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Thesis defended by **Xochitl CORMON**

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Impacts of a top-predator emergence in an exploited ecosystem: North Sea hake and saithe.

Which interactions? What consequences?

Thesis supervised by	Paul MARCHAL	Supervisor
	Youen VERMARD	Co-Monitor

Committee members

Referees	Henrik GISLASON	Professor at DTU Aqua, Copenhaguen	
	Christian MÖLLMAN	Professor at IHF, Hamburg	
Examiners	Sébastien LEFEBVRE	Professor at LOG UMR 8187, Lille	Committee president
	Georg ENGELHARD	Senior Researcher at CEFAS, Lowestoft	
Supervisor	Paul MARCHAL	Senior Researcher at IFREMER, Boulogne-sur-Mer	

Institut français de l'exploitation de la mer

École doctorale **Ecole Doctorale Sciences de la Matière, du Rayonnement et de l'Environnement**

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Thèse présentée par **Xochitl Cormon**

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Discipline **Biologie**

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Impacts de l'émergence d'un top-prédateur dans un ecosystème exploité : le merlu et le lieu noir de mer du Nord.

Quelles interactions ? Quelles conséquences ?

Thèse dirigée par	Paul Marchal	Directeur
	Youen Vermard	Co-encadrant

Composition du jury

Rapporteurs	Henrik Gislason	Professeur au DTU Aqua, Copenhaguen	
	Christian Möllman	Professeur à l'IHF, Hamburg	
Examinateurs	Sébastien Lefebvre	Professeur au LOG UMR 8187, Lille	Président du jury
	Georg Engelhard	Directeur de recherche au CEFAS, Lowestoft	
Directeur de thèse	Paul Marchal	Directeur de recherche à l'IFREMER, Boulogne-sur-Mer	

A Jeannot,

Alive without breath,
As cold as death,
Never thirsty, ever drinking,
All in mail never clinging.

J.R.R. Tolkien, The Hobbit

An expert is a person who has made all the mistakes that can be made in a very narrow field.

Niels Bohr

Time is a drug.
Too much of it kills you.

Terry Pratchett, Small Gods

IMPACTS OF A TOP-PREDATOR EMERGENCE IN AN EXPLOITED ECOSYSTEM: NORTH SEA HAKE AND SAITHE.

Which interactions? What consequences?

Abstract

North Sea saithe (*Pollachius virens*) has high economic value for European fisheries. In recent years, North Sea saithe abundance has decreased, while abundance of hake (*Merluccius merluccius*), which was rarely fished in the North Sea, has increased dramatically in the area. This work investigate the nature of the ecological interactions between saithe and hake in the North Sea, in order to understand if recent hake emergence in this area could explain, at least partially, the recent decline of the saithe stock. The results obtained during this research suggested competitive interactions between saithe and hake predators in the area. In addition, this investigation revealed potential negative effects of hake on the resident saithe stock. Therefore, hake emergence in the North Sea must be taken into account when managing commercial fish stocks, the sustainability of which may be threatened by this up-coming predator. Finally, the results obtained within this PhD study highlight the importance of hake as an up-coming predator and competitor in the North Sea, and provide the necessary basis for further investigations of hake potential ecological and economic function in this exploited ecosystem.

Keywords: exploitative competition, saithe, hake, simple foodweb, up-coming predator, north sea

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IMPACTS DE L'ÉMERGENCE D'UN TOP-PRÉDATEUR DANS UN ECOSYSTÈME EXPLOITÉ : LE MERLU ET LE LIEU NOIR DE MER DU NORD.

Quelles interactions ? Quelles conséquences ?

Résumé

La population de lieu noir (*Pollachius virens*) de mer du Nord a une importance économique élevée pour les pêcheries européennes. Depuis une dizaine d'années, l'abondance du lieu noir a décliné, alors que le merlu (*Merluccius merluccius*), qui était peu pêché dans cette zone, a vu son abondance fortement augmenter. Ce travail se concentre sur la nature des interactions écologiques entre le lieu noir et le merlu en Mer du Nord afin de déterminer si la récente émergence du merlu dans cette zone pourrait expliquer, au moins en partie, le récent déclin du stock de lieu noir. Les résultats obtenus lors de ce travail de recherche ont permis de valider l'hypothèse de compétition entre le lieu noir et le merlu. De plus, cette étude a révélé un impact potentiellement négatif de l'augmentation du merlu sur la biomasse de lieu noir. L'émergence du merlu en mer du Nord doit donc être sérieusement prise en compte dans les avis scientifiques supportant les décisions de gestion encadrant la pêche du lieu noir, mais aussi des autres espèces de mer du Nord que l'émergence du merlu est susceptible d'affecter. Finalement, ce travail fournit donc les premières bases écologiques nécessaires à une investigation plus détaillée des conséquences de l'émergence du merlu dans un écosystème hautement exploité tel que la mer du Nord.

Mots clés : compétition, lieu noir, merlu, simple réseau trophique, émergence d'un prédateur, mer du nord

IFREMER, Channel and North Sea Fisheries Research Unit
150 quai Gambetta – B.P. 699, 62321, Boulogne-sur-Mer – France

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Acronyms

AIC Akaike Information Criterion

AICc corrected Akaike Information Criterion (AIC)

ALK Age-Length Keys

AR AutoRegressive model

ARMA AutoRegressive Moving Average model

BIC Bayesian Information Criterion

CHARM Channel Habitat Atlas for marine Resource Management

CPUE Catch Per Unit Effort

CTD Sonde

DATRAS ICES online DAtabase of TRAwling Survey

DBL Dogger Bank Line

EAF Ecosystem Approach to Fisheries

GLM Generalized Linear Models

GLS Generalized Least Squares

GoF Goodness-of-Fit

IBTS International Bottom Trawl Survey

ICES International Council for the Exploration of the Sea

I-RI Index of Relative Importance

LME Large Marine Ecosystem

MA Moving Average model

MEV Moran's EigenVectors

MIK Methot Isaac Kidd like net

MRM Minimum Realistic Models

MRT Multivariate Regression Tree

MSTY Maximum Short-Term Yield

MSVPA MultiSpecies Virtual Population Analysis

MSY Maximum Sustainable Yield

NLS Non-linear Least Squares

OCEAN ICES Oceanographic online database

OLS Ordinary Least Squares

RI Relative Importance index

SMS Stochastic MultiSpecies

SSB Spawning Stock Biomass

TAC Total Allowable Catch

TSB Total Stock Biomass

VBGF von Bertalanffy Growth Function

VIF Variance Inflation Factor

WGNSSK Working Group on the assessment of demersal stocks in the North Sea and SkagerraK

WGSAM Working Group on multiSpecies Assessment Methods

Fish species

Blue whiting *Micromesistius poutassou*

Capelin *Mallotus villosus*

Cod *Gadus morhua*

Common sole *Solea solea*

Grey gurnard *Eutrigla gurnardus*

Haddock *Melanogrammus aeglefinus*

Hake *Merluccius merluccius*

Herring *Clupea harengus*

Horse mackerel *Trachurus trachurus*

Mackerel *Scomber scombrus*

Norway pout *Trisopterus esmarkii*

Plaice *Pleuronectes platessa*

Poor cod *Trisopterus minutus*

Saithe *Pollachius virens*

Sandeel *Ammodytes sp.*

Silvery lightfish *Maurolicus muelleri*

Silvery pout *Gadiculus argenteus*

Sprat *Sprattus sprattus*

Whiting *Merlangius merlangus*

> Que ceux qui veulent danser dansent, que ceux qui peuvent s'éveiller s'éveillent.
>
> René Barjavel, La nuit de temps

Introduction

Today, living marine resources represent a primary source of proteins for more than 2.6 billion people and support the livelihoods of about 11 percent of the world's population (UN, 2012; FAO, 2014). Seas and oceans worldwide concentrate dense and diversified human activities, *e.g.* fishing, tourism, shipping, offshore energy production, while experiencing many environmental changes, *e.g.* acidification, increase of water temperature (Boyd *et al.*, 2014). These anthropogenic and environmental pressures may threaten the integrity and sustainability of marine ecosystems.

The diverse environmental and/or human pressures may alter the different components of the ecosystem directly or indirectly, simultaneously or sequentially, coherently or contradictorily. One example is the effect on cod (*Gadus morhua*) recruitment of the temperature and wind regime shift observed in the eighties in the North Sea (Beaugrand, 2004). Another example is the collapse of forage fish stocks across many regions worldwide enhanced by high fishing pressure (Essington *et al.*, 2015b). Those pressures, as well as their effects, are entangled. For instance, the collapse of the Barents Sea cod stock has been explained by recruitment and growth failures of its main prey stock, capelin (*Mallotus villosus*), climate change, and high fishing pressure (Blindheim and Skjoldal, 1993). These alterations may have great socio-economic impacts when associated with high-value commercial species such as cod and capelin in the Barents Sea.

In this context, the World Summit on Sustainable Development in Johannesburg (2002) provided a legally binding framework to implement an Ecosystem Approach to Fisheries (EAF) management and to encourage scientific activities relevant to the EAF (FAO, 2003). A major challenge for fisheries scientists is then to improve knowledge on ecosystem functioning, structure and dynamics (Cury *et al.*, 2003). The structure of an ecosystem is represented by its composition in terms of species and/or populations, *i.e* community, and also its abiotic properties, *e.g.* chemical properties or temperature (Frontier, 2008). The dynamics of an ecosystem then characterises the ecological interactions occurring between the different biotic and abiotic elements composing its structure.

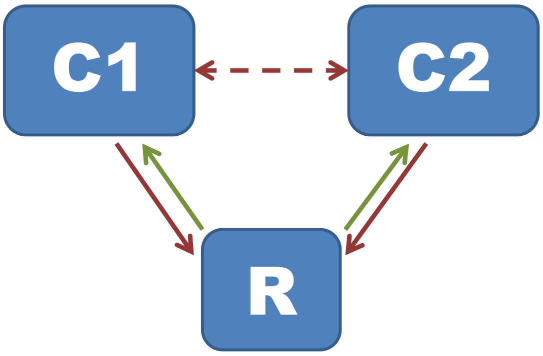


Figure 1 – Exploitative competition diagram. C1: competitor 1. C2: competitor 2. R: resource. Arrows represent the interactions and their directions. Solid line: direct interaction. Dashed line: indirect interaction. Red: negative effect. Green: positive effect.

The nature of ecological interactions depends on the abiotic environment in which they occur as well as their evolutionary context. Ecological interactions are broad and diverse and can be intra- or interspecific. Intraspecific interactions occur between individuals belonging to the same species. Interspecific interactions occur between different species. In marine ecosystems, one of the key ecological interactions is represented by the relationship between predators and prey (Jennings *et al.*, 2001; Volterra, 1928). Predator-prey interactions may regulate both predator and prey populations through top-down control, *i.e.* by the predators, and bottom-up control, *i.e.* by the prey resource (Cury *et al.*, 2003). Predation mortality is considered the main source of mortality for exploited marine living resources (Cury *et al.*, 2003).

Another type of interactions potentially regulating the ecosystem is competition (Volterra, 1928; Lotka, 1932; Gause, 1934). "Biological competition is the active demand by two or more individuals [...] for a common resource or requirement that is actually or potentially limiting" (Miller, 1967). Competitors interact directly or indirectly which results in adverse effects for all of them. Exploitative competition (indirect) (Miller, 1967), occurs when competitors, species or populations, deplete each other resources (Figure 1). Availability reduction of the resource shared may impact all competitors in the short term (Williamson, 1957). However, in the longer term, the situation may become unbalanced with a competitor taking advantage leading to the reduction of fecundity, survivorship and/or growth of the others. This phenomenon is referred to as the competitive exclusion principle (Hardin, 1960).

In marine ecosystems, competition is more difficult to evidence and has been less studied than predation, particularly at large scales (Link and Auster, 2013).

However, competition effects, particularly when combined with fishing, have been evidenced to disturb the functioning of marine ecosystems (Jennings and Kaiser, 1998; Hollowed *et al.*, 2000), thereby threatening the sustainability of their exploitation. Challenges associated with the evaluation of competition in Large Marine Ecosystem (LME) were recently reviewed by Link and Auster (2013). In order to assume competition between two species at the population level and, at spatio-temporal scales consistent with the level of which fishery management operates, Link and Auster (2013) proposed a protocol based upon four requirements:

1. **contrasted trends requirement**, which assumes opposite population trajectories resulting from the competitive exclusion principle;
2. **spatio-temporal overlap requirement**, which indicates that both species are at the same place at the same time and therefore compete for space;
3. **dietary overlap requirement**, which indicates that both species feed on same type of preys and therefore compete for food;
4. **resource limitation requirement**, which is required to demonstrate competition instead of coexistence (Jones, 1978). This is particularly challenging at large scales such as LME where it is difficult or even impossible to conclude directly about resource restriction. Indirect methods, such as the study of species condition factor, have been suggested in that context (Link and Auster, 2013).

The North Sea LME (Figure 2) has historically been one of the most heavily exploited marine ecosystem in the world, particularly concerning fish and seafood exploitation (Ducrotoy *et al.*, 2000). North Sea bathymetry is positively correlated with latitude (Knijn *et al.*, 1993) and is characterised by two different temperature gradients. In the northern region, temperature increases towards the north because of the entrance of the relatively warm North Atlantic Current (Reid and Valdés, 2011). In the southern region where several big rivers discharge, temperature increases with latitude in winter while the gradient is reversed in summer with temperature decreasing towards north (Knijn *et al.*, 1993; Janssen *et al.*, 1999).

Changes in environmental factors were reported during the last 20 years in the North Sea (ICES, 2008). Concerning temperature, the North Sea is often described as the *cauldron of climate change*, with sea temperature increasing four times faster than the global average warming over the past 30 years (Boyd *et al.*, 2014). Climate change may have altered species distribution and abundances (Beaugrand, 2004; Perry *et al.*, 2005; Jones *et al.*, 2013), as well as ecosystem functioning (Floeter *et al.*, 2005; Raab *et al.*, 2012). In this context, the International

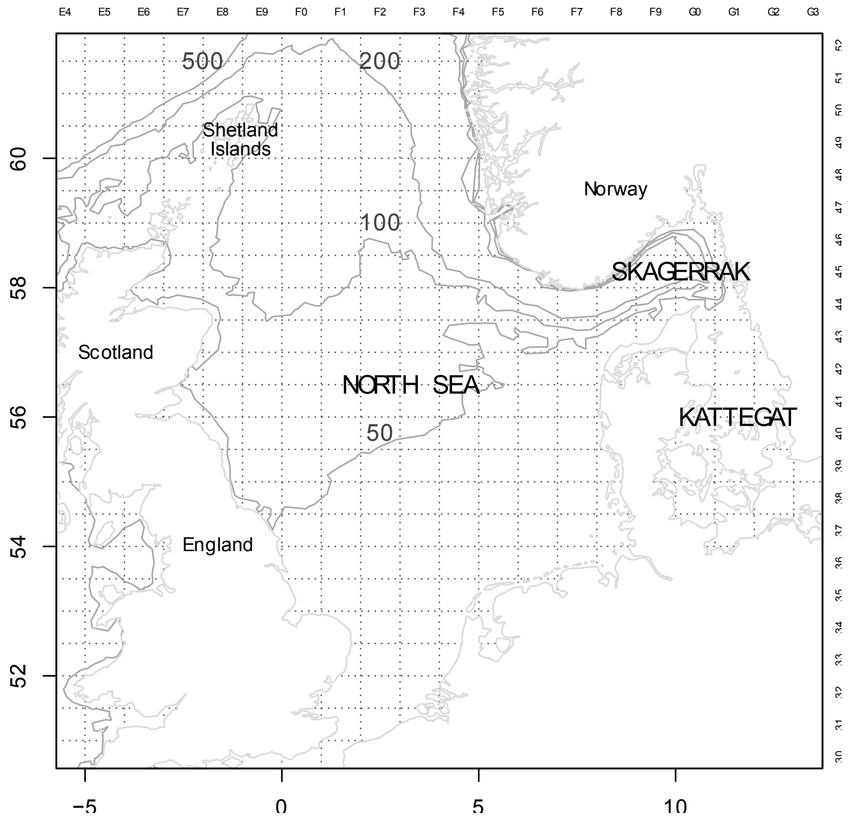


Figure 2 – Map of the study area. In upper case, maritime area names and in lower case country names. Grey lines represent depth contours accompanied by their corresponding depth value in meters. The dotted grid in the background represents the ICES statistical rectangle grid (1° longitude × 0.5° latitude).

Council for the Exploration of the Sea (ICES), which is the main advisory body for the management of Northeast Atlantic marine living resources, estimated the adverse effects of ecosystem functioning alterations.

In the Baltic and the North Sea, ICES has drawn particular attention to the inclusion of species interactions in fish stock assessments, the outputs of which represent an important source of scientific advice informing fisheries management (ICES, 2013b, 2014b). In this context, the ICES Working Group on multiSpecies Assessment Methods (WGSAM) started using the multispecies stock assessment model Stochastic MultiSpecies (SMS), as a basis for multispecies advice in these areas. This model estimates predation mortalities ($M2$) exerted on prey populations (top-down control), in addition to the usual single-species stock assessment parameters, to take into account predator-prey interactions in commercial fish stock assessment.

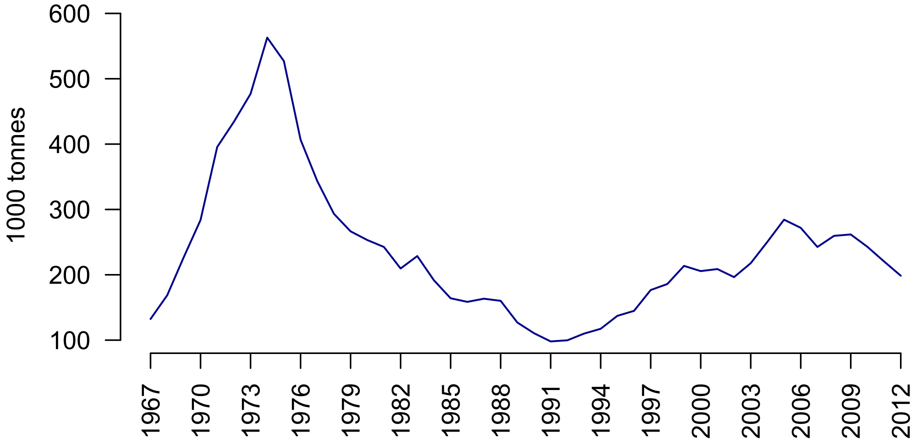
In the North Sea, demersal fisheries landed 675000 tonnes of fish in 2010, of which 12 percent were large gadoid species, mainly cod, haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and saithe (*Pollachius virens*) (ICES, 2014b; Pauly and Zeller, 2015). Currently, saithe is the most important demersal species landed in this area, and supports the fishery economy of several European countries including Norway, the United Kingdom, France and Germany (ICES, 2014b; Pauly and Zeller, 2015). The North Sea saithe stock is considered to inhabit the North Sea, but also the Skagerrak and Kattegat (Figure 2) and the area west of Scotland (ICES, 2014b). North Sea saithe (including all its geographical components) will from hereafter simply referred to as saithe.

Saithe (Figure 3) is a major top-predator fish species in the North Sea. Its commercial importance and its potential impacts on other exploited fish populations, through predation, made it a well-studied species along with other gadoids, particularly after the gadoid outburst in the 1970's (Cushing, 1984; Daan, 1989; Bergstad, 1991a,b; Du Buit, 1991; ICES, 1997a; Hoines and Bergstad, 1999). Saithe has a northerly distribution (mainly above 57° of latitude), with clear differences between adult and juvenile distributions (ICES, 2014b). Indeed, while adults generally live offshore, saithe nursery grounds are inshore with the most important nursery being located along the Norwegian west coast. Fishery recruitment occurs at age 3 when individuals migrate from coastal areas seaward while age at 50 percent maturity (A_{50}) is between 4 and 5 years old. Spawning occurs from January to March at about 200m depth (ICES, 2014b).

Recent stock assessments suggest that North Sea saithe recruitment, growth, mean weight-at-age and Spawning Stock Biomass (SSB) have decreased in recent years (Figure 4) notwithstanding an exploitation around Maximum Sustainable Yield (MSY) levels for several years (ICES, 2014b). The reasons of these declines are largely unknown and might result from environment-induced changes,

Figure 3 – Saithe. ©Ifremer, P. Porcher, 2011

(a) Saithe SSB



(b) Saithe mean weight-at-age

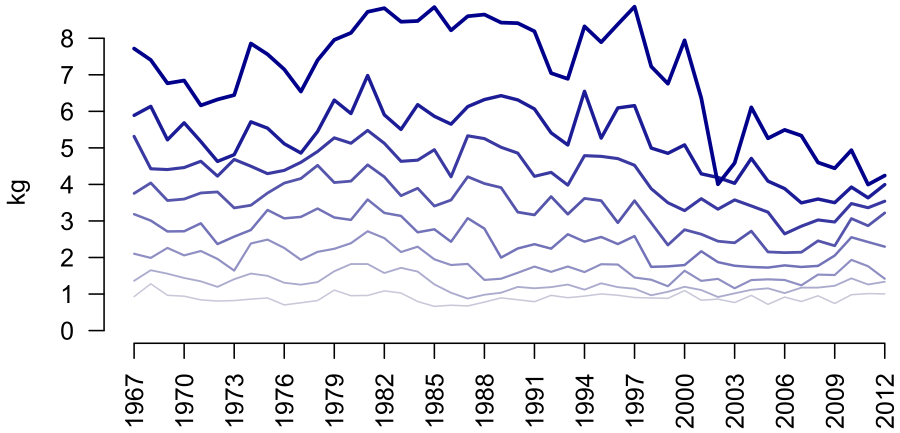


Figure 4 – North Sea saithe stock trends from 1967 to 2012 (ICES, 2014b). (a) Spawning Stock Biomass. (b) Mean weight-at-age from age 3 (thin light blue line) to age 10 (thick darkblue).

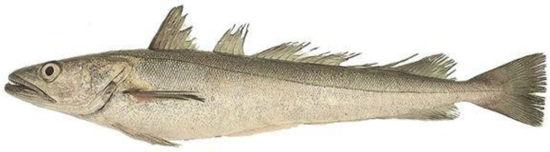


Figure 5 – European hake. ©Ifremer

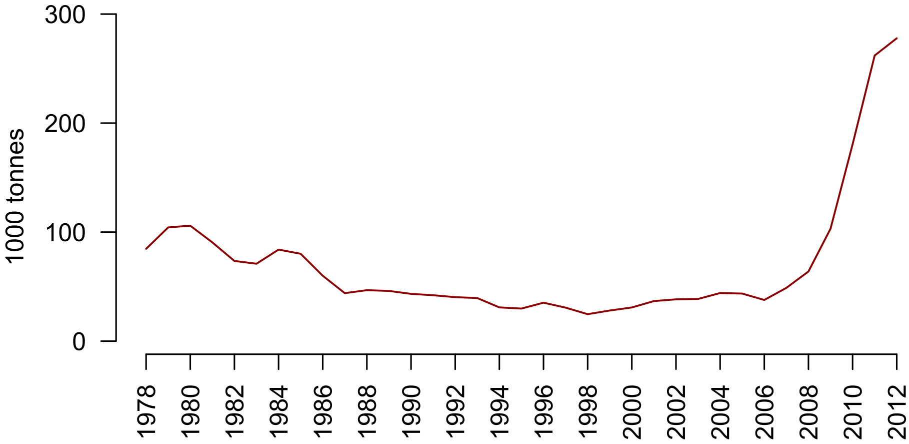


Figure 6 – Northern European hake Spawning Stock Biomass trends from 1978 to 2012 (ICES, 2013a).

trophic induced-changes and/or fishery-induced changes. Saithe is primarily caught in the North Sea by directed fisheries operating along the shelf with significant discards only observed in Scottish demersal mixed fisheries operating inshore (ICES, 2014b). However, North Sea saithe fisheries reported recently a substantial increase in their European hake (*Merluccius merluccius*) bycatch.

European hake (Figure 5) is a large top-predator gadoid species which primarily feeds on fish (Cohen *et al.*, 1990; Bergstad, 1991b; DuBuit, 1996). European hake in the North Sea is a component of the larger Northern hake stock, which is distributed over, as for saithe, the North Sea, the Skagerrak, the Kattegat and West Scotland but also the Celtic Sea, the Channel and the Bay of Biscay where the bulk of its distribution is located (ICES, 2013a). European hake is a batch spawner with spawning occurring all year through (Murua, 2010). Northern hake, which will from now on be more simply referred to as hake, has two main nursery grounds located in the Bay of Biscay and the Celtic Seas (ICES, 2013a). In addition to its wide geographical distribution, hake can be found over a wide range of water depths (Casey and Pereiro, 1995).

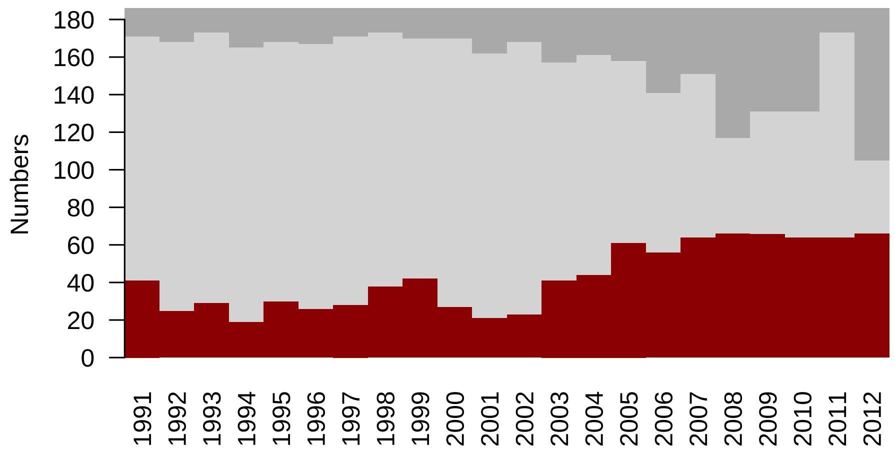
The quasi-absence of hake in the North Sea during the last 50 years made it a species with little commercial interest in this area and led to very limited hake quota attributed to North Sea fisheries. Hence, an increase of bycatch may have potential economic impact for North Sea demersal fisheries, particularly in the context of a landing obligation scheme that will gradually be implemented to all EU fleets over the period 2015-2019, as part of the 2013 Common Fishery Policy.

During the last decade, hake SSB has increased to reach historically high levels in 2010 onwards (Figure 6). This increase matches with an expansion of hake distribution area (Baudron and Fernandes, 2014). In the North Sea, the number of ICES statistical rectangles where hake was caught during the International Bottom Trawl Survey (IBTS) increased gradually from 2002 to 2008, in both winter and summer (Figure 7). Recently, Baudron and Fernandes (2014) showed an increase in hake abundance in the North Sea and warned the scientific community about the potential economic impacts for North Sea demersal fisheries. There is, however, no study yet about potential impacts of hake emergence on the North Sea ecosystem, and more particularly on the main commercial species of the area.

As largely piscivorous, hake may have a direct impact on prey stocks such as forage fish, by increasing their predation mortality. The potential impact on forage fishes might in turn affect other predators feeding on them, which would highlight indirect competitive interactions between those predators and hake in the North Sea (Figure 1). In this context, we first compared the SSB of saithe and hake in the North Sea and found opposite trajectories between the two species from 2005 onwards (Figure 8) which fulfils the contrasted trends requirement (1st condition of competition theory in LME; Link and Auster (2013)).

In order to understand ecological interactions between saithe and hake in the North Sea, it is indispensable to improve knowledge about their ecology in this area. As mentioned previously, saithe was well studied after the gadoid outburst. However, most of the studies available concerning its distribution and diet in the North Sea date back to the nineties. Hake is well studied in the Bay of Biscay, the Celtic Seas and the Mediterranean Sea (DuBuit, 1996; Kacher and Amara, 2005; Mahé *et al.*, 2007; Harmelin-Vivien *et al.*, 2012). However, due to its historical low abundance and limited commercial interest in the North Sea, information on hake ecology in this area is very scarce. In this context, saithe and hake ecology in the North Sea, for which knowledge is either outdated, or even absent, need to be investigated.

(a) Winter



(b) Summer

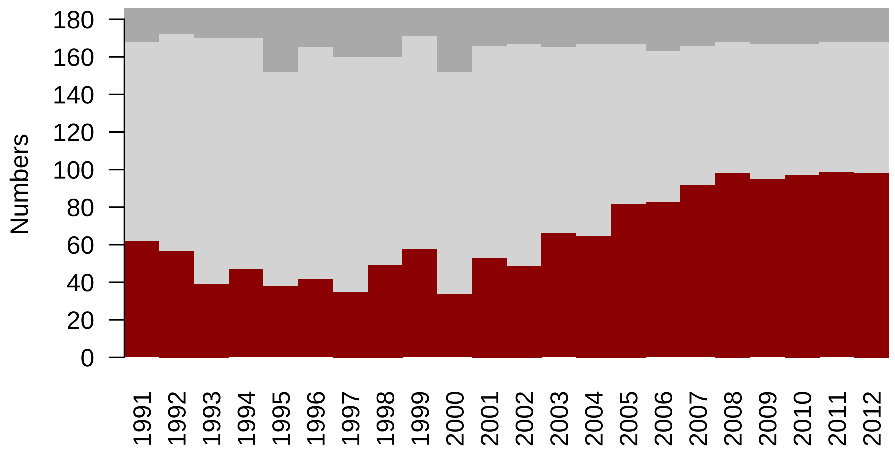


Figure 7 – Number of North Sea ICES rectangles where hake presence was recorded during seasonal IBTS survey from 1991 to 2012. Red: hake presence. Light grey: hake absence. Dark grey: non covered rectangle.

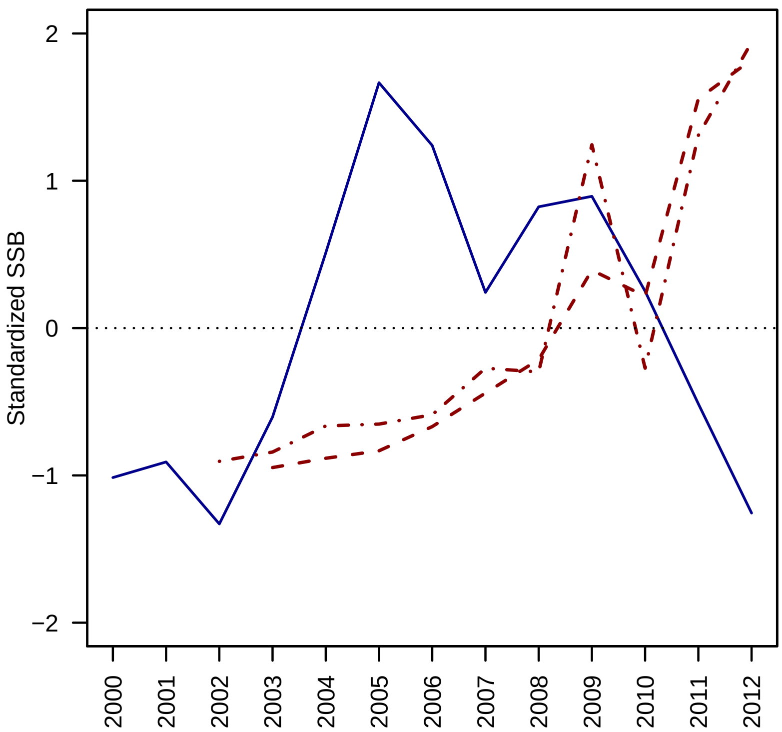


Figure 8 – Standardised Spawning Stock Biomass of saithe and hake in the North Sea from 2000 to 2012. Blue line: saithe (ICES, 2014b). Red line: hake (Baudron and Fernandes, 2014). Mixed line: winter. Dashed line: summer.

> Everything must be made as simple as possible. But not simpler.
>
> Albert Einstein

Objectives and strategy

This thesis was motivated by the recent decline of North Sea saithe stock in terms of biomass, growth and weight-at-age, the opposite trajectories of North Sea saithe population and hake in the area, and the lack of recent knowledge about saithe and hake ecology in the North Sea. Ultimately, this work seeks to understand the nature of the ecological interactions between saithe and hake in the North Sea in order to understand if recent hake emergence in this area could explain, at least partially, the recent decline of saithe stock.

What is the nature of saithe and hake ecological interactions in the North Sea? Based on current trajectories of saithe and hake populations in the North Sea and the similar size of these two demersal species, competitive interactions were assumed. In order to validate, or reject, the competition theory between saithe and hake in the North Sea, the different requirements expressed in the Introduction were investigated.

1. **How are saithe and hake spatial distributed within the North Sea and to what extent do they overlap?** The spatial dynamics of saithe and hake and their potential spatial interactions were explored in Chapter 1. First, both saithe and hake probabilities of presence were investigated separately, by season (winter and summer) and related to their environment. In this study, the environment was defined by abiotic factors, *i.e.* sea surface temperature, depth, sediment type, and by biotic factors, *i.e.* presence of potential competitors and presence of potential prey. Saithe and hake presence/absence was defined based on the 1991-2012 IBTS observations at ICES statistical rectangle scale. The changes in distribution patterns of these two species were investigated by comparing species' presence probabilities predicted over an early (1991–1996) and a late period (2007–2012). Subsequently, similar investigation was carried out on spatial overlap between the two species, which was defined as their co-occurrence at the statistical rectangle scale.

2. **What are saithe and hake diet in the North Sea and do they overlap?** This question was explored in Chapter 2 using saithe and hake gut contents data collected in winter and summer 2013. Samples were collected onboard commercial vessels (in collaboration with the French saithe fishery company EURONOR) and research vessels (German and Norwegian vessels during IBTS 2013) in the northern North Sea and around the Shetland Islands. First, saithe and hake diet dissimilarities were investigated to determine how these two predators share the food resource (food resource partitioning) in this area. Second, diet was described for each predator group. Third, dietary overlap between saithe and hake was estimated.
3. **Are prey resources, shared between saithe and hake, limited?** Indirect limitation of the resource was explored in Chapter 3 through an investigation of environmental factors regulating saithe growth. Annual growth variations were first investigated through the study of saithe mean weight-at-age increment from 1986 to 2012. Second, saithe age-length relationship characteristics were estimated for the period 1991-2012 using three candidate models. The model best describing saithe annual average growth was selected and the relationships between saithe growth and the environment were investigated. In this study, the environment was defined by the temperature and by biotic factors, *i.e.* density-dependence (intraspecific competition), and prey availability.

What are the effects of saithe and hake ecological interactions on North Sea saithe? The results obtained in Chapters 1 to 3 were used to study the potential impacts of hake emergence on saithe. Indeed, potential impact of hake on saithe must be understood and taken into account to manage the saithe stock. In addition, this might either confirm or refute, our assumption about the nature of the two species interactions in the North Sea. Exploitative competition, with hake as the advantaged species, would lead to negative effects on saithe, while coexistence would lead to none. The assumption of exploitative competition with saithe as the advantaged species was not considered due to the current trends of the two stocks (see more details in the the Introduction).

4. **How might hake emergence in the North Sea affect saithe?** The potential impacts of hake emergence in the North Sea on saithe stock were investigated in Chapter 4. A multispecies stock assessment model, parametrised for the North Sea was modified to integrate, in addition of top-down processes already included, bottom-up processes between saithe growth and the environment highlighted in Chapter 3. This modified model was used to assess hake direct impact on preys populations three different abundance scenarios. Then, saithe stock was assessed in function of hake abundance

> and fishery context using different forecast scenarios. In addition, an exploration of MSY levels for saithe was realised in a multispecies context, particularly, taking into account interactions with hake.

Briefly, this step-by-step study first investigated North Sea saithe and hake habitat, and food, resources, partitioning and overlap, as well as saithe prey-dependent, and thus limited, growth, in order to assume competition (opposed to coexistence) between North Sea saithe and hake. Secondly, the trophic impacts of hake recent emergence were inferred to explain, at least partially, North Sea saithe most recent declining trends in order to highlight the significance of little economic importance species, such as North Sea hake, in the EAF implementation for the management of heavily exploited ecosystems, particularly in a changing environment context.

Part I

What is the nature of saithe and hake ecological interactions in the North Sea?

All new explorers must answer a
science question.
You live in what kind of home?

Mr Ray, Finding Nemo

Chapter 1

Spatial interactions between saithe and hake in the North Sea

Cormon, X., Loots, C., Vaz, S., Vermard, Y., and Marchal, P. 2014, Chapter 1. Spatial interactions between saithe (*Pollachius virens*) and hake (*Merluccius merluccius*) in the North Sea. ICES Journal of Marine Science, 71: 1342–1355

Abstract
Spatial interactions between saithe and hake were investigated in the North Sea. Saithe is a well-established species in the North Sea, while occurrence of the less common hake has recently increased in the area. Spatial dynamics of these two species and their potential spatial interactions were explored using binomial Generalized Linear Models (GLM) applied to the IBTS data from 1991 to 2012. Models included different types of variables: (i) abiotic variables including sediment types, temperature and bathymetry; (ii) biotic variables including potential competitors and potential preys presence and (iii) spatial variables. The models were reduced and used to predict and map probable habitats of saithe, hake but also, for the first time in the North Sea, the distribution of the spatial overlap between these two species. Changes in distribution patterns of these two species and of their overlap were also investigated by comparing species' presence and overlap probabilities predicted over an early (1991-1996) and a late period (2007-2012). The results show an increase in the probability over time of the overlap between saithe and hake along with an expansion towards the south-west and Scottish waters. These shifts follow trends observed in temperature data and might be indirectly induced by climate changes. Saithe, hake and their overlap are positively influenced by potential preys and/or competitors, which confirms spatial co-occurrence of the species concerned and leads to the questions of predator-prey relationships and competition. Finally, the present study provides robust predictions concerning the spatial distribution of saithe, hake and of their overlap in the North Sea, which may be of interest for fishery managers.

Keywords: Species Distribution Modelling; Generalized Linear Models; saithe; hake; spatial overlap; biotic interactions; predator-prey relationship; competition; North Sea

1.1 Introduction

Spatial distributions of fish species shifted in the North Sea over the past twenty years as a result of environmental and ecosystem changes (Perry *et al.*, 2005; ICES, 2008; Reid and Valdés, 2011; Loots *et al.*, 2011). Importantly, shifts in species distribution may alter the nature of biological interactions, through changes in the spatial overlap between predators, their competitors and their preys, which may consequently affect fisheries through changes in catch composition. In the case of mixed fisheries, these rearrangements may lead to an increase in bycatch (Jones *et al.*, 2013), but also of discarding, when fishing vessels do not have a sufficient catch quota provision to match these bycatch. In a fluctuating environment context (Boyd *et al.*, 2014), it appears essential to better understand the interactions between commercial species through, for example, their spatial overlap. The related changes need to be quantified in order to improve fisheries management strategies under sustainable exploitation regimes.

In this context, this study focuses on two widely distributed gadiform species of the Northeast Atlantic: saithe (*Pollachius virens*) and hake (*Merluccius merluccius*). Because of their importance for European fisheries, saithe and hake are mainly managed through single-stock Total Allowable Catch (TAC), the setting of which depends to a large extent on the outcomes of stock assessments carried out by the International Council for the Exploration of the Sea (ICES). The North Sea saithe stock covers the North Sea, the Skagerrak, the Kattegat and Western Scotland (ICES, 2013d). The northern hake stock covers, as for saithe, the North Sea, the Skagerrak, the Kattegat and Western Scotland but also the Celtic Seas, the Channel and the Bay of Biscay where the bulk of its distribution is located (ICES, 2013a). On the one hand, North Sea saithe, mainly landed by Norway, France and Germany, has been exploited at around Maximum Sustainable Yield (MSY) level for several years. However its Spawning Stock Biomass (SSB) began to decline most recently (Figure 4a). On the other hand, the SSB of northern hake, mainly landed by France and Spain, increased dramatically since the late 2000's (Figure 6). During the same period, North Sea saithe fisheries reported a substantial increase in their hake bycatch. These fisheries have a very limited hake quota and therefore may be forced to discard this species, which could affect them economically (Baudron and Fernandes, 2014) but also adversely affect the perception of stock status (Jones *et al.*, 2013). Therefore the study of the overlap between saithe and hake, referring from now to the component of these two species stocks covering the North Sea, the Skagerrak and the Kattegat, is timely to inform fisheries managers and stock assessment scientists.

