cod (*Gadus morhua*) on the European continental shelf. *Can. J. Fish. Aquat. Sci.* **63**(5)**:**1027-1048.

Bivand, R.S., Pebesma, E.J. and Gomez-Rubio, V. (2008) *Applied spatial data analysis with R. Use R!* Gentleman, R., Hornik, K., and Parmigiani, G. NY: Springer, 374 pp.

Björnsson, B. and Steinarsson, A. (2002) The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **59**(3)**:**494-502.

Bolz, G.R. and Lough, R.G. (1988) Growth Through the 1st 6 Months of Atlantic Cod, *Gadus morhua*, and Haddock, *Melanogrammus aeglefinus*, Based on Daily Otolith Increments. *Fisher. Bull.* **86**(2)**:**223-235.

Brander, K.M. (1994) The Location and Timing of Cod Spawning Around the British Isles. *Ices. J. Mar. Sci.* **51**(1)**:**71-89.

Chen, Q.X., Chan, K.S., Lekve, K., Torstensen, E., Gjosaeter, J., Ottersen, G. and Stenseth, N.C. (2005) Population dynamics of cod *Gadus morhua* in the North Sea region: biological density-dependent and climatic density-independent effects. *Mar. Ecol. Prog. Ser.* **302:**219-232.

Clark, R.A., Fox, C.J., Viner, D. and Livermore, M. (2003) North Sea cod and climate change - modelling the effects of temperature on population dynamics. *Glob. Change Biol.* **9**(11)**:**1669-1680.

Cushing, D.H. (1984) The Gadoid Outburst in the North Sea. *J. Conseil.* **41**(2)**:**159-166.

Daan, N. (1978) Changes in cod stocks and cod fisheries in the North Sea. *Rapp. P. -v. Réun. Cons. Int. Explor. Mer.* **172:**39-57.

ESRI (2010) ArcGis. (Version 10.0) Redlands, CA: Environmental Research Institute Inc.

EUSeaMap (4-2-2011) Modelled Seabed Habitats in the Celtic Sea and North Sea http://jncc.gov.uk/euseamap

Fox, C.J., Taylor, M., Dickey-Collas, M., Fossum, P., Kraus, G., Rohlf, N., Munk, P., van Damme, C.J.G., Bolle, L.J., Maxwell, D.L. and Wright, P.J. (2008) Mapping the spawning grounds of North Sea cod (*Gadus morhua*) by direct and indirect means. *P. Roy. Soc. B-Biol. Sci.* **275**(1642)**:**1543-1548.

Fraser, S., Gotceitas, V. and Brown, J.A. (1996) Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. *Can. J. Fish. Aquat. Sci.* **53**(2)**:**305-314.

Gotceitas, V., Fraser, S. and Brown, J.A. (1997) Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **54**(6)**:**1306-1319.

Heath, M.R., Kunzlik, P.A., Gallego, A., Holmes, S. and Wright, P.J. (2008) A model of meta-population dynamics for North Sea and West of Scotland cod - The dynamic consequences of natal fidelity. *Fish. Res.* **93**(1-2)**:**92-116.

Höffle, H., Fox, C., Loots, C., Nash, R.D.M., Vaz, S., Wright, P. and Munk, P. (submitted (a)) Egg distribution of four common North Sea fishes - Local variation in spawning area usage *Fish. Oceanogr.* 28pp.

Holden, M.J. (1981) The North Sea International 0-Group Gadoid Surveys 1969-1978. *ICES Coop. Res. Rep. No. 99,* 74pp.

Holmes, S.J., Wright, P.J. and Fryer, R.J. (2008) Evidence from survey data for regional variability in cod dynamics in the North Sea and West of Scotland. *Ices. J. Mar. Sci.* **65**(2)**:**206-215.

Hüssy, K., Stjohn, M.A. and Bottcher, U. (1997) Food resource utilization by juvenile Baltic cod *Gadus morhua*: a mechanism potentially influencing recruitment success at the demersal juvenile stage? *Mar. Ecol. Prog. Ser.* **155:**199-208.

ICES (2010a) Manual for the International Bottom Trawl Surveys. International Council for the Exploration of the Sea, *Revision VIII,* 73pp.

ICES (2010b) Report of the ICES Advisory Committee 2010. *Book 6,* 309pp.

ICES (8-3-2012a) DATRAS - Database of trawl surveys

ICES (8-3-2012b) ICES Dataset on Ocean Hydrography. http://www.ices.dk/ocean/

IPCC (Intergovernmental Panel on Climate Change) (2000) Special Report on Emissions Scenarios. Cambridge, UK: Cambridge University Press, 570 pp.

Juanes, F. (2007) Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. *J Fish Biol.* **70**(3)**:**661-677.

Kamenos, N.A., Moore, P.G. and Hall-Spencer, J.M. (2004) Small-scale distribution of juvenile gadoids in shallow inshore waters; what role does maerl play? *Ices. J. Mar. Sci.* **61**(3)**:**422-429.

Laurel, B.J. and Brown, J.A. (2006) Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. *J Exp. Mar. Biol. Ecol.* **329**(1)**:**34-46.

Lindholm, J.B., Auster, P.J. and Kaufman, L.S. (1999) Habitat-mediated survivorship of juvenile (0-year) Atlantic cod Gadus morhua. *Mar. Ecol. Prog. Ser.* **180:**247-255.

