Governing factors for the size-at-age: the influence of sex, food availability, temperature and fishery on the growth performance of North Sea whiting *Merlangius merlangus* and cod *Gadus morhua*

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CONTENTS

SUMMARY

The present thesis evaluates the temporal development of the growth performance of whiting *Merlangius merlangus* and cod *Gadus morhua* in the North Sea ecosystem during recent decades. Both representatives of the family gadidae are essential components of the North Sea demersal fish community and therefore of pronounced scientific interest. Whiting, as well as cod showed marked changes in abundance during the large-scale fluctuations in the North Sea ecosystem. Therefore, it was assessed to which extend selected factors influence the physiological ecology, population dynamics and species interactions of whiting and cod in the North Sea. The results of this thesis reveal that whiting and cod distinctively differ in their physiological ecology, life history and population dynamics. This leads to species specific implications and consequences in the assessment and management decisions concerning both stocks in the North Sea.

In the 1^{st} **chapter** "**Sex-specific food intake in whiting *Merlangius merlangus***", the magnitude and the underlying mechanisms of sexual growth dimorphism in North Sea whiting were examined. Although more than half a century ago scientific literature already described and addressed sexual dimorphism in whiting, the current stock assessment as well as most recent studies on life history (*e.g.* length-at-age), ecology (*e.g.* predatory effect) or physiology (*e.g.* gastric evacuation) of whiting do not address sex-specific differences. However, sex-specific differences in the mentioned traits could have implications for the stock assessment and management of whiting as well as for multispecies assessment in the North Sea. To address questions regarding sexual dimorphism in whiting, North Sea International Bottom Trawl Survey (NS-IBTS) data and two additional datasets from the third quarter of 2007 and the first quarter of 2012 were analysed in chapter 1. Whiting expressed marked differences in growth parameters between females and males with females growing distinctively faster. These differences in somatic growth could in principle result from three different factors: (1) dissimilarities in metabolic costs, (2) different energy allocation patterns or (3) unequal energy uptake levels between female and male fish. The energy uptake level in

turn could be influenced either by the quantity or the quality of the food ingested, or by a sex-specific difference of the energy assimilation capacity. In this chapter, the influence of those factors was evaluated. The quantity and the quality of the diet of whiting in the North Sea were investigated to compare the sex-specific energy uptake levels. While no difference was detected in the diet composition, females had significantly higher amounts of food in their stomachs compared to males of the same length. Moreover, female whiting generally had lower proportions of empty stomachs than male fish. In addition, female liver and empty stomach masses were higher in comparison with the traits of same sized males. This indicates additional sex-specific differences in the metabolic costs and energy allocation patterns.

The **2nd chapter** “**Forage fish controlling population dynamics of North Sea whiting—evidence from field data and bioenergetics modelling”** evaluates the influence of forage fish abundance on whiting. Since the 1960s the North Sea ecosystem has experienced large-scale ecological fluctuations. At the beginning of the 21st century, several forage fish stocks (herring, sprat, sandeel and Norway pout) suffered from successive years of recruitment failure in large parts of the North Sea. Adult whiting, as one of the dominating predators of the demersal fish community in the North Sea, is known to be almost exclusively piscivorous and relies on only a few species that dominate its diet. Likewise to the forage fish stocks, the abundance of whiting has fluctuated dramatically throughout the last four decades. Therefore, the core hypothesis of the 2nd chapter is that a deficiency in forage fish should negatively affect the growth or the condition of such a predator that relies on a few prey fish species. To address this hypothesis, North Sea International bottom trawl survey time series on forage fish abundance and whiting growth and condition regarding contrasting periods with high and low forage fish abundance were analysed. A simultaneous decrease in forage fish abundance and whiting growth between 2000 and 2007 followed by a parallel increase in forage fish abundance and whiting growth after 2008 was observed in the North Sea. In addition, an analysis of multiple sets of stomach content data of whiting collected in several years between 1991 and 1999, as well as in 2012 compared to data collected during the period 2000 to 2007, revealed that the average stomach content masses were substantially lower during the period of observed low forage fish abundance. A second approach in the form of a bioenergetics calculation also showed, that the measured food amounts in whiting stomachs could theoretically account for the observed magnitude of the decrease in growth of whiting in the North Sea. The possible implications of these findings are discussed regarding single and multi-species assessment.

In the **3rd chapter** of the present thesis “**Influence of fishing mortality, temperature and prey abundance on the length-at-age and individual growth of North Sea cod *Gadus morhua***”, the influence of selected anthropogenic and natural factors on the life history of North Sea cod was evaluated. Cod is a commercially very important food fish that used to be a dominant component of the North Sea ecosystem. Along with the large-scale ecosystem changes in the North Sea during the last four decades, the stock has decreased notably. Therefore, it is of major interest to assess which factors contributed to the observed decrease in the North Sea cod stock. The population structure and life history of cod was analysed using data from the International Bottom trawl survey in addition to individual growth data inferred by otolith macrostructure analysis. The analysis revealed markedly different growth parameters between the southern and northern North Sea stock components with faster growth in the south. Changes in the mean length-at-age of cod were caused by a negative influence of

the fishing mortality in addition to the effect of decreasing shares of the southern component of the stock. Both effects were probably interlaced since fishing causes a reduction of the fast growing proportion of the southern stock component. In addition, the temperature was negatively correlated with the mean length-at-age of North Sea cod. The analysis of the individual cod otoliths revealed no general depression in growth of North Sea cod during the period 1975–2005. In addition, otolith analysis showed a distinct temperature dependence of the growth of the southern component of the North Sea cod stock.

ZUSAMMENFASSUNG

Die vorliegende Dissertation befasst sich mit der zeitlichen Entwicklung der Lebensgeschichten von Wittling (*Merlangius merlangus*) und Kabeljau (*Gadus morhua*) während der letzten Jahrzehnte im Ökosystem der Nordsee. Beide Vertreter der Familie der Gadidae sind essentielle Bestandteile der demersalen Fischfauna dieses Gewässers, und daher von enormem wissenschaftlichem Interesse. Im Zuge großskaliger Fluktuationen im Nordseeökosystem zeigen sowohl Wittling als auch Kabeljau drastische Bestandsveränderungen. Aus diesem Grund untersucht die vorliegende Arbeit, in welchem Maße ausgewählte Faktoren die physiologische Ökologie, die Populationsdynamik und die Arteninteraktion von Wittling und Kabeljau in der Nordsee beeinflussen. Die Ergebnisse dieser Dissertation zeigen, dass Wittling und Kabeljau sich hinsichtlich ihrer physiologischen Ökologie, Lebensgeschichte und Populationsdynamik stark unterscheiden. Daraus folgen artspezifische Auswirkungen für die Bestandsabschätzungen und Entscheidungen in der Bestandssteuerung für beide Arten in der Nordsee.

In **Kapitel 1 „Geschlechtsspezifische Futteraufnahme des Wittlings *Merlangius merlangus*”** wurden sowohl die Größenordnung, als auch die dem geschlechtsspezifischen Wachstumsdimorphismus zugrundeliegenden Mechanismen beim Nordseewittling untersucht. Obwohl Geschlechterdimorphismus beim Wittling bereits vor mehr als einem halben Jahrhundert in der wissenschaftlichen Literatur beschrieben und berücksichtigt wurde, wird dieser sowohl in heutigen Bestandseinschätzungen (stock assessments), als auch in den meisten wissenschaftlichen Studien über die Lebensgeschichte (z. B. Längen-Alters-Beziehungen), die Ökologie (z.B. Auswirkungen der Räuber) und die Physiologie (z.B. Magenleerung) des Wittlings weitestgehend ignoriert. Nichtsdestotrotz haben geschlechtsspezifische Unterschiede in den eben genannten Merkmalen möglicherweise Auswirkungen, die sowohl für die Bestandseinschätzungen und die Steuerung des Wittlingsbestandes, als auch zusätzlich für die Mehrarteneinschätzungen (multispecies assessments) in der Nordsee wichtig sind. Aus diesem Grund wurden in Kapitel 1 Daten aus der Internationalen Bodenschleppnetzerfassung der Nordsee (NS-IBTS), sowie zwei zusätzliche Datensätze die im 3. Quartal 2007 und im 1. Quartal 2012 erhoben wurden, im Hinblick auf geschlechtsspezifischen Dimorphismus untersucht.

Die Wachstumsparameter des Wittlings weisen deutliche Unterschiede zwischen Weibchen und Männchen auf, wobei die Weibchen wesentlich schneller wachsen als ihre männlichen Artgenossen. Die besagten Unterschiede im somatischen Wachstum können grundsätzlich drei verschiedene Ursachen haben: (1) Unterschiede in metabolischen Kosten, (2) Unterschiede in Energieverteilungsmustern oder (3) ungleiche Energieaufnahmemengen zwischen weiblichen und männlichen Tieren. Die Energieaufnahmemenge selbst kann entweder durch die Quantität oder die Qualität des aufgenommenen Futters, oder die Assimilationskapazität beeinflusst werden.

Dieses Kapitel bewertet den Einfluss dieser möglichen Ursachen. Quantität sowie Qualität der Nahrung des Nordseewittlings wurden untersucht um die geschlechtsspezifische Energieaufnahmemenge zu vergleichen. Obwohl kein Unterschied in der Nahrungszusammensetzung ermittelt werden konnte, wiesen Weibchen verglichen mit Männchen derselben Körperlänge eine deutlich höhere Futtermenge in ihren Mägen auf. Des Weiteren wurden bei weiblichen Wittlingen generell kleinere Anteile leerer Mägen gefunden als bei den männlichen Fischen. Zudem waren die Lebern und die leeren Mägen der Weibchen schwerer, verglichen mit denen der Männchen bei gleicher Körperlänge. Dies weist daraufhin, dass zusätzlich zu den Unterschieden in der Energieaufnahmemenge ein geschlechtsspezifischer Unterschied zwischen den metabolischen Kosten und den Energieverteilungsmustern vorliegt.

Das **2. Kapitel „Steuerung der Populationsdynamik des Nordseewittlings durch Beutefisch — Nachweise in Felddaten und durch bioenergetische Modellierung“**, beschäftigt sich mit dem Einfluss des Beutefischaufkommens auf den Wittling.

Seit den 1960er Jahren ist das Nordseeökosystem Fluktuationen unterworfen. Zu Beginn des 21. Jahrhunderts wurden mehrjährige Rekrutierungseinbrüche einiger Beutefischbestände (forage fish; Hering, Sprotte, Sandaale und Stintdorsch) in großen Teilen der Nordsee dokumentiert. Adulte Wittlinge, die eine der dominierenden Räuberarten der bodennahlebenden Fischfauna der Nordsee sind, ernähren sich fast ausschließlich piscivor und sind zudem auf wenige Arten, die ihr Nahrungsspektrum dominieren, angewiesen. Ebenso wie die Beutefischbestände ist auch die Abundanz des Wittlings in den letzten vier Jahrzehnten drastischen Schwankungen unterworfen. Aus diesen Gründen lautet die Kernhypothese des zweiten Kapitels, dass ein Mangel an Beutefisch sich negativ auf die Kondition und/oder das Wachstum eines Räubers mit einem derart eingeschränkten Nahrungsspektrum auswirkt.

Um diese Hypothese zu überprüfen, wurden Zeitserien bezüglich Beutefischabundanzen und Wachstum des Wittlings aus der Internationalen Bodenschleppnetzerfassung der Nordsee (NS-IBTS) hinsichtlich kontrastierender Phasen (gekennzeichnet durch hohe und niedrige Beutefischabundanz) analysiert. In der Nordsee wurde ein simultaner Einbruch der Beutefischabundanz und des Wittlingswachstums zwischen 2000 und 2007, gefolgt von einem gleichzeitigen Anstieg beider Kenngrößen nach 2008 festgestellt. Zudem ergab ein Vergleich von Wittlingsmageninhalten die zwischen 1991 und 1999, sowie 2012 erhoben wurden, im Vergleich zu Mageninhalten die in der Phase 2000–2007 gesammelt wurden, dass die durchschnittlichen Mageninhaltsgewichte der Wittlinge welche innerhalb der Phase mit niedriger Beutefischabundanz erhoben wurden, deutlich niedriger ausfielen. Das als zweiten Ansatz berechnete bioenergetische Modell zeigte ebenfalls, dass die gemessenen Futtermengen in den Wittlingsmägen theoretisch den gemessenen Wachstumseinbruch erzeugt haben könnten. Die Relevanz dieser Ergebnisse hinsichtlich Einzel- und Mehrartenbestandsabschätzungen werden diskutiert.

Kapitel 3 der vorliegenden Dissertation **„Einfluss von fischereilicher Sterblichkeit, Temperatur und Beuteabundanz auf die Länge der Altersklassen und das Individualwachstum des Nordseekabeljaus *Gadus morhua*"** befasst sich mit dem Einfluss ausgewählter anthropogener und natürlicher Faktoren auf die Lebensgeschichte des Nordseekabeljaus. Der Kabeljau ist ein kommerziell sehr bedeutsamer Speisefisch, der ursprünglich in der gesamten Nordsee eine dominierende Art des Ökosystems war. Im Zuge der weitreichenden Veränderungen des Nordseeökosystems verkleinerte sich der Bestand innerhalb der letzten vier Jahrzehnte merklich. Aus diesem Grund ist die Fragestellung, welche Faktoren zur beobachteten Abundanzabnahme des Nordseekabeljaubestandes beitragen besonders wichtig. Die Populationsstruktur und die Lebensgeschichte des Kabeljaus wurden anhand von Daten aus der Internationalen Bodenschleppnetzerfassung der Nordsee (NS-IBTS) und individuellen Wachstumsdaten, die aus der Makrostrukturanalyse von Otolithen gewonnen wurden untersucht. Die Analyse ergab merkliche Unterschiede in den Wachstumsparametern zwischen der südlichen und der nördlichen Bestandskomponente des Nordseekabeljaus, wobei Fische in der südlichen Nordsee schneller wachsen. Die Unterschiede in der spezifischen Länge der Altersklasse (length-at-age) resultieren aus dem Zusammenspiel zwischen negativem Einfluss der fischereilichen Sterblichkeit und dem geringeren Anteil der südlichen Bestandskomponente. Beide Faktoren sind wahrscheinlich miteinander verknüpft, da die Fischerei die schnellwachsende südliche Bestandskomponente direkt dezimiert. Zusätzlich korrelierte die Länge einer Altersklasse negativ mit der Temperatur. Die Untersuchung des individuellen Wachstums anhand von Otolithen ergab, dass es keinen generellen Wachstumseinbruch beim Nordseekabeljau gab. Zudem zeigte sich das individuelle Wachstum der südlichen Bestandskomponente temperaturabhängig.