Saithe and hake are found at depths ranging from 37 to 364 meters, and 70 to 200 meters, respectively (Scott and Scott, 1988; Kacher and Amara, 2005). These two species are generally considered as demersal but have both pelagic behaviour (Scott and Scott, 1988; Cohen *et al.*, 1990; Bergstad, 1991a), particularly regarding feeding (Cohen *et al.*, 1990; Homrum *et al.*, 2013). In addition to the top-down pressure exerted by fisheries, the populations of these two top-predators may importantly be controlled by bottom-up processes, through *e.g.* forage fishes availability (Frederiksen *et al.*, 2006). Saithe and hake present diet similarities, particularly concerning fish preys and seasonal patterns (Bergstad, 1991b; Du Buit, 1991; DuBuit, 1996), which may lead to competition for food (Link and Auster, 2013). However, the spatial overlap and subsequently the trophic interactions between hake and saithe were very limited in the North Sea, until the late 2000's, since the abundance of northern hake was low compared to saithe (Figures 4a and 6) and its distribution was mostly concentrated in the Celtic Seas (Baudron and Fernandes, 2014). Northern hake was therefore barely studied in the North Sea area and its relative abundance was never considered as a potential issue for the North Sea mixed demersal fisheries until very recently (Baudron and Fernandes, 2014). Given their recent biomass trends, it appears critical to investigate saithe and hake spatial overlap in the North Sea, in order to understand their potential effects on saithe fisheries but also on saithe population, through *e.g.* competitive interactions.

While saithe and hake are both included in the ICES North Sea atlas, FishMap, available online (`http://www.ices.dk/marine-data/maps/Pages/ICES-FishMap.aspx`), the information concerning their spatial distribution in the North Sea region is scarce and their overlap was never studied. Bergstad (1991a) mapped saithe and hake spatial distribution in the Norwegian Deep from trawl data and highlighted seasonal differences of occurrence and abundance of the two species, particularly in relation to depth. More recently, Perry *et al.* (2005) and Jones *et al.* (2013) studied spatial distribution shifts of a number of North Sea species, including saithe and hake, in relation to climate change. Concerning saithe, the results obtained differ as Perry *et al.* (2005) did not found any shift while Jones *et al.* (2013) highlighted a northward shift of saithe spatial distribution related to temperature increase. Homrum *et al.* (2013) used tagging experiment to study migration and distribution of saithe in the Northeast Atlantic, including Icelandic, Faroese and Norwegian waters. The authors highlighted migration patterns from Norwegian to Icelandic and Faroese waters that might reflect feeding migration of saithe pursuing fish preys like herring (*Clupea harengus*). Also, Baudron and Fernandes (2014) used survey and commercial data to study changes in abundance of northern hake in the different areas occupied, including the North Sea and the Skagerrak. The authors showed a large increase in hake abundance in the North Sea reflecting the trends of the overall stock (Figure 6) but also an expansion of the area historically occupied by hake which they related to the availability of suitable habitat under density-dependent pressure.

In this context, the study of saithe and hake relative habitats appears indispensable to better understand the spatial interactions between these two species. However, the definition of habitats "must surely be among the least rigorous of any in science" (Mitchell, 2005). Kearney (2006) redefined the habitat, as a function of its abiotic and biotic features, without including explicit mechanisms affecting the fitness of the species of interest. These biotic features may allow the inclusion of biotic interactions, like predator-prey relationships and/or competition. Although many studies highlighted the need of including biotic features in habitat models (Guisan and Zimmermann, 2000; Ciannelli *et al.*, 2007; Planque *et al.*, 2011; Robinson *et al.*, 2011), abiotic features are always preferred at large spatial scales (Johnson *et al.*, 2013). The paucity of habitat modelling studies including biotic interactions at large scales might result from the common assumption that biotic interactions take place at small spatial scales while abiotic features are the overall drivers of species distribution. Another reason why habitat studies have often focused almost solely on abiotic features might be a lack of information on non-commercial species abundance and/or a lack of knowledge on biotic interactions (Johnson *et al.*, 2013). For Northeast Atlantic marine ecosystems, there are only few examples of species distribution modelling including prey abundance through explanatory variables *e.g.* Wright and Begg (1997), Sveegaard *et al.* (2012) and Hjermann *et al.* (2013), who all noted the importance of prey to model predators spatial distribution. Prey abundance was also integrated in a study on demersal fishes distribution in the Balearic Islands (Johnson *et al.*, 2012) but no significant relationship was found between the distribution of hake abundance and of its preys.

Dormann (2007) considered that neglecting biotic interactions could induce spatial autocorrelation in species distribution models. Because the probability of presence of a species in an area may be more similar in its close neighbourhood than farther apart (Legendre, 1993; Quinn and Keough, 2002; Fortin and Dale, 2005) the risk of falsely rejecting the null hypothesis, or error type I might increase (Dormann *et al.*, 2007; Zuur *et al.*, 2009). In order to explore correlation between spatial distributions and changing environmental conditions, it is common to use Generalized Linear Models (GLM) which aim to reproduce the average of the species response *e.g.* species probability of presence, and allow the description and prediction of species probable habitat *i.e.* area where species may be present (Guisan and Zimmermann, 2000). The inclusion of underlying spatial structure, in order to reduce error type I, is possible including spatial eigenvectors in the GLM (Dray *et al.*, 2006; Legendre and Legendre, 2012). However this method is recent and was only applied twice to North Sea fish species (Loots *et al.*, 2010, 2011).

The specific goals of this study were (i) to investigate the distribution of saithe and hake in the North Sea; (ii) to define their probable habitat including both abiotic and biotic features; (iii) to analyse their spatial overlap and (iv) to compare the different distributions over an early (1991-1996) and recent period (2007-2012).

1.2 Materials and methods

1.2.1 Study coverage and area presentation

The study covers the North Sea, the Skagerrak and the Kattegat at the spatial scale of an ICES statistical rectangle, hereby referred to as "statistical rectangle", *i.e* grid of 1° longitude × 0.5° latitude (Figure 2). This area is covered by the International Bottom Trawl Survey which has been operated since 1991 both in summer and in winter. In the North Sea, bathymetry is positively correlated with latitude (Knijn *et al.*, 1993). The North Sea is characterised by two different temperature gradients. In the northern region, temperatures decrease towards south because of the entrance of the relatively warmer North Atlantic Current (Reid and Valdés, 2011). In the southern region, temperatures increase with latitude in winter while gradient is reverse in summer with temperature decreasing toward north (Knijn *et al.*, 1993; Janssen *et al.*, 1999).

1.2.2 Data

Extraction from ICES online DAtabase of TRAwling Survey (DATRAS) of Catch Per Unit Effort (CPUE) per length per statistical rectangle was undertaken for six trophically-related species (Bergstad, 1991b; Du Buit, 1991), of which saithe, hake and cod (*Gadus morhua*) were considered as potential competitors and Norway pout (*Trisopterus esmarkii*), blue whiting (*Micromesistius poutassou*) and herring as potential preys. Fixed length-at-maturity were used as a threshold to separate each species in two length groups characterising juveniles and adult: 55.4 cm for saithe, 50 cm for hake, 70 cm for cod, 18.5 cm for Norway pout, 25 cm for blue whiting and 23 cm for herring. Data were aggregated by year, season, statistical rectangle, species and length group and species abundance (CPUE) were transformed into presence/absence data. To study the overlap between saithe and hake, an extra column was created coding 1 for combination of year, season and statistical rectangle where both species could be found together, and 0 otherwise.

Abiotic data, extracted from ICES Oceanographic online database (OCEAN), were averaged by year, season and statistical rectangle and merged with biotic data. Seabed sediment types were previously extracted (Larsonneur *et al.*, 1982;

Augris *et al.*, 1995; Schlüter and Jerosch, 2009). They were reclassified into five broad categories: mud, fine sand, coarse sand, gravel and pebbles by Carpentier *et al.* (2009) in the Channel Habitat Atlas for marine Resource Management (CHARM). Land coverage was specified as a sixth category in addition to the five sediment types in order to account for areas including islands. Proportions of sediment type coverage per statistical rectangle (including land) were calculated. A polynomial function of third degree was added for temperature (here sea surface temperature) and bathymetry in order to improve the fit. Indeed, data exploration plots suggested that these two descriptor-response relationships were following a cubic polynomial. The average temperatures observed were mapped at different periods and seasons (Figure S1.1).

Seasonal subsets were created, winter data covered January, February and March while summer data covered July, August and September. Also, for model development, seasonal datasets were split into two subsets exhibiting similar range of the different variables and spatial autocorrelation: *datafit* included years 1991, 1992, 1995, 1996, 1999, 2000, 2003, 2004, 2007, 2008, 2011 and 2012 and *datapred* included years 1993, 1994, 1997, 1998, 2001, 2002, 2005, 2006, 2009 and 2010.

1.2.3 Model formulation

Conceptual framework

A correlative approach based on presence/absence data was chosen to fulfil the study objectives concerning saithe, hake and their spatial overlap distributions. Assuming a binomial distribution of the binary data under investigation, GLM (McCullagh and Nelder, 1989) may be considered as the most parsimonious approach (Guisan *et al.*, 2002) and therefore was used for this study. A logistic multiple regression was applied to relate occurrence or probability of presence (pp) to explanatory variables or predictors (x) by fitting data to a logistic curve (Quinn and Keough, 2002):

$$pp(x_1, x_2, ..., x_n) = \frac{e^{\beta_0+\beta_1 \cdot x_1+\beta_2 \cdot x_2+...+\beta_n \cdot x_n}}{1+e^{\beta_0+\beta_1 \cdot x_1+\beta_2 \cdot x_2+...+\beta_n \cdot x_n}} \tag{1.1}$$

where β are the regression parameters or coefficients.

Environmental models

Three environmental models per season were created, one for each species and a third one for the overlap. All models initially included all biotic and abiotic variables presented in previous section (1.2.2). Both types of variable were tested for collinearity (Dormann *et al.*, 2013) and separation, which is an outcome of binary model fitting (Albert and Anderson, 1984). In order to limit the collinearity of independent variables, Spearman correlation coefficient and Variance Inflation Factor (VIF) were analysed, with thresholds set to 0.85 and 2.5, respectively. Concerning model potential convergence problems through infinite estimates of one or several coefficients β, separation of the data was tested using R package {`brglm`} (Kosmidis, 2013).

Concerning biotic variables, saithe, hake, Norway pout and blue whiting presented a high positive correlation (over 0.85) between total presence (irrespective of length groups) and at least one of the length group (juveniles and adult). Following the parsimony principle, only total presence of these four species were conserved. For cod and herring, the two length groups contrasted enough so that total presence were discarded in order to discriminate length groups of these two species in the analysis. The VIF analysis did not suggest to discard any biotic variables. For the abiotic ones, Spearman coefficients were all below the chosen threshold $(0,85)$ but the VIF analysis led to discard mud proportion. The separation test depended on the response studied and led to discard coarse sand proportion from the overlap models.

Table 1.1 presents the explanatory variables with their description, their units and their sources while Equations 1.2 to 1.4 present the final formulas of the environmental models including (i) potential competitors presence, (ii) potential preys presence, (iii) sediment types, (iv) temperature and (v) bathymetry:

Saithe occurrence environmental model:

$$\begin{aligned} \mathrm{S.Tot} \sim\ & \mathrm{H.Tot} + \mathrm{C.Adu} + \mathrm{C.Juv} + \mathrm{NP.Tot} + \mathrm{BW.Tot} + \mathrm{HG.Juv} + \mathrm{HG.Adu} \\ & + \mathrm{CSpp} + \mathrm{FSpp} + \mathrm{Gpp} + \mathrm{Ppp} + \mathrm{Lpp} + \mathrm{Temp} + \mathrm{Temp2} + \mathrm{Temp3} \\ & + \mathrm{Depth} + \mathrm{Depth2} + \mathrm{Depth3} \end{aligned} \tag{1.2}$$

Hake occurrence environmental model:

$$\begin{aligned} \mathrm{H.Tot} \sim\ & \mathrm{S.Tot} + \mathrm{C.Adu} + \mathrm{C.Juv} + \mathrm{NP.Tot} + \mathrm{BW.Tot} + \mathrm{HG.Juv} + \mathrm{HG.Adu} \\ & + \mathrm{CSpp} + \mathrm{FSpp} + \mathrm{Gpp} + \mathrm{Ppp} + \mathrm{Lpp} + \mathrm{Temp} + \mathrm{Temp2} + \mathrm{Temp3} \\ & + \mathrm{Depth} + \mathrm{Depth2} + \mathrm{Depth3} \end{aligned} \tag{1.3}$$

Overlap environmental model:

$$\begin{aligned}\text{Overlap} \sim &+ \text{C.Adu} + \text{C.Juv} + \text{NP.Tot} + \text{BW.Tot} + \text{HG.Juv} + \text{HG.Adu}\\ &+ \text{FSpp} + \text{Gpp} + \text{Ppp} + \text{Lpp} + \text{Temp} + \text{Temp2} + \text{Temp3}\\ &+ \text{Depth} + \text{Depth2} + \text{Depth3}\end{aligned} \tag{1.4}$$

Table 1.1 – Biotic and abiotic variables used to build saithe, hake and overlap models during winter and summer period. Total presence and overlap include both juvenile and adult individuals.
Comp.: potential competitors; Preys: potential preys; Sedi.: sediment type; Temp.: temperature; Bathy.: bathymetry.
cm: centimeter; –: no units; %: percentage; °C: degree Celsius; m: meter.

Type		Name	Description	Units	Source
Biotic	Comp.	S.Tot	Total presence saithe	–	DATRAS
		H.Tot	Total presence hake	–	DATRAS
		Overlap	Presence of both saithe and hake	–	DATRAS
		C.Adu	Presence of adult cod ($\geq$ 70cm)	–	DATRAS
	Preys	C.Juv	Presence of juvenile cod ($<$ 70cm)	–	DATRAS
		NP.Tot	Total presence Norway pout	–	DATRAS
		BW.Tot	Total presence blue whiting	–	DATRAS
		HG.Adu	Presence of adult herring ($\geq$ 23cm)	–	DATRAS
		HG.Juv	Presence of juvenile herring ($<$ 23cm)	–	DATRAS
Abiotic	Sedi.	CSpp	Proportion of coarse sand coverage	%	CHARM
		FSpp	Proportion of fine sand coverage	%	CHARM
		Gpp	Proportion of gravel coverage	%	CHARM
		Ppp	Proportion of pebble coverage	%	CHARM
		Lpp	Proportion of land coverage	%	CHARM
	Temp.	Temp	Average temperature	°C	OCEAN
		Temp2	Average squared temperature	°C	OCEAN
		Temp3	Average cubic temperature	°C	OCEAN
	Bathy.	Depth	Average bottom depth	m	OCEAN
		Depth2	Average squared depth	m	OCEAN
		Depth3	Average cubic depth	m	OCEAN

Spatial models

In order to accomodate the independence assumption (Zuur *et al.*, 2009; Legendre and Legendre, 2012) and to capture spatial patterns at different scales, the Moran's EigenVectors (MEV) mapping method was chosen. This method allows the translation of the spatial arrangement of the data directly into explanatory variables through the eigenvector decomposition of data coordinate connectivity matrix (Dormann *et al.*, 2007; Dray, 2008; Legendre and Legendre, 2012).

MEV were extracted from the connectivity matrix based on relative neighbourhood (Toussaint, 1980) and weighted as a function of the inverse of Euclidian distance calculated from the scaled and centred latitudes and corrected longitudes ($cos(\text{latitude} \times \pi/180)$) of statistical rectangle central points (Borcard *et al.*, 2011). This was undertaken using R package {spdep} (Bivand *et al.*, 2013). MEV were computed and their Moran's index was calculated using 999 permutations and {spacemakeR} (Dray, 2013). Significant ($p < 0.01$) and positive MEV were selected. MEV significance relative to the detrended response was tested by forward selection with double criteria (Dormann *et al.*, 2007; Borcard *et al.*, 2011). The forward selection was performed using {packfor} (Dray *et al.*, 2013) with significance level (α) and cumulated coefficient determination (R^2_{more}) set both to 0.001. The forward selection stopped when either the R^2 of the last variable added was lower than R^2_{more} or when its significance level was higher than α. The residuals obtained after fitting responses to a second-order polynomial ($X + X^2 + X \times Y + Y + Y^2$) based on corrected longitude (X) and latitude (Y) were used as detrended responses. At the end of the process, the number of spatial variables (*i.e.* MEV) selected depended on the response. 7, 13 and 8 spatial variables were added to winter environmental models and 6, 7 and 6 to summer ones, completing Equations 1.2 to 1.4, respectively.

1.2.4 Model calibration

Model calibration was realised using *datafit* dataset described earlier. Model reduction started from the six initial full models: three environmental-only models and three spatial models that included environmental variables and spatial ones (*i.e.* MEV). Environmental variables were eliminated by forward, backward and both stepwise selection using three common criteria: Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and Chi squared (χ^2). MEV were selected *a priori* as described in the previous section (1.2.3) and these were not changed (Dormann *et al.*, 2007). Consequently for spatial models, minimum or null models included all (and only) MEV *a priori* selected and reduction operated only on environmental variables. This procedure, similar to the one presented by Lelièvre *et al.*, resulted (including initial full models) in twenty models per response and per season *i.e.* ten environmental-only models and ten spatial ones.

1.2.5 Model selection

Model selection was based on the predictive abilities of the different models (Planque *et al.*, 2011; Lelièvre *et al.*) using the True Positive Rate (TPR), or sensitivity. Sensitivity represents the prediction rate of observed presence. It was preferred to the, more commonly used, receiver operating characteristic because of false absence which often characterise marine ecosystem sampling (Hirzel *et al.*, 2002). Predictions of presence probability (ranging from 0 to 1) were made based on *datapred* dataset described earlier and transformed into observation predictions (absence, 0 or presence, 1) using a threshold value. This threshold was calculated for each model in order to maximise the sensitivity (Jimenez-Valverde and Lobo, 2007). Each model sensitivity was then calculated and the different values were compared: models with sensitivity values closer to 1 indicate a better ability to predict presence. When sensitivity was not discriminant, *i.e* difference of sensitivity < 0.05, variables were counted and the most parsimonious models were selected. Six models per season were selected for evaluation (three environmental-only models and three spatial ones) which is a total of twelve models.

1.2.6 Model evaluation

Spatial autocorrelation was checked for detrended residuals of selected models using Moran's I coefficient and correlograms (Fortin and Dale, 2005; Borcard *et al.*, 2011; Legendre and Legendre, 2012). Moran's I coefficient characterises spatial autocorrelation going from -1 to 1 with values close to 0 characterising random arrangement, *i.e.* few or no spatial autocorrelation. Correlograms are a graphical tool used to visualise spatial correlation by plotting Moran's I coefficient by spatial lags, here ten lags separated by 75 ± 10 kilometres each. Moran's I coefficient, their significance and associate correlograms were computed using {spdep} (Bivand *et al.*, 2013). The final six least spatially autocorrelated models, three per season, were selected for further evaluation. Goodness-of-Fit (GoF) was evaluated using the adjusted coefficient of determination (adjR^2) and the dispersion parameter (φ). Descriptor coefficients were calculated, tested using χ^2 test and the percentage of deviance explained by each of them was examined. Finally, maps of absolute fitting error (absolute Student residuals) were produced to complete the evaluation.

1.2.7 Model prediction

After evaluation, the six final models were used to predict seasonal probable habitat and overlap of saithe and hake within the modelled area. Predictions were made following Equation 1.1, using values of predictors x and associated regression parameters β calculated during calibration (section 1.2.4). In order to study the changes of probable habitat and overlap between the two species, predictions were averaged on two time periods: 1991-1996, the early period, and 2007-2012, the recent one. The early period averaged predictions were then subtracted to the recent ones in order to provide an overview of the changes of the different responses over the last twenty years. The results were mapped using R version 2.15.3.

1.3 Results

1.3.1 Environmental predictors

A comparison of environmental-only and spatial models variable significance and estimated coefficients is presented in the supplementary material (Tables S1.1 to S1.3). However, only the outputs of spatial models, which explicitly account for spatial autocorrelation were further investigated (Tables 1.2 and 1.3).

For each of the selected models, there are differences in explanatory variable selection and in the contribution of these selected variables to the total deviance explained by the model. These differences depend on the response variable and on the season (Tables 1.2 and 1.3). However, the signs of the models estimated coefficients are consistent for all response variables and seasons. When they are significant, saithe, hake and overlap response variables are always positively influenced by the presence of potential preys, Norway pout, blue whiting and adult herring, potential competitors, saithe, hake and adult cod, temperature (polynom) and bathymetry (polynom). In contrast, these response variables are always negatively influenced by the presence of juvenile herring and the percentage cover of fine sand or pebbles (Table 1.2). Abiotic and biotic variables have the highest contribution to explain saithe and overlap occurrences while spatial variables have the lowest one. Only hake presence variations are generally much better explained by adding spatial variables (9.78% of deviance explained in winter and 11.48% in summer) than by using only biotic and abiotic ones (Table 1.3).

Concerning abiotic variables, temperature and bathymetry are the most important in terms of deviance explained. However, the importance of these two variables varies depending on the models and once again hake models differ from the two others. Indeed, hake presence variations are generally less

Table 1.2 – Estimated coefficient β signs for selected variables for saithe, hake and their overlap final models in the two seasons. W: winter. S: summer. See Table 1.1 for environmental variables description.

			Saithe		Hake		Overlap	
			W	S	W	S	W	S
Biotic	Comp.	S.Tot			+	+		
		H.Tot	+	+				
		C.Adu	+	+		+	+	+
	Preys	C.Juv		+				+
		NP.Tot	+		+		+	+
		BW.Tot			+			+
		HG.Adu			+		+	
		HG.Juv	−	−			−	−
Abiotic	Sedi.	CSpp				−		
		FSpp		−	−	−	−	−
		Gpp	+	+		+		
		Ppp			−	−		
		Lpp		+				
	Temp.	Temp				+		+
		Temp2			−			−
		Temp3			+	−		
	Bathy.	Depth	+	+	+	+	+	+
		Depth2			−		−	−
		Depth3	−	−	+			+

explained by bathymetry with only 1.02% of deviance explained in summer and 19.26% in winter. This contrasts with the bathymetry explanatory power ranging from 25.18% for overlap winter model to 40.84% for saithe summer one. The relationship with temperature is more important for hake presence than for saithe (not selected at all) or overlap (selected only in summer), particularly in summer where it is the most important abiotic variable with 5.04% of deviance explained.

Concerning biotic variables, both species presence are positively influenced by potential preys presence (Norway pout, blue whiting and adult herring), particularly in winter. The mutual relationship with Norway pout explaining 1.35% and 0.35% of saithe and hake winter presence variations, respectively, is consistent with the relation between overlap and Norway pout presence (1.30%

Table 1.3 – Deviance explained (%) for selected variable for saithe, hake and their overlap final models in the two seasons. W: winter. S: summer. MEV : Moran's EigenVectors. See Table 1.1 for environmental variables description.

			Saithe		Hake		Overlap	
			W	S	W	S	W	S
Biotic	Comp.	S.Tot			1.61	10.89		
		H.Tot	1.60	1.96				
		C.Adu	2.59	3.96		0.99	1.67	2.98
	Preys	C.Juv		1.41				0.47
		NP.Tot	1.35		0.35		1.30	1.13
		BW.Tot			0.59			0.63
		HG.Adu			0.91		0.85	
		HG.Juv	1.25	1.10			1.03	1.36
Subtotal			6.79	8.43	3.46	11.88	4.85	6.57
Abiotic	Sedi.	CSpp				0.46		
		FSpp		0.53	4.00	0.40	0.94	0.76
		Gpp	0.53	0.56		0.57		
		Ppp			1.75	0.37		
		Lpp		0.37				
	Temp.	Temp				3.54		0.40
		Temp2			0.44			1.63
		Temp3			1.13	1.50		
	Bathy.	Depth	31.35	38.99	14.18	1.02	21.91	24.62
		Depth2			3.48		3.27	3.59
		Depth3	0.68	1.85	1.60			0.40
Subtotal			32.56	42.3	26.58	7.86	26.12	31.4
Spatial		MEV	2.66	2.84	9.78	11.48	3.79	4.83
TOTAL			42.01	53.57	39.82	31.22	34.76	42.80

of deviance explained in winter and 1.13% in summer). The relation between saithe and hake presence is independent of the season and saithe presence explains 10.89% of hake presence in summer. In addition, for saithe and overlap models, adult cod presence is, independently of the season, the most important biotic variable in terms of response presence variation with 2.59% and 3.96% of deviance explained in winter and 1.67% and 2.98% in summer, respectively.

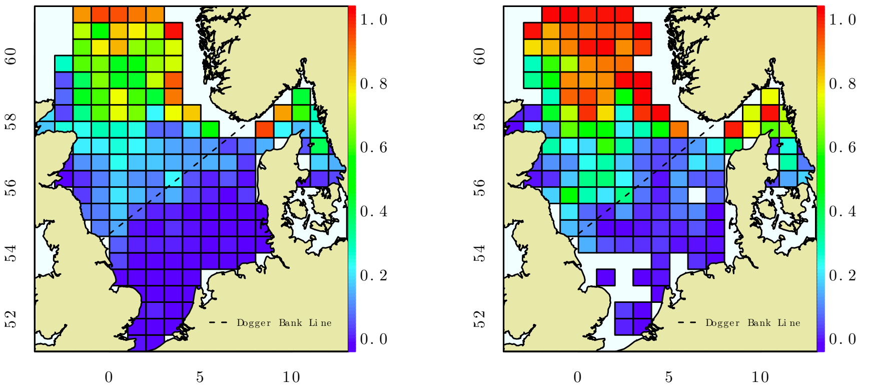
1.3.2 Predicted distributions

An increase of presence probabilities of saithe, hake and of their overlap is generally observed in the regions above the line hereby termed as Dogger Bank Line (DBL), irrespective of the seasons. This increase occurs generally in association with a south-west expansion of the distribution towards Scottish and English waters (Figures 1.1 to 1.3). However, seasonal and period-related differences are revealed when each distribution is more thoroughly investigated.

Saithe is mainly found in the northern region of the North Sea and the Skagerrak. However, seasonal differences can be noted, particularly in the early period distributions. In winter (Figure 1.1a), saithe distribution is concentrated above 57.5° of latitude. This region indicates high probabilities of presence (pp) ranging from 0.6 to 0.9 at its northern boundary. In the early period and in summer (Figure 1.1b), presence probabilities are even higher in this area ($0.8 < pp < 1$) and distribution expands to the Central North Sea above the DBL where saithe can be found at medium presence probabilities ($pp > 0.4$). In the most recent years (Figures 1.1c and 1.1d), a notable increase in presence probabilities is observed in the northern region with positive differences in presence probabilities ($dpp > 0.1$) along with a south-west expansion of the distribution, particularly in winter.

Hake is mainly found in the northern region of the North Sea, in the Skagerrak and in the Kattegat. However, compared to saithe, hake is more widely spread and has a lower presence probability in the area where both species are present *i.e.* above 57.5° of latitude. In winter and during the early period (Figure 1.2a) hake is intermediately present in the area with medium presence probabilities ranging from 0.4 to 0.8. In summer and during the early period (Figure 1.2b), hake presence probabilities above the DBL are higher ($0.6 < pp < 1$) and its northern distribution expands towards south-west and the Scottish waters. There is also medium presence probabilities in the south-east region, below the DBL ($0.4 < pp < 0.8$). Regarding the most recent years, hake winter area of distribution (Figure 1.2c) did not change much except for a slight expansion towards the English waters and an increase of presence probabilities in the region where hake was already present during the early period ($ddp > 0.2$). In the most recent years and in summer (Figure 1.2d), a decrease of presence probabilities is observed in the Skagerrak, the Kattegat and the region south of the DBL ($dpp < -0.1$) while in the region above the DBL, an increase of presence probabilities ($ddp > 0.1$) and a south-west expansion towards English waters is notable.

The two species mainly overlap in the Northern North Sea, above 57.5° of latitude. Overlap distribution in winter and during the early period (Figure 1.3a), indicates medium overlap probabilities in the central part of the Northern North Sea, the Skagerrak and also along the Norwegian coast ($0.3 < pp < 0.7$). In



(a) Winter, early period, *pp*

(b) Summer, early period, *pp*

(c) Winter, difference with recent period, *dpp*

(d) Summer, difference with recent period, *dpp*

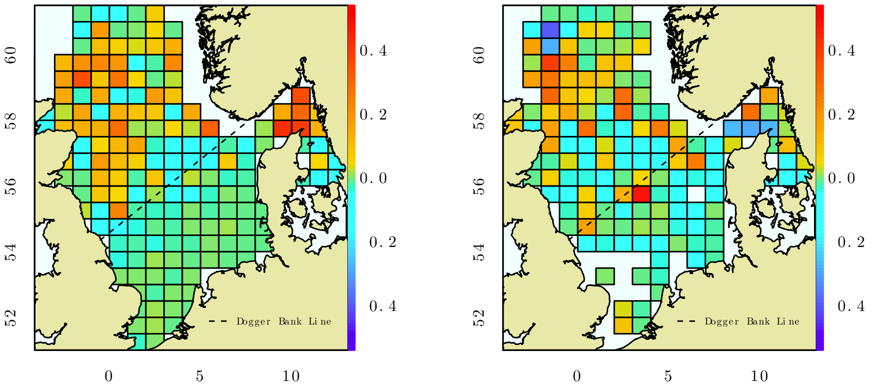
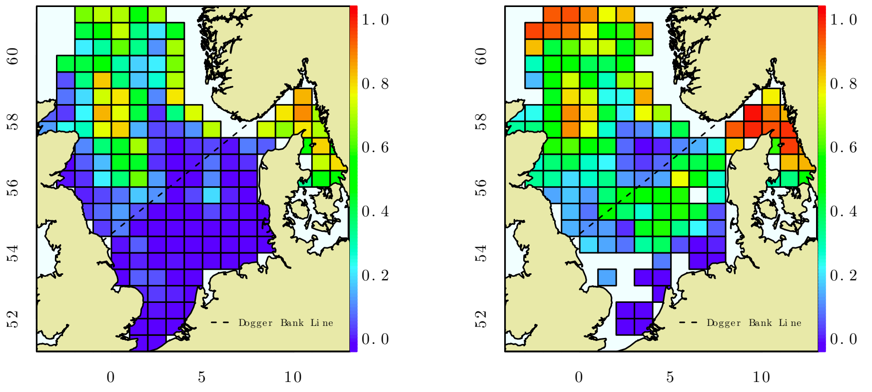
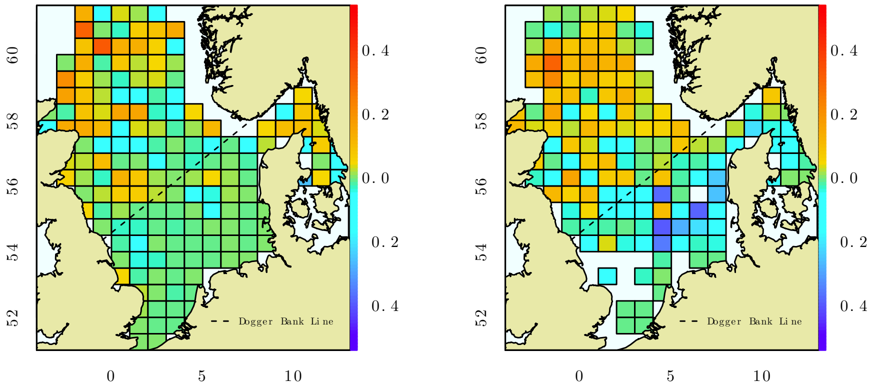


Figure 1.1 – Saithe presence probabilities, *pp*, predictions maps for the early period, 1991-1996, in (a) winter and in (b) summer. Changes in saithe distributions over the last twenty years resulting from the difference between recent, 2007-2012, and early period in (c) winter and in (d) summer. Note the difference of scale for (c) and (d) where the colour gradient displays a difference of presence probabilities, *dpp*.

summer and during the early period (Figure 1.3b), the area is similar in terms of latitude but wider in terms of longitude ranges, and it is characterised by generally higher overlap probabilities ($0.4 < pp < 0.9$). The southern boundary of the overlap distribution is, generally, consistent with saithe distribution patterns. In the most recent years, a notable increase of winter overlap (Figure 1.2c), is observed at the edges of the northern region (Norwegian and Scottish coast) and in the Skagerrak ($ddp > 0.2$) along with a slight expansion towards south-west. Similar trends are observed in summer (Figure 1.2d) with the increase of overlap probabilities in the northern region and the persistence of the south-west


(a) Winter, early period, *pp*

(b) Summer, early period, *pp*


(c) Winter, difference with recent period, *dpp*

(d) Summer, difference with recent period, *dpp*

Figure 1.2 – Hake presence probabilities, *pp*, predictions maps for the early period, 1991-1996, in (a) winter and in (b) summer. Changes in hake distributions over the last twenty years resulting from the difference between recent, 2007-2012, and early period in (c) winter and in (d) summer. Note the difference of scale for (c) and (d) where the colour gradient displays a difference of presence probabilities, *dpp*.

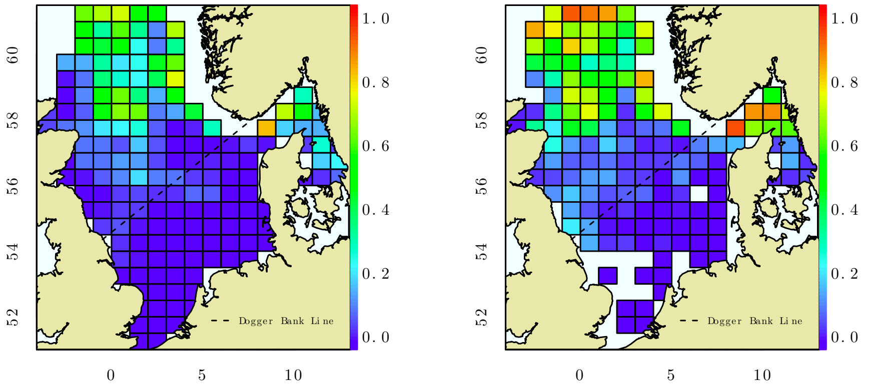
expansion towards the Scottish and English waters.

1.3.3 Evaluation

Models evaluation reveals, first, that there is only few spatial autocorrelation left in the detrended residuals of spatial models (Figure 1.4) in comparison to environmental-only models (Figure S1.3). The number of significant spatially correlated lags ranges from 0 to 1, with a maximum Moran's I coefficient absolute value equal to 0.05 in hake summer model. These results mean that only very

(a) Winter, early period, *pp*

(b) Summer, early period, *pp*



(c) Winter, difference with recent period, *dpp*

(d) Summer, difference with recent period, *dpp*

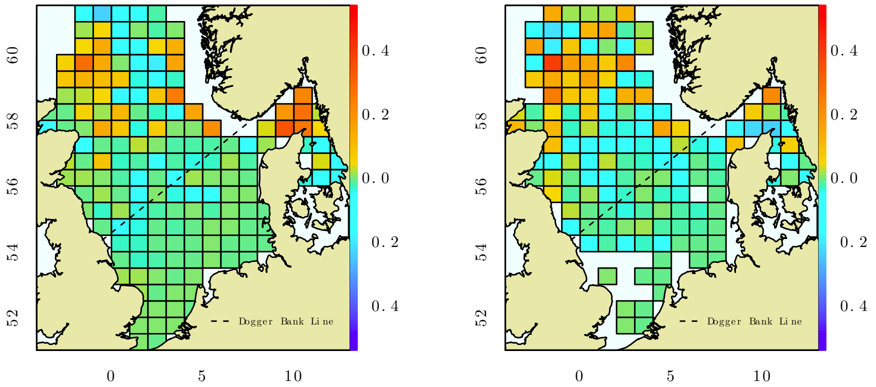


Figure 1.3 – Overlap between saithe and hake probabilities, *pp*, predictions maps for the early period, 1991-1996, in (a) winter and in (b) summer. Changes in overlap over the last twenty years resulting from the difference between recent, 2007-2012, and early period in (c) winter and in (d) summer. Note the difference of scale for (c) and (d) where the colour gradient displays a difference of presence probabilities, *dpp*.

small arrangement patterns are detected in radius of 75 ± 10 kilometres and validate the selection of spatial models in order to reduce the chances of falsely rejecting the null hypothesis (no effect of one variable), also called error type I. However, the results also show that the coefficients estimated with the hake models are more biased than for the saithe and overlap ones (Tables S1.1 to S1.3), due to higher spatial autocorrelation remaining in the residuals and therefore that their selected variables are more subject to error type I than those selected for saithe and overlap models. Second, all models satisfy the GoF with value ranging from a minimum adjR^2 of 0.31 and a maximum of 0.59; dispersion parameter φ close to 1 for every model and sensitivity, ranging from 0.74 to 0.84 (Table 1.4). Finally, fitting error (fe) maps indicates a very good ability of the models to predict absence ($fe < 0.25$) but a more uncertain presence prediction ($0.25 < fe < 1$) (Figure S1.2).

Table 1.4 – Goodness-of-Fit and predictive power according to different parameters of final models for saithe, hake and their overlap in the two seasons. W: winter. S: summer. adjR^2: adjusted coefficient of determination, TPR: True Positive Rate, or sensitivity

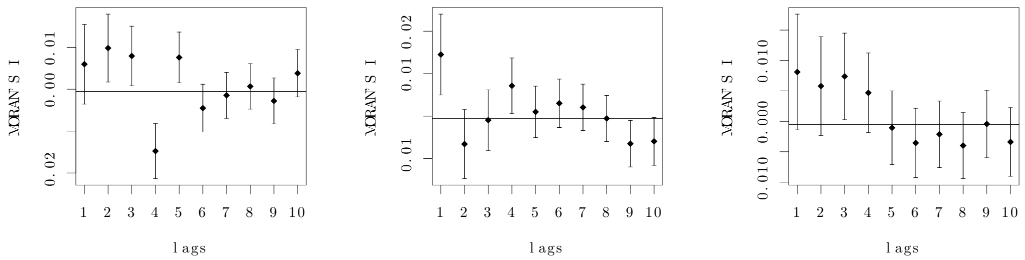
		adjR^2	dispersion (φ)	threshold	TPR
Saithe	W	0.47	1.06	0.20	0.83
	S	0.59	1.15	0.31	0.84
Hake	W	0.42	1.00	0.37	0.84
	S	0.36	1.02	0.44	0.74
Overlap	W	0.31	0.97	0.11	0.83
	S	0.46	0.97	0.26	0.81

1.4 Discussion

1.4.1 Ecological aspects

Saithe suitable habitat in the North Sea is determined by relatively deep waters (> 50 meters). Saithe distribution has slightly expanded towards southwest over the last twenty years which might be linked to an increase of temperature in the North Sea (ICES, 2008; Reid and Valdés, 2011). Indeed, in the recent period, warmer temperatures are found further south and in the Scottish waters. Hake suitable habitat in the North Sea is determined by temperatures ranging from 7°C to 15°C. Bathymetry seems less important as hake can be found in a wide spectrum of depth ranges. The strong relationship of hake distribution with temperature indicates that overall warming (Boyd *et al.*, 2014) could make the North Sea a more suitable habitat for this species. Temperature effect is confirmed by an increase of presence probabilities over the last twenty years in the northern area which has warmed up both in winter (+0.6°C) and summer (+0.9°C). In summer, the disappearance of the southern patch (below the DBL) is consistent with temperatures exceeding 15°C in the recent years. If depth is not overly restrictive within the models, a limiting temperature factor might exist around 15°C. Applied to hake, this limit could be related to reproduction

(a) Saithe, winter (b) Hake, winter (c) Overlap, winter



(d) Saithe, summer (e) Hake, summer (f) Overlap, summer

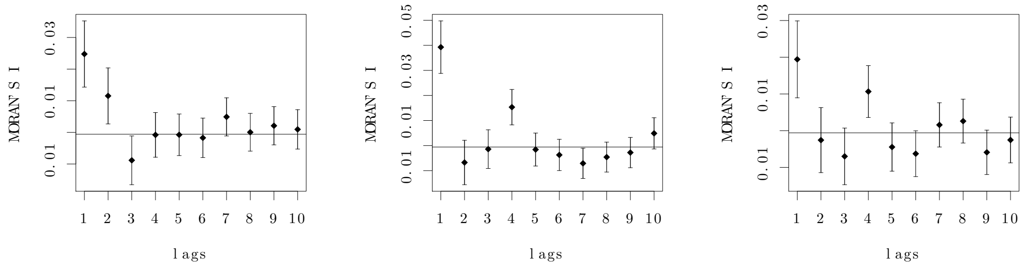


Figure 1.4 – Correlograms of detrended residuals of selected models for saithe (first column), hake (second column) and their overlap (third column) at winter (first line) and summer (second line). Moran's I coefficients depending on different spatial lags, spaced by 75 ± 10 kilometres.

as spawning occurs in temperatures of up to 15°C with an optimum between 10°C and 12.5°C (Ibaibarriaga *et al.*, 2007). The study of the overlap between saithe and hake shows highest occurrences of the two species together in the Northern North Sea with a major importance of bathymetry but also an effect of temperature in summer. There is a consistent spatial trend of increasing overlap probabilities above 57.5° of latitude along with an expansion towards southwest and the Scottish waters. These trends are consistent with saithe and hake spatial distributions changes but also with changes observed in temperature patterns. In the Northern North Sea, temperature and bathymetry are strongly correlated and present similar gradients: temperature and depth decrease with latitude (Knijn *et al.*, 1993; Reid and Valdés, 2011). Therefore, disentangling the respective effects of these two variables is a challenge.