Lindholm, J.B., Auster, P.J., Ruth, M. and Kaufman, L. (2001) Modeling the effects of fishing and implications for the design of marine protected areas: Juvenile fish responses to variations in seafloor habitat. *Conserv. Biol.* **15**(2)**:**424-437.

Loots, C., Vaz, S., Planque, B. and Koubbi, P. (2010) What controls the spatial distribution of the North Sea plaice spawning population? Confronting ecological hypotheses through a model selection framework. *Ices. J. Mar. Sci.* **67**(2)**:**244-257.

Lough, R.G. (2010) Juvenile cod (*Gadus morhua*) mortality and the importance of bottom sediment type to recruitment on Georges Bank. *Fish. Oceanogr.* **19**(2)**:**159-181.

Lough, R.G., Valentine, P.C., Potter, D.C., Auditore, P.J., Bolz, G.R., Neilson, J.D. and Perry, R.I. (1989) Ecology and Distribution of Juvenile Cod and Haddock in Relation to Sediment Type and Bottom Currents on Eastern Georges-Bank. *Mar. Ecol. Prog. Ser.* **56**(1-2)**:**1-12.

Magill, S.H. and Sayer, M.D.J. (2004) The effect of reduced temperature and salinity on the blood physiology of juvenile Atlantic cod. *J Fish Biol.* **64**(5)**:**1193-1205.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J. and Zhao, Z.-C. (2007) Global Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., and Miller, H.L. (eds) Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press, Chap. 10

Methven, D.A. and Schneider, D.C. (1998) Gear-independent patterns of variation in catch of juvenile Atlantic cod (*Gadus morhua*) in coastal habitats. *Can. J. Fish. Aquat. Sci.* **55**(6)**:**1430-1442.

Otto, L. and Zimmerman, J.T.F. (1990) Review of the Physical Oceanography of the North Sea Part 1. General Review. *Neth. J. Sea. Res.* **26**(2-4)**:**163-193.

Otto, L., Zimmerman, J.T.F., Furnes, G.K., Mork, M., Saetre, R. and Becker, G. (1990) Review of the Physical Oceanography of the North Sea. *Neth. J. Sea. Res.* **26**(2-4)**:**161-238.

Pingree, R.D. and Griffiths, D.K. (1978) Tidal Fronts on Shelf Seas Around British-Isles. *J. Geophys. Res. -Oc. Atm.* **83**(NC9)**:**4615-4622.

Pinnegar, J.K. and Stafford, R. (30-9-2009) DAPSTOM - An Integrated Database & Portal for Fish Stomach Records. Database version 1.5. Phase 1 Final Report. *http://www.cefas.co.uk/data/an-integrated-database-and-portal-for-fish-stomach-records-(dapstom)/prey-of-specified-predators.aspx*

Planque, B., Loots, C., Petitgas, P., Lindstrom, U. and Vaz, S. (2011) Understanding what controls the spatial distribution of fish populations using a multi-model approach. *Fish. Oceanogr.* **20**(1)**:**1-17.

Planque, B., Bellier, E. and Lazure, P. (2007) Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. *Fish. Oceanogr.* **16**(1)**:**16-30.

R Development Core Team (2008) R: A language and environment for statistical computing. (Version 2.14.0) Vienna, Austria: R Foundation for Statistical Computing, http://www.R-project.org

Rätz, H.J. and Lloret, J. (2003) Variation in fish condition between Atlantic cod (*Gadus morhua*) stocks, the effect on their productivity and management implications. *Fish. Res.* **60**(2-3)**:**369-380.

Righton, D., Quayle, V.A., Hetherington, S. and Burt, G. (2007) Movements and distribution of cod (*Gadus morhua*) in the southern North Sea and English Channel: results from conventional and electronic tagging experiments. *J. Mar. Biol. Assoc. UK* **87**(2)**:**599-613.

Riley, J.D. and Parnell, W.G. (1984) The distribution of young cod. *Flødevigen rapportser. 1,* pp. 563-580.

Rindorf, A. and Lewy, P. (2006) Warm, windy winters drive cod north and homing of spawners keeps them there. *J. Appl. Ecol.* **43**(3)**:**445-453.

Serchuck, F.M., Grosslein, M.D., Lough, R.G. and Mountain, D.G. (1994) Fishery and environmental factors affecting trends and fluctuations in the Georges Bank and Gulf of Maine Atlantic cod stocks: an overview. *ICES mar. Sci. Symp.* **198:**77-109.

Simpson, J.H. (1997) Physical processes in the ROFI regime. *Journal of Marine Systems* **12**(1-4)**:**3-15.

Sissenwine, M.P. (1984) Why do fish populations vary? In: *Workshop on exploitation of marine communities.* May, R. (ed.) Berlin: Springer, pp. 59-94.

Stenseth, N.C., Jorde, P.E., Chan, K.S., Hansen, E., Knutsen, H., Andre, C., Skogen, M.D. and Lekve, K. (2006) Ecological and genetic impact of Atlantic cod larval drift in the Skagerrak. *P. Roy. Soc. B-Biol. Sci.* **273**(1590)**:**1085-1092.

Weiergang, J. (1995) Dynocs inception report. Danish Hydraulic Institute, *Technical Report.*

Wood, S.N. (2006) *Generalized Additive Models: An Introduction with R.* London: Chapman & Hall, 410pp.

Wood, S.N. and Augustin, N.H. (2002) GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. *Ecol. Model.* **157**(2-3)**:**157-177.

”... Da steh ich nun, ich armer Tor!
Und bin so klug als wie zuvor; ...”

Faust I (J. W. v. Goethe, 1808)