GENERAL INTRODUCTION

WHITING AND COD IN A GLOBAL CONTEXT

Whiting *Merlangius merlangus* (L. 1758), with a maximum size of 70 cm, is a medium sized representative of the family Gadidae and the only species within its genus. Whiting has a long body with a dark blotch at the upper base of the pectoral fin and no or a microscopic chin barbel (Cohen *et al.*, 1990). Whiting is of secondary commercial importance. It is caught especially in European Atlantic waters. Total annual catch in 2012 was 42 056 tonnes (FAO, 2012). The distribution range of whiting is rather broad but covers only shelf-waters. It occurs in the south-western Barents Sea and the eastern North Atlantic from Iceland to the northern coast of Portugal and in the North Sea and the Baltic Sea. The subspecies *M. merlangius euxinus* (Nordmann, 1840) expand the distribution range of whiting from the western Mediterranean, where also the subspecies *M. merlangius merlangus* occurs, and the Adriatic Sea, to the Aegean Sea, the Sea of Marmara, to the Black sea and to the Sea of Azov (Ehrenbaum, 1909; Svetnovidov, 1986; Cohen *et al.*, 1990) (Fig. 1). Due to its southwards distribution, whiting is considered as a Lusitian species (Yang, 1982). The habitat of whiting shifts from a more pelagic life in coastal areas as juveniles to deeper waters as fish get older. Adult whiting can be found near the bottom in depths of 10 to 200 m (Ehrenbaum, 1909). Whiting shows an impressive growth performance during its first year of live after which growth slows down. Amongst gadoids whiting has a relatively high fecundity and maturation starts at age 1 year (Bowers, 1954; Hawkins, 1970; Hislop & Hall, 1974).

Cod *Gadus morhua* L. 1758 with a maximum size of 200 cm, is one of the largest representatives of the family Gadidae. The body of cod is covered with small dark blotches. The head is relatively narrow and has a well-developed chin barbel (Cohen, 1990). Atlantic cod is globally amongst the most important commercially exploited fish species. It is caught in large targeted fisheries. Total annual catch in 2012 was 1 114 401 tonnes (FAO, 2012). Cod is distributed throughout the North Atlantic from brackish to marine waters usually inhabiting temperatures between 0 and 12°C (Drinkwater, 2005). Western distribution ranges from Cape Hatteras to Labrador along the North American coast. Cod occurs along the south-western and -eastern Greenland coast and around Iceland. North-eastern distribution ranges from the northern Bay of Biscay over the North Sea and the Baltic Sea to the Barents Sea up to Novaya Zemlya (Fig. 1). According to its occurrence, only on the northern hemisphere, cod is regarded as a boreal species (Yang, 1982). Adult cod is a cold temperate, demersal species encountering very diverse habitats from shorelines to well below the continental shelf, covering depths of 50 m to over 600 m (Cohen *et al.*, 1990). The growth rates of cod are very divergent depending on the habitat. Atlantic cod matures at age 2 years at the earliest in the eastern and at age 4 years at the earliest in the western parts of the North Atlantic (Cohen *et al.*, 1990).

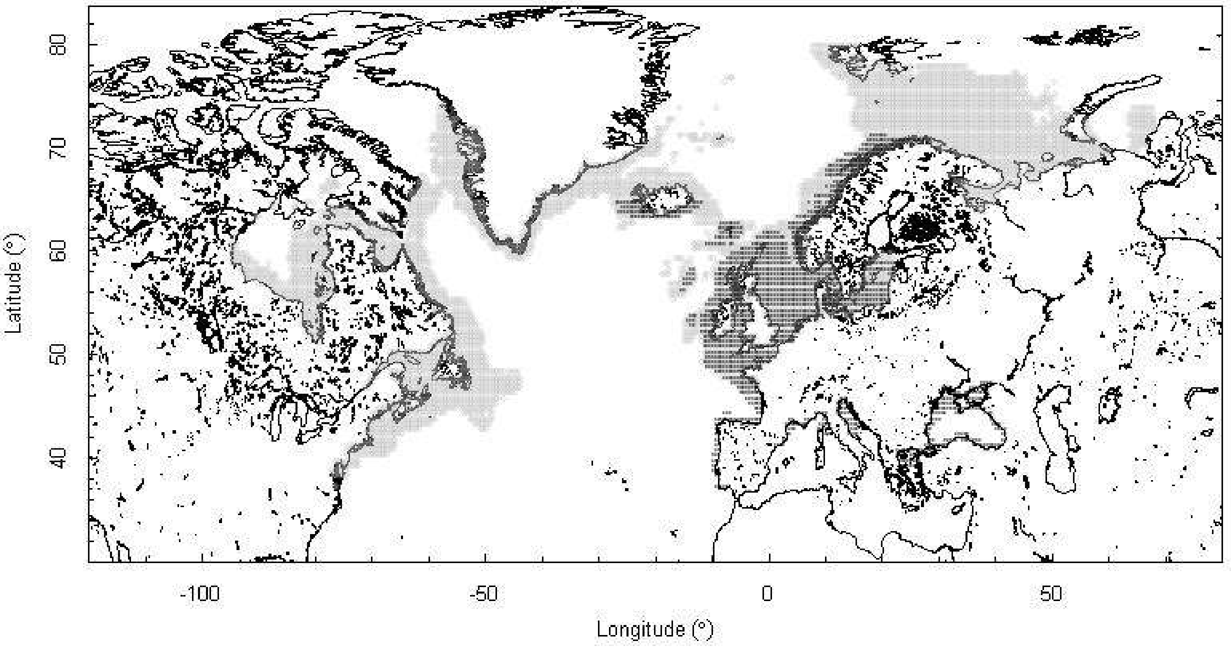

FIGURE 1. Global distribution of whiting (dark grey) and cod (light grey). (Data obtained from http://www.aquamaps.org).

Whiting and cod, as most members of the family Gadidae, are economically, ecologically and culturally important species in many of the world's ecosystems (Patterson *et al.*, 1985; Frank *et al.*, 2005; Link *et al.*, 2008; Reed *et al.*, 2013). Within their habitat, whiting and cod incorporate the role of secondary and tertiary consumers, feeding on prey that is either planktivorous or piscivorous itself. In turn, they are preyed upon by themselves, birds, marine mammals and humans. As a result of these traits, it is of general interest to understand the biology, ecological characteristics and life history of whiting and cod in order to conserve, protect and sustainably manage those resources. As described above, both species possess similar features but also characteristics that are different between them. This makes it of particular interest to examine those two typical yet different representatives of the family gadidae in a comparative approach. As this requires exploring a habitat where both species are endemic, this was realised in the North Sea ecosystem.

THE NORTH SEA ECOSYSTEM

The North Sea is one of the most intensively anthropogenic used areas in the Northeast Atlantic. It is an important European supplier of resources, such as fossil fuels with large oil fields in the central and northern parts and natural gas reserves in the southern areas, to name just a few (Clark & Frid, 2001). Moreover, it is amongst the most exploited fishing grounds worldwide (Hempel, 1978; Rogers & Stocks, 2001). In terms of mass, the industrial fisheries, mainly targeting sandeels *Ammodytes* spp. L. 1758, Norway pout *Trisopterus esmarkii* (Nilsson 1855) and sprat *Sprattus sprattus* (L. 1758) is the most important. Pelagic trawlers extensively catch herring *Clupea harengus* L. 1758 and mackerel *Scomber scombrus* L. 1758 for human consumption. In terms of value, demersal fisheries, targeting fishes inhabiting the water column close to the sea floor, is the most important. Major bottom trawling fisheries are the mixed flatfish fishery targeting plaice *Pleuronectes platessa* L. 1758 and common sole *Solea solea* (L. 1758) in the southern North Sea and the mixed demersal fishery catching cod, haddock *Melanogrammus aeglefinus* (L. 1758) and whiting in the northern North Sea. Moreover, fisheries on crustaceans, mainly Norway lobster *Nephrops norvegicus* L. 1758, Pink shrimp *Pandalus* spp. Leach 1814 or Brown shrimp *Crangon crangon* L. 1758 are locally very intensive (Rogers & Stocks, 2001).

The North Sea is a geologically relatively old European Shelf Sea enclosed in the east, south and west by land masses, and in the North open to the Northeast Atlantic. The English Channel in the south is the second connection to the Atlantic and the Skagerak and Kattegat in the east connects the North Sea to the Baltic Sea. Considering its hydrography and soil morphology, the North Sea is an extremely heterogeneous habitat. It is a relatively shallow basin with average depths ranging from 30 m in the southeast along the German and the southern Bight, over 50–100 m depths in the central parts to about 200 m in the northern areas. The Norwegian Trench in the north runs along the Norwegian coastline to the Skagerak with depths up to 600 m (Knijn *et al.*, 1993). The Dogger Bank separates the southern from the central parts with an average water depth of 25 m (Veenstra, 1965). Large currents from the Atlantic enter the North Sea mainly in the North and to a lesser extend through the English Channel. Water masses of the North Sea are usually transported in an anticlockwise gyre driven by wind forces. Salinities range from 35 in the northern to 29 in the south-eastern North Sea. Great regional variation exists in substrata including mud, sand, gravel and rock. Moreover, regional differences in the seasonal vertical structuring of the water column are present. While large parts of the central and northern North Sea show distinct stratification from spring to autumn, the water column in the shallow areas in the south are well mixed throughout the whole year. During the winter no stratification exists in virtually the whole North Sea. Stratified water masses in the North Sea develop a strong thermocline during the summer months, which is caused by a fast warming of the upper water layers. Compared to relatively little seasonality of the bottom temperatures in the northern parts, temperatures in the German and Southern Bight are characterised by large seasonal extremes (Reid et al 1988; Otto *et al.*, 1990; Knijn *et al.*, 1993). Due to those heterogeneous physical conditions, the North Sea phytoplankton (Reid *et al.*, 1990), zooplankton (Fransz *et al.*, 1991) and meiofauna (Heip *et al.*, 1990) communities are spatially very divergent. The 224 species of North Sea fish are divided into three different origins: Boreal, Lusitanian and Atlantic. According to species composition, abundance and habitat, spatially divergent fish communities can be found in the North Sea ecosystem (Yang, 1982).

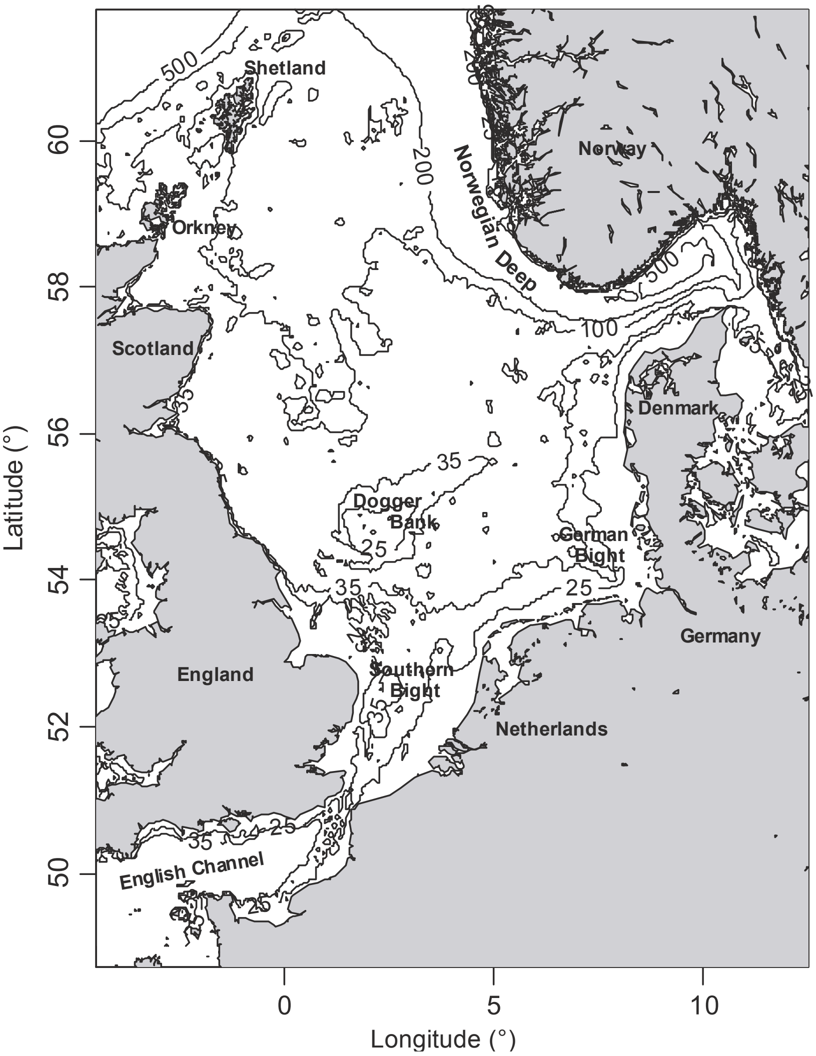

FIGURE 2. Map of the North Sea with depth contour (grey lines).

The North Sea ecosystem experienced large-scale changes in hydrographical conditions as well as on several community levels during the last five decades (Weijermann *et al.*, 2005). Since the 1980s the North Sea surface temperature as well as the oceanic inflow had increased (Reid *et al.*, 2001; Belkin, 2009). Community alterations were documented for phytoplankton abundance and composition (Reid, 1975), benthos composition and distribution (Kröncke *et al.*, 2011) and zooplankton distribution and composition (Beaugrand & Ibanez, 2002). Furthermore, changes on higher trophic levels like fish (e.g. Reid *et al.*, 2001), birds (e.g. Wanless *et al.*, 2005) and mammals (e.g. Fredricksen *et al.*, 2004) were documented. Generally, warm-water species increased while cold-water species decreased (Beaugrand, 2004). Concerning the historical development of major gadoid stocks in the North Sea ecosystem, a prominent feature is the so-called ‘gadoid outburst’ (Cushing, 1984). Starting in 1962, during the 1960s and 70s almost always one of the gadoid species (whiting, cod, haddock, saithe *Pollachius virens* (L. 1758) and Norway pout) produced above-average year classes in the North Sea (Hempel, 1978). Consequently, stocks were on high levels in the late 1960s and early 70s, followed by subsequent decline to low stock levels in the early 1990s. Likewise, the North Sea forage fish communities, feeding on zooplankton and being in turn preyed by higher trophic levels (Alder *et al.*, 2008), showed substantial fluctuations during the last 40 years (Dickey-Collas *et al.*, 2013; Engelhard *et al.*, 2013). At the beginning of the 21st century, a number of forage fish species namely sandeels, Norway pout, herring and sprat showed a marked decline in their spawning stock biomass and produced some of the smallest year classes ever recorded: the spawning stock biomass of sandeels was low in the period between 2000 and 2006, starting in 2002 herring and sprat produced below-average year classes and the recruitment of Norway pout reached historic minima in 2003 and 2004. From 2007 onwards, the spawning stocks of sandeels, sprat and Norway pout increased again and Norway pout stock produced very strong year classes in 2009 and 2012 (ICES, 2013).

Due to its high ecological and economical value, it is essential that the resources of the North Sea are protected, conserved and sustainably managed. A general problem for conservation measures is the incomplete knowledge about the biology of the species within the ecosystem. Specifically for many species, knowledge gaps exist with regard to life history parameters such as the size-at-age, and the physiological ecology and species interactions, which are required for an understanding of the functioning of the ecosystem and of possible implications of an ecosystem change. In the present thesis, two key demersal predatory fishes of the North Sea ecosystem are investigated, regarding the above mentioned attributes to improve the knowledge and to provide scientific basis for sustainable management: whiting and cod.