The seasonal differences and the relations with depth and temperature are consistent with Bergstad (1991a) and Jones *et al.* (2013). The direction of the shifts in the North Sea, towards south-west, differs from Perry *et al.* (2005) who found no shift at all and Jones *et al.* (2013) who predicted a northwards shift. However, the authors focused on global long-term climate change effects and covered large temporal scale compared to the twenty years investigated here.

In addition, the southeastern region of the North Sea (below the DBL) presents inverse gradients of temperature in winter and summer. This area might be too cold in winter and too warm in summer which might the limited expansion towards south-west in the Scottish and English waters. Baudron and Fernandes (2014) noted an eastward shift for hake and rejected the hypothesis of a climate-induced change on the basis of the absence of latitude centroids shifts in the other areas occupied by northern hake. The authors suggested that hake expansion may result from density-dependent pressure due to hake recent increase of abundance. They related this increase of abundance to fishery management decisions applied in 2004. Indirect climate-induced changes through *e.g* changes in marine communities (Beaugrand *et al.*, 2003; Beaugrand, 2004; Perry *et al.*, 2005) might explain the changes in habitat suitability of the Scottish and English waters, as they could affect prey availability and therefore may supplement density-dependent induced changes assumption (Baudron and Fernandes, 2014).

The present study considers potential competitors and preys occurrence in modelling saithe, hake and their overlap spatial distributions. Species occurrence have been used to describe biotic interactions. Norway pout, blue whiting, herring and juvenile cod were considered as potential preys while saithe, hake and adult cod were considered as potential competitors (Bergstad, 1991b; Du Buit, 1991; DuBuit, 1996). The positive relationships between potential competitors highlighted in the present study agrees with Baudron and Fernandes (2014) assumption concerning an impact of fishery management restriction adopted in 2004 within the Northern hake recovery plan. The same year, cod recovery plan was adopted in the North Sea which substantially reduced TAC for cod. The resulting economical impacts for demersal mixed fisheries could lead to an avoidance of cod presence areas by these fleets and therefore induced side-effects on other species abundance. This is consistent with the relative importance of adult cod in almost all the models. Link and Auster (2013) suggested that competitors feeding on the same resource are likely to be found in the same areas, which would be characterised by positive relationships at the population scale. Therefore, potential competitive interactions of saithe and hake with cod but also potential competition between saithe and hake assumptions are strengthen by their mutual positive relationships.

Interspecific positive relationships indicate spatial co-occurrence of the different species but do not imply any causal relationship. They could reflect a covariate of major importance missing (Guisan and Thuiller, 2005) and thus they might illustrate indirect biotic effects. Based on the current knowledge concerning saithe and hake diet and the results obtained here, the assumption of predator-prey relationships with Norway pout, blue whiting and adult herring appears reasonable. The percentages of deviance explained by these different species occurrences are consistent with Bergstad (1991b), Du Buit (1991) and DuBuit (1996) who recorded Norway pout and blue whiting as major preys for saithe and hake, respectively. These authors also noted a seasonal diet difference with an increased importance of fish-based diet in winter while saithe and hake fed mostly on zooplankton in summer. This is consistent with the non-selection of fish preys in the models for this season. Johnson *et al.* (2012) did not find prey abundance as significant while studying hake abundance in the Balearic Islands but highlighted an importance of prey size. In order to increase the meaningfulness of the estimated coefficients and improve the interpretation of the relationships, the integration of size groups for potential preys could be of interest, particularly regarding hake. The positive relationships of the overlap with Norway pout, blue whiting, juvenile cod and adult herring confirm the assumption that both saithe and hake feed on these preys.

The present study supplements Baudron and Fernandes (2014) results and suggests that the North Sea warming may have had direct and indirect effects on saithe and hake distribution as well as on their overlap. The similarities between saithe and hake relationships with the different explanatory variables (abiotic and biotic ones) strengthen the assumption that spatial overlap between the two species could keep increasing in the future years. In order to investigate direct effects of climate changes, the study could benefit from the use of global indices representing warming processes better than the average temperatures used here. Indirect effects may be trophically related. Perry *et al.* (2005) showed a southwards shift of Norway pout distribution in relation to the North Sea warming. Therefore, the positive relationship between Norway pout presence and the presence of saithe, hake as well as their overlap supports the hypothesis of trophically-related changes and is consistent with Homrum *et al.* (2013) who highlighted feeding migration behaviour of saithe. As a result, the importance of integrating biotic variables at large scale for species distribution modelling is confirmed by the present study which suggest a participation of other species presence in habitat suitability. The substantial amount of information brought by the biotic variables confirms the importance of integrating potential competitors and preys occurrence in predators habitat models (Torres *et al.*, 2008; Schick and Lutcavage, 2009). The inclusion of biotic features, through other species presence/absence, also increase the robustness of the predictions with spatial autocorrelation quantitative bias far smaller than the 25% assessed by Dormann (2007) in environmental-only models (see Supplementary material for detailed comparison of coefficients).

The interspecific positive relationships provide a first step towards the study of potential bottom-up processes involved in predators spatial distribution through an estimation of their relations with potential preys. In order to confirm these assumptions, it is essential to investigate saithe and hake respective diets in the North Sea as they are currently lacking. The outcomes of diet analyses would in particular allow defining different group sizes for preys, but also modelling species by length groups based on potential diet differences as length-at-maturity used in this study was not discriminant. Ontogenetic variation are not considered in this study because of the high correlation between the total presence of both saithe and hake (juveniles and adult mixed) and at least one of the related length group. This lack of consideration might cause misinterpretation of the results particularly concerning hake. Indeed, juveniles saithe stay in deep waters along the Norwegian coast till they reach maturity which might explain the high correlation between total presence and adult group. For hake, the lack of knowledge concerning maturation in the North Sea but also concerning the presence (or not) of nursery ground in the area are aspects which need to be further investigated. Diet analysis and interspecific comparison would also facilitate the investigation of these two species potential competition. Indeed, even if it could be part of long-term natural fluctuations, the opposite abundance trends of saithe and hake in the North Sea (ICES, 2013d; Baudron and Fernandes, 2014) fulfil the first requirement to demonstrate competition in a large marine ecosystem between two marine species according to Link and Auster (2013). The second requirement these authors suggested concerned spatial overlap which has been established in the present study.

1.4.2 Modelling aspects

Hake emergence in the North Sea and its potential impacts on commercial species and related fisheries could be further investigated. Hake's spatial distribution is currently expanding and this species could in the future years populate areas where it is currently absent (Baudron and Fernandes, 2014). This is consistent with the particular results obtained for hake models concerning the importance of spatial autocorrelation and spatial variables. Quantiles regression techniques may supplement the results obtained here by determining hake potential habitat *i.e* area with suitable conditions for species to be present (Vaz *et al.*, 2008) and give a better overview of hake potential future distribution in the North Sea. Also, modelling the early and late period separately could be of interest in order to compare the importance of the different variables at the two periods. Concerning potential preys, this is particularly interesting for opportunistic feeders which is generally the case of gadiforms fishes in the North Sea. Finally, the study of hake's models performance in a new area, presenting similar range of predictor variables like for example West-Scotland, could also provide an external validation (Guisan *et al.*, 2006; Robinson *et al.*, 2011). Alternatively, the inclusion of West-Scotland data in model calibration could potentially improve the understanding of spatial interactions between saithe and hake in all the area of distribution of North Sea saithe.

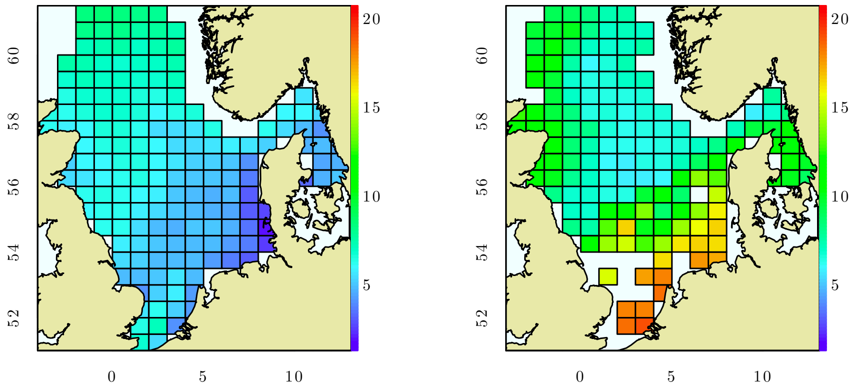
1.4.3 Conclusion

The increasing interest on the effects of global warming (Boyd *et al.*, 2014) lead to a large number of studies which undertook species spatial distribution shifts in the North Sea (Beaugrand, 2004; Perry *et al.*, 2005; Reid and Valdés, 2011; Jones *et al.*, 2013). However, the potential new interactions resulting from these shifts were less examined. In addition, the lack of biotic features used in species distribution modelling (Johnson *et al.*, 2013) may lead to an incomplete view of the situation and to poor predictions (Guisan and Zimmermann, 2000; Mitchell, 2005; Dormann, 2007; Planque *et al.*, 2011; Robinson *et al.*, 2011), which may become a problem for fishery management (Johnson *et al.*, 2013). In this context, the present study investigated saithe and hake spatial distribution in the North Sea, defined their probable habitat and addressed hake recent emergence in the North Sea in relation with saithe through the study of their spatial overlap. This investigation was undertaken through the exploration of the different species presence relationships with abiotic features like temperature and bathymetry. However the novelty of the method was to also include biotic interactions into saithe and hake distribution models through the presence/absence of other species recorded in the literature as potential competitors or preys.

An increasing overlap between saithe and hake over time has been established, which could be induced by climate and trophic changes. These results provide a solid basis to further investigate competition between saithe and hake in the North Sea. In addition, the important contribution of biotic features in the models confirms the importance of including such variables while modelling species distribution at the population scale. The relations between predator occurrence and prey availability were statistically estimated. The results obtained increase our understanding of interspecific interactions and more particularly of bottom-up processes and are of interest in a climate change context. These results would valuably be complemented by a thorough comparative analysis of saithe and hake respective diets. Finally, the present study provided robust predictions concerning saithe and hake spatial distribution in the North Sea. In a context of multi-specific fisheries management, these results may be considered by managers in their decisions (*e.g.* setting of the TACs) concerning saithe, hake and their related fisheries in the area.

1.5 Supplementary material

Supplementary materials presents maps of temperatures in the area of interest (Figure S1.1), correlograms of non-selected environmental-only models (Figure S1.3) and absolute models fitting errors from early period (Figure S1.2). In addition, this section includes three regression parameters tables (Tables S1.1 to S1.3), for saithe, hake and their overlap, respectively, allowing the comparison between non-selected environmental-only models and selected spatial ones.


(a) Winter, early period (b) Summer, early period

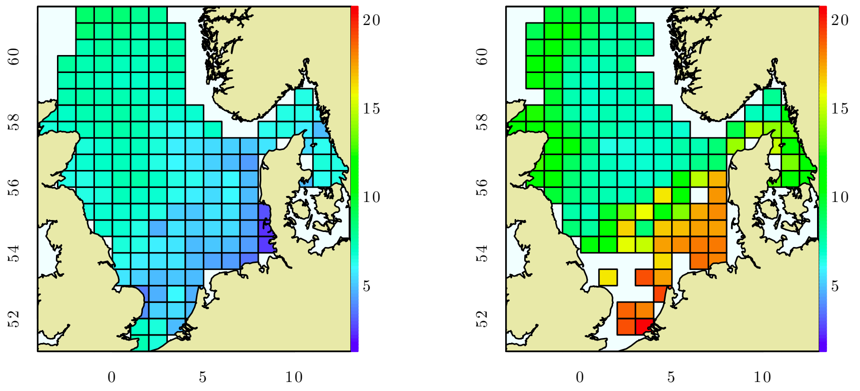
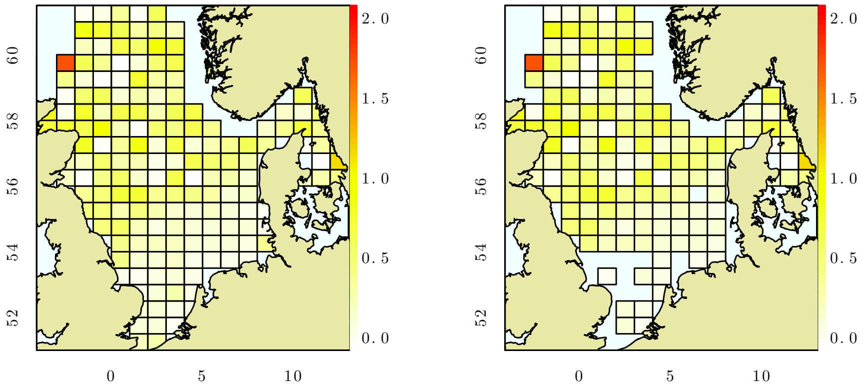
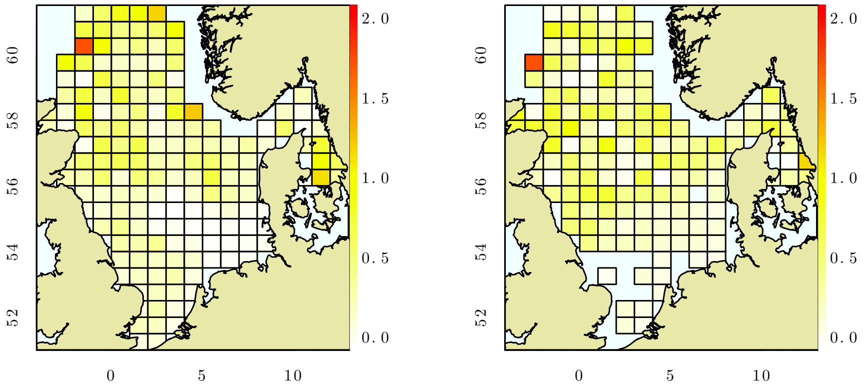

(c) Winter, recent period (d) Summer, recent period

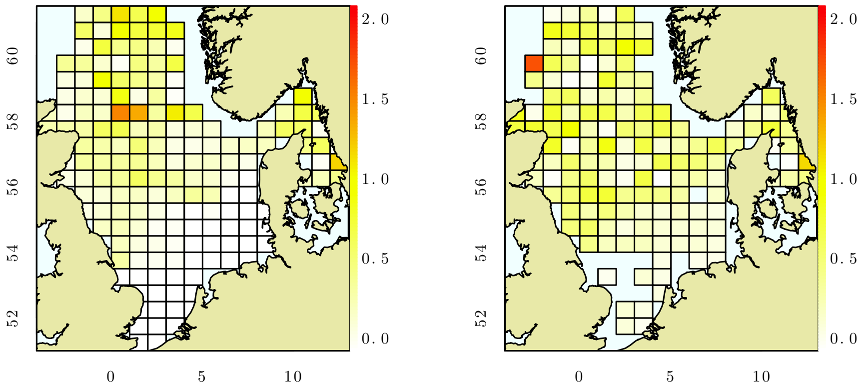
Figure S1.1 – Temperature observation maps (in degree Celsius) for the early period (1991-1996), in (a) winter and in (b) summer and for the recent period (2007-2012) in (c) winter and in (d) summer.


(a) Saithe, winter, early period

(b) Saithe, summer, early period

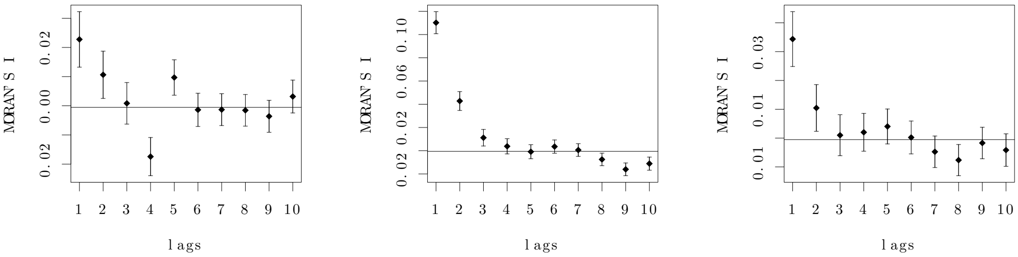

(c) Hake, winter, early period

(d) Hake, summer, early period

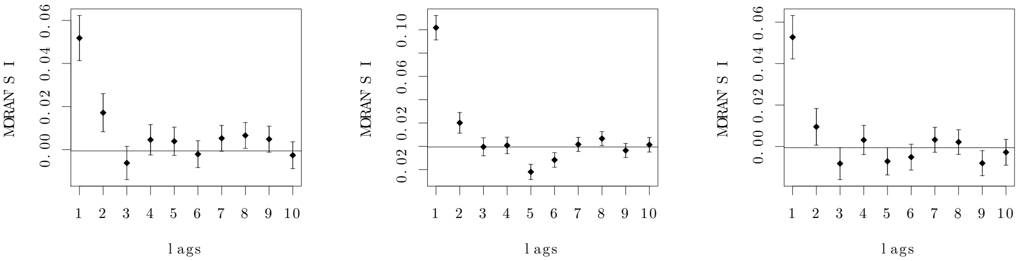

(e) Overlap, winter, early period

(f) Overlap, summer, early period

Figure S1.2 – Maps of spatial models absolute fitting error, error between observations and predictions, calculated for the early period (1991-1996) for saithe (a) in winter and (b) in summer; for hake (c) in winter and (d) in summer; for overlap (e) in winter and (f) in summer.



(a) Saithe, winter (b) Hake, winter (c) Overlap, winter



(d) Saithe, summer (e) Hake, summer (f) Overlap, summer

Figure S1.3 – Correlograms of detrended residuals of environmental-only models for saithe (first column), hake (second column) and their overlap (third column) at winter (first line) and summer (second line). Moran's *I* coefficients depending on different spatial lags, spaced by 75 ± 10 kilometres.

Table S1.1 – Environmental-only and spatial saithe distribution models parameters β per variables (Table 1.1) and for each season. All coefficients are significant with $p < 0.001$, except for those marked with a letter as exposant. ^{a}: $p < 0.01$.

	Winter		Summer	
	ENV	ENV+SP	ENV	ENV+SP
H.Tot	7.92×10^{-1}	7.89×10^{-1}	9.57×10^{-1}	9.22×10^{-1}
C.Adu	1.05	1.05	1.02	1.09
C.Juv			1.58	1.61
NP.Tot	1.18	1.18		
BW.Tot				
HG.Adu				
HG.Juv	-8.29×10^{-1}	-8.46×10^{-1}	-1.02	-9.04×10^{-1}
CSpp				
FSpp			-1.13	-9.77×10^{-1}
Gpp	3.96^a	4.23	5.71	6.60
Ppp				
Lpp				3.72×10^{1a}
Temp				
Temp2				
Temp3				
Depth	2.84×10^{-2}	2.83×10^{-2}	6.27×10^{-2}	4.77×10^{-2}
Depth2			-1.09×10^{-4}	
Depth3	-6.98×10^{-8}	-6.52×10^{-8}		-1.66×10^{-7}

Table S1.2 – Environmental-only and spatial hake distribution models parameters β per variables (Table 1.1) and for each season. All coefficients are significant with $p < 0.001$, except for those marked with a letter as exposant. ^{a}: $p < 0.01$; ^{b}: $p < 0.05$.

	Winter		Summer	
	ENV	ENV+SP	ENV	ENV+SP
S.Tot	6.10×10^{-1}	7.86×10^{-1}	1.02	1.09
C.Adu			5.01×10^{-1}	$4.40 \times 10^{-1\,a}$
C.Juv				
NP.Tot	9.89×10^{-1}	$7.82 \times 10^{-1\,a}$		
BW.Tot	7.85×10^{-1}	7.76×10^{-1}	$6.47 \times 10^{-1\,a}$	
HG.Adu	1.31	1.25		
HG.Juv				
CSpp				-1.97^{a}
FSpp	-2.92	-2.75	-1.13	-8.60×10^{-1}
Gpp				5.17
Ppp	-3.28	-4.62	-2.71	-2.43
Lpp				
Temp	5.07^{b}		1.13	1.06
Temp2	-1.01^{a}	-1.56×10^{-1}		
Temp3	$6.41 \times 10^{-2\,a}$	1.79×10^{-2}	-2.79×10^{-3}	-2.57×10^{-3}
Depth	4.04×10^{-2}	4.37×10^{-2}	6.76×10^{-3}	7.87×10^{-3}
Depth2	-2.07×10^{-4}	-2.09×10^{-4}		
Depth3	2.73×10^{-7}	2.59×10^{-7}		

Table S1.3 – Environmental-only and spatial overlap models parameters β per variables (Table 1.1) and for each season. All coefficients are significant with $p < 0.001$, except for those marked with a letter as exposant. ^{a}: $p < 0.01$.

	Winter		Summer	
	ENV	ENV+SP	ENV	ENV+SP
C.Adu	7.24×10^{-1}	7.73×10^{-1}	1.02	9.80×10^{-1}
C.Juv			$8.81 \times 10^{-1\,a}$	$9.37 \times 10^{-1\,a}$
NP.Tot	1.17^{a}	1.41	$9.37 \times 10^{-1\,a}$	$9.51 \times 10^{-1\,a}$
BW.Tot			7.64×10^{-1}	7.12×10^{-1}
HG.Adu	1.33	1.28		
HG.Juv	-7.94×10^{-1}	-1.11	-8.23×10^{-1}	-9.16×10^{-1}
FSpp	-1.54	-1.02	-1.34	-1.09
Gpp				
Ppp				
Lpp				
Temp	$1.07 \times 10^{1\,a}$		1.63	1.65
Temp2	-1.91^{a}		-7.04×10^{-2}	-7.19×10^{-2}
Temp3	1.08×10^{-1}			
Depth	5.53×10^{-2}	2.75×10^{-2}	6.78×10^{-2}	6.03×10^{-2}
Depth2	-2.00×10^{-4}	-3.88×10^{-5}	-2.53×10^{-4}	-2.12×10^{-4}
Depth3	$2.31 \times 10^{-7\,a}$		2.91×10^{-7}	$2.32 \times 10^{-7\,a}$

Here we eat fish.
Under the sea, the fish eat us.
I know, I know, oh, oh, oh.

George R.R. Martin, A Song of Ice and Fire, A Clash of Kings

Chapter 2

Trophic competition between saithe and hake in the North Sea

Cormon, X., Cresson, P., Denis, J., Rabhi, K., Rouquette, M., Tiedemann, F., and Marchal, P. Manuscript, Chapter 2. Could there be a dietary overlap between well-established saithe (*Pollachuis virens*) and emerging hake (*Merluccius merluccius*) in the North Sea?

Abstract
Recent emergence of European hake in the North Sea might result in trophic competition with co-occurring species such as saithe. Saithe diet in the North Sea was not investigated since 1991 while hake diet was never investigated in this area. In this context, we examined saithe and hake diets to understand their feeding behaviour and measure the dietary overlap between these two predators. Diet was studied through the analysis of gut contents collected in 2013 in the Northern North Sea. A robust and informative index combining traditional prey occurrence and abundance frequencies was chosen to describe saithe and hake diet and calculate their dietary overlap. Results suggested a partitioning of food resources based on predator length. Saithe and hake presented dietary overlap within length groups which deserves consideration, particularly concerning prey types with high energetic values such as silvery lightfish (*Maurolicus muelleri*).

Keywords: trophic competition; resource partitioning; co-occurring gadoids; saithe; hake; North Sea; dietary measure index; Horn overlap index; overlap significance

2.1 Introduction

Environmental factors changed in the North Sea (ICES, 2008) in the last 20 years, resulting in changes in community structure (Beaugrand, 2004) and in species spatial relocation (Beare *et al.*, 2004). These changes are expected to alter regional food-web linkages by modifying species interactions (Poloczanska *et al.*, 2008). As shown for grey gurnard (*Eutrigla gurnardus*) (Floeter *et al.*, 2005), the emergence of a predator in a heavily exploited area such as the North Sea may impact the whole ecosystem including species of high commercial importance such as cod (*Gadus morhua*). In addition, new competitive interactions may appear and indirectly impact well-established species through a reduction of their food availability (Frederiksen *et al.*, 2006).

In order to study trophic competition, one approach consists of investigating prey-resource partitioning and predators dietary overlap. Within fish communities, these questions are largely studied with stomach or gut content analyses (Hislop, 1980). There are, however, many ways of characterising fish diet. Since more than 30 years, scientists have attempted to best characterise diet (Hislop, 1980; Ross, 1986; Cortés, 1997; Hansson, 1998; Baker *et al.*, 2014). Traditional dietary indices are prey occurrence, abundance and weight frequencies (Bowen, 1996). Each of these indices provides different information about diet and has it own merits and weaknesses. For example, prey frequency of occurrence is the least biased of the three indices but poorly reflects dietary overlap. Prey abundance frequency tends to overestimate the importance of small prey types while, to the contrary, prey weight tends to overestimate the importance of larger preys.

Compound dietary indices combining two or more measures *e.g.* Pinkas *et al.* (1970) Index of Relative Importance (I-RI) have been widely used (Hislop, 1980; Cortés, 1997; Hart *et al.*, 2002). However, some scientists argue that compound indices are redundant with traditional dietary indices (Macdonald and Green, 1983), lack of biological meaning (Bowen, 1996), or are simply too sensitive *e.g.* to prey taxonomic level resolution (Hansson, 1998). The adequacy of dietary overlap indices (Horn, 1966; Schoener, 1968; Linton *et al.*, 1981; Wallace, 1981) and the way overlap significance must be established (Mueller and Altenberg, 1985; Cortés, 1997; Link and Auster, 2013; Krebs, 2014) have also been investigated.

North Sea gadoids, *e.g.* cod, saithe (*Pollachius virens*), whiting (*Merlangius merlangus*), are major predators of the North Sea ecosystem, and investigating their respective diet is of particular interest (Bergstad, 1991b; Hislop *et al.*, 1991; Hoines and Bergstad, 1999; Adlerstein *et al.*, 2002) in an Ecosystem Approach to Fisheries (EAF) management context. It is thus of primary importance to get better insights into multispecies interactions in the North Sea (ICES, 2013b), to estimate predation mortalities and assess interacting stocks simultaneously. A major requirement to conduct such multispecies assessments and analyses, is to enhance knowledge about the diet of species structuring the exploited ecosystem. This requirement led to large sampling programs such as the 1981 and 1991 Stomach Sampling Projects of the North Sea or, more recently, the EU-funded project MARE/2012/02 "Study on stomach content of fish to support the assessment of good environmental status of marine food webs and the prediction of MSY after stock restoration".

While both the 1981 and 1991 stomach sampling programs focused exclusively on cod, saithe, whiting, haddock (*Melanogrammus aeglefinus*) and mackerel (*Scomber scombrus*) (Daan, 1989; ICES, 1997a), the more recent MARE/2012/02 project also considered two North Sea upcoming predators: grey gurnard (Floeter *et al.*, 2005) and hake (*Merluccius merluccius*) (Baudron and Fernandes, 2014; Cormon *et al.*, 2014, Chapter 1). Hake diet, in particular, was never studied at a large scale in the area even if its potential predation on fish prey populations are expected to be high, particularly since its abundance increased (Cohen *et al.*, 1990; Bergstad, 1991b; DuBuit, 1996; Mahé *et al.*, 2007). For this reason, hake was recently included in Stochastic MultiSpecies (SMS), the multispecies model that has most recently been operated by the International Council for the Exploration of the Sea (ICES) to assess North Sea fish stocks (ICES, 2014a). Unfortunately, prey groups as described by ICES (2014a) are too aggregated to allow a fine study of hake diet. This aggregation, pooling all non-commercial species together (fishes, crustaceans, molluscs, *etc.*), also hamper the diet comparison between hake and other species. Indeed, in addition to a new predation pressure exerted on prey populations, hake emergence could also have indirect effects on other species through trophic competition.

In particular, the increasing spatial overlap between hake and saithe (Cormon *et al.*, 2014, Chapter 1) might have negative consequences for saithe population in case of high dietary overlap. For instance, saithe growth in the North Sea was shown to depend on Norway pout (*Trisopterus esmarkii*) availability (Cormon *et al.*, 2016, Chapter 3). Carruthers *et al.* (2005) also evidenced a link between Scotian Shelf saithe condition and euphausiids availability. In the North Sea and its surroundings, saithe diet was studied more than 20 years ago (Daan, 1989; Bergstad, 1991b; Du Buit, 1991; ICES, 1997a). Since then, environmental and species distribution changes might have altered saithe diet. The decreasing trend of saithe Spawning Stock Biomass (SSB) over the last few years along with decreasing mean weight-at-age (ICES, 2014b) and growth (Cormon *et al.*, 2016, Chapter 3) might partly result from competitive interactions with hake (Cormon *et al.*, 2016, Chapter 4) and confirm the need of comparing saithe and hake diets.

The aim of this study is to investigate specific diets of saithe and hake, as

Table 2.1 – Characteristics of saithe and hake samples collected in 2013. Numbers of non-empty samples collected are separated with a dash from numbers of samples selected for prey identification by sub-sampling.

	Winter		Summer		Total
	Saithe	Hake	Saithe	Hake	
Devaginated	2	32	0	22	56
Empty	7	10	0	33	50
Non-empty	96-71	38-38	104-56	68-49	306-214
Total	105	80	104	123	412

well as the dietary overlap between these two potential competitors. In addition, we suggest a method to choose a dietary index, particularly for dietary overlap calculations, building on ecological meaning but also robustness to sampling error properties. Finally, different methods to assess dietary overlap index significance were used and compared.

2.2 Materials and methods

2.2.1 Sample collection

Saithe and hake samples were collected in winter (January-February) and summer (July-August) 2013 in the Northern part of the North Sea (above 57°N of latitude) from the Norwegian coast (6°E of longitude) to West Scotland (8°W of longitude). Most of the sampling was operated by the crew of two freezer bottom trawlers (*Cap Nord* and *Klondyke*) belonging to the EURONOR fishing company. Saithe and hake samples were retrieved by pairs of similar sizes during five weeks of fishing operations. In order to ensure a reasonable amount of exploitable samples (non-empty and non-devaginated guts), we collected at least twice as much fishes as required for the diet analysis. Targeted sizes ranged from 40 centimetres to maximum size encountered. Sampling was realised during catch sorting and selected fishes were immediately frozen at -40°C.

After landing, all EURONOR samples were sized, weighted and sex-typed before fish guts were extracted at IFREMER in Boulogne-sur-Mer where all laboratory work took place. Gut contents were stored in Petri-dishes and refrozen at -20°C for potential prey identification. Empty and devaginated samples were also recorded (Table 2.1). The high amount of devaginated hake guts recorded in winter led to an increase of sampling effort in summer. We proceeded to the sub-sampling of the EURONOR exploitable samples (non-empty and non-devaginated guts) based on classification. This classification regrouped the most similar individuals, in terms of total length, sex, maturity, geographical position (latitude and longitude), time (day or night), and depth (when available), in order to obtain representative sub-samples.

A reduced number of the smallest hake and saithe size categories (from 20 cm to 40 cm) was collected during winter and summer International Bottom Trawl Survey (IBTS) aboard Norwegian and German research vessels, *G.O. Sars* and *Walther Herwig III*, respectively. After being sized, weighted and sex-typed, fish guts were directly extracted on board and frozen at −40°C.

In total, 412 samples of saithe and hake were collected in 2013 (Table S2.1) and, after sub-sampling, 214 non-empty samples were prepared for prey identification (Table 2.1).

2.2.2 Prey identification and classification

Preys included in gut contents (stomach and intestines) were identified with both unaided eye and binocular microscope. Commercial samples collected by fishing vessels may have stayed in trawls for several hours leading to advanced digestion of the prey and transfer into intestines. Considering whole gut contents provide thus a longer time-integrated view of feeding patterns. Prey items were sorted and identified at their lowest possible taxonomic level (ICES, 2010). Occurrence and abundance of prey items were recorded. The advanced digestion of most preys present in guts did not allow using prey weight in the subsequent analyses.

In order to identify rare prey taxons and to group preys of minor importance, frequencies of occurrence (F_{O_i}, Equation 2.1), and frequencies of abundance (F_{O_i}, Equation 2.2), were calculated for each prey item i over the whole pool of data. When both F_{O_i} and F_{N_i} were lower than 5%, preys were pooled based on their taxonomic level but also on their habitat, *e.g.* pelagic and demersal fish species were separated. Pooling was realised cautiously, *e.g.* *Trisopterus sp.* remains were separated from clearly identified remains of Norway pout to facilitate unbiased interpretation. In total, 20 groups, including 9 fish groups (Table 2.2), 6 crustaceans groups (Table 2.3) and 5 other invertebrates groups (Table 2.4), were used in saithe and hake diet analysis.

$$F_{O_i} = \frac{J_i}{S} \tag{2.1}$$

where J represents the number of guts containing prey item i and S the total number of full guts; and

$$F_{N_i} = \frac{N_i}{\sum_{i=1}^{T} N_i} \tag{2.2}$$

where N_i represents the number (abundance) of prey items i and T the number of prey types.

2.2.3 Diet analysis

Predator characterisation

A Multivariate Regression Tree (MRT), a clustering analysis technique which allows constrained partitioning by *a priori* chosen variables (De'Ath, 2002), was used to distinguish between diet types. The partitioning of our diet data, 20 prey groups abundance at the individual level (one sample = 1 row), was constrained by fishing season, predators species and predators length. This constrained partitioning aimed at identifying of the diet's most driving factors among the three tested, by minimising the within-group sums of squares. The minimum number of observations in terminal MRT leaves was set to 20 to prevent final groups from being too small to be further investigated. Finally, alternative trees were build after randomly removing one sample from dataset for a total of 999 iterations. This cross-validation procedure allowed us to choose the tree with best predictive power.

Costello (1990) graphical techniques were used to investigate prey dominance and predator feeding strategy within predator groups resulting from the previously described MRT analysis. We, therefore, related for each prey, i, the frequency of abundance (F_{N_i}) to its frequency of occurrence (F_{O_i}).

Diet overlap

Dietary index selection To study dietary overlap between saithe and hake, we considered several indices combining abundance and occurrence. Four indices were computed, in addition to F_O and F_N. Prey specific abundance frequency, F_{NS_i}, allowed the calculation of prey abundance frequency conditional to this prey occurrence (Equation 2.3). The weighted abundance frequency, F_{NW_i} (Amundsen *et al.*, 1996), was calculated with abundance, N_i, weighted by F_{O_i} (Equation 2.4). Indices of relative importance from Pinkas *et al.* (1970) and George and Hadley (1979) were modified in F_{M_i} and F_{S_i}, respectively, in order to combine occurrence and abundance frequencies without taking into account weight (Equations 2.5 and 2.6).

Table 2.2 – Fish groups used for saithe and hake diet analysis.

Groups	Prey items	Abbreviations
Norway pout		NP
	Trisopterus esmarkii	
Trisopterus spp.		TSP
	Trisopterus sp.	
	Trisopterus minutus	
Silvery pout		SP
	Gadiculus argenteus	
Blue whiting		BW
	Micromesistus poutassou	
Gadoids non-identified		GNI
	Gadiformes	
	Gadidae	
Silvery lightfish		SL
	Maurolicus muelleri	
Other pelagic fishes		OPF
	Clupeidae	
	Clupea harengus	
	Scomber scombrus	
Other demersal fishes		ODF
	Merlangius merlangus	
	Melanogrammus aeglefinus	
	Merluccius merluccius	
	Argentinidae	
	Argentina sphyraena	
	Ammodytidae	
	Ammodytes sp.	
	Callionymus maculatus	
	Pleuronectidae	
	Hippoglossoides platessoides	
	Limanda limanda	
	Helicolenus dactylopterus	
Fishes non-identified		FNI
	Actinopterygii	
	Stomiiformes	
	Myctophiformes	

Table 2.3 – Crustacean groups used for saithe and hake diet analysis.

Groups	Prey items	Abbreviations
Hyperiids		HYP
	Hyperiidae	
	Hyperia sp.	
	Hyperia galba	
Euphausiids		EUP
	Euphausiacea	
	Euphausiidae	
	Meganyctiphanes norvegica	
Copepods		COP
	Copepoda	
	Calanoida	
	Calanus sp.	
	Paraenchaeta norvegica	
	Caligus sp.	
Other amphipods		OA
	Amphipoda	
	Gammaridae	
Other malacostraca		OM
	Malacostraca	
	Eucarida	
	Cumacea	
	Decapoda	
	Brachyura	
	Crangon allmanni	
	Philocheras echinulatus	
	Galathea	
	Liocarcinus holsatus	
	Isopoda	
	Mysida	
	Praunus flexuosus	
	Peracaridea	
Crustaceans non-identified		CNI
	Crustacea	

Table 2.4 – Other invertebrate groups used for saithe and hake in diet analysis.