WHITING AND COD IN THE NORTH SEA ECOSYSTEM

Whiting is widely distributed throughout the North Sea and one of the dominating species in the demersal predator community of this ecosystem (Knijn *et al*., 1993; Greenstreet and Hall, 1996). The population of North Sea whiting reached an all-time maximum during the ‘gadoid outburst’ in the 1960s and 70s and decreased continuously thereafter. Whiting is a gadoid of secondary commercial importance, which is caught in large numbers, but mainly as by-catch in mixed demersal or in Norway lobster fisheries. Total annual landings in 2013 in the North Sea were 13 354 tonnes (ICES, 2014). Regularly, in the North Sea whiting may reach ages of up to 8 years and maximum lengths of about 50 cm. Females start spawning after they complete their 2nd year of life (~22 cm body length), whereas males become mature at the end of age 1 year (~19 cm body length) (Messtorf, 1959). Female whiting are very fecund, with an average egg production of 1,900 eggs per gram body mass (Hislop & Hall, 1974). The relatively small pelagic eggs (0.97–1.32 mm; Russel, 1976) are spawned in multiple batches over a period of up to 14 weeks (Hawkins, 1970). Spawning takes place from January in the southern parts to September in the more northern areas of the North Sea (Ehrenbaum, 1909). After an egg development of approximately 10 days, the pelagic larvae hatch and start to prey already within the yolk-sac stage at sizes < 3 mm, mainly on nauplii and copepodite stages of calanoid copepods (Last, 1978). Whiting is a highly selective predator, feeding almost exclusively on fish once a body size of 25 cm is reached (Fig. 3). Moreover, whiting relies mainly on selected commercially important species, such as common brown shrimp as juveniles, and sandeels, Norway pout, herring and sprat as adults (Hislop *et al*., 1991; Knijn *et al*., 1993). The predation of whiting on other fish focuses mainly on age 0- and age 1- cohorts. Temming *et al.* (2007) showed that North Sea whiting is capable of wiping out a substantial fraction of a year class of cod within only a few days. Likewise, whiting in the North Sea consumes annually approximately 700 000 tonnes of sandeel, which exceeds the total annual landings since 2003 (ICES, unpubl. data cited in Temming et al 2004). Therefore, whiting is a voracious fish predator and has occasionally the highest impact on the ecosystem amongst other predatory fishes. Whiting can be considered as highly sensitive to changes in the fish community, regarding its few preferred prey species. In turn, juvenile whiting is an important prey for larger gadoids and other demersal fishes (Hislop *et al.*, 1997).

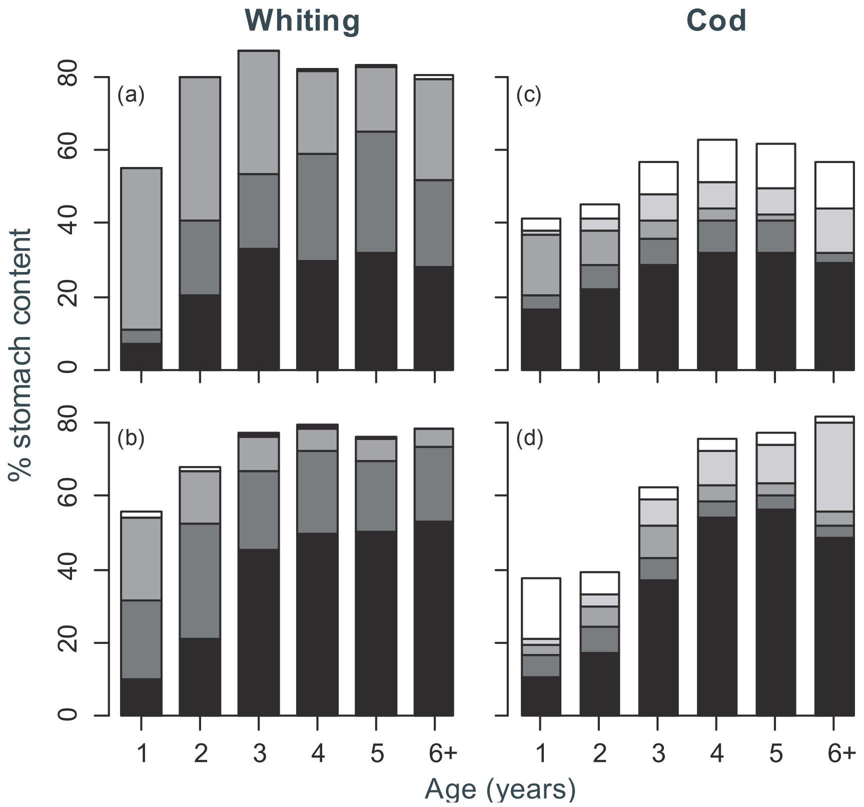

FIGURE 3. Food composition in whiting ((a) & (b)) and cod ((c) & (d)) stomachs by mass percentage of commercial important species (Data obtained from Daan, 1989); crustaceans (□), flatfishes (░), sandeels (▒), herring and sprat (▓) and gadoids (■). Top panels represent summer values (2nd and 3rd quarter) and bottom panels show winter values (1st and 4th quarter) of North Sea samples from 1981.

Cod was historically widely distributed throughout the North Sea and one of the most important commercially exploited species within this ecosystem. During the 'gadoid outburst' some very strong year classes led to a capacious spawning stock. This era ended in the mid 1980s when a marked decline in recruitment was observed reaching a historical minimum in the 2000s (Olsen *et al.*, 2010). However, cod is still an important component of the North Sea demersal fish community and as ever a highly valuable species for human consumption. Total annual landings in 2013 were 25 784 tonnes (ICES, 2014). In the North Sea, cod rarely exceed an age of 20 years and sizes of 110 cm (Muus & Nielsen, 1999). While a small proportion of males start spawning at age 2 years, females participate in spawning at age 3 years at the earliest, but it is not until age 6 years when they are all mature (Wagner & Dethloff, 1985; ICES, 2012). Spawning takes place from January to April (Brander, 1994). On average, a female North Sea cod produces 570 eggs per gram body mass and releases the relatively big eggs (1.16–1.89 mm; Russel, 1976) periodically in multiple batches over a period of up to 8 weeks (Oosthuizen & Daan, 1974; Kjesbu 1989). Larvae hatch after 10 to 28 days depending on temperature (Thompson & Riley, 1978) and start to feed on nauplii and copepodite stages of calanoid copepods at sizes of > 3mm when they are still in their yolk-sac stage (Last, 1978). Cod is an omnivorous opportunistic predator with a very diverse diet. Juveniles feed predominantly on crustaceans and with increasing size the proportion of fish in the diet increases. Adults feed mainly on fish including commercial important gadoids, clupeids, flatfish and sandeel. However, due to its hardly selective food preferences and depending on season and region, invertebrate prey is still a major component of adult cod diet (Daan, 1973) (Fig. 3). In turn, cod is an important prey for other piscivorous predators in the North Sea ecosystem. Juveniles are eaten by grey gurnard *Eutrigla gurnardus* (L. 1758), whiting, cod itself as well as by marine birds and mammals. Due to its large body size, adult cod is mainly preyed upon by man.

Following from the above, inhabiting the same ecosystem whiting and cod exhibit differences in life history characteristics, food web links and population dynamics. While both whiting and cod are of high ecological relevance being amongst the top predators within the demersal fish community in the North Sea ecosystem, the reduction in the cod stock has especially economic relevance. Moreover, it remains unclear which mechanisms are the basis for those differences and recent individual information on the temporal development of those traits is rare. Therefore, it is of particular interest to study cod and whiting in the North Sea ecosystem in a comparative approach. How both species respond to the large-scale changes in hydrographic conditions, as well as on multiple ecosystem levels in the North Sea, can give important information about the underlying species-specific physiological ecology, life history and population dynamics.

PHYSIOLOGICAL ECOLOGY AND FACTORS INFLUENCING THE SIZE-AT-AGE

Physiological ecology encompasses a rather broad scientific field that ultimately aims to understand the functioning of living systems. Generally, the central focus lies on the adaptations or mechanisms by which organisms interact with their ever-changing environment. Aside from morphology, anatomy, and behaviour, the adaptations usually incorporate physiological processes (Tracy *et al.*, 1982). Apart from the genetic predispositions physiological processes determine the traits individual organisms express, experiencing different environmental conditions, i.e. phenotypic plasticity. How these traits are expressed, controls the life history parameters and thus population dynamics of a species. The population dynamics in turn lead to interactions within one species and between species within an ecosystem.

Traits commonly studied in commercially exploited fish stocks are condition and size-at-age. The condition of fishes is morpho-physiologically indicated by the ratio between either body length and body mass of a fish, or the ratios between the mass of an organ (e.g. gonads or liver) and fish body mass (Shulman & Love, 1999). The general assumption is that a heavier fish at a given length, or a fish with a heavier organ at a given mass, is of greater fitness (Bolger & Connolly, 1989). The size-at-age in a stock is crucial for the conservation and the management of a stock, since it is used to determine the stock structure and the biomass of fish that can be removed from an exploited stock ideally, to sustain the optimum biomass without provoking growth, recruitment or ecosystem overfishing. On the other hand the size-at-age influences the production of a stock due to its influence on the individual fecundity, which in turn determines the production of a fish stock (Trippel, 1999; Barot *et al.*, 2004). Moreover, studying spatial and temporal differences in the size-at-age might give insights to the species environment interactions.

While the temporal development of the length-at-age of North Sea cod has been subject to several scientific studies because of the species economic relevance (e.g. Rindorf et al., 2008), no recent scientific studies analysed the temporal development of the length-at-age of North Sea whiting. Likewise, there is only a small amount of available information on the factors influencing the life history processes and population dynamics of North Sea whiting (e.g. Messtorf 1959). However, for cod there is also a lack of information on the individual growth history during the large-scale changes that occurred in the North Sea ecosystem.

The size-at-age depends on both, mechanisms which affect the composition of an age class of the stock and mechanisms which affect the growth rates of fish. The growth rates of fish affect the size-at-age in a fish population. Therefore, the identification of the factors determining the growth of a natural fish population has been subject to numerous publications (e.g. Crozier, 1926; van Poorten & Walters, 2015). Growth represents the ultimate expression of the general health or fitness of an individual or a population since it is the synergy of the increase in body length, condition and tissue energy concentration (Booth & Keast, 1986; Bolger & Connolly, 1989). Generally, individual growth is a result of the interaction between multiple intrinsic (e.g. sex & condition) and extrinsic (e.g. temperature & food) factors influencing the physiological processes in fish.

One striking intrinsic factor affecting the physiology, and thus the growth of fish, is the sex. In many fish species females and males exhibit different growth rates (Shulman, 1974). In most species sex-specific differences exist in the age at which they become sexual mature. Commonly, sexual maturity is the inflection point in the life history of a fish where growth switches between the phase of comparatively rapid immature growth and adult growth which is relatively slow due to additional investment into reproduction (Dutta, 1994). Thus, the sex-specific age at first maturation determines the length of the phase of immature fast growth. Moreover, mature fish have different sex-specific expenditures during spawning. During maturation female fish break down energy reserves much faster compared to males since their gonads are larger. On the other hand, male fish show higher physical activity levels compared to females and thus have larger energy expenditures during spawning. Moreover, associated with maturation, sex-specific differences in the quantity and quality of the liver tissue might occur (Shulman & Love, 1999). For North Sea whiting in particular, there are indications that sexual size dimorphism exists, which was addressed in the literature more than half a century ago (e.g. Messtorf, 1958). However, this knowledge was somehow forgotten and most recent studies on life history, ecology or physiology of whiting do not address sex-specific differences (e.g. Hislop *et al.*, 1991; Andersen, 1999; Temming & Mergardt, 2002). Moreover, the energetic consequences and underlying mechanisms are still unknown. Therefore, it is important to resume the topic of sexual dimorphism in whiting to quantify the magnitude as well as to understand the underlying mechanisms and thus, to fill this knowledge gap.

The obtainment of energy is one essential extrinsic factor influencing physiological processes such as growth in fish, since the ultimate impulse common to all living systems is the acquisition of energy and matter, which are needed to realize life processes. Within an organism the available energy has to be partitioned between the processes of maintenance, growth, energy storage and reproduction. Since those four processes are competing, low energy resources lead to trade-offs between them (Congdon *et al.*, 1982). In heterotrophic organisms such as fish, the required energy and carbon is purchased by the intake of organic material provided by other organisms. Thus, the metabolism of fishes is linked to other trophic levels in an ecosystem because it is affected by the abundance, accessibility, and the composition of food (Shulman & Love, 1999).

Considering the large-scale fluctuations in prey fish in the North Sea described above, it is of particular interest to investigate how predators respond to these changes in food availability. While no information of the effect of prey abundance on the length-at-age of North Sea whiting is available, Rindorf *et al.* (2008) found that the size-at-age of North Sea cod increased with increasing demersal prey biomass. While whiting in the North Sea is a very selective piscivorous feeder, cod is a carnivorous generalist with markedly lower proportions of fish in its diet (Fig. 3). In addition, the diet of cod directly reflects the abundance of a certain prey species (Floeter & Temming, 2003) which indicates the opportunistic feeding behaviour of cod. Due to these contradictory findings, it is important to revise the influence of prey fish on cod while it is of particular interest to assess the effects of prey abundance on very selective feeders, such as whiting.

Being ectothermic, one of the most important and influential abiotic factor affecting fishes is the temperature (Fry, 1971). Temperature controls the rates of chemical reactions in such way, as an increase in temperature leads to a faster reaction. Thus, the metabolism of living organisms as an omnium-gatherum of mainly enzyme-catalysed chemical reactions is influenced by temperature (Reynolds & Casterlin, 1980). Usually, with increasing temperature, enzyme activity and thus metabolic processes increase until a certain level where metabolic enzymes are structurally damaged (Shulman & Love, 1999). As a consequence, various life processes of fishes have shown to be affected by temperature: with increasing temperatures, egg developmental rates increase (Pauly & Pullin, 1988) and under ad libitum feeding conditions, adult growth rates increases with temperature to an optimum, beyond which growth decreases (Beitinger & Fitzpatrick, 1979), as does rates of gut emptying (Hofer *et al.*, 1982) and food absorption (Riddle, 1909).

While there is no information of the influence of temperature on the length-at-age of North Sea whiting in North Sea cod, the effect of temperature on growth is ambiguous: while some studies found no effect of temperature on adult cod growth (Sinclair *et al.*, 2002; Rindorf *et al.*, 2008), other publications detected an influence of temperature on the growth of cod (e.g. Brander 2007). Therefore, it is important to re-evaluate the effect of temperature on the growth of North Sea cod; on an individual level, as well as on the population mean length-at-age.

The second mechanism influencing the size-at-age in a fish population is size-selective mortality. The selective removal of the fast or the slow growing proportions of an age class that is naturally composed of a cohort of fish showing large individual variation in size, results in a decrease or an increase in the size-at-age. One major cause of size-selective mortality in an exploited fish stock is the fishery that usually selectively removes larger individuals (Hanson & Chouinard, 1992). In the southern Gulf of St. Lawrence and the West Greenland cod stocks, size-selective mortality was shown to have negatively affected the size-at-age (Riget & Engelstoft, 1998; Sinclair *et al.*, 2002). In the North Sea stock however, up until now no analysis of the effect of size-selective mortality on the length-at-age has been realised. Likewise, in North Sea whiting no scientific study has assessed the influence of size-selective mortality. Therefore, the present thesis addresses this knowledge gap.

GENERAL HYPOTHESES—SCOPE OF THE THESIS

The objective of this thesis was to (i) evaluate the temporal development of the length-at-age in the North Sea ecosystem and to (ii) determine to which extend selected factors influence the physiological ecology, population dynamics and species interactions of whiting and cod. Based on the general biology and distribution of whiting and cod, divergent temporal developments of the length-at-age and different species-specific responses to alterations in the North Sea ecosystem between these representatives of the family gadidae, were hypothesised.

In **chapter I** the topic of sexual size dimorphism in North Sea whiting was examined. Based on studies by Bowers (1954), Messtorf (1959) and recent data, it was expected to find significant sexual differences in growth. The general hypothesis was that sex-specific differences in the energy uptake levels exist which lead to differences in the growth between female and male whiting. This hypothesis was tested by evaluating the mass of the stomach content and the prey composition in the stomachs of whiting to detect potential sex-specific differences in the quantity and the quality of the diet. Two alternative hypotheses were addressed by evaluating possible sex-specific differences in the liver masses and the empty stomach masses which could indicate different energy allocation patterns or different metabolic costs between female and male whiting. In addition, year specific differences in the mentioned metrics between 2007 and 2012 were examined.

The aim of **chapter II** was to evaluate the influence of changing energy resources on North Sea whiting. The temporal development of the length-at-age of whiting and the temporal development of the prey fish abundance in the North Sea was evaluated. Moreover, the stomach contents and the condition of whiting during different feeding regimes were analysed. The central hypothesis was that changes in the food web, particularly in the forage fish community in the early 2000s in the North Sea ecosystem, affected the condition and the growth of whiting. The period from 2000 to 2007 was characterised by low prey abundance, while in contrast the years from 2008 onwards represent a period of sufficient food supply. Moreover, the hypothesis that a lack of food induced a decrease in the length-at-age of whiting was tested by applying a bioenergetics model. Additionally, possible alternative mechanisms (temperature, fishing) that could have contributed to the observed differences in whiting were discussed.

In **chapter III** the influences of multiple factors on the length-at-age and growth of North Sea cod were evaluated. The central hypothesis was that fishing affects the growth of this extensively exploited species. The influence of temperature, prey abundance and fishing mortality on the length-at-age of North Sea cod was tested. Moreover, spatial differences in the length-at-age were assessed to determine to which extend the composition of the North Sea stock is responsible for the observed differences in the average length-at-age. A more precise analysis of the growth history of cod from the southern North Sea based on otolith macrostructure analysis should give insight into the influence of these effects on the individual growth in the former main territory of North Sea cod.

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Chapter I

Sex-specific food intake in whiting *Merlangius merlangus*

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ABSTRACT

In this study, the topic of sexual growth dimorphism in whiting *Merlangius merlangus* is examined. To quantify the magnitude and to understand underlying mechanisms, North Sea International Bottom Trawl Survey (NS-IBTS) data and two additional datasets from the third quarter of 2007 and the first quarter of 2012 were analysed. Whiting displays distinct differences in growth parameters between males and females, with females reaching a higher asymptotic length than males. To identify the mechanisms which lead to higher growth in females, the quantity and the quality of the diet of whiting in the North Sea were investigated to compare the sex-specific energy uptake levels. The diet composition did not differ between the sexes, but females had higher stomach content masses than males of the same total length, and showed lower proportions of empty stomachs. Moreover, female whiting had higher liver and empty stomach masses compared with males of the same size, which indicates additional sex-specific differences in the metabolic costs and energy allocation patterns. Finally, interannual differences were found in the stomach contents, the share of empty stomachs and liver masses of whiting in the North Sea.

INTRODUCTION

The systematic difference in the phenotypes between females and males of the same species, *i. e.* sexual dimorphism, is a prominent phenomenon in nature, attributed to the adaptation of sexes to their different reproductive roles (Helfman *et al.*, 2009). A very common distinction between the sexes is the difference in body size, ascribed to evolutionary differences in sexual selection, parental investment and resource partitioning (Alexander *et al.*, 1979; Roff, 1981; Carothers, 1984). In the marine environment, sexual size dimorphism, more precisely the difference in maximum observed body length or the difference in mean asymptotic length ($L\infty$), is common in numerous species. Probably, the most notable example of fishes is a deep-sea anglerfish, of the suborder Ceratioidei, where females of the species *Ceratias holboelli* Kroyer 1845 reach more than 60 times the maximum observed body length of males (Pietsch, 2005).

Far less pronounced, yet subject to a lot of studies and very well described, is sexual size dimorphism in many families of Pleuronectiformes (Beverton & Holt, 1959; de Veen, 1976; Rijnsdorp & Ibelings, 1989; Imsland *et al.*, 1997). Mahe & Moguedet (1991) described the mean asymptotic length of American plaice *Hippoglossoides platessoides* (Fabricius, 1780) where females reach an average mean asymptotic length of 90 cm compared with 66 cm in males. In the North Sea, another commercially important flatfish species, the European plaice *Pleuronectes platessa* L. 1758, also exhibits distinct sex-specific growth parameters. VanWalraven *et al.* (2010) showed average mean asymptotic length of 90 and of 51 cm for female and male plaice, respectively.

In gadoids, however, sexual size dimorphism also exists, but is less pronounced than in the earlier mentioned species. For example, in Norway pout *Trisopterus esmarkii* (Nilsson 1855) and in Pacific cod *Gadus macrocephalus* Tilesius 1810, differences of 1 cm for both species (Stark, 2007; Lambert *et al.*, 2009) were observed in the $L\infty$ between the sexes. Consequently, many recent studies on the life history, physiology or ecology of gadoid species neglect the influence of sex, or simply do not consider sex as an influencing factor (Jobling, 1982; Eliassen & Vahl, 1982; Andersen, 2001; Vinther, 2001; Michalsen *et al.*, 2008; ICES, 2012b).

Whiting *Merlangius merlangus* (L. 1758), a medium sized gadoid, is widely distributed in the north-east Atlantic Ocean from the northern coast of Portugal to Iceland and the south-western Barents Sea (Svetnovidov, 1986). In the North Sea, whiting is a common fish species of secondary commercial importance that is caught in large numbers, but mainly as by-catch. Among gadoids, whiting is a highly selective feeder, which from a total length of >25 cm is almost exclusively piscivorous. It is considered to be a key predator, feeding on many commercially important species, such as crangonids, as a juvenile, and on sandeels *Ammodytes spp.* L. 1758, *T. esmarkii*, herring *Clupea harengus* L. 1758 and sprat *Sprattus sprattus* (L. 1758) as an adult (Hislop *et al.*, 1991). In addition, Temming *et al.* (2007) demonstrated that whiting is a voracious predator on 0 year-group gadoids, including its own offspring but especially juvenile Atlantic cod *Gadus morhua* L. 1758. Compared with other batch spawning gadoids, whiting exhibit relatively high fecundity. In the North Sea, the stock has an extended spawning period that may last from January until July (Messtorff, 1959). During that period, a female of 35 cm total length may produce up to 760 000 ripe eggs and release them periodically at *c.* 2 day intervals over a period of up to 10 weeks (Hawkins, 1970; Hislop & Hall, 1974; Hislop, 1975). The reproductive strategy varies between the sexes of whiting. While a large proportion of males participate in spawning at an age of 1 year, the age of maturity for female fish is 2 years at the earliest (Messtorff, 1959). Hislop (1975) deduced, from lower post-spawning condition factors in female whiting, that the spawning-related energy expenditure is greater in females than in males. Moreover, the courtship and mating behaviour of whiting have been shown to differ between the sexes. Males generally appear to be more active during spawning, showing aggressive territorial behaviour and intrusive courting, whereas female whiting are more passive during that period (Hawkins, 1970). More than a half century ago, sexual dimorphic life history was commonly addressed in studies on whiting and differences in total length-at-age up to 13 cm (22%) between males and females were described (Desbrosses, 1948; Bowers, 1954; Messtorff, 1959). Despite these differences, most recent studies on the life history (*e.g.* length-at-age), ecology (*e.g.* predatory effect) or physiology (*e.g.* gastric evacuation) of whiting do not address sex-specific differences (Hislop *et al.*, 1991; Seyhan *et al.*, 1998; Andersen, 1999; Pedersen, 2000; Temming & Mergardt, 2002; Gerritsen *et al.*, 2003).

In general, somatic growth differences between males and females could result from three intrinsic factors: (1) dissimilarities in metabolic costs, (2) different energy allocation patterns or (3) unequal energy uptake levels between female and male fish. The energy uptake level in turn could be influenced either by the quantity or the quality of the food ingested, or by a sex-specific difference of the energy assimilation capacity. In teleosts, studies on the mechanisms underlying sexual size dimorphism are rare, but generally conclude that often, more than one of the above-mentioned intrinsic factors contributes to the observed sexual growth dimorphism. Rennie *et al.* (2008) applied bioenergetic mass-balance modelling in two species of the family Percidae, and found that different metabolic costs, along with differences in energy allocation patterns, as well as a difference in energy uptake level, were involved in the sexual size dimorphism in those species. Males mature earlier and at a smaller body size, and reach a smaller mean asymptotic length than females. Additionally, in both species, mature males consumed lower amounts of food, but exhibited lower food conversion efficiencies and metabolic costs than females. A further experimental study on perch *Perca fluviatilis* L. 1758 confirmed that androgens could cause lower growth rates in males by decreasing the food intake (Mandiki *et al.*, 2005). Field studies on sex-specific growth differences in the common dab *Limanda limanda* L.1758 considered lower masses of both the stomach content and the tissue of the empty intestines in males, indicating lower food consumption as well as possibly differential food conversion efficiency as the causes of sexual size dimorphism (Lozan, 1992; Temming & Hammer, 1994). In plaice, the energetic causes and related management implications of sexual dimorphic growth have been subject to several scientific studies. Lower growth in male flatfishes results from their earlier maturation, which causes an energy allocation shift towards reproductive tissue. Moreover, adult males invest a higher proportion of the available energy into reproduction than females and, therefore, have less energy left for somatic growth (Roff, 1982; Rijnsdorp & Ibelings, 1989). As a consequence of the differences in growth and maturation, the catchability of males and females of the same age is likely to differ in the beam trawl used in flatfish fisheries. Thus, the proportion of males in an age class discarded would be higher than in the stock. If the discards are not included in the assessment, estimates on the status of the stock would be biased and in turn mislead management advice (Kell & Bromley, 2004).

The objective of this study was to examine the topic of sexual dimorphism in whiting in the North Sea. Considering the studies of Bowers (1954), Messtorff (1959) and recent data, significant sexual differences in somatic growth were expected. To explore the potential underlying mechanisms, North Sea International Bottom Trawl Survey (NS-IBTS; ICES, 2012a) data and two additional data sets from 2007 and 2012 were analysed. The central hypothesis of this study is that female whiting have higher energy uptake levels than males of the same size, which leads to higher somatic growth. In order to test this hypothesis, the stomach content masses and the prey composition of female and male whiting were compared to find potential differences in the quantity or quality of the diet. Moreover, the masses of the empty stomachs and the livers were compared to address two alternative explanations for sexual size dimorphism: differences in metabolic costs and differences in energy allocation patterns. Additionally, interannual differences between the investigated metrics were evaluated.

MATERIALS AND METHODS

DATA SOURCES AND SAMPLING

To examine growth and condition differences between male and female whiting in the North Sea, NS-IBTS data on total length and mass at age of North Sea whiting were obtained from the International Council for the Exploration of the Sea (ICES) DATRAS database (http://ices.dk/marine-data/data-portals/Pages/DATRAS.aspx/). Fishes from that database have been aged using otolith macrostructure analysis, according to the NS-IBTS manual (ICES, 2012a). To avoid seasonal bias, sub-sets of the first quarters of 2007 and 2012 were used for further analyses.

To obtain individual information on stomach contents and the masses of the livers, fish were acquired from two North Sea research cruises with the German IBTS standard vessel (R.V. *Walther Herwig III*) in 2007 and 2012. During both cruises, sample collection followed the standardized NS-IBTS sampling scheme (ICES, 2012a). A GOV (grande ouverture verticale) survey trawl, which has been described in the IBTS manual (ICES, 2012a), was deployed for 30 min, granting equal catchabilities. In 2007, fish were trawled during the German small-scale bottom trawl survey (GSBTS) from four 10 nautical mile (nmi) × 10 nmi boxes in July–August. A total of six to eight hauls were carried out on three consecutive days per box (Ehrich *et al.*, 2007). From each haul, if possible, five fish from the total length classes 20–24.9, 25–29.9, 30–34.9, 35–39.9 and >40 cm were immediately frozen at -40°C. In April 2012, whiting were caught during a research cruise contributing to the EU-project VECTORS (www.marine-vectors.eu), covering a larger area of the North Sea, with a total of 69 trawl hauls. If possible, 10 fish of the same total length classes defined for 2007 sampling were individually numbered and frozen immediately for later analysis. Whenever possible, 10 fish of the total length classes <15 cm and 15–20 cm were sampled. In the laboratory, total length and standard length (1 mm) and total body mass (0.01 g) were recorded. Fish were cut open and internal organs were removed from the body cavity by gently detaching the mesentery tissue and cutting the pharyngeal end of the oesophagus. The non-gastro and intestinal organs were isolated carefully by removing the connecting tissues and weighed individually (0.001 g). The sex of the fish was recorded and the gutted body mass was determined (0.01 g) individually. Fish that showed signs of regurgitation were discarded prior to the analysis of stomach contents to reduce bias introduced by the fishing method. The pyloric caeca and the adjacent intestine were sectioned off the stomach prior to recording the mass (0·001 g) of the full and the empty stomach, as well as the mass of the stomach content (0.001 g).

In 2007, for all 437 stomachs collected, and in 2012, for a sub-set of 535 stomachs, contents were identified to prey species level if possible. Lengths (mm) and masses (0.001 g) of larger undigested prey organisms were obtained. An overview of samples used for later analysis is presented in Table I-I and the geographic positions of the hauls are shown in Figure I-1.

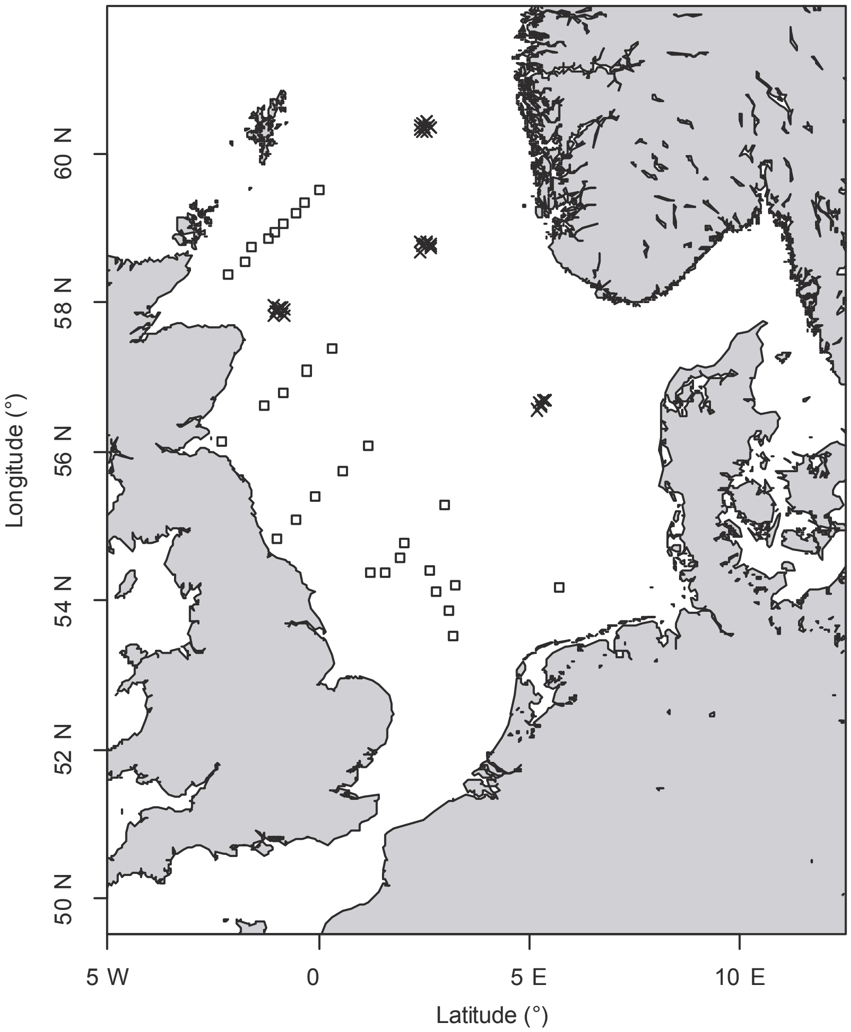

FIGURE I-1. Distribution of whiting samples, collected during research cruises in 2007 (×) and 2012 (□) within the North Sea.