Groups	Prey items	Abbreviations
Annelids		ANN
	Annelida	
	Polychaeta	
	Nereis sp.	
Cephalopods		CEP
	Cephalopoda	
	Sepiolidae	
	Teuthida	
	Loliginidae	
	Alloteuthis subulata	
Gastropods		GAS
	Gastropoda	
	Clione limacina	
	Rissoella diaphana	
	Euspira pulchella	
	Obtusella sp.	
	Obtusella intersecta	
Other invertebrates		OI
	Mollusca	
	Ostracoda	
	Echinoidea	
	Bivalvia	
	Mytilus sp.	
	Venus verruscosa	
Invertebrates n.i.		INI
	Invertebrata	

$$F_{NS_i} = \frac{N_i}{\sum_{i=1}^{Q} N_i} \tag{2.3}$$

where Q represents the number of prey types in guts containing prey i has been identified.

$$F_{NW_i} = \frac{N_i \times F_{O_i}}{\sum_{i=1}^{T}(N_i \times F_{O_i})} \tag{2.4}$$

$$F_{M_i} = F_{N_i} \times F_{O_i} \tag{2.5}$$

and

$$F_{S_i} = F_{N_i} + F_{O_i} \tag{2.6}$$

A bootstrapping procedure was carried out for the six indices to quantify their robustness to sampling error. 1000 samples were drawn with replacement and distribution per prey of each index was studied to characterise and compare the sensitivity of indices estimates to sampling error. To that purpose, we calculated the weighted average coefficient of variation ($\overline{CV}_W$) for each index over the whole pool of data (Equation 2.7). Finally, the dietary index maximising both ecological meaning and robustness to sampling error (relatively small $\overline{CV}_W$) was chosen for overlap index calculation.

$$\overline{CV}_W = \frac{\sum_i^T (CV_{x_i} \times x_i)}{\sum_{i=1}^{T} x_i} \tag{2.7}$$

where x is any dietary index and CV the coefficient of variation calculated as in Equation 2.8.

$$CV = \frac{\sigma_{x_i}}{\mu_{x_i}} \tag{2.8}$$

where σ is the standard deviation and μ the mean.

Overlap index calculation Seasonal variations of saithe and hake diet overlap were considered for each predators groups defined by the MRT analysis. The Horn (1966) index (Equation 2.9) was chosen to evaluate trophic overlap, since it can be used for any of the six dietary indices previously described. The Horn's index is a modification of the Morisita's index, based on information theory and allowing the comparison of proportions. It is appropriate when foraging habitat overlap are of interest (Horn, 1966) and provides relatively less biased overlap values compared to other indices (Cortés, 1997; Jost, 2007; Krebs, 2014).

$$R_{jk} = \frac{\sum(p_{ij} + p_{ik}) \times log(p_{ij} + p_{ik}) - \sum p_{ij} \times log(p_{ij}) - \sum p_{ik} \times log(p_{ik})}{2 \times log(2)} \tag{2.9}$$

where R_{jk} is Horn's index of diet overlap between group j and group k, p_{ij} the proportional importance of prey item i eaten by predator group j and p_{ik} the proportional importance of prey item i eaten by predator group k. Predator groups j and k may represent any group of predators based on chosen characteristic *e.g.* species, length, sex.

Overlap index significance In order to evaluate Horn's indices representativeness and draw conclusion about their significance, we followed a procedure in three steps. For each group, we first checked whether the observed Horn's index (R_{obs}) was included within the 95% confidence interval of the distribution obtained by a bootstrap procedure of 1000 resamples ($D1$). R_{obs} was also compared to the median of $D1$ here referred to as R_m.

Second, we evaluated whether the observed Horn overlap index (R_{obs}) was significantly different to theoretical Horn index (R_{th}) values derived from 500 random permutations of hake prey importance proportion (p_{ik} in Equation 2.9). The resulting theoretical distribution ($D2$) was then examined and a pvalue P_p was calculated as the ratio between the number of $R_{\text{th}} > R_{\text{obs}}$ and the total number of permutations ($n = 500$).

Third, the robustness of the conclusions about overlap significance to sampling error was assessed. To that purpose, we used the bootstrap distribution $D1$ (as in step 1), and we permuted 500 times each of the 1000 thousands resamples (as in step 2) resulting in half a million of theoretical Horn's overlap indices, the distribution of which is referred to as $D3$. We checked the robustness to sampling error of the conclusions about overlap significance drawn in step 2 by comparing R_m to $D3$. As in step 2, a pvalue was calculated (P_{bp}) as the ratio between the number of $R_{\text{th}} > R_m$ and the total number of permutations ($n = 500000$).

Finally, conclusions drawn in steps 2 and 3 about overlap significance were compared to conclusions drawn using Ross (1986) simple rule of thumb (RT) which suggest a significant overlap when overlap index exceeded 0.6.

2.3 Results

2.3.1 Predator groups

The classification analysis, constrained by season, predator species and length, indicates four groups based on season and predators length. However, predator species were not selected as discriminant in this analysis (Figure 2.1). The vari-

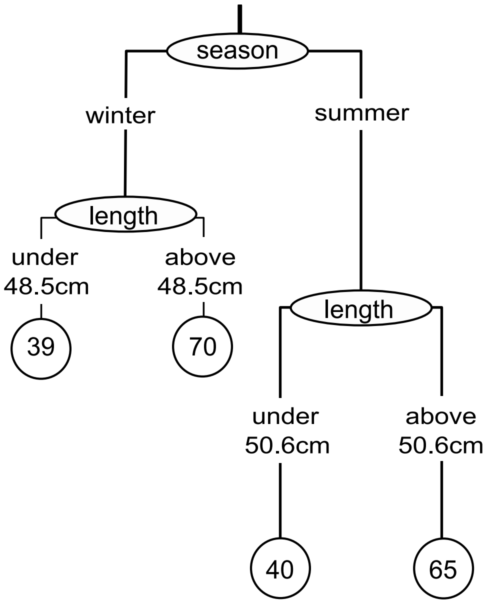
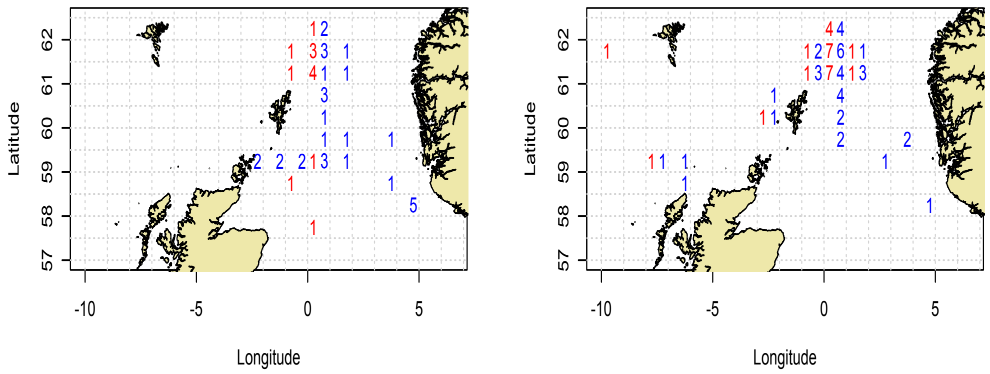


Figure 2.1 – Partitioning of prey abundance constrained by season, predator's species and length obtained with Multivariate Regression Tree analysis. Ellipses indicate split characteristics, rectangles group characteristics, and circles numbers of individuals in final groups.

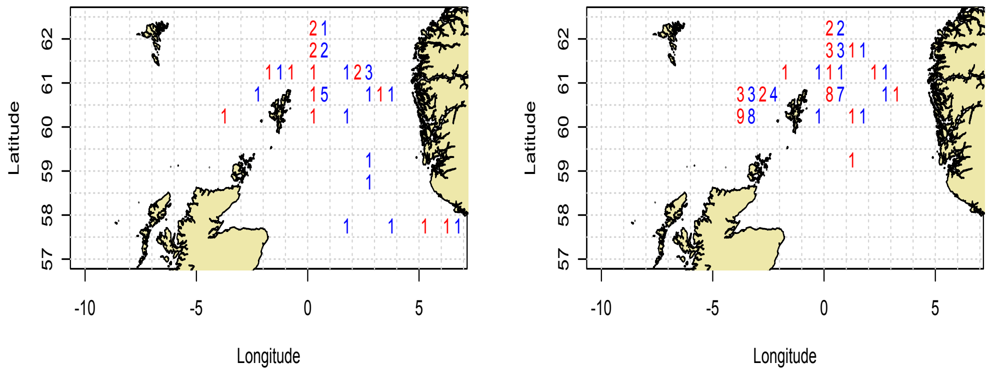
ability explained by the MRT was very low, with a coefficient of determination (R^2) around 0.07, and a predictive power of the tree equal to zero.

The classification based on season and predator length did not appear sufficient to differentiate between diets, and highlighted the need of studying saithe and hake diets within groups. To be consistent, both seasons were divided in two length classes with threshold set to 50 cm. The spatial distribution of individuals with non-empty guts available for diet identification was checked by species (Figure 2.2), to ensure a sufficient number of individuals per predator group. In winter, there were more saithe than hake samples analysed for both length classes: 31 and 13 samples, respectively, for individuals ≤ 50 cm; and 40 and 25 samples, respectively, for individuals > 50 cm (Figures 2.2a and 2.2b). In summer, proportions of saithe and hake samples analysed were similar for both length classes (due to the increase of hake sampling effort in summer), with 22 and 15 samples for saithe and hake ≤ 50 cm, respectively; and 34 samples each for individuals > 50 cm (Figures 2.2c and 2.2d). Spatial coverage was satisfactory.



(a) Winter ≤ 50cm, 44 individuals

(b) Winter > 50cm, 65 individuals



(c) Summer ≤ 50cm, 37 individuals

(d) Summer > 50cm, 68 individuals

Figure 2.2 – Spatial distribution of saithe and hake per groups (season and predator length) for which diet has been analysed (non-empty samples). In red, counts per ICES statistical rectangle of hake, and in blue, counts per ICES statistical rectangle of saithe.

2.3.2 Diet description

Winter Smaller hake fed exclusively on fish preys while smaller saithe diet was more diverse, including crustaceans and other invertebrates (Tables 2.5 and 2.6). Costello plot (Figure 2.3a) indicated a specialisation of saithe on euphausiids and copepods which were found in about 13% and 16%, respectively, of saithe guts analysed (Table 2.5), but represented about 49% and 30%, respectively, of saithe total preys consumption (Table 2.6). Norway pout was hake's dominant prey, found in about 50% of hake guts (Table 2.5) and representing about 60% of hake total prey consumption (Table 2.6). Norway pout was also eaten by 60% of saithe but represented only 20% of its total prey consumption.

In contrast, winter diet of larger saithe and hake (> 50 cm) was less partitioned (Figure 2.3b). Both predators had always mainly consumed fish preys. Although hake was still more piscivorous than saithe in terms of prey abundance ($80.39\% > 66.20\%$, Table 2.6), its diet was more diverse than that of smaller hake with a larger consumption of crustaceans and other invertebrates *e.g.* gastropods. Costello plot (Figure 2.3b) showed similar importance of silvery pout (*Gadiculus argenteus*) for both saithe and hake with 20% of both predators found with silvery pout in their guts while this prey represents about 20% of saithe and hake total prey consumption (Tables 2.5 and 2.6). There were similar occurrences of all other fish preys in saithe and hake guts except for the other demersal fishes (see Table 2.2 for prey group composition) which were only eaten by saithe. These results highlight diet similarities between the two predators. Only Norway pout and silvery lightfish (*Maurolicus muelleri*) abundance were higher for saithe than for hake. Larger saithe were still specialised on euphausiids while gastropods represented a larger diet fraction for hake (Figure 2.3b).

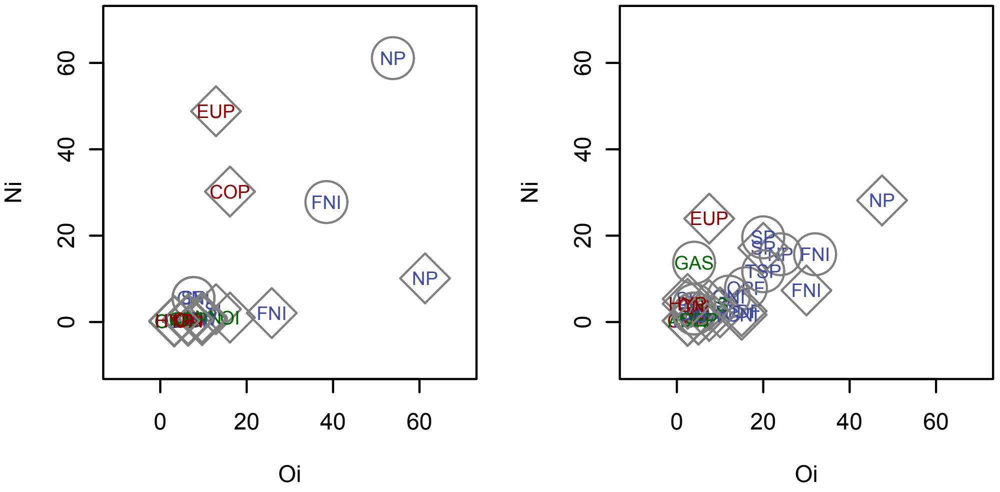
Summer Smaller saithe (≤ 50 cm) had a generalist diet, *sensu* Costello (1990), based on fish and crustaceans with occurrences of about 86% and 91%, respectively (Table 2.5). Smaller hake were more piscivorous than saithe, with about 93% of fish prey occurrence, while crustaceans were found in only 13% of their guts (Table 2.5). For saithe, the main occurring preys ($F_0 \geq 40\%$) were silvery lightfish, hyperiids, euphausiids and other malacostraca as well as non-identified fish and crustaceans. The dominance of silvery lightfish was confirmed as representing more than 40% of saithe total prey consumption (Table 2.6). In comparison, preys often consumed ($F_0 \geq 25\%$), *i.e* Norway pout, copepods and gastropods were less important (Figure 2.3c). Norway pout and euphausiids were also found in hake guts (40% and 7%, respectively). These preys were important for hake representing at least 25% each of hake total prey consumption. However, a bulk of fish preys could not be identified in hake guts, thereby hindering more detailed analyses.

Table 2.5 – Percentages of prey type occurrence calculated for saithe and hake in each predator group. S: saithe. H: hake. See Tables 2.2 to 2.4 for prey groups and prey abbreviations definition.

		Winter				Summer			
		≤ 50cm		> 50cm		≤ 50cm		> 50cm	
		S	H	S	H	S	H	S	H
Fish		83.87	100.00	100.00	100.00	86.36	93.33	97.06	97.06
	NP	61.29	53.85	47.50	24.00	27.27	40.00	29.41	5.88
	TSP			2.50	20.00		13.33	20.59	
	SP	9.68	7.69	20.00	20.00			23.53	8.82
	BW	9.68		7.50	4.00	13.64		29.41	11.76
	GNI		7.69	15.00	12.00	18.18	13.33	8.82	
	SL	12.90		2.50	4.00	40.91		50.00	11.76
	OPF			10.00	16.00			5.88	17.65
	ODF	3.23		15.00		13.64		2.94	8.82
	FNI	25.81	38.46	30.00	32.00	45.45	40.00	50.00	58.82
Crustaceans		41.94		15.00	8.00	90.91	13.33	70.59	11.76
	HYP	3.23		2.50		59.09		41.18	5.88
	EUP	12.90		7.50		59.09	6.67	35.29	
	COP	16.13		2.50		22.73		11.76	
	OA	6.45				9.09		8.82	2.94
	OM	12.90		2.50	4.00	40.91		50.00	11.76
	CNI	6.45			4.00	40.91	6.67	29.41	8.82
Other invertebrates		32.26		15.00	4.00	50.00		35.29	14.71
	ANN	9.68		2.50		31.82		2.94	2.94
	CEP	6.45		5.00				11.76	8.82
	GAS	3.23		7.50	4.00	27.27		11.76	5.88
	OI	16.13				4.55			
	INI					9.09		20.59	2.94

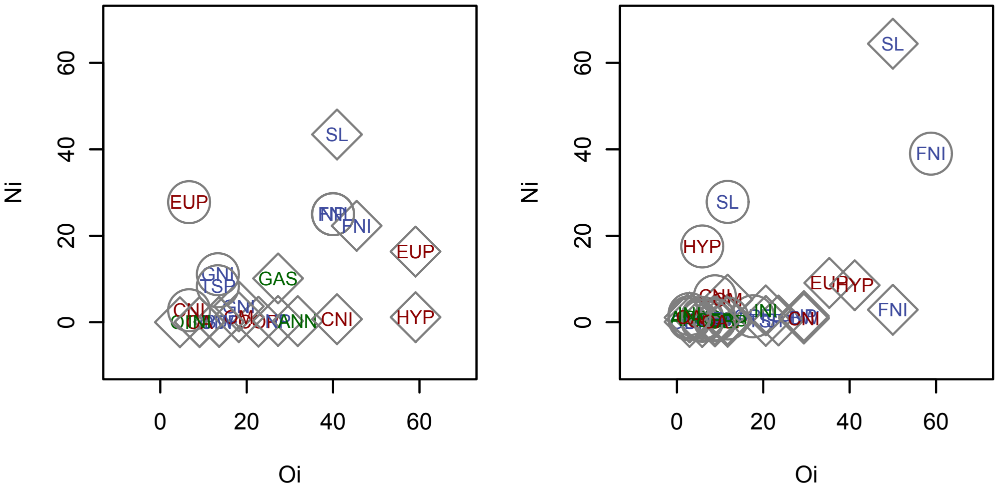
Table 2.6 – Percentages of prey type abundance calculated for saithe and hake in each predator group. S: saithe. H: hake. See Tables 2.2 to 2.4 for prey groups and prey abbreviations definition.

		Winter				Summer			
		≤ 50cm		> 50cm		≤ 50cm		> 50cm	
		S	H	S	H	S	H	S	H
Fish		16.52	100.00	66.20	80.39	69.90	69.44	71.29	70.79
	NP	10.12	61.11	28.17	15.69	0.31	25.00	1.43	0.52
	TSP			0.28	11.76		8.33	0.32	
	SP	0.45	5.56	17.18	19.61			0.41	0.69
	BW	0.74		1.41	1.96	0.09		1.05	0.86
	GNI		5.56	1.69	5.88	3.67	11.11	0.59	
	SL	2.98		5.35	1.96	43.44		64.43	27.84
	OPF			2.25	7.84			0.08	1.37
	ODF	0.15		2.54		0.08		0.08	0.52
	FNI	2.08	27.78	7.32	15.69	22.31	25.00	2.89	39.00
Crustaceans		80.65		29.01	5.88	19.59	30.56	24.09	25.09
	HYP	0.30		4.23		1.18		8.56	17.53
	EUP	48.81		23.94		16.35	27.78	9.10	
	COP	30.21		0.28		0.14		0.14	
	OA	0.45				0.03		0.19	1.20
	OM	0.30		0.56	1.96	1.18		5.24	0.34
	CNI	0.60			3.92	0.71	2.78	0.86	6.01
Other invertebrates		2.83		4.79	13.73	10.51		4.62	4.12
	ANN	1.04		0.28		0.27		1.11	0.69
	CEP	0.60		0.56				0.14	0.52
	GAS	0.15		3.94	13.73	10.14		0.62	1.03
	OI	1.04				0.01			
	INI					0.09		2.75	1.89



(a) Winter ≤ 50cm

(b) Winter > 50cm



(c) Summer ≤ 50cm

(d) Summer > 50cm

Figure 2.3 – Prey frequencies of abundance percentages as a function of their occurrence frequencies percentages found for saithe and hake (Costello, 1990). Circles indicate prey eaten by hakes and diamonds indicate prey eaten by saithe. Blue prey items represent fish preys (Table 2.2), red prey items represent crustaceans preys (Table 2.3) and green prey items represent other invertebrates preys (Table 2.4). See Tables 2.2 to 2.4 for prey groups and prey abbreviations.

Table 2.7 – Weighted average coefficient of variation ($\overline{CV}_W$) of the different dietary indices after bootstrap on the whole pool of data ($n = 1000$). See Sections 2.2.2 and 2.2.3 for details about dietary indices.

Index	$\overline{CV}_W$
F_O	0.17
F_N	0.40
F_{NS}	0.41
F_{NW}	0.43
F_M	0.47
F_S	0.21

Larger saithe and hake (> 50 cm) presented a highly piscivorous diet with fish preys occurring in about 97% of both predators species guts (Table 2.5) and representing about 70% of total preys consumed (Table 2.6). The dominance of silvery lightfish for saithe was maintained (Figure 2.3d). Even if silvery lightfish was relatively abundant in hake diet ($F_N \approx 27\%$), it was twice less dominant than for saithe ($F_N \approx 65\%$). However, the figures obtained for hake could be underestimated because of the high frequencies of non-identified fish preys. We also noted the lower importance of Norway pout for both predators ($F_N < 2\%$, Table 2.6). Concerning crustaceans, there was a slight tendency for hake to specialise on hyperiids while saithe was more generalist, preying upon hyperiids and euphausiids as well (Figure 2.3d).

2.3.3 Diet overlap

Selection of best dietary index

Occurrence frequency, F_O was the most robust dietary index to sampling error with weighted average coefficient of variation ($\overline{CV}_W$) estimated to 0.17 (Table 2.7). The compound index summing occurrence and abundance frequencies, F_S, was quite robust with $\overline{CV}_W = 0.21$ while the other indices studied were more sensitive to sampling bias with $\overline{CV}_W > 0.40$.

Summation of occurrence and abundance frequencies also allowed to overcome weaknesses of its summands by increasing amount of information and by giving the same weight to both dietary indices (Figure 2.4). For example, two crustaceans with similar sizes such as hyperiids and euphausiids and which had similar occurrence (Figure 2.4a) were ranked by their abundance (Figure 2.4b) when using the compound index F_S (Figure 2.4c). On the other hand, a fish such as Norway pout which was relatively occurrent ($F_O \approx 0.35$) would have been ignored if using only F_N due to the high amount of the smaller prey, silvery lightfish. This was overcome by the use of the compound index F_S.

For these reasons, F_S, was chosen as the best index to represent prey importance and was used to measure dietary overlap between saithe and hake within predator groups.

Saithe and hake diet overlap

Larger individuals Saithe and hake larger than 50 cm had a high and significant ($P_p \leq 0.05$) diet overlap in both winter and summer, with $R_{\text{obs}} \approx 0.8$ (Table 2.8).

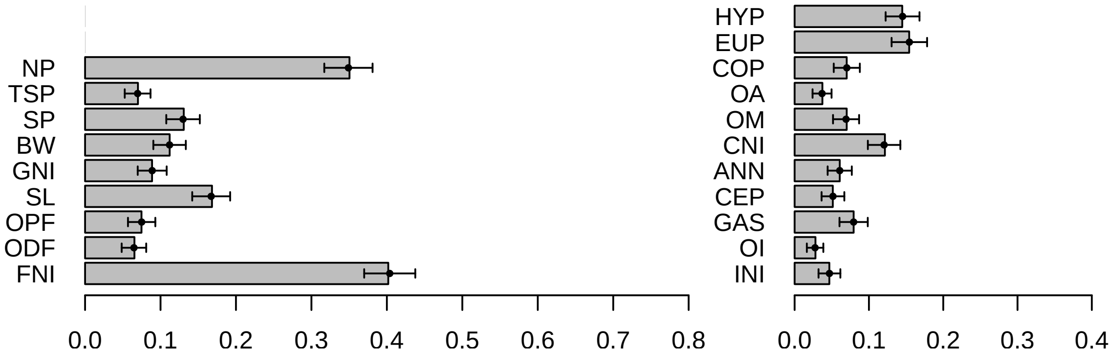
In winter, Norway pout and silvery pout were the main preys shared between larger saithe and hake and represented together, in terms of prey importance, about 40% and 32% of saithe and hake diets, respectively (Figure 2.5b). In addition, non-identified fish preys and relatively less important preys such as other pelagic fishes, non-identified gadoid fishes and gastropods were also shared between both species. Euphausiids were only important for saithe, representing about 11% of their diet in winter. The dietary overlap of 0.79 was significant ($P_p \leq 0.01$).

In summer, silvery lightfish was the main prey shared between saithe and hake, representing about 20% of these two predator groups diet (Figure 2.5d). Although saithe and hake diets were more diverse, other preys such as hyperiids, non-identified crustaceans, silvery pout, blue whiting (*Micromesistius poutassou*), gastropods and cephalopods had similar importance for both predators. Similar to winter, larger saithe in summer specialized in feeding on euphausiids, which represented about 9% of their diet. Diet overlap is once again significant ($P_p \leq 0.01$).

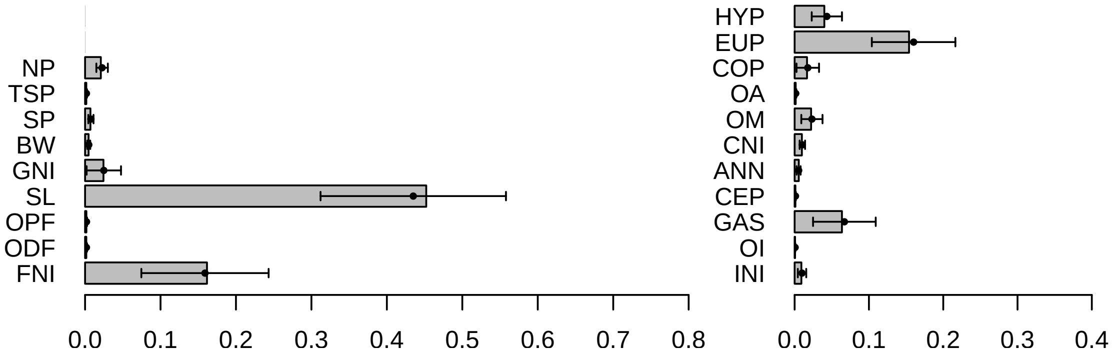
Smaller individuals Individuals smaller than 50 cm showed similarities in diet but had reduced diet overlap, relatively to larger individuals, with $R_{\text{obs}} \approx 0.55$ (Table 2.8).

In winter, Norway pout and silvery pout were the main preys shared between smaller saithe and hake. However, these preys were twice as important for hake than for saithe, representing together about 26% and 60% of saithe and hake diet, respectively (Figure 2.5a). The significant overlap ($P_p \leq 0.05$) should be interpreted cautiously though, due to the large amount of non-identified fishes, representing about 32% of hake diet. In summer, euphausiids were the main shared prey, with similar importance (about 15%) for both smaller saithe and smaller hake diet. Like in winter, Norway pout was common to the two species but was more important for hake diet ($\approx 30\%$) than for saithe diet ($\approx 5\%$). The overlap was not significant ($P_p > 0.05$).

(a) Frequencies of occurrence, F_O



(b) Frequencies of abundance, F_N



(c) Sum of occurrence and abundance frequencies, F_S

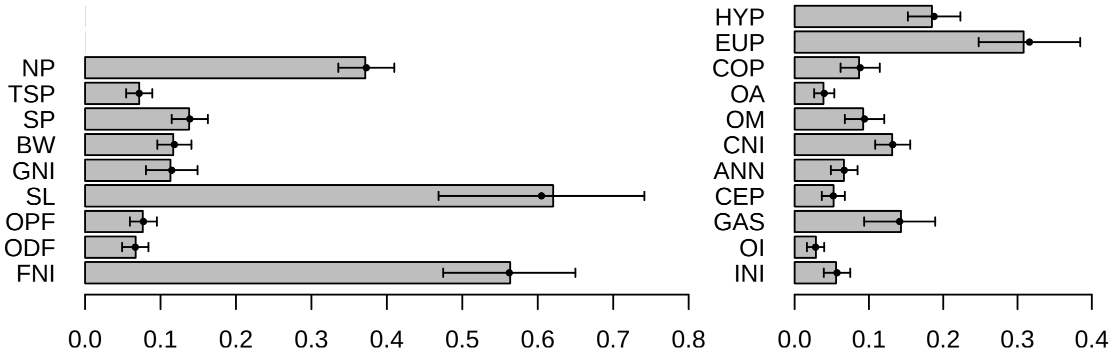
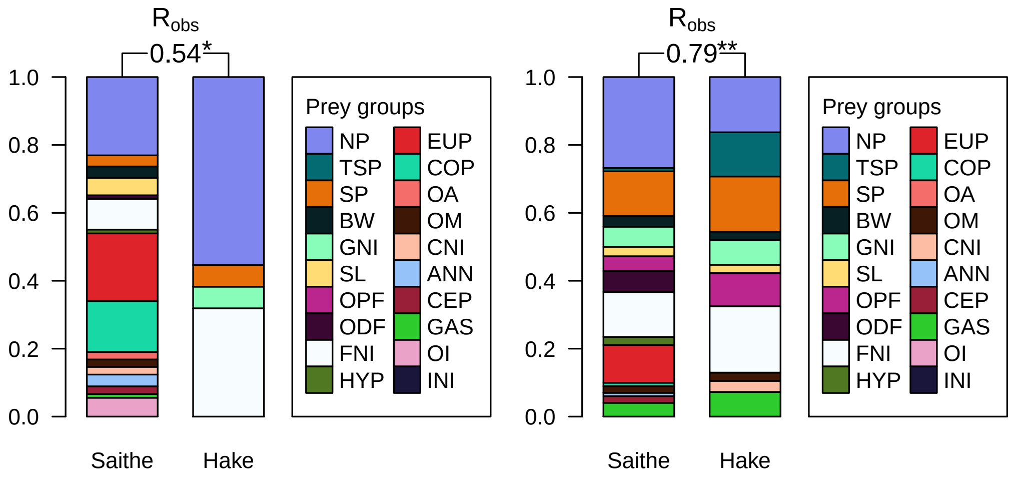


Figure 2.4 – Three dietary measures calculated for each prey types on the whole pool of data with standard deviation and mean obtained after bootstrapping procedure ($n = 1000$). Dots represent the mean wrapped by the associated error bars representing standard deviation. For graphical purposes, fish groups are plotted on the left panel (Table 2.2) while crustaceans and other invertebrates groups (Tables 2.3 and 2.4) are plotted on the right panel.

(a) Winter ≤ 50cm (b) Winter > 50cm



(c) Summer ≤ 50cm (d) Summer > 50cm

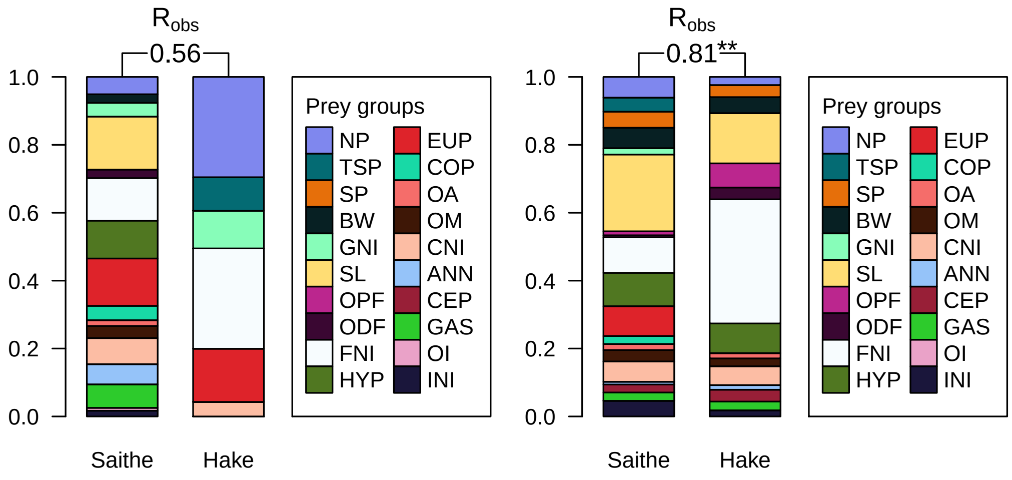


Figure 2.5 – Prey importance (F_S) proportions for saithe and hake diet within predators groups and dietary overlap between the two species. R_{obs} is the observed overlap value between the two species associated with its significance (*: $\alpha = 5\%$, **: $\alpha = 1\%$). See Tables 2.2 to 2.4 for prey groups and prey abbreviations.

Table 2.8 – Dietary overlap measures (R_{obs}) between saithe and hake observed per season and length group and their associated pvalue (P_p). See Section 2.2.3 for details about dietary and significance assessment of dietary overlap indices. *: $\alpha = 5\%$. **: $\alpha = 1\%$.

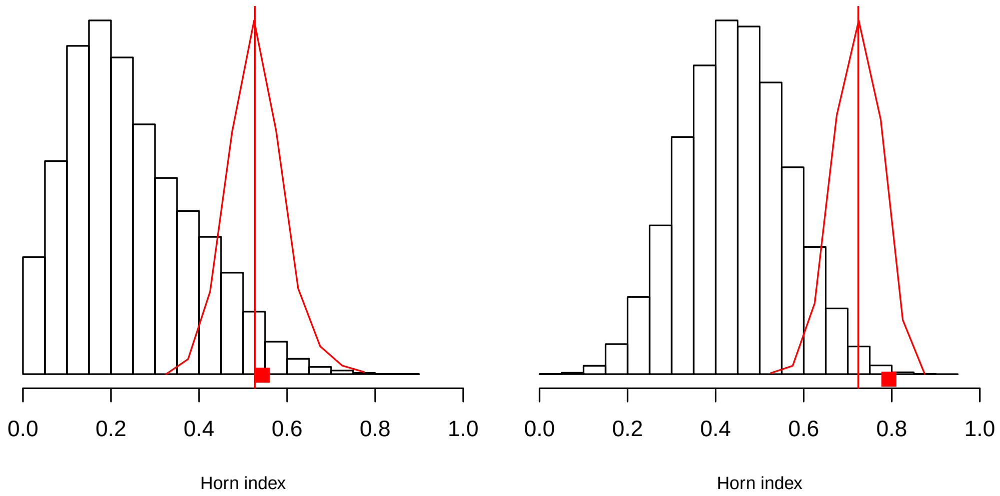
	Index	R_{obs}	P_p	
Winter				
$\leq$ 50cm	F_S	0.54	0.020	*
$>$ 50cm	F_S	0.79	0.002	**
Summer				
$\leq$ 50cm	F_S	0.56	0.064	
$>$ 50cm	F_S	0.81	0.010	**

Overlap significance The comparison of the overlap significance based on the different methods indicated that Ross (1986) rule of thumb would have led to the same conclusions than those drawn from the previously described P_p analysis, for large individuals in both seasons (significant diet overlap) and also for small individuals in summer (non-significant diet overlap). Only overlap between smaller saithe and smaller hake in winter would have been considered non-significant, while permutation test suggests a significant overlap ($P_p \leq 0.05$, Table 2.9). Also, even if we tend to overestimate Horn's overlap indices, the distributions obtained after bootstrap were quite narrow and therefore our observed diet index (R_{obs}) was close to the inferred overlap index (R_{m}) or median of the distribution (Figure 2.6).

P_{bp} were calculated after comparing the inferred overlap distribution obtained by bootstrap with theoretical distribution obtained randomly through permutations. This significance assessment technique, which is the most robust to sampling error, did not provide different conclusion concerning diet overlap indices significance than the comparison of observed diet overlap index with theoretical distribution obtained after permutation (P_p). This suggests that conclusions made on the diet overlap between saithe and hake are robust to sampling errors.

2.4 Discussion

The results confirm the highly piscivorous diet of hake (Cohen *et al.*, 1990; Bergstad, 1991b; DuBuit, 1996; Mahé *et al.*, 2007) and show a lower diversity of preys consumed compared to saithe, particularly for smaller individuals ($\leq$ 50 cm). In winter, Norway pout is largely dominant as a fish prey, for both


(a) Winter ≤ 50cm (b) Winter > 50cm

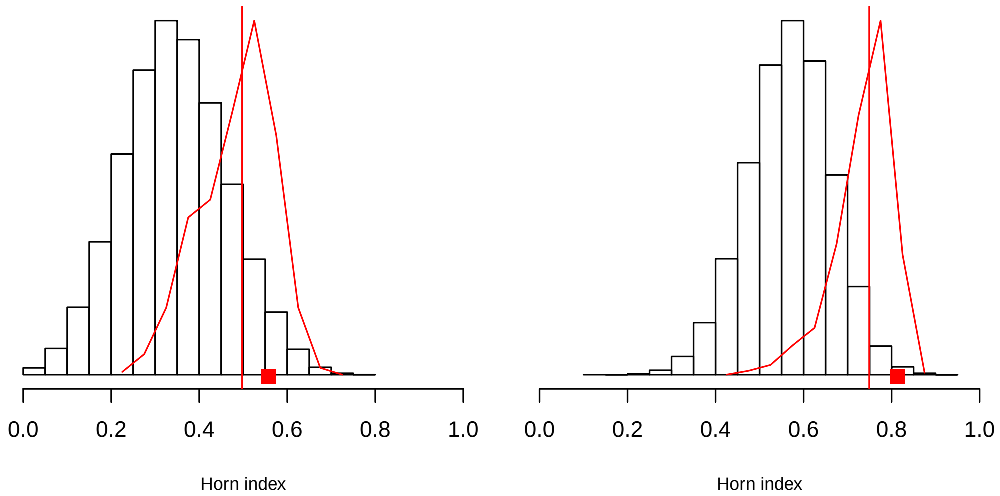

(c) Summer ≤ 50cm (d) Summer > 50cm

Figure 2.6 – Distribution of Horn's diet overlap between saithe and hake indices obtained after bootstrap and permutations for each predators groups. Red curve is the distribution obtained after bootstrap procedure ($D1$, $n = 1000$). Solid line is the median of the distribution or inferred overlap index (R_m). Red square is the observed overlap index (R_{obs}). Bars represent the cumulated frequencies of overlap indices obtained after permutations of hake proportion of prey importance (Figure 2.5) following each bootstrap ($D3$, $n = 500000$).

Table 2.9 – Significance comparison of the overlap between saithe and hake observed, per season and length group, depending on assessment method. RT: rule of thumb (Ross, 1986). P_p: pvalue calculated with R_{obs} and permutations ($n = 500$). P_{bp}: pvalue calculated with R_m and bootstrap with permutations ($n = 500000$). See Section 2.2.3 for more details. ✗: non significant overlap. ✓: significant overlap ($\alpha = 5\%$).

	Index	P_p	P_{bp}	RT
Winter				
≤ 50cm	F_S	✓	✓	✗
> 50cm	F_S	✓	✓	✓
Summer				
≤ 50cm	F_S	✗	✗	✗
> 50cm	F_S	✓	✓	✓

saithe and hake, while the importance of this prey decreases in summer. This is consistent with literature (Bergstad, 1991b; Du Buit, 1991) and confirms the results obtained by Cormon *et al.* (2014, Chapter 1) concerning the spatial overlap between Norway pout and the two predators. However, the summer switch from Norway pout to euphausiids feeding, observed in the Norwegian deep by Bergstad (1991b), could not be confirmed for saithe in the Northern North Sea. Euphausiids, which are nevertheless important all over the year for saithe, are relatively less important in summer. This is particularly true concerning individuals larger than 50 cm for which dominant prey is silvery lightfish. Silvery lightfish, which is, in the summer season, the dominant prey for larger hake as well, is a deep-sea mesopelagic fish with no commercial interest and with high energetic value (Pedersen and Hislop, 2001).

Euphausiids are also highly energetic preys (Mauchline and Fisher, 1969). The high occurrence of euphausiids recorded in summer saithe diet might result from density-dependent feeding, as zooplankton is generally more productive in summer (Francsz *et al.*, 1991). The increased importance of euphausiids shown by Bergstad (1991b) for smaller saithe is consistent with our results showing a specialisation of smaller saithe (≤ 50 cm) on euphausiids, particularly in winter. In summer, the consumption of this prey group by smaller hake (≤ 50 cm) might have consequences for smaller saithe particularly if abundance of euphausiids in the North Sea decreases over time (Beaugrand *et al.*, 2003). Indeed, Carruthers *et al.* (2005) showed a dependency between euphausiids abundance and Scotian Shelf saithe condition.

The reduced importance of euphausiids in saithe diet, compared to (Bergstad, 1991b) results, is consistent with the decrease of euphausiids importance in diet observed between 1981 and 1991 (Daan, 1989; ICES, 1997a). This decrease is consistent with euphausiids abundance decrease in the North Sea (Beaugrand *et al.*, 2003) and might confirm the density-dependent feeding behaviour assumption. The relatively small importance of herring (*Clupea harengus*), which was pooled with other pelagic fishes in this study, is at odds with earlier observations of saithe diet (Daan, 1989; ICES, 1997a). This apparent contradiction might result from the use of prey weight to characterise saithe diet in Daan (1989) and ICES (1997a), which could have over-represented the importance of relatively heavy herring as a prey in this analysis. Further comparing trends of saithe diet changes combined with temporal series of prey availability could improve our understanding of saithe feeding strategy and behaviour.

A reduction of fish prey availability in the North Sea could result from greater hake predation, particularly when hake abundance and probability of presence increase in the area (Baudron and Fernandes, 2014; Cormon *et al.*, 2014, Chapter 1; ICES, 2014a). This might have adverse consequences for saithe for which fish preys represent at least 40% of diet in terms of occurrence and abundance combined, including relatively high energetic preys *i.e.* silvery lightfish, herring and, to a smaller extent, Norway pout (Pedersen and Hislop, 2001).

In addition, the high dietary overlap between saithe and hake larger than 50 cm, in both winter and summer, suggests interspecific trophic competition between both species in the North Sea. The greater diversity of saithe diet might prevent interspecific trophic competition with hake (Jones, 1978), particularly for saithe smaller than 50 cm for which dietary overlap with hake is reduced compared to larger individuals and even non-significant in summer. However, high significant dietary overlap between larger saithe and hake and similarities between diet of the smaller individuals, particularly concerning euphausiids (Carruthers *et al.*, 2005) and Norway pout (Cormon *et al.*, 2016, Chapter 3), may threaten the coexistence of the two species in the North Sea.

Method-wise, the results obtained suggest that the use of Ross (1986) rule of thumb for the assessment of dietary overlap significance (RT) might be too conservative. However, our results concerning the significance of the overlap between smaller saithe and hake might be driven by the low diversity of prey found in hake guts. The robustness of prey occurrence frequency to sampling error bears out the conclusion of Baker *et al.* (2014). Unfortunately, prey occurrence does not characterise diet in a suitable way for dietary overlap studies. Our results support the use of the modified version of Relative Importance index (RI) (George and Hadley, 1979) disagreeing with Macdonald and Green (1983) argument about the redundancy of compound indices.

The high proportion of non-identified fish prey items occurrence and abundance in our results might result from the nature of our samples and sampling protocol. Indeed, samples collected during commercial fishery operations may have stayed several hours in trawls. In addition, freezing of our sample was not instantaneous, particularly for large fishes. The higher amount of non-identified fish found in hake samples may be explained by the large amount of mucus found in hake guts during content analyses. However, the limitations resulting from this high amount of non-identified fish preys are slightly overcome by the use the modified RI index.

Finally, hake emergence in the North Sea needs to be monitored, particularly concerning trophic impacts on North Sea forage species population. Forage species, which are particularly sensitive to predation mortality and environmental changes (Engelhard *et al.*, 2014), are key species for the ecosystem functioning sustaining a large range of predators in the North Sea (Plaganyi, 2007; Engelhard *et al.*, 2014; Pikitch *et al.*, 2014). In particular, non-commercial species of high energetic value such as euphausiids and silvery lightfish, need to be studied as current knowledge about their ecology is scarce. Concerning trophic interactions, the resource partitioning between saithe and hake is generally low and dietary overlap generally high, particularly for individuals larger than 50 cm. For these reasons, trophic competition between saithe and hake in the Northern North Sea may be assumed. Most of shared preys, i.e. silvery lightfish, Norway pout and euphausiids have high energy content (Mauchline and Fisher, 1969; Pedersen and Hislop, 2001). Their lowering abundance might represent a decrease of energy input for saithe. Therefore, this trophic competition combined with the increasing spatial overlap between saithe and hake (Cormon *et al.*, 2014, Chapter 1) might threaten the sustainability of saithe stock in the North Sea (Link and Auster, 2013).

2.5 Supplementary material

Supplementary materials presents the synthesis of saithe and hake samples collected for the study (Table S2.1).

Table S2.1 – Synthesis of saithe and hake samples collected in 2013.

	Winter		Summer	
	Saithe	Hake	Saithe	Hake
Cap Nord	37	18	40	59
Klondyke	36	45	29	29
G.O. Sars	22	1	20	20
Walter Herwig III	10	15	15	15
Total	105	79	104	123

> Petit poisson deviendra grand.
>
> Jean de la Fontaine, Le petit
> Poisson et le Pêcheur

Chapter 3

Environmental factors potentially limiting saithe growth in the North Sea

Cormon, X., Ernande, B., Kempf, A., Vermard, Y., and Marchal, P. 2016, Chapter 3. North sea saithe (*Pollachius virens*) growth in relation to food availability, density dependence and temperature. Marine Ecological Progress Series, 542: 141–151

Abstract

North Sea saithe, a major top predator in the area, supports the fishery economy of several European countries. However, recent stock assessments suggested a decrease of SSB along with a decline of saithe growth. In this context we investigated North Sea saithe growth characteristics at the population level. First, saithe annual weight increment and age-length relationship were studied. Modelling of saithe age-length relationship was carried out using (i) the traditional von Bertalanffy Growth Function (VBGF) model; (ii) the Verhulst logistic model; and (iii) a pragmatic linear model. Secondly, environmental factors effects on saithe growth were investigated. Explanatory environmental factors included (i) food availability, represented by the total biomass of Norway pout; (ii) intraspecific competition *i.e.* density-dependence, represented by saithe abundance; and (iii) temperature. This study revealed that the Verhulst logistic model was the best descriptor of saithe growth and that density-dependence and food availability had significant effects on saithe growth coefficient while no effect of temperature was shown. Therefore, we suggest that reduced food availability and increased competition may explain the recent decrease of saithe growth coefficient.

Keywords: bottom-up processes; Von Bertalanffy growth function; logistic growth; Norway pout; prey availability effects; density-dependence; predator-prey interactions; resource limitation; competition

3.1 Introduction

Understanding factors regulating population dynamics is a cornerstone in ecology, particularly in exploited ecosystems (Frederiksen *et al.*, 2006; Laundré *et al.*, 2014). The size of a population is strongly influenced by its position within the trophic network to which it belongs (Cury *et al.*, 2003) and by the productivity of the ecosystem, its carrying capacity. In heavily exploited marine ecosystems, assessing the size (biomass and/or abundance) of commercial fish stocks with a sufficient accuracy is of primary importance to support fisheries management.

In an ecosystem approach to fisheries management (FAO, 2003), multi-species stock assessment tools have been developed to better integrate trophic interactions in fisheries diagnostics (ICES, 2012). These tools generally allow the estimation of top-down effects, *i.e.* control exerted by predators on prey populations, through an estimation of predation mortalities, see Plaganyi (2007), section 2.2, for a review. However, the reverse effects (bottom-up), *i.e.* the potential regulation of predator populations through prey availability, are often not estimated despite their recognized importance (Frederiksen *et al.*, 2006). Understanding these bottom-up processes is necessary to gain insights into interspecific competition which involves relationships through shared preys in both directions (top-down and bottom-up).

Saithe (*Pollachius virens*) is a major top-predator fish species in the North Sea, and it is commercially important for several European countries, *i.e.* Germany, France, United-Kingdom and Norway. Recent stock assessments suggest that North Sea saithe Spawning Stock Biomass (SSB), mean weight-at-age (Figure 4b) and growth have decreased in recent years (ICES, 2014b). This decrease might affect stock productivity and the sustainability of dependent fisheries (Brander, 2007). Many factors, related to genetic and/or phenotypic plasticity may affect fish growth (Sinclair *et al.*, 2002). Genetic effects may be induced by fisheries (Stokes and Law, 2000). The resulting changes on growth rate are supposedly slow: 0.1% per year according to Andersen and Brander (2009), and therefore might be highlighted only in long-term studies. In contrast, substantial changes related to phenotypic plasticity can be observed on shorter time scales.

Three environmental factors are commonly assumed to affect fish growth: density-dependence (Lorenzen and Enberg, 2002; Sinclair *et al.*, 2002), temperature (Brunel and Dickey-Collas, 2010; Baudron *et al.*, 2011), and food availability (Krohn *et al.*, 1997; Gjøsaeter *et al.*, 2009). Density-dependent regulation generally results from an increased intraspecific competition for food at large stock size (Sinclair *et al.*, 2002; Brunel and Dickey-Collas, 2010). Density-dependent growth was recognized as a common process for marine species (Lorenzen and Enberg, 2002; Sinclair *et al.*, 2002). Density-dependent effects need to be taken into account while managing species as their removal and/or conservation might decrease or increase these effects (Lorenzen and Enberg, 2002).

Changes in temperature might also affect food availability (Möllmann *et al.*, 2005; Baudron *et al.*, 2011) or have more direct effects on fish physiology. Indeed, there is an optimum temperature for growth (Jennings *et al.*, 2001), which declines with decrease of food rations (Sinclair *et al.*, 2002). In the theoretical case of unlimited food availability, growth would be determined by temperature only (Brett and Groves, 1979). There is currently insufficient available information to relate saithe growth to environmental changes and density-dependent effects are currently neglected (ICES, 2014b). Hence, regulation through food availability, which is entangled with density-dependence and temperature, needs to be investigated.

Saithe growth may be controlled by food availability, resulting from changes in temperatures, intra- or interspecific competition, and thereby could be linked to densities of mid-trophic level species such as forage fishes (Frederiksen *et al.*, 2006; Engelhard *et al.*, 2014; Plaganyi and Essington, 2014). These key species have been evidenced to either positively affect predator fish growth (Krohn *et al.*, 1997; Huse *et al.*, 2004; Gjøsaeter *et al.*, 2009; Engelhard *et al.*, 2014) or, on the contrary, negatively affect predator fish abundance through predation of the predators' eggs or larvae (Engelhard *et al.*, 2014). Saithe diet is generally based on forage species among which Norway pout (*Trisopterus esmarkii*) is of major importance (Bergstad, 1991b; Du Buit, 1991; DuBuit, 1996; Engelhard *et al.*, 2014).

In the North Sea, the recent emergence of the highly piscivorous hake (*Merluccius merluccius*), highlighted by Baudron and Fernandes (2014) and Cormon *et al.* (2014, Chapter 1), might have impacts on the North Sea ecosystem. These impacts could be direct, *e.g.* on prey species, or indirect, *e.g.* on other predator species feeding on similar prey assemblage. Saithe and hake have similar feeding habits, particularly concerning Norway pout (Bergstad, 1991b; Du Buit, 1991; DuBuit, 1996). In addition, Cormon *et al.* (2014, Chapter 1) showed an increasing spatial overlap between hake and saithe correlated with Norway pout presence. Therefore, hake emergence might affect Norway pout biomass, which has been declining since 2009 (ICES, 2014b), with a knock-off effect on saithe growth.

In order to understand the potential impacts of hake on saithe population in the North Sea, it appears necessary to first understand the potential relationships between Norway pout biomass and saithe growth characteristics that were never investigated in this area. Norway pout is a short-lived species, and its dynamics are driven by changes in recruitment and/or predation mortality rather than by fishing mortality that is relatively low for this species (ICES, 2014b). The environmental factors driving Norway pout recruitment are highly variable.

Predation mortalities are exerted on all ages by both saithe and hake (Lambert *et al.*, 2009; ICES, 2014b,a).

Both Norway pout and saithe are northern species with overlapping areas of distribution in the North Sea and Skagerrak (Lambert *et al.*, 2009; ICES, 2014b). However, only adult saithe show spatial overlap with Norway pout. Saithe juveniles are distributed inshore where Norway pout (and adult saithe) are rarely present (ICES, 2014b). Hence, high Norway pout biomass (or saithe abundance) is expected to have only little negative impacts on saithe through predation (or cannibalism) on juveniles, which allows to disentangle top-down and bottom-up effects. In addition, Cormon *et al.* (2014, Chapter 1) (Chapter 1) showed a positive relationship between Norway pout and saithe probability of presence in the North Sea while Lynam *et al.* (2015) showed a positive correlation between Norway pout and saithe biomass. For these reasons, it may be reasonable to assume that Norway pout biomass is a suitable descriptor of food available to saithe, particularly when investigating limitation of resources due to potential competition between saithe and hake. Evidencing resource limitation is a requirement to assume competitive interactions between two species (Link and Auster, 2013). While difficult to highlight at large scale,this process may be evaluated through indirect methods such as the study of relationship between prey availability and predator growth.

Growth characterisation generally involves the determination of the size of an organism (length or weight) in relation to time. Numerous models have been used to describe fish growth, of which the von Bertalanffy Growth Function (VBGF) model is probably the most common (Jennings *et al.*, 2001; Katsanevakis, 2006; Haddon, 2011). VBGF describes an organism's length in relation to its age. It is based on three parameters: (i) an asymptotic length representing the maximum size the organism can reach; (ii) a growth constant representing how swiftly the organism's size converges towards its asymptotic value; and (iii) the theoretical age of an organism of size 0. The *a priori* use of the VBGF, even when providing a good description of most fish species growth (Jennings *et al.*, 2001), may be problematic (Katsanevakis, 2006). Particularly, asymptotic length and age-at-size 0 estimations must be extrapolated and might lack biological meaning (Haddon, 2011). Kienzle (2005) recognised the issue of using VBGF for the description of saithe growth, which does not show an asymptotic length. In this context, different characterisations of saithe growth need to be investigated. Finally, to study potential effects of the environment on saithe growth, biologically meaningful growth parameters must be used.

In this study, we investigated the interannual variability of North Sea saithe growth in relation to different biotic and abiotic environmental factors. Saithe growth was first described using annual mean weight-at-age increments. Secondly, the relationship between saithe length and age was investigated. To this purpose, three models, describing saithe growth through either linear or asymptotic age-length relationships, were considered. Environmental factors considered were (i) main prey availability, represented by the total total biomass of Norway pout, a prey that also represents a major component of hake diet; (ii) density-dependence, represented by saithe abundance; and (iii) temperature.

3.2 Material and methods

3.2.1 Data

Saithe size-at-age characteristics

Saithe mean weight-at-age (kg), from age 3 to age 10 (yrs), were extracted from ICES (2014b), over the period 1987-2012. Age-Length Keys (ALK) were compiled on the basis of length measurements and age-reading on otoliths, using both survey and commercial data sources. ALK survey data were collected during the North Sea International Bottom Trawl Survey (IBTS) and subsequently extracted from the ICES online DAtabase of TRAwling Survey (DATRAS) for the period 1991-2012 (except for 2006 for which data were missing). Data were explored by age for length values and outliers (extreme values considered biologically meaningless) were ignored in subsequent analyses. The final survey database included ALK from ages 2 to 10 years (Table 3.1).

Environmental factors

Annual Norway pout Total Stock Biomass (TSB) (t), and saithe abundance, in total number of individuals, were extracted from Working Group on the assessment of demersal stocks in the North Sea and SkagerraK (WGNSSK) assessment report (ICES, 2014b) for the period 1987-2012. Sea bottom temperatures (°C), measured using Sonde (CTD) devices, were extracted from the ICES Oceanographic online database (OCEAN) at quarter and statistical rectangle (1° longitude × 0.5° latitude) resolution. Bottom temperatures were averaged annually from 1987 to 2012 over the study area (Figure 3.1).

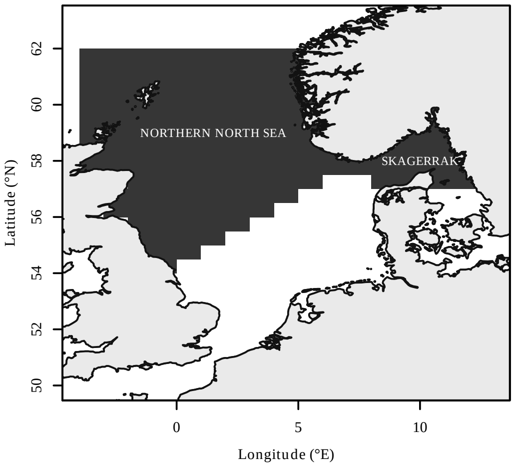


Figure 3.1 – Map of the study area.

Table 3.1 – Overview of population size characteristics data, their units, and their age and time coverage. *2006 year is missing.

Data	Units	Age	Time
Mean weight-at-age	kg	3 -10	1987-2012
Annual mean weight increment	kg	4 - 9	1988-2012
Length-at-age	cm	2 -10	1991-2012*

3.2.2 Saithe growth characteristics

Annual mean weight increments

First, saithe annual mean weight increments were calculated (Equation 3.1) for each age using mean weight-at-age data described previously. Because age 2 saithe individuals are not in the North Sea (ICES, 2014b), we did not calculate the annual weight increment between ages 2 and 3. Age 10 is considered as a *plus* group (age 10 and older) by ICES (2014b). Therefore, the calculation of an annual weight increment between age 9 and age 10 was not possible (Table 3.1).

$$\delta w_{a_t} = w_{a_t} - w_{{a-1}_{t-1}} \tag{3.1}$$

where δw is the annual average weight (w) increment in kilos; a the age in years; and t the time in years.

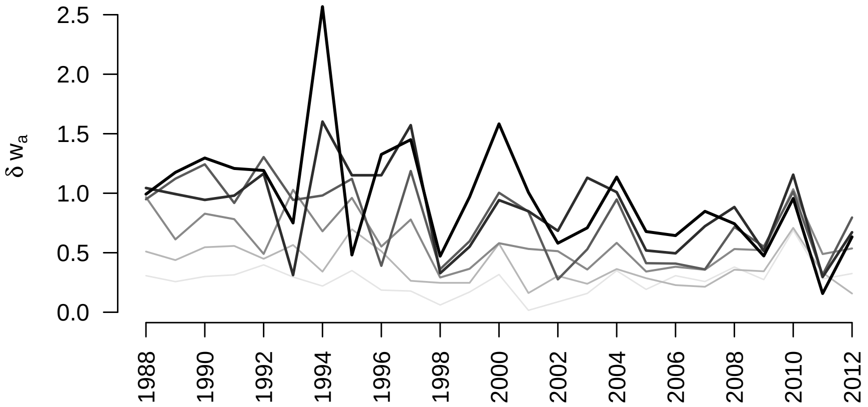


Figure 3.2 – Temporal trends in North Sea saithe annual mean weight-at-age increment (δw_a) over the 1988-2012 period. Increments between age 3 and age 4 (δw_4, light grey thin line) to increments between age 8 and age 9 (δw_9, black thick line).

Age-length relationship

Three candidate growth models were fitted to saithe age-length data. First, the traditional VBGF was fitted (Equation 3.2). Second, a Verhulst logistic growth model (Equation 3.3) was fitted and, third, a more pragmatic linear model was fitted (Equation 3.4).

The VBGF model (VB) assumes an asymptotic relationship between length, l, and age, a, depending upon three parameters: an asymptotic length, l_∞, a growth coefficient, K_{VB}, which determines how swiftly length, l, converges towards its asymptotic value, and a_0 which represents the theoretical age at which individuals are of size null.

$$l_a = l_\infty \times (1 - e^{-K_{\mathrm{VB}} \times (a - a_0)})) \tag{3.2}$$

where l_∞ is in centimetres; K_{VB} in year^{-1}; and a_0 in years.

The logistic model (LG) assumes a sigmoidal relationship between length, l, and age, a, depending upon three parameters: an asymptotic length, l_∞; a relative growth coefficient, K_{LG}; and a_i, a sigmoidal curve inflection point, which represents the theoretical age at which individuals growth trajectory changes.

$$l_a = l_\infty \times \frac{1}{(1 + e^{-K_{\mathrm{LG}} \times (a - a_i)}))} \tag{3.3}$$

where l_∞ is in centimetres; K_{LG} in year^{-1}; and a_i in years.

The linear model (LM) assumes that within the range of data available, length, l, is linearly related to age, a, depending upon an intercept, l_0 which represents the length at age 0 and a regression coefficient, K_{LM}, here representing growth.

$$l_a = l_0 + K_{\mathrm{LM}} \times a \tag{3.4}$$

where l is in centimetres; a in years; and K_{LM} in centimetres per year.

Age proportions within each year were checked to ensure sufficient and similar representation of the different ages. As different ages represented within a year belong to different cohorts and in order to reduce the cohort-related correlation, the three models were fitted for each year separately (ICES, 1991). Therefore, each year was considered as an independent sub-population allowing us to identify potential short-term variations by representing saithe annual average growth (Haddon, 2011) rather than focus on cohort average growth, which may involve longer-term effects. Linear models (Equation 3.4) were fitted using linear regression, while asymptotic models (Equations 3.2 and 3.3) were fitted using Non-linear Least Squares (NLS) regression. NLS iterations were optimized using Marquadt's algorithm and starting values set as follows: $K = 0.07$ (Jennings *et al.*, 1998); $l_\infty = 177.1$ cm (Jennings *et al.*, 1998); $a_0 = -0.8$ years (Froese and Pauly, 2014); and, $a_i = 5$ years based on saithe age at first maturity (Froese and Pauly, 2014; ICES, 2014b). NLS regressions were optimized using R 2.15.3 and `nlxb{nlmrt}` (Nash, 2013). The three candidate model were evaluated based on the comparison of their corrected Akaike Information Criterion (AIC) (AICc), which is used to compare non-nested models Goodness-of-Fit (GoF) (Burnham and Anderson, 2002). Differences between all models ($\Delta\mathrm{AIC}_c$) were calculated and the model with smallest AICc was selected.

3.2.3 Effect of the environment

Annual mean weight increment analysis

Generalized Least Squares (GLS) were used to fit the relationships between saithe annual mean weight increment, δw_{a_t}, and environmental factors prevailing during the year of the increment $(t-1)$ as described by Equation 3.5,

$$\delta w_{a_t} \sim \mu + \beta_1 . n_{TSB_{t-1}} + \beta_2 . s_{NB_{t-1}} + \beta_3 . \Theta_{t-1} + \epsilon_t \tag{3.5}$$

where a is the age; t the time in years; μ the intercept; β_1, β_2 and β_3 are the coefficients associated to Norway pout TSB (n_{TSB}) representing food availability, saithe abundance (s_{NB}) representing density dependence and mean bottom temperature (Θ), respectively; and ϵ the residual error. Residuals were checked for time autocorrelation using correlograms.

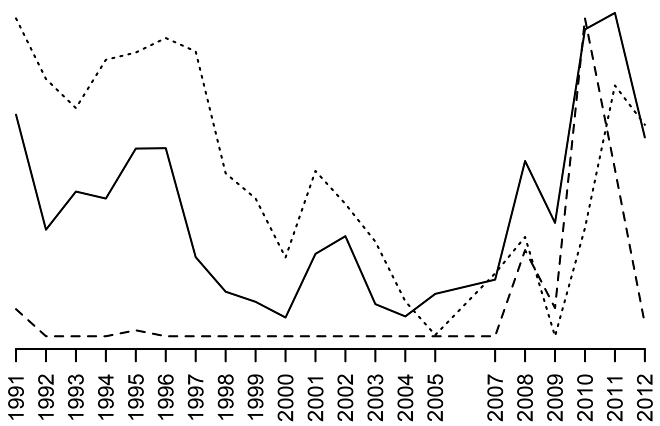


Figure 3.3 – Growth coefficients, K, estimated for period covering 1991 to 2012 using the linear model, the Verhulst logistic growth model and the Von Bertalanffy Growth Function. The dotted line shows the linear model growth coefficient estimates, K_{LM} (Equation 3.4); the solid line shows the Verhulst logistic model growth estimates, K_{LG} (Equation 3.3); and the dashed line shows the VBGF model estimates, K_{VB} (Equation 3.2). Y-axis are not plotted as absolute values of the different growth coefficients are not of interest.

When significantly autocorrelated, the residuals' error structure could be described by, either an AutoRegressive model (AR) where residuals (ϵ_t), depend upon lagged (s) residuals (ϵ_{t-s}); a Moving Average model (MA) where (ϵ_t) depends upon both random noise indexed at time t (υ_t), and its lagged value(υ_{t-s}); or an AutoRegressive Moving Average model (ARMA), combining both (Zuur *et al.*, 2009). The error structure was determined by examining the autocorrelation and partial autocorrelation functions (Zuur *et al.*, 2009; Groeger *et al.*, 2014). The regression described by Equation 3.5 was modified to include in the residuals, ϵ_t, the suitable time correlation structure chosen among the previously mentioned ones. The GoF of the error-structured model was compared to original models based on AIC. Equation 3.6 describes a first order (1,1) ARMA process.

$$\epsilon_t = \phi.\epsilon_{t-1} + \upsilon_t + \theta.\upsilon_{t-1} \tag{3.6}$$

where t is the time in years, ϕ the AR parameter, υ the random noise and θ the MA parameter. When residuals were not autocorrelated, the regression was equivalent to an Ordinary Least Squares (OLS) regression. Least-squares optimisation was made using Nelder and Mead (1965) algorithm.

Contribution of the different descriptors was tested using either *F-test*, when residual errors were not significantly autocorrelated, or *Wald-test*, when residuals autocorrelation was taken into account. Variables with the highest p-values were dropped one by one to select significant variables by backward elimination ($\alpha < 0.05$). As multiple tests were carried out (one test per mean weight-at-age increment), p-values were adjusted using Holm correction (Wright, 1992) to keep the family-wise type I error rate at level $\alpha = 0.05$. In total six regression models, from age increment 3-4 (δw_4) to age increment 8-9 (δw_9), with different descriptor coefficients and descriptor significance per model, were fitted. Regression residuals, after autocorrelation was taken into account if necessary, were tested for trends, normality and homoscedasticity.

Growth coefficient analysis

The study of environmental effects focused on temporal variations of saithe growth coefficient, K, as other growth parameter might result from extrapolation or are biologically meaningless (Kienzle, 2005; Haddon, 2011). First, the trends of the three environmental variables (n_{TSB}, s_{NB} and Θ) were compared to annual K trends estimated with selected growth models. Pearson correlation coefficients (r) between K and environment time-series were calculated. To study the short-term variations of growth, we used a 1 year time-lag for the exploration of environmental effects. Thus, we focused on short-term environmental effects (conditions prevailing the year before) on saithe annual average growth. Secondly, the relationships between K and the environment were investigated with regression techniques similarly to annual mean weight-at-age increments (see section 3.2.3). Regression residuals were checked for autocorrelation, resulting in the error term potentially including adequate ARMA model (Equation 3.6). Contribution of the different descriptors was tested using either *F-test*, when no significant time autocorrelation was found, or *Wald-test*, otherwise. Significant variables were selected by backward elimination ($\alpha < 0.05$). Regression residuals, after autocorrelation was taken into account if necessary, were tested for trends, normality and homoscedasticity.

3.3 Results

3.3.1 Saithe growth characteristics

Trends in mean weight-at-age annual increment showed a general decrease for saithe of all ages between 1988 and 2000 (Figure 3.2). In addition, weights-at-age increments of the older fish were subject to large interannual variations.

Based on AICc metrics, saithe age-length relationship was generally best described by a logistic growth model (Table 3.3). The three candidate models, the

Table 3.2 – Parameters estimates distribution depending on growth model used.

Estimate parameter	Minimum	Median	Maximum
Linear model (Equation 3.4)			
l_0	16.41	22.40	30.41
K_{LM}	4.73	6.47	8.12
Logistic model (Equation 3.3)			
a_i	2.62	8.88	138.40
K_{LG}	0.10	0.18	0.39
l_∞	82	165	26.7e06
von Bertalanffy Growth Function model (Equation 3.2)			
a_0	−6.10	−3.14	−0.93
K_{VB}	3.7e-07	7.6e-07	0.16
l_∞	95.00	8.4e06	17.6e06

LM, the LG and the VB, after being adjusted to our range of data, were not equally meaningful in biological terms. The pragmatic LM model, which assumed an infinite growth (no asymptote), estimated growth parameters in a biologically meaningful range with length-at-age 0, l_0, ranging from 16.41 cm to 30.41 cm and K_{LM} ranging from a length increase per year of 4.73 cm to 8.12 cm (Table 3.2). By contrast, the VB model, which builds on ecological theory, led to biologically meaningless estimations of l_∞ (median $l_\infty > 80\,000$ m). In comparison, l_∞ estimated using LG model were more realistic (median $l_\infty = 165$ cm) even if estimates for 5 years (1998-2000, 2003, 2004) were also meaningless (maximum $l_\infty > 260\,000$ m). These extreme values of l_∞ must be caused by the age range of our data which does not cover completely saithe lifespan (Cohen *et al.*, 1990, 25 years old), thus not allowing to estimate the asymptotic plateau.

The comparison of the three models GoF highlighted a better fit of LG models that had the smallest AICc for all years except in 2010, for which VB model had the best fit (Table 3.3). The LM and VB models had similar GoF, except for years 2008, 2010 and 2011. In order to model saithe growth consistently over years, and based on the models' biological meaningness and GoF, the logistic model was selected as the best descriptor of saithe growth (Figure S3.1). Saithe growth coefficient (K_{LG}) globally decreased from 1991 to 2004. At finer scale, K_{LG} decreased (1991-1992; 1996-2000; 2002-2004) and increased (1992-1996; 2000-2002) alternatively (Figure 3.3). From 2004 to 2011, there was a general increase of K_{LG} except in 2009. The increase in K_{LG} observed from 2009 until 2010 was consistent with that of K_{VB}, the growth coefficient of VB that had a better fit for this particular year, thereby confirming that the use of the LG model in 2010 did

Table 3.3 – Differences of AIC_c (ΔAIC_c) by pairs of model (between brackets). $\Delta\text{AIC}_c(1/2) = \text{AIC}_c(\text{model 1}) - \text{AIC}_c(\text{model 2})$. LM: linear model. LG: logistic model. VB: von Bertalanffy Growth Function model.

Year	ΔAIC_c(LM/LG)	ΔAIC_c(LM/VB)	ΔAIC_c(LG/VB)
1991	100.17	5.70	-94.47
1992	281.86	-1.00	-282.86
1993	111.92	-1.01	-112.92
1994	143.85	-1.00	-144.85
1995	-5.51	-0.67	4.83
1996	121.04	-1.00	-122.04
1997	247.85	-1.01	-248.85
1998	348.21	-1.00	-349.22
1999	560.41	-1.00	-561.42
2000	239.14	-1.00	-240.15
2001	212.69	-1.00	-213.70
2002	122.59	-1.00	-123.60
2003	533.72	-1.01	-534.73
2004	615.62	-1.00	-616.62
2005	7.16	-1.00	-8.17
2007	97.05	-1.00	-98.06
2008	71.49	74.55	3.05
2009	31.93	3.45	-28.49
2010	989.94	1222.62	232.68
2011	1304.48	672.73	-631.74
2012	358.49	2.41	-356.08

not affect general trends of annual saithe growth coefficient. Finally, K_{LG} started to decrease again from 2011 to 2012. General trends were consistent between all three K estimates (Figure 3.3) which comforted us in the trends observed (Figure 3.3).

3.3.2 Environmental effects

There was evidence that environmental factors, particularly Norway pout biomass and saithe abundance, affected annual average growth of saithe. Indeed, K_{LG}, was found to be negatively correlated (with a 1 year time lag) with saithe total abundance (s_{NB}, $r = -0.67$, Figure 3.4a) and, to a smaller extent, with temperature (Θ, $r = -0.13$, Figure 3.4c). The correlation was positive with Norway pout biomass (n_{TSB}, $r = 0.41$, Figure 3.4b). These effects were confirmed by regression analyses of K_{LG} against the environment which highlighted negative density-dependent effects and positive food availability effects on saithe annual average growth with a time lag of 1 year (Table 3.4). Temperature, which showed little variations over the studied time period (Figure 3.4c) was not significantly related to K_{LG} ($\alpha = 5\%$). In addition, K_{LG} observed time-series comparison with fitted time-series *i.e.* predicted from models including significant environmental factors, indicated a relatively smoother estimation of K_{LG}, particularly after 2003 (Figure 3.6).

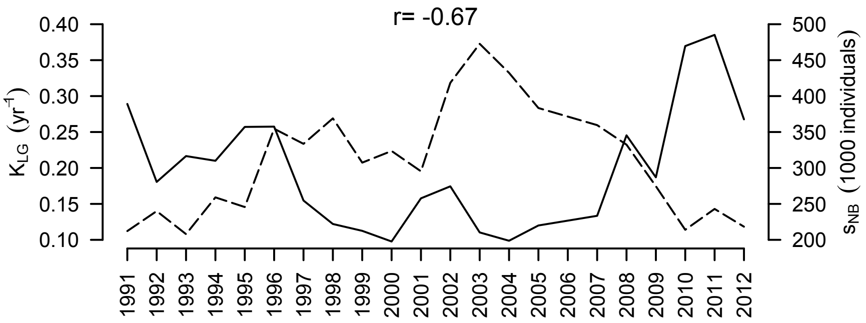
Density-dependence and prey availability explained together 46.79% of the model deviance (not shown). When saithe abundance increased by 659 000 individuals, saithe annual average growth, K_{LG}, dropped by 0.01 in the following year. Likewise, a 503 000 t increase of Norway pout total biomass led to a K_{LG} increase of 0.001 in the following year. Density-dependent effects on saithe annual average growth were strong and were the main driver of K_{LG} trends explaining 29.67% of deviance against 17.12% deviance explained by food availability. Graphical observations of different effects may suggest that food availability becomes a limiting factor only when density-dependence is reduced (Figure 3.5). To summarise, saithe grew slower when density-dependence was higher independently of the food available. However, when density-dependence was reduced ($s_{NB} < 200\,000$ t) saithe tended to grow faster when more food was available.

Density-dependence was the only environmental factor which had a significant effect on saithe annual mean weight-at-age increment (Table 3.4). In addition, this negative effect was limited to annual weight increment between ages 5-6 ($\delta w6$) and ages 6-7 ($\delta w7$).

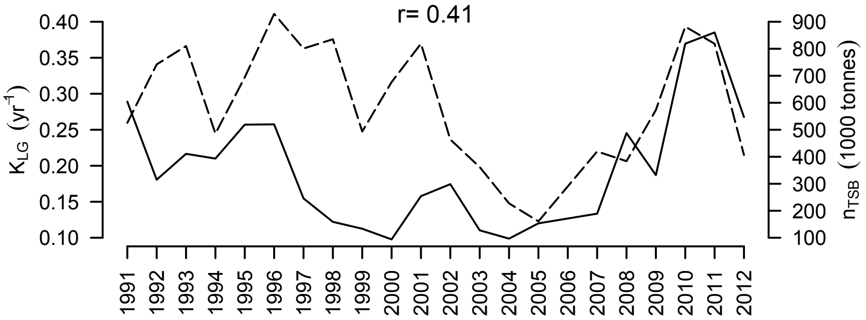
Table 3.4 – Significant relationships of North Sea saithe growth characteristics with environmental variables. Descriptor variables are noted n_{TSB}, for Norway pout total biomass; s_{NB}, for saithe abundance; and Θ, for temperature. ACF indicates the autocorrelation structure. *Pvalues were obtained after Holm adjustment concerning w_a.

Response	Descriptor	ACF	Coefficient	Pvalue*
Annual mean weight-at-age increment (δw_a)				
δw_6	s_{NB}	None	−1.57e-06	$p < 0.05$
δw_7	s_{NB}	None	−2.21e-06	$p < 0.05$
Growth coefficient (K_{LG})				
	s_{NB}	None	−6.59e-07	$p < 0.01$
	n_{TSB}	None	5.03e-08	$p < 0.05$

(a) Density dependence



(b) Food availability



(c) Temperature

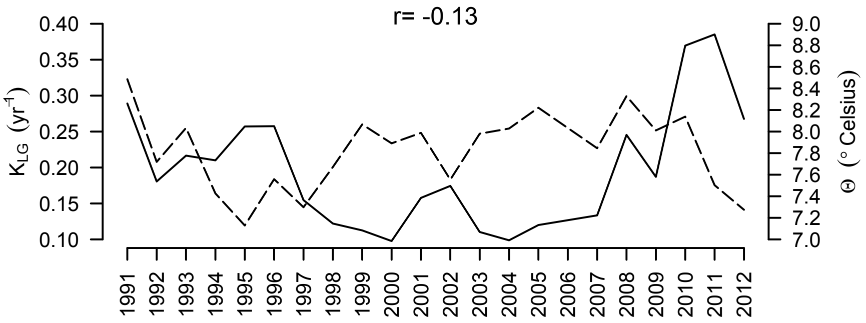


Figure 3.4 – Environmental factors time series from 1991 to 2012 compared to saithe growth coefficient estimates and the corresponding Pearson correlation coefficient (r). Solid lines represent the growth coefficient from logistic growth model, K_{LG}; and dashed lines represent the environmental variables of the year before (a) saithe abundance, S_{NB}; (b) Norway pout Total Stock Biomass, n_{TSB}; and (c) temperature, θ.

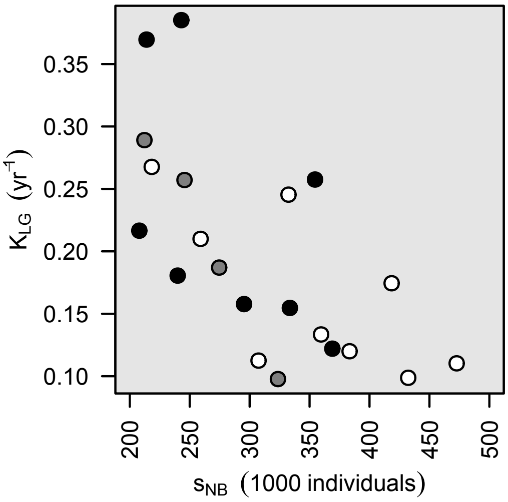


Figure 3.5 – Saithe average growth (K_{LG}) as function of saithe total abundance (s_{NB}). Color filling represents Norway pout availability (n_{TSB}). White: low availability (n_{TSB} < 500 000 t). Grey: medium avialability (500 000 t < n_{TSB} < 700 000 t). Black: high availability (n_{TSB} > 700 000 t).

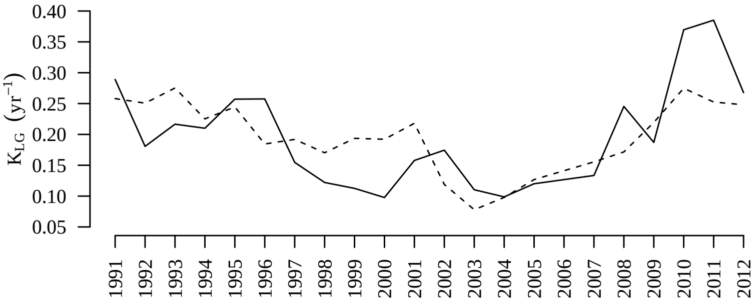


Figure 3.6 – Observed saithe growth coefficient, K_{LG} (solid line), and K_{LG} fitted with models including significant environmental factors (dashed line).

3.4 Discussion

In this study, we found that, given the limitations of our data (older age missing), saithe growth is best described by a logistic relationship between age and length. In addition, density-dependence and food availability had, respectively, negative and positive significant effects on saithe growth, while temperature was never found significant.

The generally poor performance of the VBGF to model saithe annual growth in terms of GoF, as well as the lack of biological meaning of some of the growth parameters estimated, confirms the unsuitability of the VBGF to model saithe growth where the range of age-length data is generally located well away from the asymptotic plateau (Kienzle, 2005). The non-asymptotic behaviour of saithe growth curve, within our observation window, is confirmed by the suitability of the linear model to describe saithe growth, which globally performed similarly to the VBGF model. The difficulties to estimate l_∞ may also question the suitability of the logistic model, which is asymptotic as well. However, the high GoF of the logistic model when fitted to saithe age-length data and the reasonable range of the estimated parameters confirm its suitability. The yearly-based estimation, instead of the cohort-based estimation often used in growth studies, presents the advantage of reducing temporal correlation (ICES, 1991), thus allowing to consider each year's populations as independent. This reduces the age-related correlation (different ages represented within a year belong to different cohorts) and enhances the focus on short-term environmental effect by averaging saithe growth for each year.