DATA ANALYSIS

All statistical analyses were performed in R 3.0.2; (R Development Core Team, 2013). The length-at-age data and the empty stomach mass data were analysed applying non-linear mixed effect (NLME) models using the nlme-package 3.1-111in R (Pinheiro *et al.*, 2013) NLME models were chosen, as they allow the analysis of unbalanced data, repeated measurements on the same factor level, and can take heterogeneities into account. Moreover, NLME models provide the possibility to incorporate random factors to explain the variability between the factor levels (Lindstrom & Bates, 1990; Pinheiro & Bates, 2000; Aggrey, 2009). The total length (L_T) of whiting in relation to age (t) and the ICES roundfish area where the fish were caught were modelled for both sexes together, by fitting the von Bertalanffy growth function:

$$L_{Tij} = L\infty_i \times \left(1 - e^{-k_i(t_{ij} - t_{0i})}\right) + \varepsilon_{ij},\ \ \varepsilon_{ij} \sim N(0, \sigma^2), \tag{1}$$

where L_{Tij} (mm) is the jth observation of L_T of the $_i$th Roundfish Area (i=1,…,M;j=1,…,m$_i$). M is the total Number of areas, and m$_i$ is the total number of observations in the ith area. t_{ij} is the corresponding age (years) of whiting. $L\infty_i$, k_i and t_{0i} are the Roundfish Area-specific growth parameters. We set t_{0i} to be 0 in all Areas to assure the comparability of the models. ε_{ij} is a normally distributed error term; and σ^2 is the residual variance. We introduced sex and year as covariates to describe the variation of $L\infty_i$ and k_i between the areas (Pinheiro and Bates 2000). Thus, the parameters $L\infty_i$ and k_i are modeled as the sum of the following components:

$$\begin{array}{l} L\infty_i = \beta_1 + \gamma_1 x_{1i} + \gamma_3 x_{2i} + \gamma_5 x_{1i} x_{2i} + b_{1i}, \\ k_i = \beta_2 + \gamma_2 x_{1i} + \gamma_4 x_{2i} + \gamma_6 x_{1i} x_{2i} + b_{2i}, \end{array} \quad x_{1i} \begin{cases} -1, year\ i = 2007, \\ 1, year\ i = 2012, \end{cases} \quad x_{2i} \begin{cases} -1, sex\ i = females, \\ 1, sex\ i = males, \end{cases} \tag{2}$$

where β_1 and β_2 are fixed effects parameters equal for all Roundfish Areas, that describe the average maximum length $L\infty_i$ (intercept) and parameter k_i (intercept). The binary variables x_{1i} and x_{2i} define the covariates year and sex. γ_1 and γ_2 are the main effect of the year on $L\infty_i$ ($L\infty$ Year) and k_i (k Year); γ_3 and γ_4 are the main effect of sex on $L\infty_i$ ($L\infty$ Sex) and k_i (k Sex), and γ_5 and γ_6 represent the year-sex interaction effect on $L\infty_i$ ($L\infty$ Year:Sex) and k_i (k Year:Sex). In addition, β_1 and β_2, γ_1 and $\gamma_2$represent the $L\infty_i$ and k_i for female whiting from 2007 and 2012, respectively; γ_3 and γ_4, γ_5 and $\gamma_6$represent the $L\infty_i$ and k_i for male whiting from 2007 and 2012, respectively; b_{1i} and b_{2i} are random effects parameters of area i, which represent the deviation of the Roundfish Area - specific parameters from the population average (Lindstrom and Bates 1990; Pinheiro and Bates 2000, Zuur et al., 2009). The mass of the digestive tract affects the metabolic costs in fishes (Goolish and Adelman, 1988). Thus, we analysed the empty stomach masses (M_{ES}) of whiting, based on the assumption that the M_{ES} is a first approximation to sex-specific differences in the metabolic costs. We modelled the M_{ES} as a power function of total length:

$$M_{ESij} = a_i\, LT_{ij}^{\ r_i} + \varepsilon_{ij},\ \varepsilon_{ij} \sim N(o, \sigma^2), \tag{3}$$

where $M_{ES_{ij}}$ (g) is the jth observation of the M_{ES} of the ith station (i=1,…,M;j=1,…,mi). M is the total number of stations, and mi is the total number of observations in the ith station. LT_{ij} is the corresponding total fish length (mm) of whiting. a_i and r_i are the multiplier and the exponent of the power function. Again, εij is a normally distributed error term and σ^2 is the residual variance. We also introduced year and sex as covariates and the parameters a_i and r_i are modelled as follows:

$$\begin{array}{l} a_i = \beta_1 + \gamma_1 x_{1i} + \gamma_3 x_{2i} + \gamma_5 x_{1i} x_{2i} + b_{1i}, \\ r_i = \beta_2 + \gamma_2 x_{1i} + \gamma_4 x_{2i} + \gamma_6 x_{1i} x_{2i} + b_{2i}, \end{array} \quad x_{1i} \begin{cases} -1, year\ i = 2007, \\ 1, year\ i = 2012, \end{cases} \quad x_{2i} \begin{cases} -1, sex\ i = females, \\ 1, sex\ i = males, \end{cases} \tag{4}$$

where β_1 and β_2 are fixed effects parameters equal for all stations, that describe the average maximum a_i (intercept) and parameter r_i (intercept). The binary variables x_{1i} and x_{2i} define the covariates year and sex. γ_1 and γ_2 are the main effect of the year on a_i (a Year) and r_i (r Year); γ_3 and γ_4 are the main effect of sex on a_i (a Sex) and r_i (r Sex), and γ_5 and γ_6 represent the year - sex interaction effect on a_i (a Year:Sex) and r_i (r Year:Sex). In addition, β_1 and β_2, γ_1 and $\gamma_2$represent the a_i and r_i for female whiting from 2007 and 2012, respectively; γ_3 and γ_4, γ_5 and $\gamma_6$represent the a_i and r_i for male whiting from 2007 and 2012, respectively; b_{1i} and b_{2i} are random effects parameters of the station i, which represent the deviation of the station - specific parameters from the population average (Lindstrom & Bates 1990; Pinheiro and Bates 2000, Zuur *et al.*, 2009).

To examine the relationship between the total body mass (M_{TB}) and the total length (L_{T}) of male and female whiting, we applied nonlinear regression on the IBTS length- and mass-at-age data, using the nls function of the stats-package (version 3.0.2; R Core Team 2013).

The M_{TB} of the fish was described by: $M_{TB} = q\ LT^b$, where the isometric growth exponent b of the L_T was set to 3, to allow the comparison of annual and sex-specific changes in the coefficient q, which reflects the condition of the fish, while neutralising the influence of parameter b. The application is fully described in Bates & Watts (2008). To test for statistical differences in the length - M_{TB} relationships between the year sampled and the sex of whiting length and mass was logarithmised and a linear model with b=3 was fitted to the data. An ANOVA was applied on the linear double logarithmic length-mass relationship.
To compare the masses of the liver (M_L) of females and males on a statistical basis, M_L expressed as percentage of the total body mass (M_{LREL}) were pooled according to 5 cm length groups and either a Welch Two Sample t-test or a Wilcoxon rank - sum test with continuity correction were applied, depending on normality and variance structure of the pooled samples.

TABLE I-I. Number of stomachs analysed in 2007 and 2012 in the North Sea, by year, sex and length of whiting.

	2007				2012			
	Females		Males		Females		Males	
LT class (cm)	N_{total}	N_{PC}	N_{total}	N_{PC}	N_{total}	N_{PC}	N_{total}	N_{PC}
< 15					28	10	15	10
15- 19.9					58	10	64	17
20- 24.9	45	45	63	63	125	11	130	14
25- 29.9	99	99	91	91	134	49	159	66
30- 34.9	65	65	45	45	194	123	126	70
35- 39.9	18	18	8	8	105	90	15	11
> 40	3	3			42	55		
Total	230	230	207	207	686	347	509	188

N_{total} the total number of stomachs; N_{PC} number of stomachs used for prey composition analysis

To analyse the diet composition of whiting, the subsample of 972 fish, where stomach contents were analysed to species level, were pooled in 5 cm length classes and prey items were assigned to the following seven categories: sandeels, clupeids, Norway pout, other gadidae, other fish prey, non-fish prey and unknown prey. Relative mass proportions of each prey category were then compared between males and females. To test for statistical differences in the diet composition Wilcoxon rank - sum tests were applied to compare the mean relative proportions of each prey group based on the variabilities between the stations.
To quantify the feeding of whiting in the North Sea we used the total fullness index (TFI), the proportion of empty stomachs, and the amount of food in stomachs of feeding fish expressed as percentage of total fish body mass, separately. The mass of the stomach content, expressed in mg, as percentage of total, or gutted body mass, exhibited a non-Gaussian distribution, together with increasing variance with increasing fish size as well as non-normal distribution

of errors. Therefore, non-parametric statistics were used to analyse possible differences between male and female whiting.

The TFI accounts for differences in stomach contents of feeding and non-feeding fish caused by different fish length and is determined by: $TFI = (10^4\ M_{SC})\ (L^3)^{-1}$, where the parameter M_{SC} is the total mass of stomach content (0.001 g) and L is the total body length of the fish (mm). The TFI is estimated for both, fish with food in the stomach and fish with empty stomachs. We tested for differences in the TFI between the sexes and the year/quarter sampled, applying a Kruskal–Wallis rank sum test, followed by a post-hoc paired Wilcoxon rank-sum test.

In addition, the proportion of empty stomachs in whiting samples were analysed separately from the mass of the stomach content of the nonempty stomachs, since the act of not feeding or feeding was considered additionally, to the amount of food consumed (Stefánsson and Pálsson 1997, Waiwood *et al.* 1991). We performed χ^2-tests on proportions of empty stomach pooled in 5 cm length classes to analyse differences in the percentages of empty stomach between males and females. To compare the mass of the stomach content as percentage of the total body mass, stomachs were pooled according to 5 cm length classes and Wilcoxon rank-sum tests were applied on the pooled samples to test for differences between male and female whiting. For stomach and liver analyses, individual data from the research cruises in 2007 and 2012 were not spatially analysed, but pooled for all stations together. The spatial effect of the sampling station on mass of the stomach content, mass of the empty stomach, and the liver mass of whiting is assumed to be equal for both sexes, since the distribution of male and female whiting on the stations in 2007 and 2012 showed no significant difference (Wilcoxon rank - sum test, W= 20016, n_1= n_2=208, P> 0.05).

RESULTS

GROWTH DIFFERENCES

Mean total body length- and body mass-at-age of whiting of both sexes were lower in 2007 compared with 2012. On average, a 6 year-old female was 1.5 times heavier and 1.1 times larger in 2012 than in 2007. In both years, the total body mass and total body length of female whiting were higher than of male whiting. Mean body mass- and length- at-age 5 years were 1.7 and 1.2 times higher in females than in males of the same age in 2007, as well as in 2012 (Table I-II).

TABLE I-II. Mean total length (L_T) and total body mass (M_{TB}) at age of North Sea whiting in first quarters of 2007 and 2012, obtained from the ICES North Sea International Bottom Trawl Survey dataset

	2007				2012			
	Females		Males		Females		Males	
Age (years)	L_T (cm)	M_{TB} (g)	L_T (cm)	M_{TB} (g)	L_T (cm)	M_{TB} (g)	L_T (cm)	M_{TB} (g)
1	16.4	34.6	16.6	35.0	16.9	38.1	16.5	36.3
2	23.3	106.4	21.1	72.9	24.0	114.2	22.0	86.2
3	29.2	219.6	26.2	140.9	30.1	242.8	26.8	164.1
4	33.0	306.2	28.1	180.8	34.8	391.4	29.9	229.5
5	34.1	331.4	29.3	200.1	37.9	502.5	32.4	288.0
6	34.9	374.2	31.1	268.8	39.4	574.4	34.4	362.3
7	35.9	404.2	31.7	266.1	40.8	605.9	35.7	397.5

The length-at-age of female and male whiting was best described by a von Bertalanffy growth function fitted to the NS-IBTS data from 2007 and 2012, using the varPower (Pinheiro & Bates, 2000) variance function (Fig. I-2). The t-statistics of the NLME model fitted to the length-at-age of whiting indicated a significant effect of year (t=−6.22, d.f. = 6040, P<0.001) and sex (t =3.19, d.f. = 6040, P<0.01) on the parameter k of the von Bertalanffy growth curve fitted. Mean asymptotic length ($L\infty$) significantly differed between the years (t =12.10, d.f. = 6040, P<0.001), the sex (t=−12.71, d.f. = 6040, P<0.001) and the interaction of both effects (t=−4.19, d.f. = 6040, P<0.001). The estimated $L\infty$ of females was 348 mm in 2007 and 392 mm in 2012. The corresponding $L\infty$ of males were 307 and 329 mm, respectively (Table I-III). Additionally, linear regression was applied to the observed length-at-age *v.* the predicted values from the model. The coefficients of determination for female and male whiting in the 2007 sub-set were 0.71 ($F_{2,1277}$ =3067, P<0.001) and 0·68 ($F_{2,1067}$ =2307, P<0.001) and in the 2012 sub-set, r^2 was 0.72 ($F_{2,2079}$ =5304, P<0.001) and 0·71($F_{2,1627}$ =3930, P<0.001), respectively. The residuals of the model showed normal distribution and homogeneity of variances.

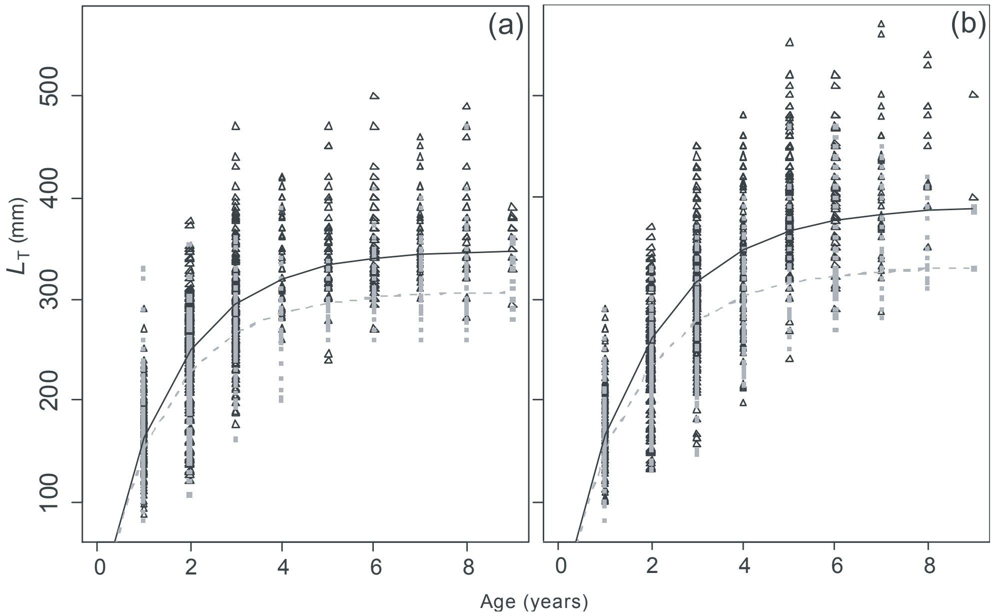

FIGURE I-2. Total length (L_T) at age of female (black triangles) and male (grey dots) whiting, obtained from 1st quarter North Sea IBTS data (a) 2007 and (b) 2012. Lines represent predicted L_T (mm) of male (dashed line) and female (solid line) received from the applied NLME- model (Table I -III).

TABLE I-III. Von Bertalanffy growth parameters and S.E. estimates from the nonlinear mixed effect model, fitted to whiting length-at-age data of the 1st quarters 2007 and 2012, obtained from the ICES North Sea IBTS dataset.

Parameter	Value	S.E	*t*-Value	*P*
L∞ intercept (females 2007)	348	12	28.858	< 0.0001
L∞ Year (females 2012)	392	4	12.095	< 0.0001
L∞ Sex (males 2007)	307	3	-12.711	< 0.0001
L∞ Year :Sex (males 2012)	329	5	-4.194	< 0.0001
k (Intercept) (females 2007)	0.63	0.06	9.958	< 0.0001
k Year (females 2012)	0.55	0.01	-6.217	< 0.0001
k Sex (males 2007)	0.68	0.02	3.189	0.001
k Year:Sex (males 2012)	0.64	0.02	0.471	0.637
$\sigma b\ ^2 k$	0.03098			
$\sigma b\ ^2$Lmax	1093.56			
$\sigma\ ^2$	1434.18			
d.f.	6040			
AIC	61027.46			
BIC	61121.36			
logLik	-30499.73			

The model was fitted by restricted maximum likelihood (REML). *L∞* = maximum total length (mm); *k* = bertalanffy growth parameter; σ2 = residual *length* variance; σb2 = the area variance in *Linf and k* within the population; AIC = Akaike information criterion; BIC = Bayesian information criterion; LogLik = log-likelihood.

DIFFERENCES IN THE EMPTY STOMACH MASS

The differences between the mass of the empty stomach of female and male whiting were analysed, applying a NLME model to individual whiting data obtained from the small-scale field studies in 2007 and 2012. For females of 35 cm, the model predicted a 0.23 g (7%) heavier mass of the empty stomach in 2007 and a 0.4 g (10%) heavier mass of the empty stomach in 2012 than in male whiting of the same size and year. The magnitude of the differences between the sexes increased with increasing total length (Fig. I–3). The results from the *t*-statistics of the mass of the empty stomach as a power function of the total length indicated no significant effect of sex (t=−1.4, d.f. = 1598, P>0.05) or year (t=−0.5, d.f. =1598, P>0.05) on parameter a. Parameter r (slope) was significantly affected by sex (t=−2.5, d.f. =1598, P<0.05). The estimated slopes of the mass of the empty stomach as a function of total length for females were r =3.06 in 2007 and r =3.15 in 2012. The analogous slopes for males were r =2.75 and r =3.08 (Table I-IV).

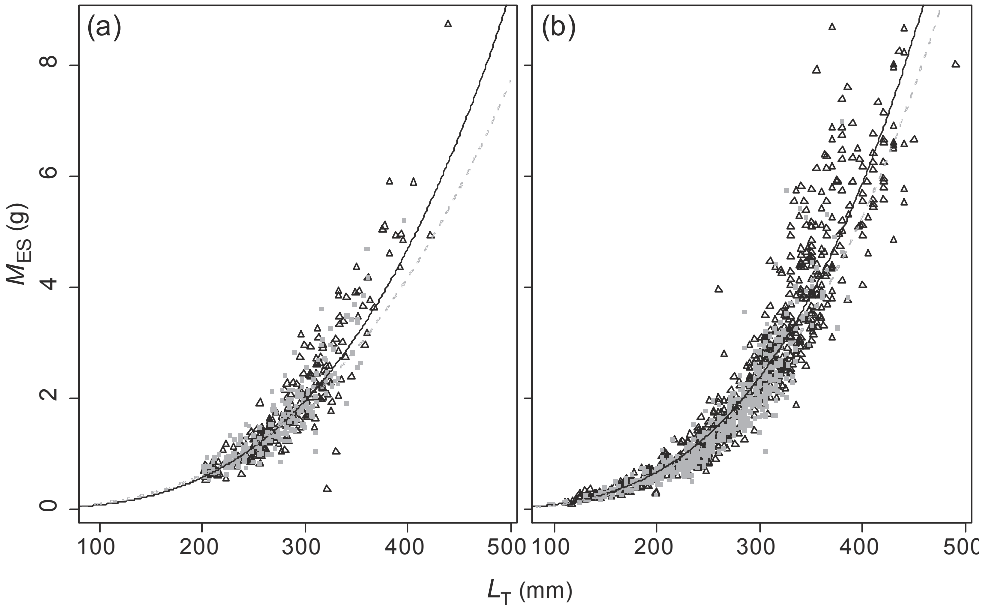

FIGURE I-3. Mass of the empty stomachs (M_{ES}) of female (black triangles) and male (grey dots) whiting, obtained from North Sea M. merlangus caught in (a) 2007 and (b) 2012. Lines represent predicted total length (L_T) of male (dashed line) and female (solid line) received from the applied NLME-model (Table I-IV).

The residuals of the model showed normal distribution and homogeneity of variances. The coefficients of determination for the linear regression applied on the observed *v*. the predicted values from the model of the mass of the empty stomach were 0.86 ($F_{2,229}$ =1441, P<0.001) for females and 0.82 ($F_{2,206}$ =912.6, P<0.001) for males in 2007. In 2012, $r2$ of applied regression for females was 0.87 ($F_{2,672}$ =4580, P<0.001) and 0.86 for males ($F_{2,500}$ =3154, P<0.001). When tested in relation to the M_{TB} of the fish, the influence of sex on mass of the empty stomach was no longer significant.

TABLE I-IV. Parameters and S.E. estimates of the nonlinear mixed effect model, fitted to empty stomach masses of whiting caught in 2012 and 2007 in the North Sea.

Parameter	Value	S.E	*t*-Value	*P*
a Intercept (females 2007)	0.0000001	0.00000003	1.812	0.070
a Year (females 2012)	0.0000001	0.00000003	-0.499	0.618
a Sex (males 2007)	0.0000003	0.00000017	1.378	0.168
a Year :Sex (males 2012)	0.0000001	0.00000017	-1.327	0.185
r (Intercept) (females 2007)	3.058	0.098	31.320	< 0.0001
r Year (females 2012)	3.151	0.101	0.922	0.356
r Sex (males 2007)	2.751	0.125	-2.453	0.014
r Year:Sex (males 2012)	3.084	0.135	1.894	0.058
б^{2}b	0.000194			
б^{2}	1.42E-16			
AIC	1191.63			
BIC	1256.18			
logLik	-583.81			

The model was fitted by restricted maximum likelihood (REML). *a* = scaling parameter; *b* = growth exponent; σ2 = residual *length* variance; σb2 = the station variance in *a and b* within the population; AIC = Akaike information criterion; BIC = Bayesian information criterion; LogLik = log-likelihood.

DIFFERENCES IN THE BODY MASS-LENGTH RELATIONSHIPS

The body mass-length relationships of female and male whiting were estimated using ICES NS-IBTS datasets of the first quarters of 2007 and 2012. The parameter *q* from the power function of total length to describe the body mass was 0.0085 for females and 0.0081 for males in 2007. In 2012, *q* was estimated at 0.0089 for females and 0.0083 for males, respectively. The body mass of female whiting of a total length of 30 cm predicted from the non-linear model was 10.8 (5%) and 16.2 g (7%) heavier than of males of the same size in 2007 and 2012, respectively (Fig. I–4). The ANOVA applied to the linear relationship of the logarithmic body mass-length data detected a significant effect of year ($F_{4,5291}$ =30.06, P<0.001) and sex ($F_{4,5291}$ =11.43, P<0.001).

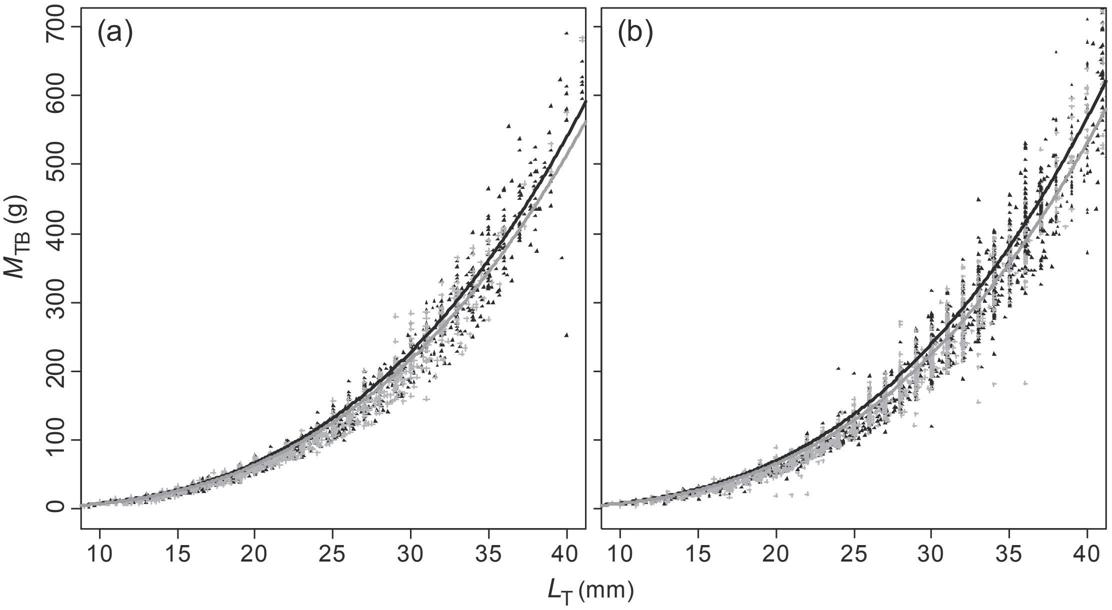

FIGURE I-4. Total body mass (M_{TB}) and total length (L_T) relationships of female (black) and male (grey) North Sea whiting obtained from North Sea International Bottom Trawl Survey data in (a) 2007 and (b) 2012. The curves were fitted by (a) female $y=0.0085x^3$ and male $y=0.0081x^3$ and (b) female $y=0.0089x^3$ and male $y=0.0083x^3$.

DIFFERENCES IN THE LIVER MASS

The relative liver mass of female whiting was higher than of the same-sized males, with a difference in the mean (and median) ranging from 0.25% (0.3%) in fish <15 cm in 2012 to 1.27% (1.35%) in 25–29.9 cm whiting in 2007 samples (Fig. I–5). Females had significantly higher *M*LREL than males of the same total length in 2007 samples in the total length groups 20–24.9 cm (Wilcoxon rank-sum test, $n1$ =45, $n2$ =63, W =1739, P<0.05), 25–29.9 cm (Wilcoxon rank-sum test, W =6833, $n1$ =91, $n2$ =99, P<0.001) and 30–34.9 cm (Wilcoxon rank-sum test, W =1887, $n1$ =45, $n2$ =65, P<0.05). In the total length group 35–39·9 cm, the livers of females were on average 0·74% heavier in proportion to body mass than the livers of males of the same size, but the difference was not significant (Wilcoxon rank-sum test, W =2.2, $n1$ =8, $n2$ =18, P>0.05), probably due to the small sample size of male whiting. In 2012 samples, the relative liver mass of both sexes increased with increasing total length, ranging from a mean of 1.45% in female and 1.21% in male whiting <15 cm to 3.8% in males and 4.6% in females of a total length of 35–39.9 cm. In all size classes, mean and median relative liver masses were higher in female than in male whiting of the same size. Due to normality and variance homogeneity, a Welch two-sample *t*-test was applied to the relative liver masses of fish<15 cm (t =1.28, d.f. = 30.3, P>0.05) and to fish of a total length of 20–24.9 cm (t =5.03, d.f. = 251.2, P<0.001), whereas Wilcoxon rank-sum tests with continuity correction were applied to data of size classes showing non-normality and heterogeneity of variances: 15–19·9 cm (W =2362, $n1$ =58, $n2$ =63, P<0·01), 25–29.9 cm (W =14161, $n1$ =134 , $n2$ =159, P<0.001), 30–34.9 cm(W =18415, $n1$ =126 , $n2$ =194, P<0.001) and 35–39.9 cm (W =991, $n1$ =15, $n2$ =105, P>0.05).

The analysis of the liver mass as percentage of the gutted body mass resulted in the same patterns as seen when using total body mass, but on average the values increased by 12 and 17% in females and 9 and 10% in males from 2007 and 2012, respectively.

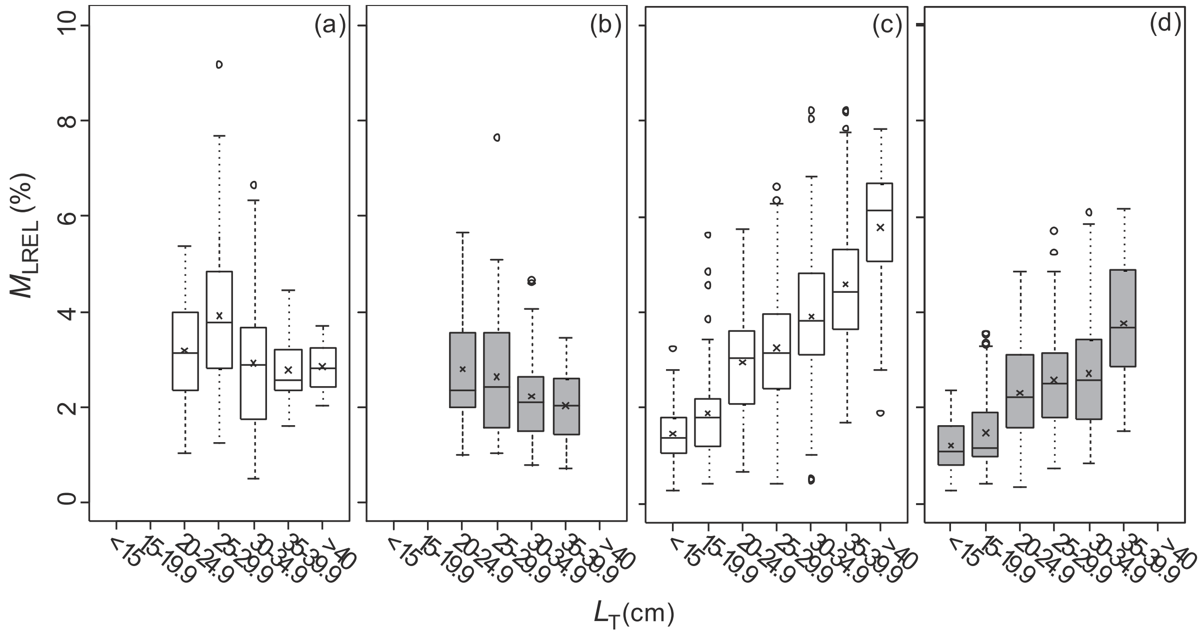

FIGURE I-5. Liver mass as percentage of total body mass (M_{LREL}) of whiting in (a,b) 2007 and (c,d) 2012 for (a, c) females and (b, d) males. Grey boxes represent males, white boxes females. ×, mean; –, median. The lower and upper ends of the box represent the 25 and 75% quartiles, respectively. The I⋯⋯I mark the most extreme data point which is not more than 1.5 times the interquartile range from the box. ○ indicate values that lie outside of this range.