Even if the absolute value of the estimated growth coefficients, K, cannot be directly compared, as not representing growth in the same way (see Equations 3.2 to 3.4), the comparison of their time trends is possible. This comparison reveals consistent trends independently of the model used to describe saithe growth. Particularly, a growth increase beginning in the second half of the 2000's can be observed in K time-series resulting from linear, logistic and VBGF estimation as well as in the mean weight increments of the younger ages ($\delta w4$, $\delta w5$, $\delta w6$). Growth coefficient K_{LG} was estimated using a logistic model, selected as the best model to describe saithe annual average growth. K_{LG} shifted in 2004 from a decreasing to an increasing trend. This trend shift coincides with the inception of three species management plans within EU-Norway agreement: North Sea saithe, Northern hake and North Sea cod (*Gadus morhua*).

This coincidence might result from fishing pressure reduction (Engelhard *et al.*, 2015), although the link is not straightforward. The different management plans, when successful, must result in abundance and/or biomass increase of the targeted species (saithe, hake and cod). In this context, significance of the negative density-dependence effects would suggest that the increase in saithe biomass (due to a decrease in fishing mortality) should, according to our result, lead to a decrease in saithe growth, which is just opposite to the observed trend. There are two explanations to this apparent paradox. First, the effects of management plans on fishing mortality and stock abundance are unlikely to be instantaneous, particularly in a changing environment context, to a more or less fast actual abundance and/or biomass increase depending on species resilience (Miller *et al.*, 2010). Second, management plans may first have an impact on young individuals which will increase the average growth rate of saithe in the first years before leading to decline. These mid-term effects may be confirmed by K_{LG} decreasing trend starting in 2010. However, fishing mortality alone is not always sufficient to explain growth as environmental factors might influence recruitment and dynamics as well as growth in shorter terms.

Considering short-term effects (one year), almost half of K_{LG} temporal variation was significantly explained by density-dependence, represented by saithe abundance, and food availability, represented by Norway pout total biomass. The opposite direction of density-dependence and food availability effects are consistent with ecological theory (Jennings *et al.*, 2001; Cury *et al.*, 2003) and confirm the entanglement of these two variables (Sinclair *et al.*, 2002; Lorenzen and Enberg, 2002). The significance of density-dependence effects on ages 5-6 increments ($\delta w6$) and ages 6-7 increments ($\delta w7$) may be related to changes in the amount of energy allocated to somatic growth caused by maturation (Brett and Groves, 1979; Day and Taylor, 1997), which occurs between age 4 and age 5 for saithe (ICES, 2014b). In this case, we would have expected older ages increments to have significant relationship with density-dependence as well. The lack of observable density-dependent effects could result from the high variability of the older ages annual mean weight increments and suggest that annual mean weight-at-age increments, particularly for the older ages, were too variable to be good descriptor of saithe growth.

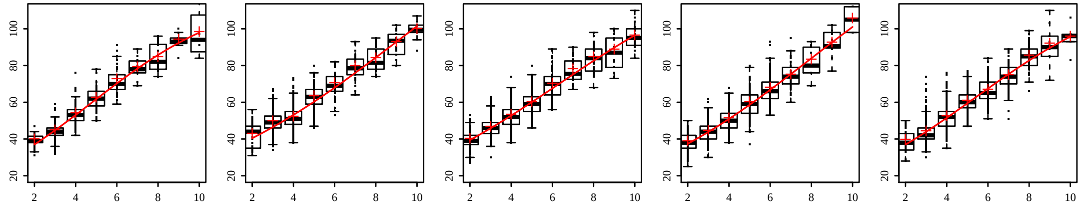
The negative correlation between temperature and K_{LG} may suggest that annual mean temperatures are over the growth optimum (Brett and Groves, 1979). The absence of significant effects of temperature on saithe growth might be explained by the narrow range of temperature variations experienced by the North Sea saithe population in the last 20 years. Because of the limited length of the times series available, and the fact that we study effects at the large scale of the whole North Sea, the best way to investigate temperature effects on saithe growth would be to conduct a study of spatial variation in growth characteristics at a broader geographical scale *e.g.* across the North Sea, the Northeast Arctic, and the Faroe Islands populations. Such comparisons would be of great interest as these saithe populations all overlap with Norway pout distribution (Lambert *et al.*, 2009). Larger coverage might allow to study the interactions between temperature, density-dependence and food availability, which are particularly meaningful when studying growth (Brett and Groves, 1979; Sinclair *et al.*, 2002; Brunel and Dickey-Collas, 2010). Also, a study of saithe growth based upon cohorts instead of years, as was done for haddock (*Melanogrammus aeglefinus*) in the North Sea (Baudron *et al.*, 2011), or using asymptotic/maximum body-size (Baudron *et al.*, 2014) might highlight temperature effects.

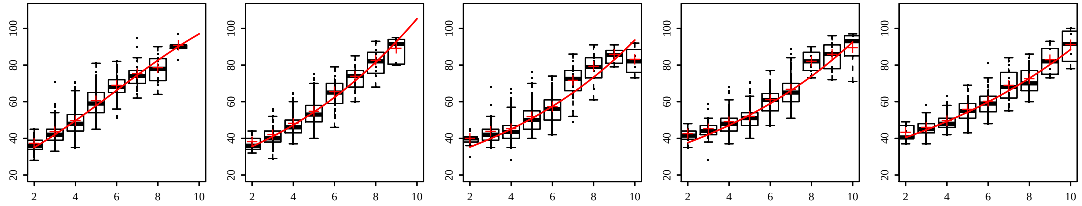
The greater effect of density-dependence relative to food availability may indicate that Norway pout alone is not a sufficient descriptor of food availability and that other forage species may be of importance. For instance, euphausiids which are high energetic value preys (Pedersen and Hislop, 2001) and which were recorded as an important prey for saithe in the North Sea (Bergstad, 1991b; Du Buit, 1991) may have an impact on saithe growth (Carruthers *et al.*, 2005). However, the significant effect of Norway pout biomass, which increased from 2004 and decreased from 2009 (ICES, 2014b), on saithe growth indicates that Norway pout is a key species for saithe and confirms previous studies results (Cormon *et al.*, 2014, Chapter 1; Lynam *et al.*, 2015). This reinforces the assumption of bottom-up processes regulating growth of North Sea saithe and, combined with density-dependence effects might confirm an increasing (intra- or interspecific) competition for food resource.

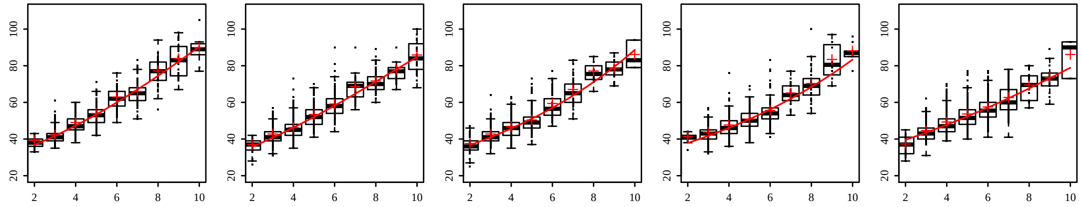
Finally, this study shows an effect of the forage fish availability on predator growth. Similar results were obtained in past studies investigating the interactions between capelin (*Mallotus villosus*) and cod (Northwest Atlantic cod, Krohn *et al.* (1997); Barent Sea cod, Gjøsaeter *et al.* (2009)) or sandeel (*Ammodytes sp.*) and their predators in the North Sea (Engelhard *et al.*, 2013). Regarding, North Sea saithe, no evidence on dependency of its main fish preys was reported before. However, Carruthers *et al.* (2005) showed a relationship between euphausiids abundance and saithe body condition in the Scotian Shelf. It is the first time that such processes are highlighted for North Sea saithe and Norway pout. This is particularly relevant to anticipate the ecological effect of the emergence of a potential competitor, such as hake (Baudron and Fernandes, 2014; Cormon *et al.*, 2014, Chapter 1), on well-established species such as North Sea saithe. Indeed, the emergence of another top-predator in the North Sea might affect food availability trough predation and, according to the results obtained here, indirectly impact the growth of its competitors, such as saithe.

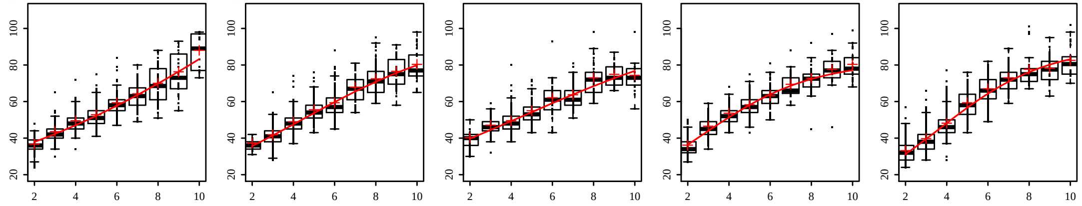
In this context, the emergence of hake in the North Sea might partially explain the decreasing saithe growth, as Norway pout is also an important ingredient of hake diet shown (ICES, 2014a). In addition, the significant relationship between Norway pout and saithe growth may push forward the saithe and hake competitive interaction hypothesis recently suggested by Cormon *et al.* (2014, Chapter 1) by highlighting a limitation of their common resource. Therefore, these results provide a further step towards a global understanding of the trophic-related processes involved at the population level in a large marine exploited ecosystem such as the North Sea, in addition to their specific interest for saithe population and/or fisheries.

3.5 Supplementary material


(a) 1991 (b) 1992 (c) 1993 (d) 1994 (e) 1995


(f) 1996 (g) 1997 (h) 1998 (i) 1999 (j) 2000


(k) 2001 (l) 2002 (m) 2003 (n) 2004 (o) 2005


(p) 2007 (q) 2008 (r) 2009 (s) 2010 (t) 2011

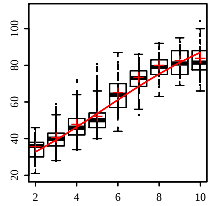

(u) 2012

Figure S3.1 – North Sea saithe length measured during the different survey years as function of the age. Red crosses represent mean length-at-age, red lines represent fitted logistic growth curves.

Part II

What are the effects of saithe and hake ecological interactions on North Sea saithe?

> He uses statistics like a drunken man uses a lamp post, more for support than illumination.
>
> Andrew Lang

Chapter 4

Potential impacts of hake emergence in the North Sea on saithe stock

Cormon, X., Kempf, A., Vermard, Y., Vinther, M., and Marchal, P. 2016, Chapter 4. Emergence of a new predator in the North Sea: evaluation of potential trophic impacts focused on hake, saithe, and Norway pout. ICES Journal of Marine Science, 73: 1357–1369

Abstract
During the last fifteen years, northern European hake has increased in abundance, and its spatial distribution has expanded in the North Sea region in correlation with temperature. In a context of global warming, this spatial shift could impact local trophic interactions: direct impacts may affect forage fishes through modified predator-prey interactions, and indirect impacts may materialise through competition with other resident predators. For instance, North Sea saithe spatial overlap with hake has increased while saithe spawning stock biomass has decreased recently notwithstanding a sustainable exploitation. In this context, we investigated the range of potential impacts resulting from most recent hake emergence in the North Sea, with a particular focus on saithe. We carried out a multispecies assessment of North Sea saithe, using the Stochastic MultiSpecies (SMS) model. In addition to top-down processes already implemented in SMS, we built in the model bottom-up processes, relating Norway pout abundance and saithe weight-at-age. We simulated the effects, on all North Sea species being considered but focusing on Norway pout and saithe, of combining different hake abundance trends scenarios with the inclusion of bottom-up processes in SMS. North Sea saithe F_{MSY} was then evaluated in a multispecies context and contrasted with single-species value. The different scenarios tested revealed a negative impact of hake emergence on saithe biomass, resulting from an increase of predation pressure on Norway pout. These results confirm the competition assumption between saithe and hake in the North Sea and might partially explain the most recent decrease of saithe biomass. This study also highlighted that taking into account bottom-up processes in the stock assessment had a limited effect on the estimation of saithe F_{MSY} which was consistent with single-species value.

Keywords: simple food-web; interspecific competition; hake; saithe; Norway pout; SMS; Maximum Sustainable Yield; multispecies stock assessment; predator-prey interactions

4.1 Introduction

In 2002, the Johannesburg World Summit on Sustainable Development provided a legally binding framework to implement and develop science relevant to the Ecosystem Approach to Fisheries (EAF) and associated management tools (FAO, 2003). In that context, Plaganyi (2007) reviewed models available to take into account species interactions in fisheries research and management. Models are ranging from complex and holistic ecosystem models to minimum realistic models, which are restricted to marine organisms known to have strong interactions with the species of interest. Such minimum realistic models have been preferred by different advisory agencies worldwide to account for multispecies interactions in stock assessment-based fisheries advice, because of their flexibility and ability to fit to observations (Plaganyi, 2007). The International Council for the Exploration of the Sea (ICES), *i.e.* the main advisory body of fisheries management in the Northeast Atlantic, has promoted a multispecies assessments, building in biological interactions since the late 1980's. ICES has recently drawn particular attention to multispecies considerations for stock management in the North Sea, and clearly expressed the objective to provide regular multispecies advice on fisheries in this area (ICES, 2013b).

A major assumption of most single-species stock assessments is that natural mortality (M) is a static and exogenous scalar. In addition to the usual single-species stock assessment parameters, multispecies stock assessment models often separate M into a static natural mortality ($M1$) and a dynamic predation mortality ($M2$) exerted on prey stocks by predator's (top-down control). The age-structured Stochastic MultiSpecies (SMS) model developed by Lewy and Vinther (2004) is used by ICES Working Group on multiSpecies Assessment Methods (WGSAM) as a basis for advice on multispecies considerations for the North Sea area. In its standard version, the SMS model assumes that consumption rates of predators are constant over time because changes in the availability of certain prey species are assumed to be of minor importance. Multispecies models focusing on top-down processes only, such as SMS, provide an improvement for the stock assessment of forage fish populations and predator juveniles. However, such models are less informative when focusing on top-predator populations where older ages are more likely impacted by decreasing prey availability and resulting consumption rates than by predation. Indeed, bottom-up control, *e.g.* dependency of predators on forage fish (Frederiksen *et al.*, 2006; Engelhard *et al.*, 2014; Pikitch *et al.*, 2014), and competitive interactions, are often not taken into account in multispecies stock assessment models, even if their importance is acknowledged (Hollowed *et al.*, 2000).

Changes in environmental factors reported during the last 20 years in the North Sea (ICES, 2008) have led to changes in species distribution and abundances (Beaugrand, 2004; Perry *et al.*, 2005; Jones *et al.*, 2013) but also in ecosystem functioning. The recent increase of Northern hake (*Merluccius merluccius*) abundance in the North Sea (Baudron and Fernandes, 2014; Cormon *et al.*, 2014, Chapter 1) could impact other exploited species through changes in the food-web. These trophic impacts could be direct, *e.g.* on prey species, or indirect, *e.g.* on other predator species feeding on similar prey assemblages *i.e.* competitors. These concerns led in 2013 to an initiative to collect hake diet data from stomach contents within an EU-funded project (MARE/2012/02) in order to include hake in the North Sea multispecies assessment. North Sea hake is currently considered as a small component of the larger Northern hake stock (ranging from the Spanish to the Norwegian coast, (ICES, 2013a)). As a result, the biomass of North Sea hake is input in SMS as an exogenous factor and it is not explicitly assessed within the model. Using the newly sampled hake diet data, the most recent predation mortality outputs (ICES, 2014a) indicate a direct impact of hake on two forage fish species: Norway pout (*Trisopterus esmarkii*), and herring (*Clupea harengus*). These two preys are also predated by other species such as saithe (*Pollachius virens*).

Saithe and hake are generally found at depth ranges that largely overlap (Scott and Scott, 1988; Cohen *et al.*, 1990). Although they are demersal species, they both exhibit pelagic behaviour (Scott and Scott, 1988; Cohen *et al.*, 1990; Bergstad, 1991a), particularly when feeding (Cohen *et al.*, 1990; Homrum *et al.*, 2013). Saithe and hake are top-predators and have similar diet with Norway pout being an important prey for both species (Bergstad, 1991b; Du Buit, 1991; DuBuit, 1996). In addition, Cormon *et al.* (2014, Chapter 1) showed an increasing spatial overlap between hake and saithe in the North Sea, which was positively correlated with Norway pout presence. For these reasons, it is reasonable to assume that both species are subject to competitive interactions (Link and Auster, 2013) particularly when feeding on Norway pout. The emergence of hake in the North Sea might then affect food availability and, as a result, the growth of North Sea saithe (Cormon *et al.*, 2016, Chapter 3) with knock-on effects on saithe biomass, spawning success, and recruitment (Jakobsen *et al.*, 2009). These might partly explain the recent decline in saithe biomass and weight-at-age, notwithstanding an exploitation at around Maximum Sustainable Yield (MSY) for several years (ICES, 2013d).

Fishing mortality corresponding to MSY or F_{MSY} is a commonly used limit or target reference point based on long-term yield predictions. Species interactions may adversely affect the estimation of F_{MSY}, and therefore the reliability of fisheries advice (ICES, 1997b; Gislason, 1999; Collie and Gislason, 2001). Gislason (1999) compared several reference points (including F_{MSY}) estimated in single- and multispecies models for the main Baltic Sea species, *i.e.* cod (*Gadus morhua*), herring and sprat (*Sprattus sprattus*). Collie and Gislason (2001) investigated the sensitivity of reference points to changes in natural mortality (changes of predation pressure on prey population) and growth changes (changes of prey availability to predators). However, to our best knowledge, the sensitivity of predator's F_{MSY} estimates to prey availability and growth changes. have never been investigated, when bottom-up processes are built in multispecies stock assessments.

This study focuses on the hake, Norway pout and saithe trio. The SMS model was extended with a correlation between Norway pout abundance and saithe growth (Cormon *et al.*, 2016, Chapter 3) and the estimation of consumption rates as a function of predator's estimated mean weight-at-age. Including these bottom-up processes allowed the investigation not only of direct impacts of hake on Norway pout, but also of the indirect impacts of hake on saithe. We investigated the effects of increased future levels of hake abundance, reflecting that in the context of global warming (Boyd *et al.*, 2014) hake might settle or even expand in the North Sea (Cormon *et al.*, 2014, Chapter 1). In addition, North Sea saithe MSY, and its associated fishing mortality F_{MSY}, were investigated taking into account bottom-up processes between saithe and Norway pout, and potential competitive interactions with hake.

4.2 Materials and methods

4.2.1 Model presentation

SMS model

The SMS model (Lewy and Vinther, 2004) was used to study the biological interactions between Norway pout, saithe and hake. SMS is an age-length structured model extending the MultiSpecies Virtual Population Analysis (MSVPA) (Helgason and Gislason, 1979; Pope, 1979) used by the ICES to carry out multispecies fish stock assessments in the North Sea and the Baltic Sea. SMS allows the estimation of predation mortality based on prey suitability, prey availability, predator' stomach contents and predator' consumption rates (Andersen and Ursin, 1977; Gislason and Helgason, 1985). Estimated prey suitabilities are constant over time leading to a Holling type II feeding functional response in the model (Magnusson, 1995). SMS is operated with a quarterly time-step with spawning occurring in winter (1^{st} quarter) and recruitment occurring in summer (3^{rd} quarter), while yearly biomass is calculated at the beginning of the year. The model can be used in hindcast and forecast mode and it is subject to a so-called key-run every three years within the ICES WGSAM, which aims to include and validate updates of input data and potential modifications of the model structures.

The present study is based upon the last key-run (ICES, 2014a), which includes 10 dynamically assessed fish species (predators and preys), four "other" fish predators as well as seabirds and marine mammal species (see Table 4.1 for details about species included in the model).

Implementation of bottom-up processes

As a first step, we modified SMS 2014 key-run version to model the extent to which bottom-up processes (availability of Norway pout) may limit the growth and consumption rates of saithe and ultimately impact its Spawning Stock Biomass (SSB). We focused on the hake, saithe and Norway pout trio even if methods presented here could in principle be applied to other species. The implementation of bottom-up processes in the model had two components: (i) the implementation of saithe mean weight-at-age calculation depending on Norway pout biomass and (ii) the calculation of consumption rates as a function of saithe mean weights. All parameters described below and the values used in this study are presented in Table 4.2.

Saithe weight calculation As highlighted by Cormon *et al.* (2016, Chapter 3), saithe growth was assumed to follow a sigmoidal relationship correlating length, l, and age, a, as described by Equation 4.1. The asymptotic length, l_∞, was expressed in centimetres, the relative growth constant, K_{LG}, in years^{-1}, and the sigmoidal curve inflection point, which represents the theoretical age at which individuals growth trajectory changes, a_i, in years.

$$l_a = l_\infty . \frac{1}{1 + e^{-K_{\mathrm{LG}}.(a-a_i)}} \tag{4.1}$$

The two growth parameters, a_i and l_∞, were fixed as the median values of Cormon *et al.* (2016, Chapter 3) estimations excluding years where these two parameters had no biological meaning ($l_\infty > 500$ cm and $a_i > 15$ y). Based on the empirical conclusions of Cormon *et al.* (2016, Chapter 3), saithe growth constant K_{LG} was assumed to vary linearly, at a rate defined by coefficient β_1, in relation to previous year's Norway pout Total Stock Biomass (TSB) ($\mathrm{NP}_{\mathrm{TSB}_{t-1}}$ in tonnes), see Equation 4.2.

$$K_{\mathrm{LG}_t} = \mu + \beta_1 . \mathrm{NP}_{\mathrm{TSB}_{t-1}} \tag{4.2}$$

where t is the time in years and μ the intercept.

To estimate β_1, we first realised a multiple regression of K_{LG} as a function

Table 4.1 – Species included in the Stochastic MultiSpecies model.

Assessed species
Predator only
Saithe (*Pollachius virens*)
Predator and prey
Cod (*Gadus morhua*) Haddock (*Melanogrammus aeglefinus*) Whiting (*Merlangius merlangus*)
Prey only
Norway pout (*Trisopterus esmarkii*) Herring (*Clupea harengus*) Sprat (*Sprattus sprattus*) Sandeel (*Ammodytes sp.*)
No predator-prey interaction
Common sole (*Solea solea*) Plaice (*Pleuronectes platessa*)
"Other" predators (biomass assumed known)
Fish
Hake (*Merluccius merluccius*) Grey gurnard (*Eutrigla gurnardus*) Horse mackerel (*Trachurus trachurus*) Mackerel (*Scomber scombrus*) Starry ray (*Raja radiata*)
Seabird
Fulmar (*Fulmarus sp.*) Guillemot (*Uria aalge.*) Herring gull (*Larus argentatus*) Kittiwake (*Rissa sp.*) Great-black-backed gull (*Larus marinus*) Gannet (*Morus sp.*) Puffin (*Fratercula sp.*) Razorbill (*Alca torda*)
Sea mammal
Grey seals (*Halichoerus grypus*) Harbour porpoise (*Phocoena phocoena*)

of Norway pout TSB, a_i and l_∞ using annual time-series of K_{LG} provided by Cormon *et al.* (2016, Chapter 3). The strong correlation between a_i and l_∞ led to drop the variable with the highest variance inflation factor. This procedure allowed the estimation of the partial regression coefficient β_1 describing the effect of previous year Norway pout abundance on K_{LG}, taking into account the two other parameters effects. All these preliminary analyses were conducted using R 2.15.3.

Estimated saithe length-at-ages l_a were transformed in millimetres and weights-at-age w_a in kg were derived from Equation 4.3:

$$w_{a_t} = a.l_{a_t}^{b} \tag{4.3}$$

where a and b are the allometric coefficients assumed constant over time and extracted from Froese and Pauly (2014).

Consumption rate calculation Saithe consumption rate r, at age a and time t, was calculated as a function of saithe weight-at-age w_a following Equation 4.4:

$$r_{a_t} = c_q.w_{a_t}^{d_q} \tag{4.4}$$

where c and d are the quarterly-dependent (q) allometric coefficients, estimated during model calibration or hindcast (see Section 4.2.2) using historical consumption rates and historical mean weight-at-ages.

4.2.2 Hindcast

In order to fit the model to historical data and to estimate the parameters needed for mutispecies stock assessment, a hindcast was conducted based on the last model key-run that was conducted over the period 1974-2013 (ICES, 2014a). Two changes were, however, brought about this model. First, the Ricker stock-recruitment relation used for saithe was replaced by a segmented regression (hockey stick) relation (ICES, 2013d) and was calibrated on a shortened time-series (1986-2013) to exclude the historically high recruitment values observed in the 1970's during the gadoid outburst (Cushing, 1984). Second, the described bottom-up effects on saithe mean weight-at-age and consumption rates were included.

4.2.3 Forecast

Forecasts were carried out over a period of 51 years (2014-2065) to simulate the effects of bottom-up processes in multispecies stock assessment, particularly for

Table 4.2 – Parameters used for the implementation of bottom-up process between saithe and Norway pout. q: quarter.

	Value	Equation
Growth		
K_{LG}		4.1,4.2
μ	0.17	4.2
β_1	1.01×10^{-7}	
a_i	5.9	4.1
l_∞	131	4.1
Length-weight relationship		
a	2.8322×10^{-8}	4.3
b	2.7374	
Consumption rates		
c_q		4.4
$q = 1$	0.4528	
$q = 2$	1.3127	
$q = 3$	0.6991	
$q = 4$	0.8230	
d_q		
$q = 1$	1.0334	
$q = 2$	1.0160	
$q = 3$	1.0153	
$q = 4$	1.0123	

a top-predator such as saithe, and also to evaluate the effects of hake emergence on the Norway pout and saithe stocks.

Fishery context

Three F-based fishery contexts were considered to conduct the simulations in order to reduce fishery effects on saithe and Norway pout biomass before any further investigation.

- Status-quo fishery context (*FSQ*): fishing mortality (F) of all species assessed within the model were based on F estimated at the last year of the hindcast (F_{sq}).
- Sustainable fishery context (*FST*): all species were fished at sustainable levels preferentially based on presently used recovery/management plan targets, F_{plan}, or when not available, based on either single-species F_{MSY}, or the precautionary approach F level, F_{pa} (ICES, 2014b).
- Alternative sustainable fishery context (*FST*x): all species were fished at sustainable levels (as defined above) except for Norway pout which was based on last year hindcast (F_{sq}).

All fishing mortality values are shown in Table 4.3.

Species interactions scenarios

Each of the three fishery contexts described in Section 4.2.3 were combined with four species interactions scenarios, focusing on the hake-Norway pout-saithe trio.

A baseline scenario involving saithe constant weight-at-ages and constant hake abundance over the whole period of forecast (*BAS*) was first investigated as basis of comparison with the three alternative scenarios integrating the newly implemented bottom-up processes between saithe and Norway pout. In the baseline scenarios (*BAS*, hake abundance was estimated as the average of the last three years of the hindcast (2011, 2012 and 2013). Saithe stock outputs resulting from *BAS* scenario were equivalent to outputs resulting from single-species assessment because of the absence of species interactions impacting saithe stock in the model: neither predation mortality (as saithe is an exclusive predator, Table 4.1), nor bottom-up processes were included in the model.

The three alternative scenarios, exploring hake predation pressure on Norway pout and its indirect effects on the saithe stock, were investigated through the implementation of bottom-up processes in the model as described in Equations 4.1 to 4.3. Including bottom-up preocesses results in saithe stock outputs,

Table 4.3 – Synthesis of the different scenarios explored (??). Average fishing mortalities (y^{-1}) are computed for ages indicated in square brackets. BAS: baseline scenario. CST: constant hake abundance scenario. MOD: moderate hake abundance scenario. HIG: high hake abundance scenario. Dash: constant parameter. Tilde: varying parameter. Non-constant hake abundance indicates an increase rate (%.y^{-1}) over the time period (y) indicated between brackets.

Fishery context scenario						
		Status-quo fishery (*FSQ*)	Sustainable fishery (*FST*, *FST*x)			
Fishing mortality		F	F_{plan}	F_{MSY}	F_{pa}	F
Cod	[2-4]	0.26		0.33		
Whiting	[2-6]	0.17	0.15			
Haddock	[2-6]	0.16		0.37		
Saithe	[3-6]	0.31	0.30			
Herring	[2-6]	0.26	0.25			
Sandeel	[1-2]	0.30				0.30
Norway pout	[1-2]	0.06			0.60	
Sprat	[1-2]	0.30		0.70		

Species interactions scenario				
	BAS	CST	MOD	HIG
Saithe weight-at-age	–	~	~	~
Hake abundance	–	–	+5% (11)	+10% (11)

such as biomass and consumption rates, being dependent on the level of hake abundance used in forecast (see below and Figure 4.1).

- *CST*, hake abundance was constant over the whole period of forecast and was estimated as for *BAS* scenario.
- *MOD*, hake abundance increase was moderate: 5% per year during 11 years starting in 2014 (based on the 2011-2013 averaged abundance) and reaching a plateau from 2025 onwards.
- *HIG*, hake abundance increase was high: 10% per year during 11 years starting in 2014 (based on the 2011-2013 averaged abundance) and reaching a plateau from 2025 onwards.

A summary of the four species interactions scenarios is presented in Table 4.3.

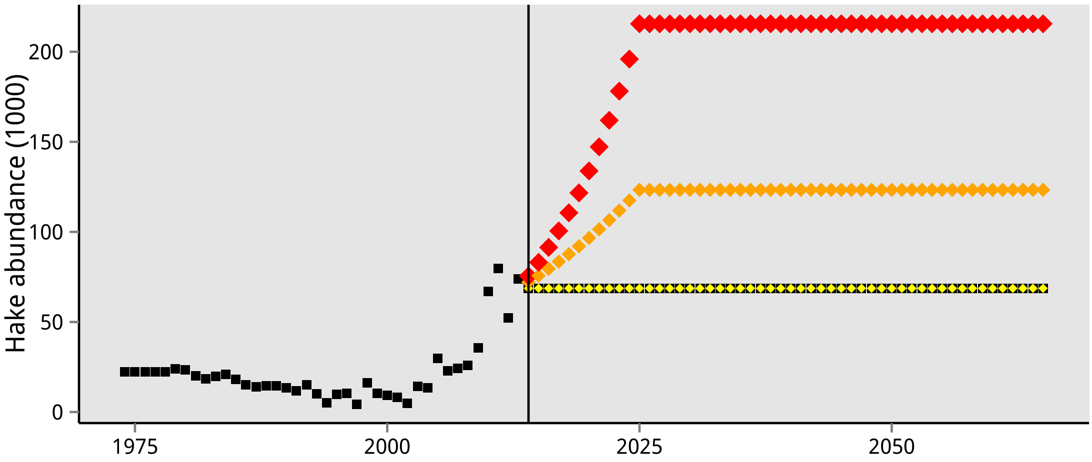


Figure 4.1 – Hake abundance in number of individuals over time depending on the four different scenarios investigated. Black square: baseline scenario where hake abundance is constant and no bottom-up processes are included (*BAS*). Small yellow diamond: constant hake abundance (*CST*). Orange diamond: moderate hake abundance (*MOD*). Large red diamond: high hake abundance (*HIG*).

Saithe yield optimization

Finally, we tested the sensitivity of saithe F_{MSY} (currently assessed within single-species model) to multispecies interations, including bottom-up control. To that purpose, we simulated North Sea saithe yield for each of the four scenarios (*BAS*, *CST*, *MOD*, *HIG*), considering the *status-quo* fishery context (*FSQ*). Only Norway pout and saithe fishing mortalities varied. Norway pout F took values of either F_{sq} or F_{pa} (Table 4.3). Saithe fishing mortality F ranged from 0 to 1, with an increment of 0.1. Saithe yield was optimized for the short-term by considering the average saithe yield over the first five years of forecast (2014-2018), and then for the long-term by considering the yield in the final forecast year (2065). These optimisations led to the estimation of F_{MSTY} (Maximum Short-Term Yield) and F_{MSY}, respectively.

4.3 Results

4.3.1 Baseline scenario and fishery context

Considering the baseline scenario (*BAS*), the comparison of different fishery context suggested to consider in subsequent analyses the alternative sustainable fishery context scenario, so to limit the effects of fishing on saithe and Norway pout biomass.

In the *FSQ*, the baseline scenario (*BAS*) forecast, presented in the Supplementary material, showed that adult Norway pout (age 1 to age 3) were mainly predated by saithe, which contributed to about half of total predation mortality (*M2*); while hake, cod and whiting (*Merlangius merlangus*) contributed to the other half (Figure S4.1). In contrast, young Norway pout (age 0) were mainly predated by other predatory fishes (about half of total *M2*). Norway pout and saithe biomass trends (Figure S4.2) were opposite with a decrease of Norway pout TSB concurrent with the increase of saithe SSB and the associated *M2* increase (Figure S4.1).

The results obtained when combining the *BAS* scenario and the *FSQ* fishery context were used as a basis for further comparisons of the three fishery contexts. Saithe SSB (Figure 4.2a) increased following the reduction of saithe *F* in the *FST* and in the *FST*x. However, Norway pout biomass (Figure 4.2b) was severely impacted by the strong increase of fishing mortality in *FST* compared to *FSQ* (×10, see Table 4.3). The alternative sustainable fishery context (*FST*x), where Norway pout *F* is at *status-quo* level, was more sustainable with an increase of Norway pout biomass compared to the two other fishery contexts (*FSQ* and *FST*). For these reasons, the alternative sustainable fishery context was selected to simulate the effects of the various hake abundance scenarios under considerations.

4.3.2 Interactions scenarios

In order to understand the differences resulting from the inclusion of bottom-up processes between saithe and Norway pout, at a constant hake abundance, we first compared the status of Norway pout and saithe stocks as derived from the baseline (*BAS*) and the constant (*CST*) scenarios. Then, th effects of increased hake abundance on both Norway pout and saithe stocks were investigated by comparing the outputs of scenarios *CST*, *MOD*, and *HIG*. As explained in Section 4.3.1, all hake abundance scenarios were simulated within alternative sustainable fishery context (*FST*x).

Inclusion of bottom-up processes between saithe and Norway pout

The inclusion of bottom-up processes between saithe and Norway pout had negative effects on both saithe and Norway pout biomass, even when hake abundance remained constant (*CST*). Norway pout and saithe biomass were reduced by around 10% (Figure 4.3a) and 17% (Figure 4.3b), respectively, compared to the baseline scenario where no bottom-up processes were included (*BAS*).

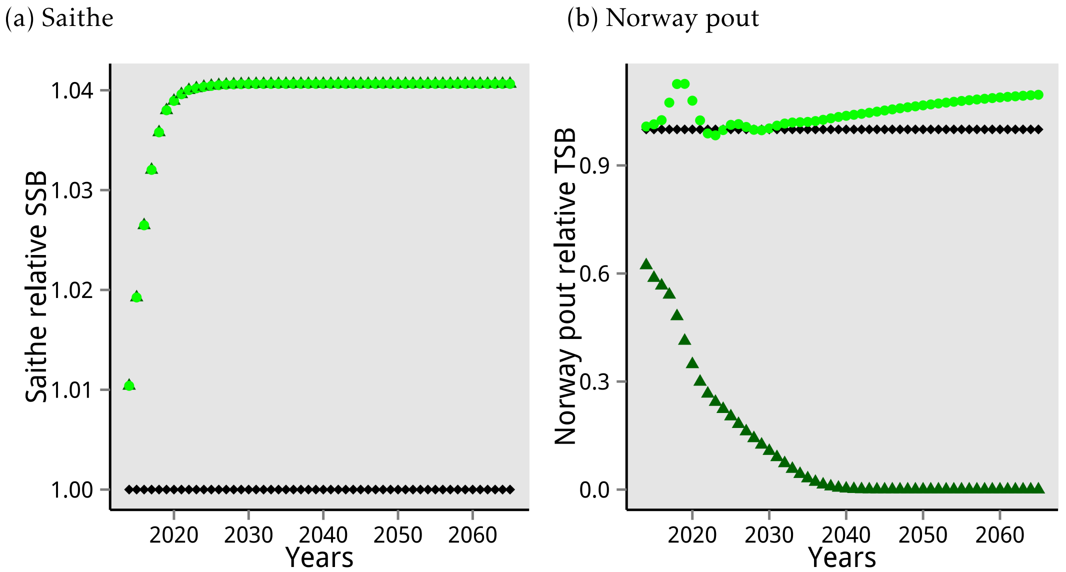


Figure 4.2 – Difference between saithe and Norway pout relative biomass depending on three fishery contexts while hake is assumed constant and no bottom-up processes between saithe and Norway pout are included (*BAS*). (a) Saithe Spawning Stock Biomass (SSB) estimates comparison. (b) Norway pout Total Stock Biomass (TSB) estimates comparison. Black diamond: status-quo fishery context (*FSQ*). Olive triangle: sustainable fishery context (*FST*). Green circle: alternative sustainable fishery context (*FST*x).

Age 1 Norway pout predation mortalities (*M2*) in the baseline scenario (Figure 4.4) were similarly distributed to the ones derived from *status-quo* fishery context (Figure S4.1): half of *M2* due to saithe predation, while hake, cod and whiting contributed to the remaining half. There was, however, a slight increase of total *M2* exerted on Norway pout when bottom-up processes were included (Figure 4.4), which is an indirect consequence of the reduction in saithe biomass (Figure 4.3b). Indeed, the lower predation exerted by saithe on young whiting and haddock (*Melanogrammus aeglefinus*) resulted in an increase of their biomass, and hence in the increase of the predation exerted by these two species on Norway pout (not shown). Accordingly, there was a slight decrease in the predation pressure induced by saithe.

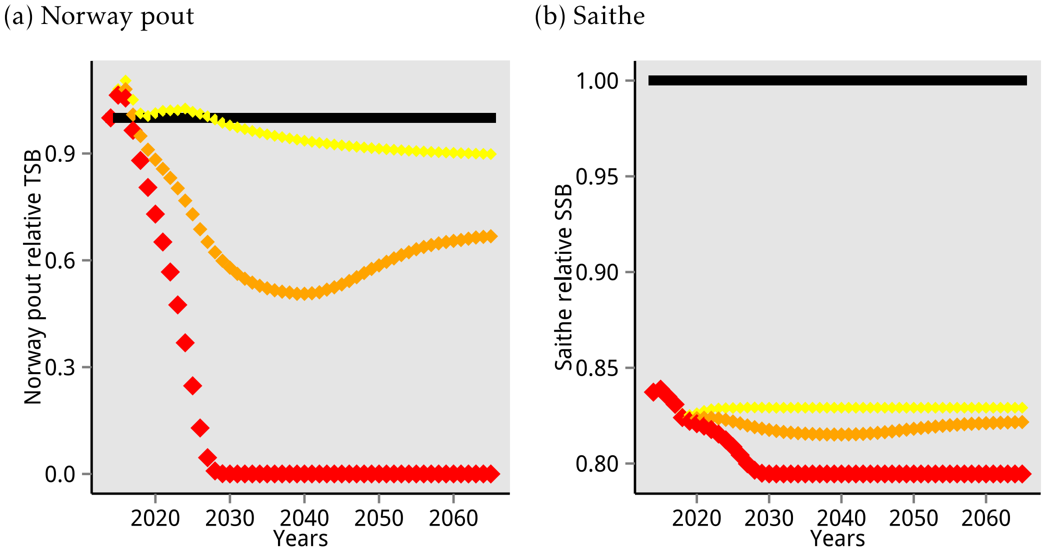
Hake abundance increase

In scenarios where hake abundance increased and bottom-up processes were included, there were negative effects on both saithe and Norway pout forecast biomass (Figure 4.3). These effects were generally proportional to the magnitude of hake abundance changes (moderate or high).

When hake abundance increased moderately (*MOD*), the resulting Norway pout biomass was about 30% lower compared to the scenario where hake abundance was kept constant (*CST*). In the high hake abundance scenario (*HIG*), Norway pout biomass decreased swiftly to finally collapse in 2030 (Figure 4.3a). Concerning indirect effects, a moderate increase of hake abundance (*MOD*) had only a slight negative impact on saithe biomass compared to the *CST* scenario (around 1%, Figure 4.3b). However, in the *HIG* scenario, saithe biomass decreased relatively swiftly to finally reach a stable level, around 5% lower compared to the *CST* scenario.