DIFFERENCES IN THE DIET COMPOSITION

Male and female whiting fed mainly on fish prey with increasing amounts in the larger size classes. In 2007, the proportion of fish in diets of female and male whiting ranged from 35 and 61% in fish of a L_T of 20–24.9 cm to 82 and 63% in 35–39.9 cm fish. In 2012, the fish fraction in diets of female and male whiting extended from 59 and 11% in whiting<15 cm to an average of 94 and 87% in 35–39.9 cm fish. In 2007, non-fish prey was found to a larger extent in the size group 30–34.9 cm (females: 15%; males: 31%) compared with 2012 (females: 3%; males: 7%). The maximum percentage of non-fish prey in 2007 whiting samples was 63% for females and 39% for males in the size group of 20 24.9 cm, compared with values of 33% for female and 23% for male whiting from 2012. Clupeids, which were found in large amounts in the 2012 stomach samples of the size group 25–29.9 cm (females: 59%; males: 41%), were not present in the 2007 samples. No statistical differences in the diet composition were found between males and females (Fig. I-6).

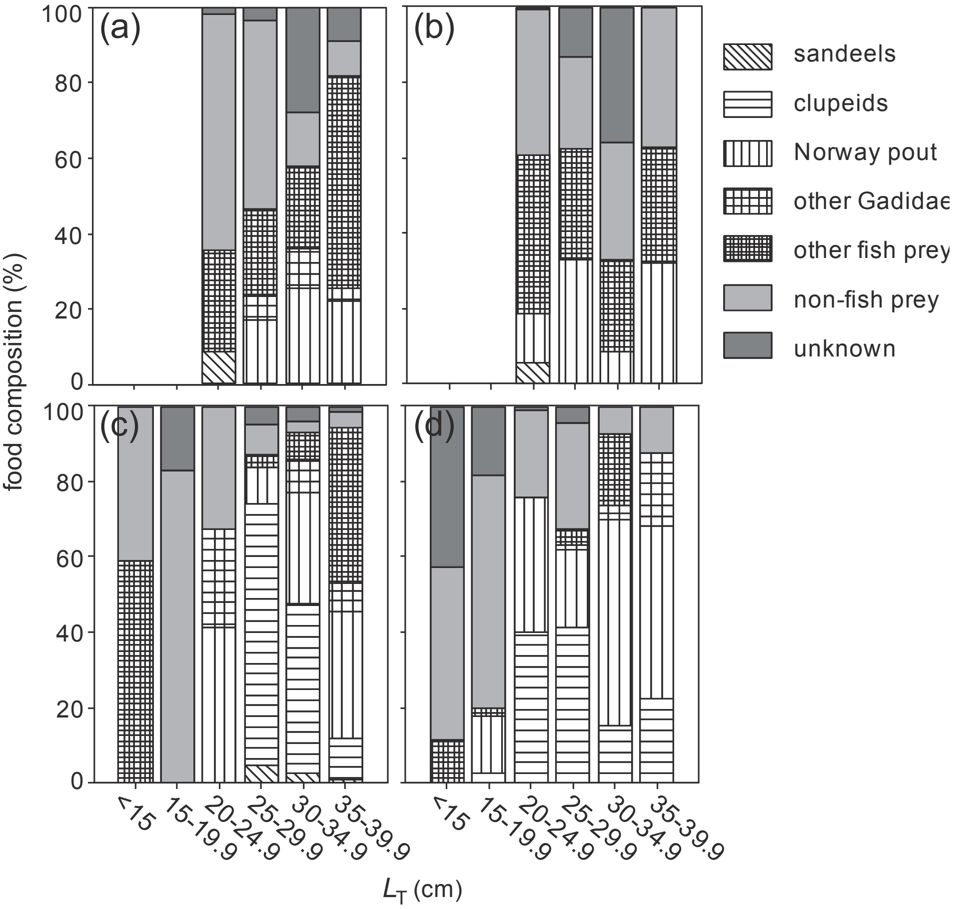

FIGURE I-6. Food composition related to total length (L_T) of (a, c) female and (b, d) male North Sea whiting from (a, b) 2007 and (c, d) 2012.

DIFFERENCES IN THE QUANTITY OF FOOD

To analyse the difference in the quantity consumed, the total fullness index (*TFI*), including feeding and non feeding fish, was compared between male and female whiting from 2007 and 2012. The mean total fullness index of females was in general higher than the mean *TFI* of males in 2007 (TFI_{females} =0.5; TFI_{males} =0.4), as well as in 2012 (TFI_{females} =0.95; TFI_{males} =0.5). The Kruskal Wallis rank-sum test of *TFI* for both sexes and both years indicated a significant difference between the groups (χ^2 = 35.25, d.f. = 3, P<0.001) and the subsequent paired Wilcoxon rank sum test with Bonferroni correction found significantly higher *TFI* for females in 2012, compared with males in 2012 (P<0·001) and males (P<0·001) and females (P<0·01) in 2007. No significant difference was detected between females and males in 2007. The analysis of the percentage of empty stomachs in North Sea whiting showed that in 2007, the average percentage of empty stomachs in both sexes was somewhat higher than in 2012 (+14% in females and +18% in males). From a size of 20 cm on, in 2007 as well as in 2012, female whiting showed similar (whiting 20–24.9 cm in 2007, both sexes: 36%) or lower amounts of empty stomachs. On average, in 2007 and 2012, stomachs were empty in 50 and 32% of males, compared with 41 and 28% of females, respectively. Female whiting had significantly fewer empty stomachs than males of the same size in the 20–24.9 cm (χ^2=4.64, d.f. =1, P<0.05) and in the 30–34.9 cm (χ^2=7.04, d.f.=1, P<0.01) total length groups in 2012 (Table I–V).

TABLE I -V. Percentages of empty stomachs in whiting samples, collected in 2007 and 2012 in the North Sea with p-values from the $\boldsymbol{x}^2$-test.

	2007			2012		
	Females	Males		Females	Males	
L_T (cm)	%Empty stomachs	%Empty stomachs	P (x^2)	%Empty stomachs	%Empty stomachs	P (x^2)
< 15				32	27	>0.05 (0.14)
15-19.9				31	20	>0.05 (1.85)
20-24.9	36	36	>0.05(0.01)	22	35	<0.05 (4.65)
25-29.9	45	48	>0.05 (0.16)	26	32	>0.05 (1.25)
30-34.9	48	56	>0.05 (0.66)	24	39	<0.01 (7.04)
35-39.9	39	63	>0.05 (1.24)	26	40	>0.05 (1.34)
> 40	33			31		

TABLE I-VI. Mean stomach content mass (M_{SC}) by year, sex and total length (L_T) of whiting sampled in 2007 and 2012 in the North Sea.

M_{SC} (g)								
	2007				2012			
	Females		Males		Females		Males	
L_T (cm)	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
< 15					0.152	0.349	0.142	0.178
15-19.9					0.242	0.486	0.401	0.834
20-24.9	0.620	0.758	0.733	1.180	0.713	1.285	0.627	1.509
25-29.9	0.866	1.452	0.651	0.987	2.003	3.696	0.850	1.869
30-34.9	1.240	2.547	0.609	1.012	4.637	7.149	1.171	2.833
35-39.9	5.600	7.113	1.351	1.907	6.993	10.54	1.885	2.668
> 40	4.022	3.510			4.637	7.231		

The mean stomach content mass of whiting in 2007 was in general lower than in 2012. Compared with 2007, female whiting from a size of 20 cm on had on average 1.3 g more food in the stomachs in 2012. The stomach content mass of analogous males was 0.29 g higher. The differences in stomach contents in 2007 were less pronounced than in 2012. In 2007, the stomach content mass of female whiting was 0.11 g lower in total length group 20–24.9 cm, but up to 3.95 g higher for the larger total length groups. In 2012, except for 15–19.9 cm fish, females fed in general more than males of the same size, exhibiting up to 5.11 g higher stomach content masses. The differences between sexes in 2012 from a size of 25 cm on were significant at the 99% level (Wilcoxon rank-sum tests; $P<0.001$). The stomach content mass as percentage of the total body mass indicated an increasing trend with total length in females in 2012, which was not observed in the 2007 samples, or in 2012 male whiting. The stomach content mas in g and as percentage of the total body mass of feeding whiting showed considerably large variability that increased with increasing size (Table I-VI and Fig. I-7). The analysis of the stomach content mass as a percentage of the gutted fish body mass resulted in the same patterns as seen when using total body mass, but on average, the values increased by 13 and 20% in female and by 9 and 13% in male whiting from 2007 and 2012, respectively.

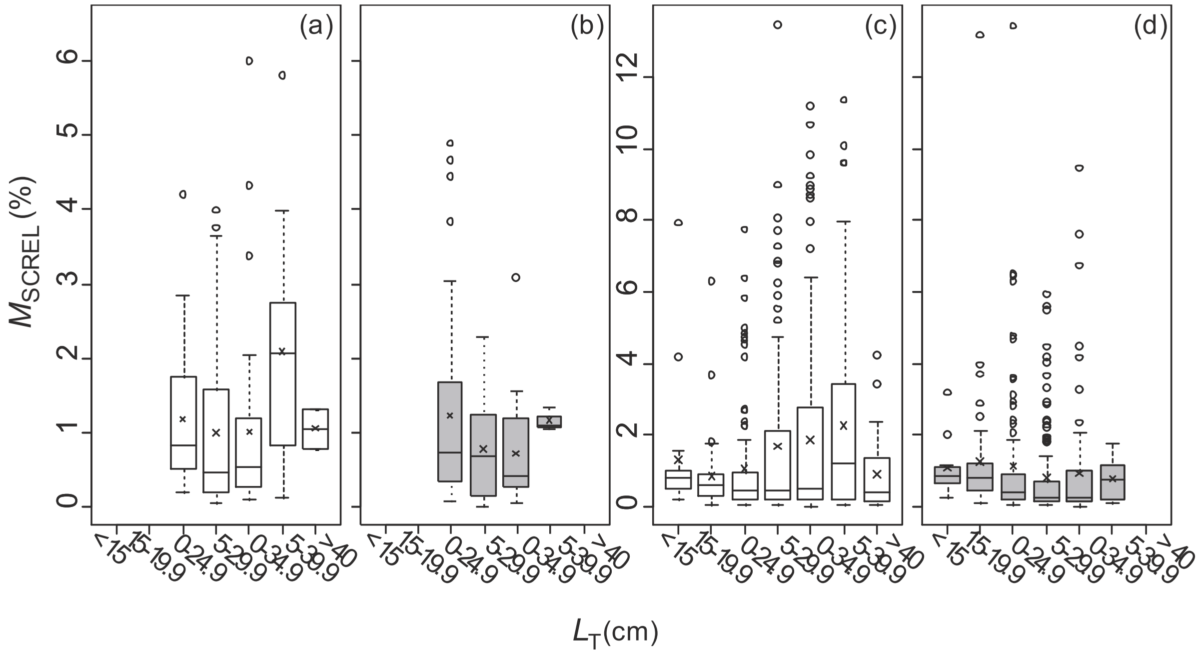

FIGURE I-7. Stomach content mass as percentage of total body mass (M_{SCREL}) of whiting in (a,b) 2007 and (c,d) 2012 for (a, c) females and (b, d) males. Grey boxes represent males, white boxes females. ×: mean; –: median. The lower and upper ends of the box represent the 25 and 75% quartiles, respectively. The |⋯⋯| mark the most extreme data point which is not more than 1·5 times the interquartile range from the box. ○indicate values that lie outside of this range. The scale of (c, d) is double the scale of (a, b).

DISCUSSION

GROWTH DIFFERENCES

In both NS-IBTS datasets from 2007 and 2012, mean total body length and mass of female whiting were higher than those of respective males of the same age. Predicted lengths from the NLME model are not only generally higher for females, but the differences also increased with age, up to a difference of 5.6 cm in 7 year-old fish in 2012. Besides these large growth differences, whiting, as most other roundfish species, does not show outer dimorphism between the sexes and has not been sampled separately in most surveys and consequently, sex-specific growth is not addressed in studies of whiting.

Larger lengths at age of female whiting have been described, however, and sexual size dimorphism was considered in research on growth and morphology of whiting in earlier studies. Messtorff (1959) described size differences of North Sea whiting ranging from 1.2 cm by the end of the first year of life to 4.3 cm differences in 7 year-old whiting. Bowers (1954), who studied whiting from Isle of Man waters, found that at the age of 7 years females were 10.5 cmlonger than males of the same age, and Desbrosses (1948) found that 6 year-old females from the French Atlantic coast were 13 cm longer than males of the same age. To summarize, female whiting grow faster than males, but this was somehow forgotten.

Faster growth in females implies that corresponding differences in the physiology or ecology between the sexes of whiting must exist to provide the excess energy for the higher growth rates in females. Three principle mechanisms are feasible: (i) dissimilarities in metabolic costs, (ii) different energy allocation patterns or (iii) unequal food intake between female and male whiting. Subsequently, to what extent present results can contribute to disentangle the role of these three mechanisms will be discussed.

DIFFERENCES IN METABOLIC COSTS

Hypothetically, higher metabolic costs of male fishes could be the cause of the observed growth differences. In general, differences in metabolic costs could result either from differences in the routine or in the activity-related metabolism (Fry, 1971). Sex-specific differences in activity levels have been described as the cause of sexual size dimorphism in numerous species in nature, mainly resulting from mating competition or parental care in one sex (Glutton-Brock & Vincent, 1991). In walleye *Sander vitreus* (Mitchill 1818), smaller length-at-age and smaller asymptotic sizes in males resulted from lower gross growth efficiencies, which in turn were determined by higher activity levels of males, mainly during the mating season (Henderson *et al.*, 2003). Higher activity levels can also be related to higher routine metabolic rates as has been shown for male Texas tarantulas *Aphonopelma anax* (Shillington, 2005) but this has not been investigated in fishes.