Changes in hake abundance induced changes of Norway pout *M2* allocation (Figure 4.4). In the *MOD* scenario, hake became almost as important as saithe and as cod, whiting and haddock combined. In the *HIG* scenario, hake became the major predator of Norway pout, followed by saithe while the predation exerted by other species became insignificant ($< 5\%$). In addition, the high level of hake abundance in *HIG* had a severe impact on Norway pout predation mortality with estimated Norway pout *M2* reaching extreme values ($M2 > 7.5$) after 15 years. These extreme *M2* values explain the decrease and subsequent collapse of Norway pout biomass in 2030.

Saithe F_{MSY} estiamted from single-species stock assessments (0.3) was not altered when derived from multispecies stock assessments, even with bottom-up processes being built in the model. However, the inclusion of bottom-up processes narrowed the plateau around the maximum long-term yield versus fishing mortality relationship, and highlighted the importance of Norway pout


(a) Norway pout

(b) Saithe

Figure 4.3 – Differences between Norway pout and saithe relative biomass estimated for each of the species interaction scenarios. (a) Norway pout Total Stock Biomass (TSB) and (b) saithe Spawning Stock Biomass (SSB). Black square: baseline scenario used for comparisons where hake abundance is constant and no bottom-up processes are included (*BAS*). Small yellow diamond: constant hake abundance and bottom-up processes (*CST*). Orange diamond: moderate hake abundance and bottom-up processes (*MOD*). Large red diamond: high hake abundance and bottom-up processes (*HIG*).

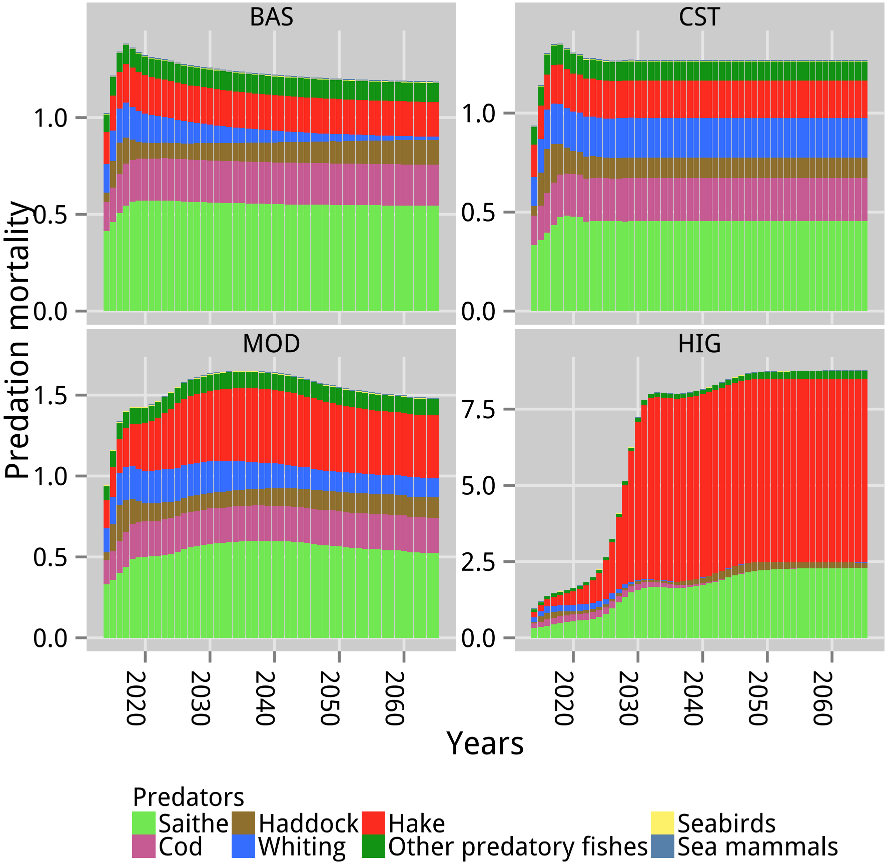


Figure 4.4 – Age 1 Norway pout predation mortalities for each of the species interaction scenarios. BAS: baseline scenario used for comparisons with constant hake abundance and no bottom-up processes included. CST: constant hake abundance and bottom-up processes. MOD: moderate hake abundance and bottom-up processes. HIG: high hake abundance and bottom-up processes.

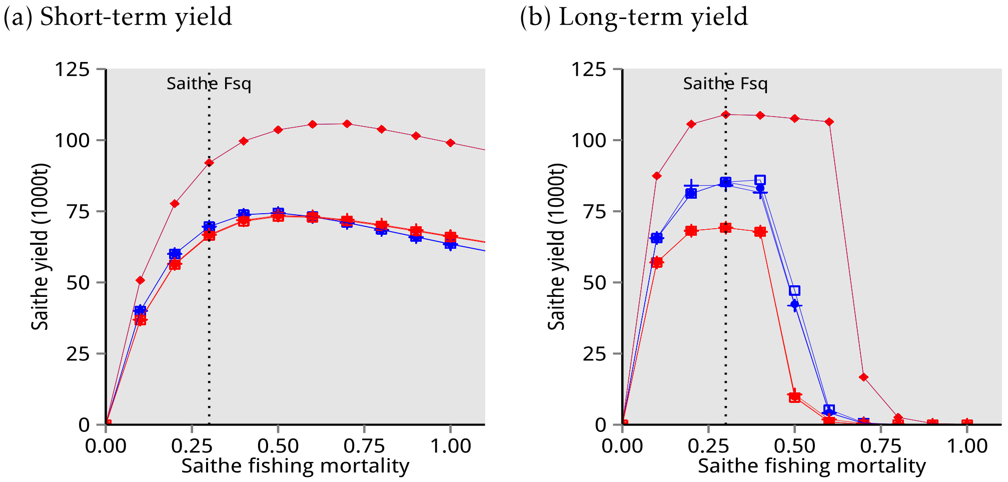


Figure 4.5 – Saithe yield as a function of saithe fishing mortality depending on the species interaction scenarios and Norway pout fishing mortality. (a) Short-term yield estimated by averaging yield from 2014 to 2018 included. (b) Long-term yield estimated at final year of the forecast period value (2065). Blue: Norway pout status-quo fishing mortality (F_{sq}). Red: Norway pout precautionary approach fishing mortality (F_{pa}). Diamond: baseline scenario where hake abundance is constant and no bottom-up processes are included (*BAS*). Plus: constant hake abundance and bottom-up processes (*CST*). Dot: moderate hake abundance and bottom-up processes (*MOD*). Square: high hake abundance and bottom-up processes (*HIG*).

fishing mortality level.

The relationship between short-term saithe yield and saithe fishing mortality (F) was similar across the different species interactions scenarios investigated (Figure 4.5a). Saithe MSTY was reached at around $F_{\mathrm{MSTY}} = 0.5$ for all scenarios. Only absolute yield estimates differed depending on whether or not bottom-up processes were included, while Norway pout fishing mortality and hake abundance had limited effects. The inclusion of the bottom-up processes between saithe and Norway pout led to lower saithe yield estimates, compared to the baseline scenario (*BAS*) for the same saithe F.

The inclusion of bottom-up processes between saithe and Norway pout affected long-term saithe yield, while hake abundance level had barely any effect (Figure 4.5b). When no bottom-up processes were included, a large plateau was found around the maximum long-term saithe yield versus F relationship, from $F = 0.2$ to $F = 0.6$, a range where F_{sq}, F_{MSY}, and F_{MSTY} were all included. Exploiting saithe within that F range, which includes the values of F_{sq}, F_{MSY}, and F_{MSTY}, woudl then lead to a long-term yield close to MSY. However, when bottom-up processes were included, the plateau including F_{MSY} narrowed (from $F = 0.2$ to $F = 0.4$). Consequently, when saithe fishing mortality was set to F_{MSTY} and bottom-up processes were not taken into account, long-term saithe yields were barely changed compared to F_{sq}, while they became very low when bottom-up processes were included. Overall, long-term saithe yields were maximised in all scenarios when F was set to current single-species target: $F_{\mathrm{MSY}_{\mathrm{multispecies}}} \simeq F_{\mathrm{MSY}_{\mathrm{single\text{-}species}}} \simeq 0.3$. Finally, the inclusion of bottom-up processes highlighted differences depending on the levels of Norway pout fishing mortality. Indeed, the general decrease of absolute saithe yield resulting from the inclusion of bottom-up processes was even more dramatic when Norway pout fishing mortality was set to $F_{pa} = 0.6$ instead of $F_{sq} = 0.06$.

4.4 Discussion

4.4.1 Species interactions in top-predator assessment

In this study, we conducted a comprehensive multispecies assessment of North Sea saithe stock, including bottom-up processes relating saithe weight-at-age to Norway pout abundance. It revealed in particular the adverse effects, on the precision of top-predator assessments, of neglecting such bottom-up processes, particularly in a context of competition for a common prey with another top-predator. This study thus highlighted that an increase of hake abundance in the North Sea would have a strong impact on Norway pout biomass through predation, resulting in indirect negative effects on saithe stock through competitive interactions.

Importance of prey availability for top-predator assessment

In the absence of bottom-up control linking saithe growth and Norway pout abundance, saithe SSB increased in the first years of the forecast period, as a result of initial saithe recruitments being set above recent average in the baseline forecast. These relatively high values used in the forecast stem from the three peaks observed in the saithe recruitment hindcast period (1986, 1995 and 2001), from which they are calculated.

The negative effect of Norway pout biomass reduction on saithe SSB, when the correlation between saithe weight-at-age and Norway pout biomass was taken into account, bears out the results of Lynam *et al.* (2015), who found a direct correlation between the SSB of these two species using Generalized Additive Models (GAMs). There are numerous examples of such bottom-up relationships between preys and predators all along the marine food web, *e.g.* Atlantic mackerel (*Scomber scombrus*) dependency on copepods (Ringuette *et al.*, 2002), North Sea demersal fishes dependency on sandeel (*Ammodytes sp.*) (Engelhard *et al.*, 2013, 2014), and bottlenose dolphins sensitivity to resource depletion in the Bay of Biscay (Lassalle *et al.*, 2012).

The importance of taking into account prey availability for predator assessment was confirmed by the differences in saithe yield prediction depending on, whether or not, bottom-up processes were built in the assessment. Indeed, when saithe growth was related to Norway pout availability, saithe long-term yield predictions were reduced by around 25% when saithe was exploited at *status-quo* (F_{sq}), compared to the scenario with no bottom-up processes.

The lower estimations of saithe long-term yield, when taking into account bottom-up processes, are consistent with recent assessment results (ICES, 2013d). Therefore, taking into account Norway pout availability in saithe assessment may lead to more realistic yield predictions that could inform management (Rice, 2011). For instance, Buchheister *et al.* (2015) showed that an increase in prey availability may have a positive impact on the Northeast U.S. Atlantic coast flounder stock and suggest that taking into account these bottom-up processes may support the management of that depleted stock. Several studies suggested similar ideas concerning management of forage fish predators worldwide (Pikitch *et al.*, 2014; Essington *et al.*, 2015a) including the North Sea (Engelhard *et al.*, 2014).

In addition, an increase of saithe F to F_{MSTY} (Maximum Short-Term Yield) would only increase slightly short-term yields, but at the expense of a dramatic decrease of long-term yields. This pattern was only revealed when bottom-up processes were built in the model, which confirms the importance of taking prey availability into account when studying long-term yields of fish predators like saithe (Rice, 2011; Plaganyi, 2013).

Finally, the inclusion of bottom-up processes in multispecies models, through prey availability, is necessary to study indirect competitive interactions effects, which may disturb the functioning of marine ecosystems, particularly when combined with fishing (Jennings and Kaiser, 1998; Hollowed *et al.*, 2000).

Increased competition revealed

Despite the dramatic increase of hake abundance in the last 12 years (Baudron and Fernandes, 2014; Cormon *et al.*, 2014, Chapter 1; ICES, 2014a), its abundance was still around four times lower than saithe abundance in the North Sea at the beginning of the forecast period. This explains the higher Norway pout predation mortality *M2* induced by saithe when hake abundance was constant. However, an increase of hake abundance led to an increase of the predation mortality M2 exerted by this predator. In the high hake abundance scenario, hake became the major predator of Norway pout leading directly to its collapse and indirectly to a decrease of saithe biomass (when bottom-up processes were built in the assessment).

The collapse of the Norway pout stock could result from the Holling functional feeding response assumed in the model. Indeed, the Holling type II function did not allow Norway pout predators to switch prey at low Norway pout abundance which compromised Norway pout stock recovery. Another functional response, *e.g.* Holling type III feeding response, could have been considered (Kempf *et al.*, 2008), although that would likely only have delayed, and not prevented, the collapse of the Norway pout stock (Floeter *et al.*, 2005). In the Scotian Shelf, Carruthers *et al.* (2005) showed that saithe persistently preyed upon euphausiids even at low euphausiids abundance, instead of switching to other preys, which resulted in a loss of saithe body condition. These results provide some support to the Holling type II assumption. In that case, the absence of prey shift coudl be expmained by the the high energetic value of euphausiids (Mauchline and Fisher, 1969).

Being a highly piscivorous predator, hake may impact other forage fish preys contributing to its diet such as herring (ICES, 2014a). Herring, which is a prey with high energetic value (Pedersen and Hislop, 2001), is also consumed by saithe. The variation of saithe growth as a function of prey availability was here reduced to a dependency on Norway pout abundance, based on Cormon *et al.* (2016, Chapter 3). The potential bottom-up processes between saithe and other preys, such as herring, need to be further investigated to be integrated, when evidenced, in future multispecies assessments. In addition, saithe is not the only predator sharing prey with hake in the North Sea. For instance, Norway pout and herring are also consumed by cod and whiting (Engelhard *et al.*, 2014; ICES, 2014a). Therefore, hake might have an impact on these other demersal species, particularly if their spatial overlap is important. These questions need to be investigated in order to broaden the understanding of the potential impact of hake on the North Sea ecosystem.

Finally, the uncertainty around the logistic growth parameters *i.e.* l_∞ and a_i, may also bias our results (Payne *et al.*, 2015). For instance, current estimates of ai are probably too high to realistically reflect actual changes in life-stage and/or maturation. Lower a_i values would have resulted in a slower growth, thereby impacting saithe weight-at-age and biomass more substantially. In addition, the absence of bottom-up processes between hake and Norway pout and the fact that hake biomass is not assessed but forced into the model suggest that our results should be interpreted with caution. The lack of information available about hake stock identity and dynamics in the North Sea is an important issue, which needs to be addressed to explicitly assess hake within the model. For instance, the question of the existence of one or two hake stocks needs to be investigated. Baudron and Fernandes (2014) assumed that the recent increase of hake abundance in the North Sea is exclusively due to density dependent effects in West Scotland, consistently with the current definition of the Northern hake stock (ICES, 2013a). However, hake is a batch spawner (Murua, 2010) and, when present around Shetland Islands during spawning, its larvae might drift, along with saithe larvae, towards Norwegian coast and Skagerrak (Munk *et al.*, 1999). These processes would lead to different dynamics than those currently assumed and would need to be further investigated to better inform the management of hake in the North Sea.

4.4.2 Multispecies advice

When bottom-up processes of Norway pout on saithe were not included, the overestimation of saithe biomass (around 17%) had no marked effect on the estimation of F_{MSY}. Saithe *status-quo* fishing mortality ($F_{\mathrm{sq}} = 0.31$) was very close to single-species and multispecies MSY and recovery plan fishing mortalities ($F_{\mathrm{MSY}} = F_{\mathrm{plan}} = 0.3$), which confirms that the exploitation of saithe in the North Sea is probably not subject to overfishing and also the robustness of F_{MSY} estimates to changes in growth, even if these changes lead to different absolute yields (Collie and Gislason, 2001).

The suitability of Norway pout single-species management measures in a multispecies context is more questionable. Indeed, single-species precautionary approach fishing mortality ($F_{pa} = 0.6$) was 10 times higher than *status-quo* fishing mortality ($F_{sq} = 0.06$). When applied in a multispecies context, F_{pa} would lead to stock collapse (even with no increase of natural mortality). Even if F_{pa} should be an upper limit reference point in an escapement strategy and not a permanent target, the sensitivity of Norway pout stock to an increase of mortality (F and/or $M2$) should be taken into account in the next management decisions concerning this key forage fish species. In addition, Norway pout recruitment, which is to a large extent determined by environmental factors during egg and larval phase, is an important driver of its stock dynamics (ICES, 2013c). The forecast are consequently largely dependent upon assumptions made concerning Norway pout recruitment. These uncertainties reinforce the fact that single- and multispecies advices are not comparable because of the different assumptions used in the different methods, *e.g.* shape of the stock-recruitment relationships and natural mortality settings.

Potential environmental disturbances were not taken into account in this study. In a context of global warming (GIEC, 2014), an increase of temperature in the North Sea might have different consequences on the ecosystem, *e.g.*

changes in predator-prey spatial overlap (Perry *et al.*, 2005; Jones *et al.*, 2013), or change in size- or age-at-maturation (Thorsen *et al.*, 2010; Baudron *et al.*, 2011), which may influence our results. Such environmental changes could be more explicitly built in our model. As an example, a more accurate estimation of hake abundance in the future years, *e.g.* by downscaling climate scenarios, could allow inferring hake distribution in the area as a function of temperature and reduce our scenarios uncertainties (Payne *et al.*, 2015). In addition, a reduction of prey availability might have consequences for predator spawning success and recruitment (Jakobsen *et al.*, 2009). Köster *et al.* (2009) showed that environmentally sensitive stock recruitment of Eastern Baltic cod might lead to unsuitable biological reference point estimations where not taken into account. As the latter processes were not included in the model this study might have underestimated the negative impacts of reduced Norway pout availability on saithe biomass. Thus, the resulting effects of saithe and hake competitive interactions may have been underestimated, which may have adversely affected the estimation of multispecies saithe F_{MSY}.

4.5 Conclusion

This study revealed the importance of taking into account bottom-up processes, in addition to more usual top-down processes, to assess the status of predators in a multispecies context. To our best knowledge, it is the first time that both processes are combined in a multispecies stock assessment model parameterised for the North Sea. We focused here on North Sea saithe, for which predator dependency on prey as well as interspecific competition were accounted for and we showed some potential negative effects of hake emergence in the area on both Norway pout and saithe biomass.

North Sea saithe was a good case to study competitive interactions with hake due to the absence of spatial overlap between adult and juvenile individuals ICES (2013b) which allowed to disentangle top-down and bottom-up effects. However, interspecific competitive processes need to be investigated for other North Sea species. For instance, cod might become another "victim" of hake emergence in the area, should it also compete for preys with hake. In the Northwest Atlantic and in the Barents Sea, cod was found to depend on capelin (*Mallotus villosus*) abundance (Krohn *et al.*, 1997; Gjøsaeter *et al.*, 2009). In the North Sea, Norway pout and/or herring may affect cod stock as these preys contribute importantly to its diet (Engelhard *et al.*, 2014).

In this study, the competition between hake and saithe was investigated through their preying on Norway pout. Actually, competition may also occur for other preys (particularly if the Norway pout stock collapses), such as herring, blue whiting (*Micromesistius poutassou*) or euphausiids. Herring and euphausiids may be key forage species in the North Sea due to their high energetic content (Mauchline and Fisher, 1969; Pedersen and Hislop, 2001). Combined with fishing and potential environmental disturbances (Beaugrand, 2004), an increased predation mortality exerted by hake on these key species might inflate some of the adverse effects of hake emergence on the North Sea ecosystem. For instance, herring density-dependency was assumed to have implications for the management of harbour porpoises and mackerel in the eastern North Sea, Skagerrak and Kattegat (Sveegaard *et al.*, 2012). In the Baltic Sea, herring was found sensitive to competition with sprat on zooplankton (Casini *et al.*, 2006) while in the North Sea it was assumed to compete with sprat and anchovy (*Engraulis encrasicolis*) (Raab *et al.*, 2012). Concerning euphausiids, the dependency of predators, such as saithe, was shown in the Scotian Sea (Carruthers *et al.*, 2005; Plaganyi, 2013). Ultimately, this work could be extended to other species if sufficient data were available. Indeed, understanding distribution and dynamics of hake, as well as of key forage species such as herring and euphausiids, would help the precision of multispecies stock assessment and thereby of the science basis supporting the management of the heavily exploited North Sea marine ecosystem.

Finally, the negative impact of hake on saithe biomass through a reduction of Norway pout availability bears out the competition hypothesis (Link and Auster, 2013), suggested between the two species by Cormon *et al.* (2014, Chapter 1) and might explain partially the most recent reduction observed in saithe biomass and weights-at-age.

4.6 Supplementary material

Supplementary materials present hindcast and status-quo fishery context forecast results.

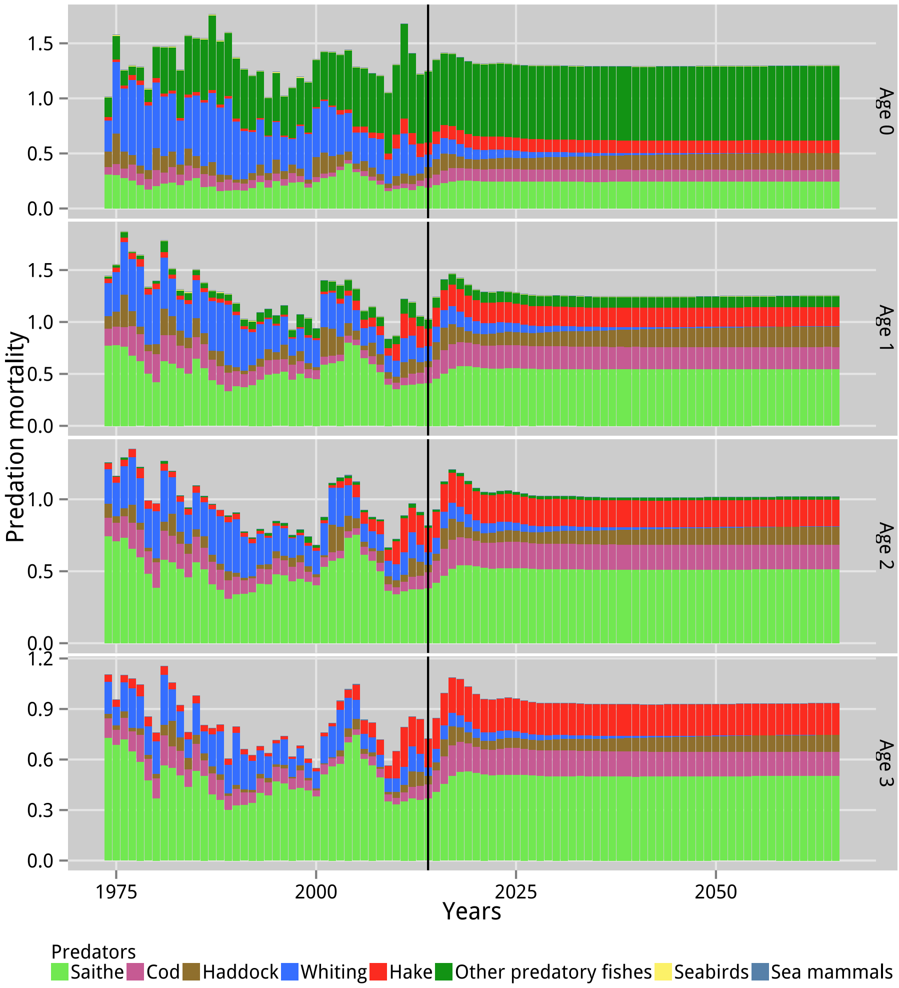
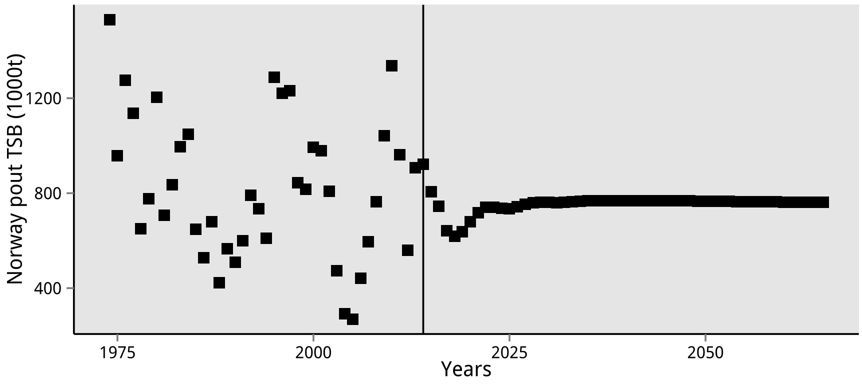
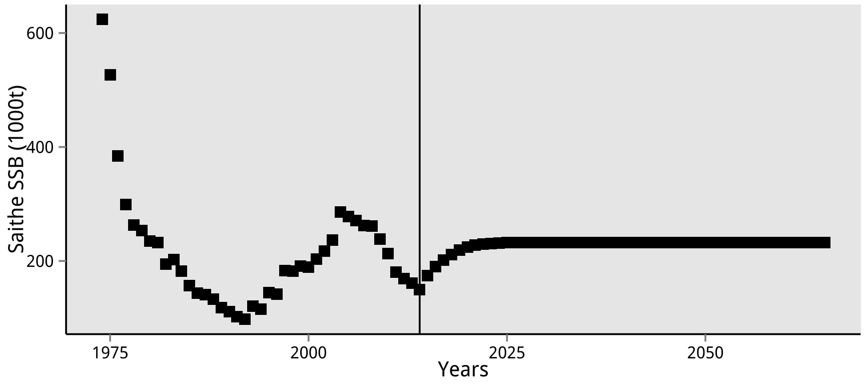


Figure S4.1 – Norway pout predation mortalities from age 0 to age 3 over time for the hindcast and the baseline scenario forecast within status-quo fishery context (*FSQ*) context (1974-2065). Vertical black line indicates first year of forecast (2014).

(a) Norway pout biomass



(b) Saithe biomass



(c) Saithe recruitment

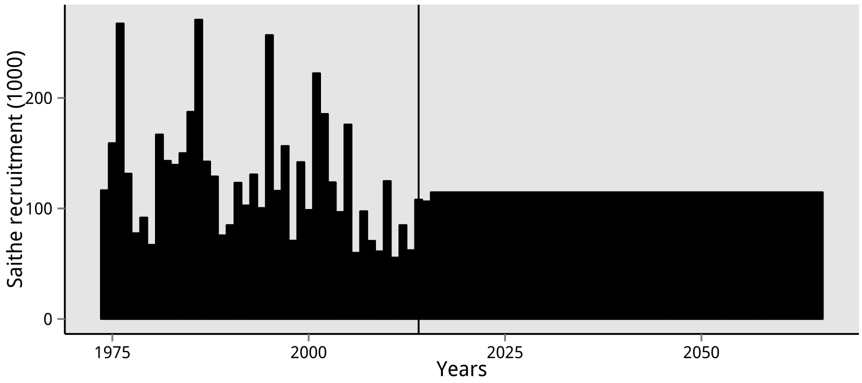


Figure S4.2 – Biological stock parameters of saithe and Norway pout over time for the hindcast and the baseline scenario forecast within status-quo fishery context (*FSQ*) context (1974-2065). (a) Norway pout Total Stock Biomass (TSB). (b) Saithe Spawning Stock Biomass (SSB). (c) Saithe recruitment (age = 3). Vertical black line indicates first year of forecast (2014).

> In God we trust. All others must bring data.
>
> W. Edwards Deming

Conclusion

Competition or coexistence?

This long-running question in ecology was the core of this PhD thesis. Competition, which is a major factor of ecosystem organisation, is expected to lead to changes of the ecosystem structure, through the dominance of one species over the other(s), while coexistence may allow all species to live together without adverse effects for any of them (Miller, 1967; Jones, 1978). In order to investigate the nature of the interactions between saithe (*Pollachius virens*) and hake (*Merluccius merluccius*) in the North Sea and, ultimately, to assess potential impact of hake emergence on saithe in the area, a step-by-step investigation was conducted to verify the four criteria required to assume competition between two species at large-scale (Link and Auster, 2013, Introduction).

Contrasted trends. Competition between two species in an exploited ecosystem must have observable effects at the population level to be of interest in a fishery management context (Link and Auster, 2013). The expansion of hake in the North Sea was shown in terms of probability of presence (Chapter 1), biomass (Baudron and Fernandes, 2014) and abundance (ICES, 2014a, Appendix A), while saithe biomass decreased steadily in the area since 2006 (ICES, 2014b).

These opposite trends are in accord with the 1st criterion to assume competition between two species at a large-scale. Yet, these opposite trends could also result from predator-prey interactions, with hake preying upon saithe. Based upon 2013 diet studies (ICES, 2014a, Chapter 2), the predator-prey interaction assumption could be rejected. However, these diet studies were based upon samples collected offshore and exclusively in the North Sea. Consequently, trophic interactions in the North Sea coastal areas and in the Skagerrak are still unknown. Werner (2015) recently found that hake along the northern coast of Norway occasionally preyed upon Northeast Arctic saithe. The North Sea coastal areas and/or in the Skagerrak, and known to be saithe nursery grounds (ICES, 2014b). As a result, predator-prey interactions between hake and saithe at larval and/or juvenile stage could not be completely ruled out, which might adversely affect North Sea saithe recruitment and hence explain to some extent the opposite population trends being observed.

Spatio-temporal overlap. Although at fine scale competitors must avoid each other, at large-scale competitors must be sympatric, meaning that they share an habitat and overlap in time and space (Link and Auster, 2013). The study of saithe and hake distributions showed a sympatry of these two species in the Northern North Sea and in the Skagerrak in both winter and summer (Chapter 1). In addition, the study of the joint distribution of these two species showed an increase of the spatial overlap between saithe and hake in both seasons over the last 20 years.

Saithe distribution, constrained by depth, limited its expansion, while hake distribution, positively correlated with temperature, expanded in southern areas. These patterns and relation with abiotic environment may suggest that under global warming pressure (GIEC, 2014), both hake abundance and the spatial overlap between saithe and hake could increase in future years. In a context of competitive interactions, this spatial overlap increase, combined with an increase of temperature may potentially lead to a reduction of habitat suitability for saithe (Rutterford *et al.*, 2015) and exacerbate adverse consequences for saithe sustainability.

The results obtained concerning large-scale spatio-temporal overlap of saithe and hake distribution in the North Sea may validate the 2nd requirement of the competition theory. However, the current assumption about saithe and hake nursery grounds, located along the Norwegian coast and in the Celtic Seas, respectively, could also bring some support to the coexistence theory. Indeed, Miller (1967) advocates that allopatric larval distributions, even in case of sympatric distributions of other stages, may prevent competitive interactions. In this context, further investigation needs to be carried out, particularly concerning hake larval ecology. For instance, larval community composition and ecology in the Norwegian coast of the North Sea and the Skagerrak, considered as gadoids "universal" nursery ground for the North Sea (Munk *et al.*, 1999; Werner, 2015), needs to be further studied, particularly regarding the presence or absence oh hake larvae in this area. A first step in learning on larval ecology could be the identification of non-commercial larvae species using Methot Isaac Kidd like net (MIK) within International Bottom Trawl Survey (IBTS), which would be of great interest to study potential hake larvae drift in the North Sea.

Dietary overlap. Once common use of the space has been established through the study of spatio-temporal overlap, food resource similarities need to be evidenced to assume trophic competition (Ross, 1986; Link and Auster, 2013).

The study of saithe and hake seasonal diet showed food resource partition by predator length, while specific diet was generally similar and highly overlapping for individuals larger than 50 cm (Chapter 2). Trophic competition between saithe and hake larger than 50 cm was mainly driven by Norway pout (*Trisopterus esmarkii*) in winter, and silvery lightfish (*Maurolicus muelleri*) and silvery pout (*Gadiculus argenteus*) in summer, while main preys shared between smaller individuals were euphausiids in winter, and Norway pout in summer.

The high amount of fish that could not be identified, particularly in hake diet, may bias our results by underestimating the importance of specific fish prey group. This bias might increase or reduce dietary overlap with saithe. In addition, the correlation between stomach content and prey abundance, which were not investigated, might reveal selective, or at contrary, opportunistic feeding. When feeding is opportunistic, changing biotic communities (Beaugrand, 2004) may lead to different saithe and hake feeding habits which may moderate or exacerbate dietary overlap between the two species.

The results obtained concerning dietary overlap of saithe and hake in the Northern North Sea may validate the 3rd requirement of the competition theory. However, there are some knowledge gaps in feeding ecology of these two predators that need to be investigated to confirm trophic competition between saithe and hake in their sympatric distribution area. For instance, diel differences in feeding activity (Carpentieri *et al.*, 2005) or prey size selectivity (Johnson *et al.*, 2012) were shown in demersal communities of the Mediterranean Sea. Such differences may favour food resource repartition between species and considerably reduce apparent trophic competition (Jones, 1978).

Resource limitation. Resource limitation is essential to assume competitive interactions. If resources were unlimited, even a complete overlap of distribution and diet between saithe and hake would have no effect on any of these two species, which would then coexist (Jones, 1978). At a large geographical scale, such as that considered in this study, this 4th requirement is, however, the most difficult to check and necessitates the use of indirect methods (Link and Auster, 2013). In this study, we studied the environmental factors impacting North Sea saithe growth, which revealed the effects of density-dependence and food availability, while temperature effect was not found significant (Chapter 3).

Density-dependence was the most driving environmental factors, the effects of which were augmented when food availability was reduced. An increase of saithe abundance was thus followed by a slowing-down of saithe growth in the next year. Combined with a decrease of Norway pout biomass, saithe growth was even slower. The dominance of density-dependent effects might suggest that intraspecific competition exerted more control on saithe growth than interspecific competition. Another explanation could be that Norway pout was not the only important prey for saithe. This assumption was confirmed by the saithe diet study (Chapter 2), which highlighted the importance of other preys such as silvery lightfish and euphausiids.

These results may validate the 4th requirement of the competition theory between saithe and hake in the North Sea, highlighting some limiting effect of Norway pout biomass. However, the lack of significant effects of temperature in our study appears questionable and should be further investigated, as could be the potential effects of other abiotic factors. The study of biotic-abiotic interacting effects may reveal different short-term responses of saithe growth and also need to be investigated. In addition, the study of medium-term effects brought about by current fishing pressure reduction, could allow to clarify the impact of competitive interactions on saithe sustainability.

So, what is the nature of saithe and hake ecological interactions in the North Sea? This step-by-step investigation of saithe and hake in the North Sea suggests competitive interactions between these two predators in the area. However, further investigations need to be carried out to confirm this assumption. Indeed, gaps in knowledge about hake ecology in the area but also about key forage species ecology *e.g.* silvery lightfish and euphausiids, limited our interpretations and need to be filled to definitely validate the competition theory.

The Others

Since the implementation of the Ecosystem Approach to Fisheries (EAF) (FAO, 2003), a large number of relevant tools have been developed to model species interactions, and take them into account in fisheries advice and management (Plaganyi, 2007). These models range from complex and holistic ecosystem models to Minimum Realistic Models (MRM) which, in a context of multispecies stock assessment, should be preferred because of their flexibility and their better ability to fit to observations. MRM, such as MultiSpecies Virtual Population Analysis (MSVPA) (Helgason and Gislason, 1979; Pope, 1979), generally tend to focus on commercial species interactions. Species of little economic importance, or for which information is too limited, are generally not assessed and/or pooled together in "Other" groups. This trade-off in complexity may impair the performances of stock assessments and forecasts. This is particularly true when these "other" species interact with those explicitly built in the model.

Other predator. In 2011, the Stochastic MultiSpecies (SMS) model (Lewy and Vinther, 2004), which is the model currently in use to conduct multispecies stock assessment and forecast in the North Sea area, included 14 "other predators", of which three were fishes, *i.e.* grey gurnard (*Eutrigla gurnardus*), mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*) (ICES, 2011). Their inclusion in SMS allowed the estimation of predation mortality for commercially important prey stocks (top-down effects, predator control exerted upon preys).

In this context, the recent emergence of hake in the North Sea led to its inclusion as an "other predator" in the SMS model (ICES, 2014a). However, due to large gaps in knowledge about hake ecology in the North Sea, important assumptions have been made, particularly concerning hake abundance and consumption rates (ICES, 2014a). The inclusion of hake in the North Sea SMS model, has been achieved within this PhD (see more details in Appendix A). Based upon the assumption of competitive interactions between saithe and hake in the North Sea, as previously discussed, the inclusion of hake in the North Sea SMS and the implementation of bottom-up effects (control of predator exerted by preys) allowed assessing both the direct effects (on preys *e.g.* Norway pout) and indirect effects (on another predator, here saithe) of hake emergence in the North Sea. In addition, saithe F_{MSY} was evaluated in a multispecies context and contrasted with traditional single-species target. Hake abundance increase scenarios were investigated, which revealed potential negative effects on both Norway pout and saithe stocks, while multispecies saithe F_{MSY} was consistent with single-species estimates (Chapter 4).

These potential negative impacts of hake on saithe may inflate the potential economic impacts for the North Sea demersal fisheries (Baudron and Fernandes, 2014). In particular, even if increasing hake abundance generally did not change F_{MSY} estiamtes, it resulted in a decreased Maximum Sustainable Yield (MSY), dut to the reduction in saithe biomass. These results highlight the ecological and economic importance of hake as an up-coming predator in the North Sea. Consequently, hake abundance in the North Sea needs to be further monitored, so to elaborate more realistic hake emergence scenarios, and to better forecast ecological and economic impacts in the area, particularly in a context of global warming. This is particularly important in the context of the newly implemented EU landing obligation as the restrictive hake Total Allowable Catch (TAC) in the North Sea will likely impact the exploitation pattern of demersal fisheries in the area. In addition, the current assumption of a single northern hake stock, needs to be verified to ensure that hake do not have their own population dynamics in the North Sea. For instance, the study of hake larval ecology, genetics and/or otolith shape may provide helpful insights in support of fisheries advisers and decision-makers.

The study of hake emergence potential impacts in the North Sea focused on the three species, saithe, hake and Norway pout (Chapter 4). However, the relationships between hake and Norway pout were investigated only in one way. Indeed, the relationships between Norway pout biomass and hake growth were not built-in in our model. European hake growth has been debated for decades and the otolith-based age estimation traditionally applied by the International Council for the Exploration of the Sea (ICES) community was countered by tagging experiments in the Bay of Biscay, revealing a hake growth in the area twice as fast as previously assumed (de Pontual *et al.*, 2006). However, correlation with potentially limiting environmental factors were never investigated.

Other food. The SMS model aims at assessing fish stocks of commercial interest taking into account species interactions and particularly predator-prey interactions. Fish preys of little commercial importance are pooled in an "other food" group. While this simplication has merits when focusing only on the top-down control exerted on commercially important fish prey stocks (*e.g.* Norway pout), it does not provide a realistic framework to assess top-predator fish stocks (*e.g.* saithe) when bottom-up control and competitive interactions are made explicit. Two directions of control are involved in exploitative competition (top-down and bottom-up, Figure 1), which are not necessarily exerted on/by prey species of commercial interest. In this context, pooling preys of ecological importance, though of low economic value (*e.g.* euphausiids), in the "other food" group hinders the assessment of the direct impact exerted by competing predators on these preys, and hence of indirect competitive interactions effects.

The key role of Norway pout in the North Sea has repetitively been evidenced throughout this dissertation: as a driver for saithe and hake spatial overlap (Chapter 1), as a shared prey of major importance for both predators (Chapter 2) and as potentially limiting factor of saithe growth (Chapter 3). Finally, these processes were built in SMS, allowing to get further insights into the effect of Norway pout dynamics, on the assessment and projection of the North Sea saithe stock (Chapter 4).

The results obtained in this dissertation also suggest that other processes than Norway pout predation may affect the dynamics of the competition between saithe and hake, including abiotic factors (Chapter 1), density-dependence (Chapter 3), and the availability of other food sources (Chapter 2). Particularly, euphausiids and silvery lightfish were highlighted as important preys for both saithe and hake in the North Sea (Chapter 2). The saithe diet study revealed a specialisation, *sensu* Costello (1990), of this predator on euphausiids which might be interpreted as a way to escape competition with hake (Miller, 1967; Jones, 1978), thus reducing potential negative effects of hake emergence. However, a decrease of euphausiids in the North Sea (Beaugrand *et al.*, 2003), combined with an increased competition with emerging hake in the area (Baudron and

Fernandes, 2014) may exacerbate negative impacts on saithe stock.

In addition, euphausiids have high energetic content (Mauchline and Fisher, 1969), and may potentially affect saithe growth. In the Scotian Shelf, Carruthers *et al.* (2005) showed that saithe condition factor was positively correlated with euphausiids abundance. Hence, euphausiids abundance reduction led to a reduction of saithe feeding activity as saithe did not compensate the lack of euphausiids with other food sources. Such observations in the North Sea could make the competition with hake even more adverse for saithe sustainability. This situation reinforces the need of further studying euphausiids ecology in the area, in relation to the sustainable exploitation of saithe stock.

Similarly, knowledge about silvery lightfish ecology, an important deep-sea forage fish for both saithe and hake is very scarce. This forage species might have a key role in the area, due to its high energy content (Pedersen and Hislop, 2001), and needs to be further investigated. For instance, when studying saithe spatial distribution (Chapter 1), we initially assumed that the lack of Norway pout presence effects in summer revealed a switch from Norway pout to euphausiids feeding. However, gut content analysis (Chapter 2) revealed that the diet switch could also be from Norway pout to silvery lightfish feeding. With available data on silvery lightfish, we could include this prey in our models to confirm (or not) its importance and increase the representation of biotic interactions involved in habitat suitability.

So, what are the effects of saithe and hake ecological interactions in the North Sea on saithe stock? This investigation revealed potential negative effects of hake emergence in the North Sea on the resident saithe stock. Thus, hake emergence might explain, at least partially, the recent decline of saithe stock even if processes related to preys of little economic importance need to be investigated to confirm our findings.

Finally...

> Alles hat ein Ende,
> nur die Wurst hat zwei.
>
> German saying

Here, we showed how the emergence of the top-predator hake in the North Sea may affect this exploited ecosystem, with a particular focus upon saithe, a commercial top-predator of the area. The results obtained highlight the importance of hake as an up-coming predator and competitor in the area, and provide the necessary basis for further investigations of hake potential ecological and economic function in this exploited ecosystem. In the context of landing obligations, an increase abundance of hake may have economical consequences for the North Sea demersal fisheries (Baudron *et al.*, 2011) leading to changes in North Sea demersal fishery fleet behaviour, with fleets modifying their fishing effort distribution to reduce hake by-catches (Marchal *et al.*, 2013). In a context of global warming, these changes might have unforeseen knock-off effects on this exploited ecosystem, which need to be investigated.

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Appendix A

Inclusion of hake in SMS model

Vinther, M., Cormon, X., and Kempf, A. 2014. Annex 5: North Sea SMS model key run, 6. Adding hake as a predator. Report of the Working Group on Multispecies Assessment Methods (WGSAM). CM 2014/SSGSUE:11, ICES

Abstract

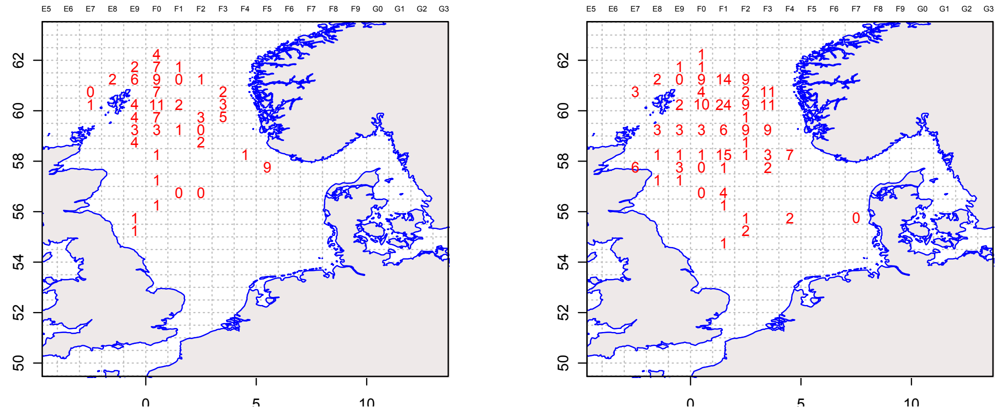
The age-structured SMS model is used for the Baltic and the North Sea area by Working Group on multiSpecies Assessment Methods (WGSAM) in order to provide multispecies advices. The North Sea SMS key-run includes and validates updates of input data and potential modifications of the model structures every three years. The last key-run was produced in October 2014 and included several modifications, revisions and updates including the addition of hake as an external predator in the model. This implementation required estimations of hake diet, abundance and consumption rates which are presented in this appendix. Its implementation allowed to assess hake role in the North Sea ecosystem and its potential impact on North Sea commercial fish stock and revealed an increasing predation pressure on Norway pout and to a smaller extent herring (*Clupea harengus*) following the increase of hake abundance in the North Sea over the most recent years (2003-2012).

Keywords: SMS key-run; external predator; hake; North Sea

A.1 Diet information

A.1.1 Sampling

Hake (*Merluccius merluccius*) diet composition was studied based on stomach content data. 300 samples were collected in winter and summer 2013 by research vessels within the EU-funded project MARE/2012/02 "Study on stomach content of fish to support the assessment of good environmental status of marine food webs and the prediction of MSY after stock restoration" and by commercial fishing vessels from EURONOR within this PhD (Chapter 2). Samples collection was realised in the Northern North Sea, above 54° of latitude, between Western Norwegian coast and Shetland Islands (Figure A.1).



(a) Winter, 109 individuals

(b) Summer, 201 individuals

Figure A.1 – Spatial distribution of hake full stomachs per season used for estimation of hake diet composition. In red, counts per ICES statistical rectangle.

A.1.2 Diet composition

Prey identification was realised at the smallest taxonomic level possible. Preys were first pooled in 13 prey categories, *i.e.* whiting (*Merlangius merlangus*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), sprat (*Sprattus sprattus*), northern and southern sandeel (*Ammodytes sp.*), Norway pout (*Trisopterus esmarkii*), poor cod (*Trisopterus minutus*), *Trisopterus sp.*, unidentified gadoids, unidentified fish and other food. Predators and prey categories were sorted by length class. Seasonal hake average weight stomach contents were calculated for each hake length classes in three steps similarly than during the "year of the stomach" in 1991 (ICES, 1997a).

1. Hake size class average weight stomach contents per haul (W_{S_h}) were calculated following Equation A.1

   $$W_{S_H} = \frac{W_{tot}}{N_F} \times \frac{N_F + N_{SR} + N_R}{N} \tag{A.1}$$

   where W_{tot} is the weight of prey in all stomach sampled in the size class; N, the sample size (number of stomach in size class); N_F, the number of full stomachs, N_{SR}, the number of stomachs containing only skeletal remains, and N_R the number of regurgitated stomachs.

2. Hake size class average weight stomach contents per International Council for the Exploration of the Sea (ICES) statistical rectangle (W_{S_R}) as average of W_{S_H} weighted by numbers of hauls in each statistical rectangle.

3. Hake size class average weight stomach contents for the whole area (W_{S_F}) were calculated as average of W_{S_R} weighted by the catch rates of each statistical rectangle or Catch Per Unit Effort (CPUE).

Poor cod, unidentified gadoids and unidentified fish average weight (W_{S_F}) needed to be reallocated as not included in Stochastic MultiSpecies (SMS). To reallocate these contents proportionally to taxonomic groups consumed by each seasonal hake length class, 4 large categories were created:

- *Trisopterus spp.*, including Norway pout and poor cod;
- gadoids, including Norway pout, poor cod, cod, whiting, haddock and other gadoids;
- clupeids, including herring and sprat;
- non identified fishes, including all fish species, other gadoids and other food.

After the averaging and reallocation, we obtained, for each hake length class and season, 8 W_{S_F} for each prey included in SMS *i.e.* whiting, cod, haddock, herring, sprat, northern and southern sandeel, Norway pout and other food. Prey of unknown length were reallocated proportionally to prey length class distribution of hake length class group contents before length class were transformed in age class based on Age-Length Keys (ALK) data. All W_{S_F} were transformed into relative values within seasonal hake length groups.

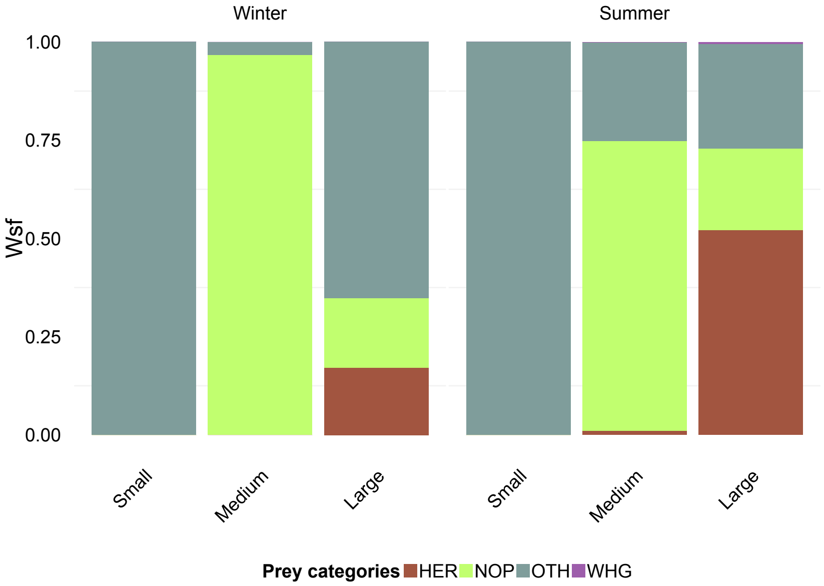


Figure A.2 – Seasonal relative stomach contents of hake length class. HER: herring. Small: < 25 cm. Medium: ≥ 25 cm and < 60 cm. Large: > 60 cm. NOP: Norway pout. WHG: whiting. OTH: other food.

A.1.3 Predator groups

The relative composition of hake diet, which was studied per season and length groups, revealed that 3 length classes were sufficient to differentiate hake diet. Indeed, individuals smaller than 25 cm only fed upon other food category while individuals larger than 60 cm fed on other food, Norway pout, herring and anecdotally whiting. The medium-size individuals (25 cm-60 cm) fed on Norway pout and other food. Therefore, the seasonal relative average weight contents were recalculated for this 3 hake length class (Figure A.2) following protocol described above (section A.1.2).

A.2 Abundance estimation

Estimation of hake abundance in the North Sea was necessary as stock assessment provides an estimation for the whole stock from which the North Sea is only a component (ICES, 2013a). Three scientific surveys covered the main area of distribution of northern hake: International Bottom Trawl Survey (IBTS), for the North Sea, the English Channel and the Skagerrak, SWC-IBTS for the West Scotland; and EVOHE for the Bay of Biscay and the Celtic Sea. These surveys covered the 1997-2013 period only during the second half of the year, thus estimations were first realised for the second semester of this period.

Hake CPUE were extracted from ICES online DAtabase of TRAwling Survey (DATRAS) and proportions of the North Sea catch rate, compared to the total area catch rate summed over all areas, were calculated for the 1997-2013 period. Based upon the number of ICES statistical rectangles in each area and the CPUE in numbers, it appeared that only 10% – 15% of hake in numbers were caught in the North Sea, while the proportion in biomass was much larger. The biomass proportions were then applied to stock assessment biomass estimations to obtain an estimation of hake biomass in the North Sea during the second half of the year. This *rough-and-ready* estimation technique was recently used for haddock in the North Sea (ICES, 2014b). First semester abundances were estimated according to the proportions found between winter and summer catch of the North Sea IBTS.

Abundance estimations from 1978 to 1996 period, for which stock assessment was available but no survey catch rates, assumed that proportions of the North Sea abundance were equal to the average of the period before hake North Sea catches increased (1997-2001). Before 1978, no stock assessment was available, hence we fixed abundance to 1978 values. Based on diet composition results abundance was estimated for 3 length groups following length distribution found in the North Sea IBTS. Final estimations are presented in Figure A.3.

A.3 Consumption rates

The lack of available information regarding hake consumption rates in the North Sea and the inconsistency of information available in other areas (Table A.1) led to using consumption rates per year and body weight based upon SMS input data for saithe (*Pollachius virens*).

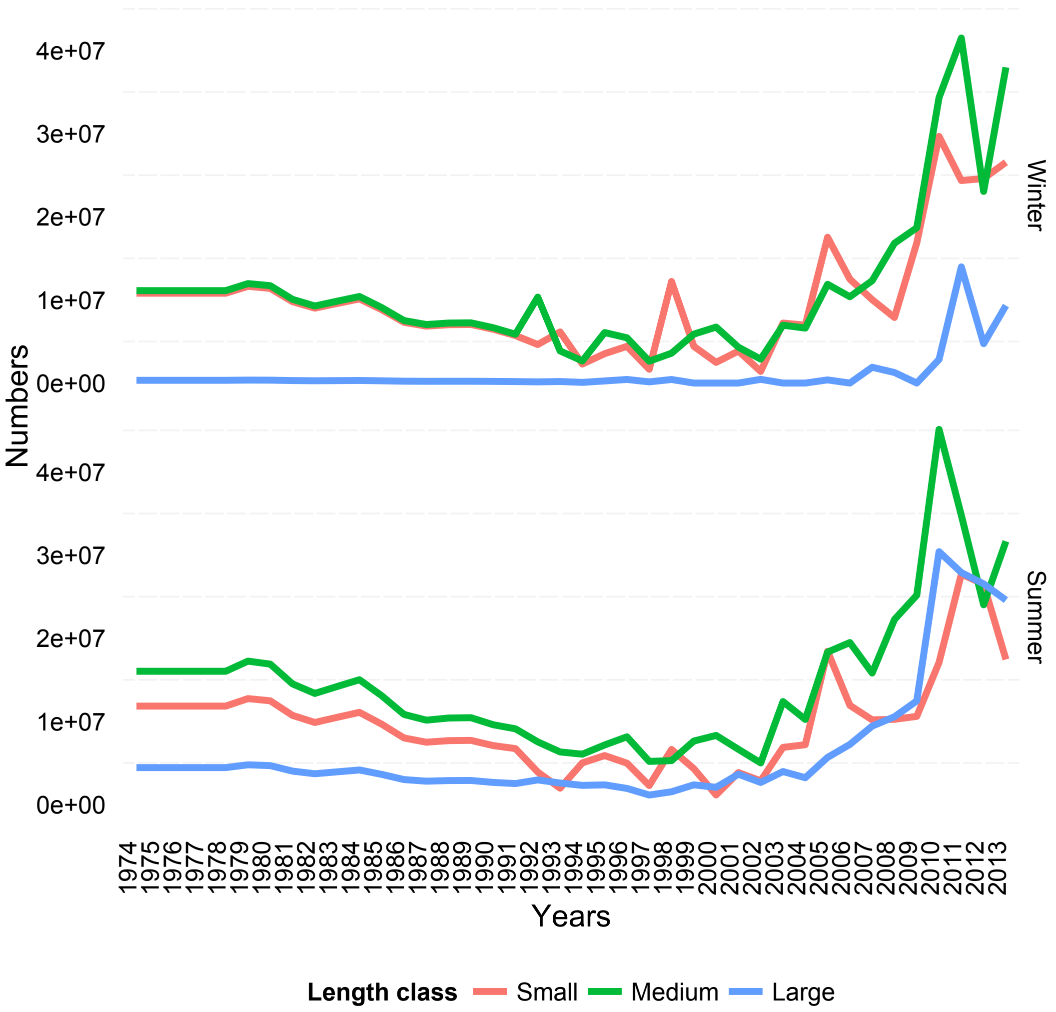


Figure A.3 – Seasonal hake length class abundance in the North Sea estimated for the 1974-2013 period.

Table A.1 – Consumption rates in year^{-1} body weight^{-1}. Small: < 25 cm. Medium: ≥ 25 cm and < 60 cm. Large: > 60 cm. Average weight (kg) of North Sea hake included in SMS between brackets.

	Small (0.0373)	Medium (0.53)	Large (2.2)	
Saithe				
North Sea	7.55	6.97	5.82	SMS input data
Northern hake				
Bay of Biscay	29.20	6.95	3.22	Cervino, pers. comm.
Celtic Sea	38.35	21.96	16.29	DuBuit (1996)
Pacific hake				
South Africa		9.1		Punt and Leslie (1995)
			4.4	Punt and Leslie (1983)

It will be okay at the end.
If it is not okay, it is not the end.

Anonymous

Afterwords and acknowledgements

It all began in July 2012. A this time, I lived in the Netherlands and had quit my alimentary job in a navigation device company for almost six months already. With my MSc in ecology I was researching a job in sciences or even better, my Graal, a PhD. This reseach revealed itself very frustrating and almost depressing. I really thought it will never happen. When I received an answer (which was not always the case!), my profile was always interesting but someone else had more experience in this particular field. Being honest, I might have been to selective in the PhD offers I applied for, thinking: "Who am I to discuss a proposal already written and funded?".

The PhD: Spatial dynamics of saithe in Skagerrak, North Sea and west of Scotland and of targeting fleets - Impact on the stock assessment. There entered Katell Hamon, she called me to tell me she just sent me an URGENT PhD offer, she knew the people who offered it and that, if I was interested, I should just call them to make a first contact. After reading the proposal, I was doubtful, PhD dealt with fisheries, modelling and stock assessment, only first axis was a bit ecological with habitat modelling. My MSc thesis, realised at IMARES building an eco-genetic model for plaice in the North Sea under Jan Jaap Poos supervision, did qualified me. But did I really wanted it? Even when my MSc thesis was a very great experience, it also taught me that doing *hard-core* modelling all my life was not my thing. I liked laboratory and field work, even if I was quite talented for programming. I was an ecologist.

Thanks to Katell I did call, and reached Youen Vermard, the main supervisor Paul Marchal was not there at the moment. I asked for the deadline, it was in May (we were mid-July!). I could send my application until Friday as they (Paul and Youen) will take a decision the next week. Four days. Four days to apply. Four days to decide to apply. After two days I did. Everything went very fast. Sent the application, they contacted Jan Jaap and Katell as referent and the next Monday I received an email inviting for a Skype interview the day after. Two hours after the interview was finished I received this most-wanted email, the one who says "Yes". I will leave the Netherlands, even if it was not ecology but fishery sciences, I was happy to go back to what I liked, scientific research.

From fishery sciences to marine ecology. Few weeks after my PhD started, Paul and Youen approached me with an idea. It appeared that French fishery targeting saithe, EURONOR, had problems with another species: hake. In this context, they asked me if I would be interested in studying hake diet based on stomach content. Of course, I said yes. 2013 started and I was putting up a sampling protocol in collaboration with EURONOR and IBTS to retrieve hake and saithe samples. I took very seriously the problematic of hake. I first included hake in my research about saithe habitat before trying to model hake habitat as well. After six months the PhD was not about saithe only anymore but about hake as well. And few month more I read it. The spark. Jason Link paper about competition in large marine ecosystems. Then it was on. A year after I began, my PhD was not anymore about fishery fleets and dynamics but about competition between two fish species. I came back to ecology thanks to fishery.

From France to Germany. At this point, I really took my research under control. I begin to have my own ideas about what I wanted to do and how I wanted to do it and I was lucky enough to be trusted by my supervisors. Laboratory work had begun, I had presented my work for the 1st time to the international scientist community at the gadoid symposium in Canada and I was writing my first paper when the project of the exchange in Germany began to take importance. Alexander Kempf had accepted to supervise me at the Thünen Institute in Hamburg, and after I wrote the proposal and obtained fundings, starting date was set to July 2014. Preparation was very stressful, room hunting was particularly difficult and frustrating. But it worked. I spent there six months. I was far from my friends and colleagues. I found love. I worked a lot. I partied a lot too. I wrote one paper. I went to the ICES conference. I learned German. I went to teach a statistic class in Dakar. I expanded my network and gain experience and skill working with Alex, who was a great supervisor.

To this. The third year of this PhD went so fast I have rough times realising it is over. In between, a two weeks round-trip to Denmark to work with Morten Vinther, the writing of the second paper, the PhD defense of two of my best friends, the conference about climate change impacts in Brazil, the writing of the third paper, the statistical analysis of diet data (finally done!), my engagement and the writing of this dissertation, I believe the year was full. I am now on the verge of getting what I worked for during three years but I am also sad it is finished. Anyway, I can now answer to my initial question "Who am I to discuss a proposal already written and funded?". I am an ecologist soon to be doctor.

Acknowledgements

I am particularly grateful to Katell and Jan Jaap without whom I am quite sure I might not have even applied to this PhD. Thank you both for your friendship and support. Thank you for believing in me.

Paul, Youen, thank you for your trust at first but also all along. I know this PhD is far from your first expectation and I hope you are not too disappointed that you still have some work on saithe fishery fleets dynamics to do. Thank you for letting me do it my way. Thanks to you I could blossom in what I did. I know I would not have done as good other way.

Alex, thank you for welcoming me at the Thünen Institute, for taking the time to work with me, but also for your sympathy and kindness. I can tell you now, I was very impressed by your ability to spot errors in huge tables. How do you do it? I hope you never forget my fish is better than your fish.

I also would like to thank all my co-authors: Morten for welcoming me at DTU Aqua and, despite a very busy schedule, for taking a lot of time to work on my project. Without you Morten I would have never been able to get the modified SMS run so fast. Bruno, thank you for taking the time to discuss with me and for enlightening me about dark statistics. Sandrine and Christophe, for your help with habitat modelling and spatial correlation. Pierre and Jérémy, thank you for your help with the diet study. I want to thank particularly Manuel and Khalef, for their incredible work in the laboratory.

Thank you to all the people who helped and/or made this research possible: Bruno Leduc from EURONOR, Jennifer Devine from IMR, Anne Sell from TI-SF, all the scientific staff and crew on board of *Cap Nord, Klondyke, G.O. Sars, Walter Herwig III*, Morgane Ramonet et Peter Samson from FFP. Also a big thank you to Denis Bitouzé who taught me LaTeX. Finally, I would like to thank the IFREMER and France Filière Pêche without which this PhD could not have been conducted.

Plus personnellement, je tiens à remercier tous mes amis, ceux qui ont été là du début à la fin, comme ceux qui n'ont été que de passages.

En particulier, un grand merci à Sylvanus, mon premier ami à Boulogne-sur-Mer sans qui les premiers mois ici auraient été bien moroses. Merci à Martinou, mon coloc pour toujours, le meilleur qu'il soit, merci pour toutes les soirées à la maison, pour les conversations de geek, pour ton humour, ton esprit et pour ton soutien dans les moments difficiles (la liste!). Merci à France, ma BFFFF! Merci d'avoir été là pour moi lorsque j'étais en Allemagne, pour les Skypes, les

conseils, et le soutien. Merci copine! Merci Raph pour ton amitié. Nous nous sommes éloignés mais je n'oublies pas les grands moments passés ensemble! Merci Tanguy pour le soutien que tu m'as apporté. Merci Maud, Rudy, Aurore et Mathias, pour votre amitié sincère, votre bonne humeur et votre folie.

Ensuite j'aimerais remercier tous les collègues de l'IFREMER, du TI-SF et de DTU qui m'ont permise où que je sois d'aller au bureau de bonne humeur. En particulier, merci Elo pour les gateaux, Mathilde pour ton efficacité, Manu pour les barres de rire au labo, Khalef pour ta gentillesse et Elvire pour venir me sauver lorsque je m'enferme dehors. Merci à tous mes potes de galère thésards, Jérémy, Henrike, Cyrielle, Bachar, Khaled, Olmo et Pierre vous y êtes bientôt! Une pensée particulière pour Tiphaine et Astrid du même cru que moi! Courage les filles!

Il me reste maintenant à dire un grand merci à toute l'équipe du beach apero volley dont Eric restera le leader incontesté à mes yeux, tous les out'grimpeurs, et tous les potes de Boubou sans oublier le personnel du RU qui m'a nourrie presque tous les midis! Je suis sûre d'avoir oublier plein de monde mais merci à tous!

Je voudrais finalement remercier ma famille qui m'a toujours soutenue dans mes choix. Merci Mam's! Tu avais raison, je suis faite pour ça! Merci Papinou! J'espère que tu es fier de moi et que tu sais enfin que je travaille sur les poissons (enfin si je change pas)! Soeurette, je te souhaite de trouver ta voie et j'ai confiance car tu es brillante. Je vous aime tous les trois très fort et je sais que c'est réciproque. Merci pour votre amour et soutien.

Enfin, merci à Florian. Merci pour ton soutien et ton amour dans les moments les plus difficiles. Merci pour avoir été à mes côtés et m'avoir supportée lors de ces derniers mois (au sens propre comme au figuré). Je ne sais pas ce que j'aurai fait sans toi. L'aventure a commencée par bien des obstacles, nous les avons passés, elle ne peut donc que continuer. J'ai hâte. Je t'aime.

Xochitl Cormon

Synthèse

Introduction

La population de lieu noir (*Pollachius virens*) de mer du Nord a une importance économique élevée pour les pêcheries européennes. Depuis une dizaine d'années, l'abondance du lieu noir a décliné, alors que le merlu (*Merluccius merluccius*), soumis à des quotas de pêche très restrictifs dans cette zone, a vu son abondance fortement augmenter. Le récent déclin du stock du lieu noir de mer du Nord, aussi bien en terme de biomasse, croissance et poids-aux-âges, les trajectoires opposées des populations du lieu noir et du merlu en Mer du Nord, et le manque de connaissances récentes sur l'écologie régionale de ces deux espèces, ont dans une très large mesure motivé ce travail de thèse.

Ce travail cherche à comprendre la nature des interactions écologiques entre le lieu noir et le merlu en Mer du Nord afin de comprendre si la récente émergence du merlu dans cette zone pourrait expliquer, au moins en partie, le récent déclin du stock de lieu noir. L'hypothèse de la compétition entre ces deux top-prédateurs a été vérifiée en trois points: (i) chevauchement spatio-temporel de la distribution géographique du lieu noir et du merlu; (ii) chevauchement trophique des ces deux espèces; et (iii) limitation de la ressource, condition essentielle aux interactions compétitives. Enfin, les conséquences d'une persistance future de l'augmentation du merlu en mer du Nord sur le stock de lieu noir ont été étudiées dans un dernier volet.

Interactions spatiales entre le lieu noir et le merlu en Mer du Nord

Les interactions spatiales entre le lieu noir et le merlu de Mer du Nord ont été étudiées en relation avec leur environnement. Nous avons pour cela utilisé des modèles linéaires généralisés intégrant les autocorrélations spatiales, que j'ai appliqués aux données saisonnières de présence/absence de lieu noir et merlu, récoltées lors de campagnes scientifiques, de 1991 à 2012. Les variables explicatives intégrées dans ces modèles incluent l'environnement abiotique (température, profondeur, type de substrat), ainsi que l'environnement biotique (présence/absence de proies et de compétiteurs potentiels). Un effet positif de la température sur la probabilité de présence du merlu a été mis en évidence, quelle que soit la saison, alors que la présence de lieu noir était majoritairement contrainte par la profondeur. La probabilité de chevauchement spatial entre ces deux espèces, est corrélée positivement avec la présence de tacaud norvégien (*Trisopterus emarkii*), ce qui a permis de souligner l'importance de cette proie pour les deux prédateurs, aussi bien en hiver qu'en été. Les changements de distribution du lieu noir, du merlu et du chevauchement spatial entre ces deux espèces, ont été étudiés par la comparaison saisonnière des probabilités de présence (spécifiques et conjointes) prédites en début (1991-1996) et en fin (2007-2012) de période. Les résultats ont montré une augmentation des probabilités de présence du merlu, liée à l'augmentation de la température, ainsi qu'une augmentation de la probabilité de présence conjointe des deux espèces, et ce quelle que soit la saison. Ces augmentations sont accompagnées d'une légère expansion des distributions en direction du sud-ouest et des côtes écossaises. L'augmentation des probabilités de présence conjointe du lieu noir et du merlu, en été comme en hiver, confirment une augmentation du chevauchement spatio-temporel de ces deux espèces et valident la première condition d'hypothèse de compétition.

Compétition trophique entre lieu noir et merlu en Mer du Nord

Les régimes alimentaires du lieu noir et du merlu de mer du Nord ont été étudiés par le biais de l'analyse de contenus digestifs, collectés en hiver et en été 2013 lors de campagnes scientifiques, mais également au cours d'opérations de pêche commerciales dans la partie septentrionale de la mer du Nord. Le régime alimentaire du lieu noir et du merlu semble plus dépendre de la saison et de la taille de ces prédateurs plutôt que de leur espèce. Dans ce contexte, un indice alimentaire combinant présence et abondance des différentes proies, sélectionné sur des bases écologiques et statistiques, a été utilisé afin de déterminer l'importance des proies pour chaque groupe de prédateurs. Cet indice a été utilisé pour quantifier le chevauchement trophique du lieu noir et du merlu de mer du Nord, en hiver comme en été. Les prédateurs ont préalablement été séparés en deux groupes de taille (plus ou moins 50 centimètres). De manière générale, le merlu s'est révélé hautement piscivore alors que le régime alimentaire du lieu noir s'est révélé plus divers. Toutefois, la compétition trophique était très importante entre les individus de plus de 50 centimètres, portant principalement sur le tacaud norvégien en hiver et sur le brossé améthyste (*Maurolicus muelleri*) en été. Les plus petits poissons, quant à eux, ont montré de fortes similarités alimentaires, même si le chevauchement trophique, plus faible, n'était pas significatif en été. Ces résultats concernant la répartition de la ressource et le chevauchement trophique du lieu noir et du merlu de mer du Nord, valident la deuxième condition de la théorie de la compétition, et nous ont amenés à nous poser la question de la limitation de la ressource.

Étude de la croissance du lieu noir en relation avec son environnement

La limitation de la ressource, très difficile à démontrer directement à une grande échelle, a été étudiée par une méthode indirecte visant à comprendre les relations entre la croissance du lieu noir de mer du Nord et son environnement. Pour ce faire, la croissance du lieu noir a été étudiée sur la base des différences de poids moyens aux âges d'une année à l'autre (1987-2012) et des données âge-longueur collectées lors des campagnes scientifiques (1991-2012). Les relations âge-longueur ont été modélisées à l'aide de trois modèles différents: un modèle linéaire simple, le modèle de von Bertalanffy, classiquement utilisé en écologie marine et un modèle de croissance logistique. Le modèle logistique a globalement permis d'obtenir le meilleur ajustement aux données de la croissance du lieu noir, ainsi que des paramètres écologiquement vraisemblables. Dans un deuxième temps, les effets de l'environnement sur la croissance du lieu noir de mer du Nord ont été étudiés, à l'aide de variables explicatives environnementales, *i.e.* température, abondance de lieu noir (pour les effets de densité-dépendance), et biomasse de tacaud norvégien (pour les effets relatifs à la disponibilité des proies). Des effets de densité-dépendance et de disponibilité des proies sur la croissance du lieu noir ont été montrés alors que la température n'a eu aucun effet significatif. Ces résultats nous permettent de valider l'hypothèse de compétition entre le lieu noir et le merlu puisqu'il a été montré que la diminution de tacaud norvégien avait un impact négatif sur la croissance du lieu noir, ce qu'il est raisonnable de considérer comme un effet limitant.

Impact de l'émergence du merlu en Mer du Nord sur le stock de lieu noir

Les résultats obtenus précédemment confirment l'importance d'étudier l'impact potentiel de l'augmentation du merlu en mer du Nord sur le stock résident de lieu noir. Pour ce faire, le merlu a été inclus dans le modèle d'évaluation de stocks multi-spécifique actuellement utilisé en mer du Nord, le modèle SMS (*Stochastic MultiSpecies*). Ce modèle a également été modifié, afin de prendre en compte la corrélation entre la biomasse de tacaud norvégien et la croissance du lieu noir en mer du Nord démontrée précédemment. Les impacts directs futurs du merlu sur ses proies ont été évalués à l'aide de différents scénarios d'abondance de merlu sur une période de 50 ans. De plus, grâce à l'inclusion de la corrélation entre la biomasse de tacaud norvégien et la croissance du lieu noir, les effets indirects de l'augmentation du merlu en mùer du Nord sur le stock de lieu noir ont également pu être évalués. Cette étude a révélé un impact négatif de l'augmentation du merlu sur la biomasse de tacaud norvégien, ainsi que sur celle de lieu noir, et ce quel que soit le scénario étudié. Enfin, l'étude a été complétée par l'évaluation multi-spécifique du niveau de mortalité par pêche du lieu noir correspondant au rendement Maximum Durable (RMD) $F_{\text{RMD}} = 0.3$, ce qui a révélé une adéquation du F_{RMD} calculé sur des bases monospécifiques pour le lieu noir avec celui calculé dans un contexte multispécifique.

Conclusion

Le merlu a jusqu'à ces dernières années été une espèce peu importante, aussi bien commercialement qu'écologiquement, en mer du Nord. La récente émergence du merlu dans cette zone pourrait avoir des répercussions sur le stock de lieu noir, qui est d'une grande importance économique pour plusieurs pays européens. Les résultats obtenus lors des trois premières parties de ce travail de recherche permettent de valider l'hypothèse de compétition entre les deux espèces. Au vu des résultats obtenus dans la dernière partie de ce travail, l'émergence du merlu en mer du Nord doit être sérieusement prise en compte dans les avis scientifiques supportant les décisions de gestion encadrant la pêche du lieu noir, mais aussi des autres espèces de mer du Nord que l'émergence du merlu est susceptible d'affecter. Ce travail fournit donc les premières bases écologiques nécessaires à une investigation plus détaillée des conséquences de l'émergence du merlu dans un écosystème hautement exploité tel que la mer du Nord.

List of publications

Original Articles

Cormon, X., Kempf, A., Vermard, Y., Vinther, M., and Marchal, P. 2016. Emergence of a new predator in the North Sea: evaluation of potential trophic impacts focused on hake, saithe, and Norway pout. ICES Journal of Marine Science, 73: 1357-1369.

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Payne, M. R., Barange, M., Cheung, W. W. L., Mackenzie, B. R., Batchelder, H. P., **Cormon, X.**, Eddy, T. D., Fernandes, J. A., Hollowed, A., Jones, M. C., Link, J. S., Neubauer, P., Ortiz, I., Queirós, A. M., and Paula, J. R. 2015. Uncertainties in projecting climate change impacts in marine ecosystems. ICES Journal of Marine Science, 73: 1272-1282.

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ICES. 2014. Annex 5: North Sea SMS model Key Run. Report of the Working Group on Multispecies Assessment Methods (WGSAM). ICES CM 2014/SSGSUE:11, London, UK.

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Cormon, X., Kempf, A., Vermard, Y., Vinther, M., and Marchal, P. 2015. Evaluation of potential trophic impacts from hake (*M. merluccius*) emergence in the North Sea. PICES 3rd International Symposium. Effects of Climate Change on the World's Oceans. 21-27 March 2015. Santos City, Brazil.

Cormon, X., Kempf, A., Vermard, Y., and Marchal, P. 2014 J:05. Evaluation of potential impacts of hake (*Merluccius merluccius*) emergence in the North Sea on saithe (*Pollachius virens*) stock growth. ICES Annual Science Conference. Sustainability in a changing ocean. 15-19 September 2014. A Coruña, Spain.

Cormon, X., Gomez, B., Rouquette, M., Vaz, S., Vermard, Y., and Marchal, P. 2013 S:10. Saithe and hake spatial interactions in the North Sea. ICES/-NAFO Symposium. Gadoid Fisheries: The ecology and Management of Rebuilding. 15-18 October 2013. St Andrews, New Brunswick, Canada.

Cormon, X., Gomez, B., Rouquette, M., Vaz, S., Vermard, Y., and Marchal, P. 2013. Interactions spatiales entre le lieu noir et le merlu en mer du Nord. Campus de la Mer. 1ères Doctoriales de la Mer. 10 October 2013. Boulogne-sur-Mer, France.

Glossary

Bottom-up Control by the resource *vs top-down*. 2, 12, 17, 35, 37, 71, 73, 87, 91, 92, 94, 95, 97, 98, 102, 105, 107–109, 118

Coexistence Interaction between individuals potentially competing, both of the same and of different species, which have no adverse effects for any individuals *vs competition*. 3, 12, 67, 113, 114

Competition Interaction between individuals, both of the same and of different species, which results in a reduction of fecundity, survivorship or growth *vs coexistence*. 2, 3, 8, 11, 12, 15, 17, 18, 34, 36, 37, 43–45, 67, 68, 70–73, 87, 91, 110, 113–116, 118, 119

Ecosystem System formed by a community of living things, their environment, and the relationships between them. 1–3, 5, 8, 16, 18, 24, 36, 44, 45, 68, 71, 72, 88, 92, 109, 110, 137

Exploitative competition Indirect competitive interaction where competitors struggle for a common resource. 2, 12, 118

Interspecific interactions Interactions between two species *vs intraspecific interactions*. 37, 113, 116, 119

Top-down Control exerted by predators on preys *vs bottom-up*. 2, 5, 12, 17, 71, 73, 92, 117, 118

Impacts of a top-predator emergence in an exploited ecosystem: North Sea hake and saithe.
Which interactions? What consequences?

Abstract

North Sea saithe (*Pollachius virens*) has high economic value for European fisheries. In recent years, North Sea saithe abundance has decreased, while abundance of hake (*Merluccius merluccius*), which was rarely fished in the North Sea, has increased dramatically in the area. This work investigate the nature of the ecological interactions between saithe and hake in the North Sea, in order to understand if recent hake emergence in this area could explain, at least partially, the recent decline of the saithe stock. The results obtained during this research suggested competitive interactions between saithe and hake predators in the area. In addition, this investigation revealed potential negative effects of hake on the resident saithe stock. Therefore, hake emergence in the North Sea must be taken into account when managing commercial fish stocks, the sustainability of which may be threatened by this up-coming predator. Finally, the results obtained within this PhD study highlight the importance of hake as an up-coming predator and competitor in the North Sea, and provide the necessary basis for further investigations of hake potential ecological and economic function in this exploited ecosystem.

Keywords: exploitative competition, saithe, hake, simple foodweb, up-coming predator, north sea

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Impacts de l'émergence d'un top-prédateur dans un ecosystème exploité : le merlu et le lieu noir de mer du Nord.
Quelles interactions ? Quelles conséquences ?

Résumé

La population de lieu noir (*Pollachius virens*) de mer du Nord a une importance économique élevée pour les pêcheries européennes. Depuis une dizaine d'années, l'abondance du lieu noir a décliné, alors que le merlu (*Merluccius merluccius*), qui était peu pêché dans cette zone, a vu son abondance fortement augmenter. Ce travail se concentre sur la nature des interactions écologiques entre le lieu noir et le merlu en Mer du Nord afin de déterminer si la récente émergence du merlu dans cette zone pourrait expliquer, au moins en partie, le récent déclin du stock de lieu noir. Les résultats obtenus lors de ce travail de recherche ont permis de valider l'hypothèse de compétition entre le lieu noir et le merlu. De plus, cette étude a révélé un impact potentiellement négatif de l'augmentation du merlu sur la biomasse de lieu noir. L'émergence du merlu en mer du Nord doit donc être sérieusement prise en compte dans les avis scientifiques supportant les décisions de gestion encadrant la pêche du lieu noir, mais aussi des autres espèces de mer du Nord que l'émergence du merlu est susceptible d'affecter. Finalement, ce travail fournit donc les premières bases écologiques nécessaires à une investigation plus détaillée des conséquences de l'émergence du merlu dans un écosystème hautement exploité tel que la mer du Nord.

Mots clés : compétition, lieu noir, merlu, simple réseau trophique, émergence d'un prédateur, mer du nord