Routine metabolic rates of fishes are influenced by different organ systems, which also change their relative effect due to allometric growth. Besides the mass of the brain, the mass of the gut has been shown to substantially affect the metabolic costs (Goolish & Adelman, 1988). Thus, the mass of the empty stomach between male and female whiting was compared, assuming that the mass of the empty stomach can serve as a first approximation to sex-specific differences in the metabolic costs. For 2007 as well as for 2012 specimens, from a size of 30 cm onwards, the model predicted a higher mass of the empty stomach for females than males of the same length. Moreover, the differences in the mass of the empty stomach between the sexes increased with increasing fish length. The slope of the NLME model fitted to the mass of the empty stomach as a function of the total length of whiting was significantly smaller for male whiting than for females (Table IV and Fig. 3). Thus, it is hypothesized that the metabolic cost approximated by the M_{ES} is higher for female whiting. Similar results were found in dab, where the masses of the total guts of females were significantly higher than those of males of the same size (Temming & Hammer, 1994). This is somewhat contrary to expectations, as lower metabolic costs cannot explain lower growth rates, but the size of the gut not only brings additional costs but it possibly also influences gastric evacuation speed and assimilation efficiency. An increase of digestive surface leads to higher turnover rates.

Thus, individuals with a larger digestive capacity may over-compensate for the additional metabolic cost with a higher consumption enabled by a faster throughput and increased assimilation efficiency (Temming & Hammer, 1994). This hypothesis is partly supported by Rennie *et al.* (2008), who studied sex-specific bioenergetic differences in percids. While disagreeing with the Henderson *et al.* (2003) hypothesis of more active males, they found that the difference in growth efficiencies between male and female walleye was not caused by higher activity metabolism, but resulted from lower metabolic costs together with lower food consumption and food conversion efficiencies in males.

DIFFERENCES IN ENERGY ALLOCATION PATTERNS

In whiting different energy allocation patterns between sexes could result from the earlier onset of sexual maturation of males. While 16% of male whiting mature at age 1 year and 73% mature at age 2 years, only 43% of females mature at age 2 years. Expressed in body length, 50% of males mature at a total length of 19.3 cm compared with 22 cm for females (Bowers, 1954; Messtorff, 1959). The energy invested in gamete production together with potentially increased activity cost of reproductive behaviour may reduce somatic growth (Roff, 1983) and could explain the observed total body length- and mass- at-age differences in whiting. The differences in growth, however, are not limited to the age and size range where males and females differ in the reproductive investment, but increase with increasing age, leading to differences in predicted mean asymptotic length from the NLME model of 6.3 (2012) and 4.1 cm (2007) between females and males. Hence, the earlier onset of maturation in males cannot explain the higher growth rates that are observed in adult female whiting.

Another hypothetical difference in energy allocation might be reflected in different condition factors between the sexes. It has been documented that fish length and body mass growth can be decoupled in gadoids such that fish continue to grow in length without gaining mass during unfavourable conditions (Pedersen & Jobling, 1989). The body mass-length relationship might theoretically differ between the sexes, with males starting to invest their energy into gaining mass instead of length at a smaller length than females, resulting in poorer growth, but better condition in male whiting. This is not, however, supported by NS-IBTS data, where females do not have lower but rather higher body masses at a given length than males (Fig. I-4).

In gadoid species, energy is primarily stored in the liver. Thus, the liver mass is a good indicator for the individual energetic status and has been shown to be an indicator for reproductive output of a fish (Lambert & Dutil, 1997; Marshall *et al.*, 1999). A sex-specific difference in investment in the lipid storage tissue could lead to differences in growth of whiting. Male whiting might have higher liver masses than female whiting of the same length due to the allocation of energy into liver growth instead of body size growth, but the analysed liver masses of 2007 and 2012 showed that females of the same lengths always had a higher liver mass as percentage of total body mass than male whiting (Fig. I–5). A higher liver mass as percentage of total body mass in females was also documented for whiting from the Black Sea (Sağlam & Sağlam, 2012). This means that females did not only show higher growth rates, but had also larger amounts of energy stored in the livers than male whiting. Thus, the allocation of energy into liver instead of body growth in male whiting cannot explain higher growth in females, but rather supports the hypothesis that there is a substantial difference in the energy acquisition through food intake. Besides the lipid storage function, in female oviparous animals, the liver also provides a specific phospholipoglycoprotein which is needed during vitellogenesis. The hepatocytes produce vitellogenin, a precursor of the yolk, prior to spawning, which is then incorporated into the eggs (Plack *et al.*, 1971, van Bohemen *et al.*, 1981). In 2012, the timing of the sampling was April, within the spawning period of whiting, which may last from January until July in the North Sea. Since batch spawning female whiting produce eggs continually for a period of up to 10 weeks, the liver mass of the April samples might partly reflect the produced vitellogenin. The energetic consequences, regarding the energy acquisition through food intake, remain the same, however, no matter which constituent the liver consists of.

DIFFERENCES IN ENERGY UPTAKE

Sex-specific differences in feeding habits and resulting adaptations are widespread in nature, and selection for niche divergence might account considerably for the evolution of sexual dimorphism (Darwin, 1871). Thus, the most likely explanation for the sex-specific growth rates are differences in the energy uptake levels, which in turn could result from different amounts of food or differences in the quality and energy content of the prey. Numerous studies describe sex-specific diets in mammals, reptiles and birds (Houston & Shine, 1993) but studies on sex-specific diet composition of marine teleosts are rare. Nevertheless, Temming & Hammer (1994) compared the diet composition of male and female dab and found a sex-specific difference, where females had higher proportions of ophiuroids in their diet than respective males. The diet composition of whiting did not show a significant difference between the sexes (Fig. I–6). The present results suggest that the food quality, which could lead to a difference in energy intake between males and females due to different prey species, is not the origin of sexual size dimorphism in whiting.

Following from the above, the most direct and most likely explanation is that differences in the total amount of food ingested by males and females lead to the observed sexual dimorphism in growth rates. The present data showed that females had lower percentages of empty stomachs than males of the same size, with on average 11.5% fewer empty stomachs in female whiting of a size of 25–39.9 cm than respective males (Table I–V). Moreover, the mean stomach content mass of female whiting from a size of 25 cm on were generally higher, ranging from 0.2 g in 2007 25–29.9 cm females samples to 5.1 g in 2012 35–39.9 cm females, than that of male whiting of the same size (Table I-VI). These results agree with other field studies on sex-specific food intake in fish displaying sexual size dimorphism (Lozan, 1992; Temming & Hammer, 1994) and with results from a bioenergetic modelling approach to explain sexual size dimorphism in percids, where males exhibited lower food consumption compared to females (Rennie *et al.*, 2008). The lower feeding activity in male whiting could be a result of an evolutionarily developed behavioural aspect: males that reduce their feeding time investment and increase their reproductive success by increasing the time spent searching for, and spawning as close as possible to a female are evolutionarily favoured (Parker, 1974). This is supported by the sex-specific behaviour of whiting, described by Hawkins (1970), during spawning in the laboratory. Males were in general continually active, displaying extensive territorial aggression and active courting behaviour, whereas females did not show an increased activity during that period. According to these aquarium observations and the timing of the sampling in April 2012, within the spawning season of whiting, the lower stomach content masses could result from increased territorial behaviour in males, which in turn decreased the time available for feeding in male whiting. Under laboratory conditions, female cod consumed greater quantities of food than males (Fordham & Trippel, 1999). These authors also found that both sexes stop feeding during spawning. This interruption of feeding cannot be confirmed for whiting from the data employed in this study, since both males and females sampled in March 2012 within the spawning season showed clear feeding activity. Likewise, Messtorff (1959) found that whiting continues feeding during spawning activity. Hence, spawning-related periods without food intake also cannot be considered as a factor contributing to the observed growth differences.

DIFFERENCES BETWEEN SAMPLES FROM 2007 AND 2012

The differences between whiting of both sexes between 2007 and 2012 were evident in most investigated metrics of this study: the NS-IBTS data revealed smaller lengths at age in 2007 compared with 2012. Whiting collected during the non-IBTS research cruises showed that fish from the third quarter in 2007 had lower liver masses expressed as percentage of the total body mass compared with first quarter samples from 2012. These results can be explained by the energetic losses due to spawning activity. Similar results were found by Sağlam & Sağlam (2012) for Black Sea whiting, where the liver mass expressed as percentage of the total body mass was low from May to October, compared with the rest of the year. Additionally, in the samples from 2007, the proportion of empty stomachs was considerably higher and the stomach contents in 2007 were somewhat lower than in 2012, with most pronounced differences in female whiting >25 cm total length, where the mean stomach content mass of individuals from 2012 was almost twice as high as compared with 2007. Moreover, in the 2007 samples, the percentage of fish in the diet of male and female whiting did not exceed a value of 82% in females of >35 cm total length. In males of that size, as well as in smaller whiting, the diet consisted of only *c*. 60% fish. This is in contrast with whiting from 2012, where in both sexes, 90% of the diet of whiting>30 cm was fish. This is in agreement with studies about the general food preferences of adult whiting (Hislop *et al.*, 1991).

Principally, the observed differences could be explained either as spatial, interannual or seasonal effects but due to a lack of samples from other quarters this cannot be resolved with present data. The ICES year of the stomach data (http://ecosystemdata.ices.dk/stomachdata/Webservices.aspx), however, can provide helpful information about the usual effect of time and space on the stomach contents of North Sea whiting but this dataset is not separated by sex. In 1981, as well as in 1991, whiting showed higher percentages of empty stomachs in the third quarter compared with the first quarter. Moreover, the stomach content mass in both years is higher in third quarter samples than in first quarters (Hislop *et al.*, 1997; Daan, 1989). For this study, these findings imply that in third quarters whiting usually feeds more than in first quarters, and the results, considering the lower energy uptake levels found in 2007, compared with 2012 samples, are presumably an interannual effect, rather than of the season sampled. In 1981, as well as in 1991, in respective quarters and ICES roundfish areas, fish is the dominant component of the diet of adult whiting. Adult whiting is almost exclusively piscivorous and a very selective feeder (Hislop *et al.*, 1991). In general, the diet of whiting from the northern North Sea consists mainly of *Trisopterus* sp., while further south clupeids (*C. harengus* and *S. sprattus*) become more important in the diet. Moreover, in all areas of the North Sea in third quarters, sandeels are a major component of adult whiting diet (Hislop *et al.*, 1997; Daan, 1989). If these prey species are not available, whiting reduces feeding rates as is indicated by frequent samples with high proportions of empty stomachs. Considering the present data on whiting for 2007 and 2012, where the differences between the whiting of the 2 years and quarters are mainly prominent in fish>25 cm, it can be assumed that it is likely that the observed discrepancies, to some extent, result from differences in the availability of prey fish in both years. In the North Sea, the abundance of Norway pout, herring, sprat and sandeels simultaneously declined at the beginning of the 2000s, followed by an increase at the end of that decade (Dickey-Collas *et al.*, 2013). Hence, the low amounts of fish in the stomach samples of 2007 are probably due to the low prey fish availability in the North Sea at that time. Whiting in 2007 showed 4 (for females) and 2 cm (for males) smaller mean asymptotic length compared with 2012 (Table I-III and Fig. I-2). There was not, however, an appreciable decrease in the condition of whiting in 2007 compared with 2012. In contradiction to these findings, cod from the Baltic Sea was shown to evolve a decrease in condition during unfavourable feeding circumstances (Eero *et al.*, 2011). The present results indicate that whiting during prolonged periods with low food availability, unlike other gadoids, respond with reduced length growth rates, while the condition of the fish varies only to a small extent. This study shows that higher somatic growth rates supplemented by larger energy reserves stored in the liver in adult female whiting probably result from higher food intake rates, as indicated by higher masses of the stomach content. Additionally, results indicate heavier empty stomach masses in females, which might suggest higher gastric assimilation capacity and evacuation rates in female whiting than in males of the same length. This hypothesis needs to be tested in physiological studies, where the effect of sex should be considered explicitly.

The present findings could also have implications for stock assessment and management of North Sea whiting. Currently, sex is not considered explicitly and input data such as M_{TB} at age and maturity at age refer to both sexes. Consequently, the outputs, such as fishing mortalities at age, are not separated. Moreover, the assessment model does not include age–length or body-mass-at-age keys that are estimated separately for by-catch (ICES, 2012b). Faster growing females will grow earlier into the selection ranges of commercial gear and hence, a higher fishing mortality can be expected. In contrast, the total mortality could be higher in males, because they could have a higher proportion in the discards or are preyed upon more heavily. Such differences in mortalities could in turn influence the reproductive output of the stock. Moreover, the mean total body mass, the length-at-age and the calculated total allowable catches (TAC) could be biased as a result of a changing sex ratio in North Sea whiting stock as seen in North Sea plaice (Kell & Bromley, 2004) and in north-east Arctic cod (Marshall *et al.*, 2006). The pronounced differences in consumption and growth could also have an effect on multispecies assessments, if possible changes in the sex ratios since the last stomach sampling in 1991 remain unaccounted for.

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Chapter II

Forage fish controlling population dynamics of North Sea whiting—evidence from field data and bioenergetics modelling

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ABSTRACT

During the last four decades the North Sea ecosystem went through pronounced ecological changes. In the early 2000s within large parts of the North Sea several fish stocks suffered from successive years of recruitment failure, namely herring, sprat, sandeels and Norway pout. Whiting *Merlangius merlangus* is one of the most important predators in the North Sea ecosystem and moreover known to be almost exclusively piscivorous with low proportions of invertebrates in its adult diet. Its abundance has fluctuated dramatically throughout recent decades.

This lead us to our hypothesis, that a shortage in forage fish should lead most likely to negative effects on growth or condition of such a predator that relies on a few dominant prey fish species. Here we used ICES IBTS time series data on forage fish abundance and whiting growth and condition to analyse contrasting periods with high and low forage fish availability. We found a simultaneous decrease in forage fish availability and whiting growth in the period from 2000-2007 and a subsequent parallel increase in prey abundance and growth after about 2008. We supported this finding with additional analysis of multiple sets of stomach data collected in the 80s, 90s and 2012 in comparison to data collected during, the period 2000 to 2007. In the period of low forage fish availability (2000-2007) the mean stomach content masss were substantially lower (on average 60% less) than in the reference periods. A simple bioenergetic calculation revealed that the lower amount of food consumed could be responsible for the magnitude of the decrease in growth. We discuss the implications of these findings for single and multi-species population modelling.

INTRODUCTION

Energy is the fuel of all ecosystems. Along with matter the amount of available energy ultimately limits the carrying capacity of a habitat and determines population sizes and population growth within a habitat. The availability of energy for species within an ecosystem in turn is regulated via different mechanisms such as trophic level specific heat loss or inter- and intra-specific competition. As a result, on an individual basis the energy available is limited. In response, the available energy has to be allocated between the competing processes of maintenance, growth, energy storage and reproduction. If energy resources are low trade-offs between those three processes will occur (Fitzpatrick, 1973; Congdon *et al.*, 1982).

In terrestrial ecosystems a lot of work has been carried out to examine the influence of low energy resources i. e. low prey abundance on energy allocation trade-offs. Laboratory experiments showed that limited food availability in the Marbled Salamander *Ambystoma opacum* Gravenhorst 1807 led to lower growth rates and lipid levels, lower proportions of total lipids and lower clutch sizes compared to individuals with higher food supply. Moreover, the proportion of reproductive individuals was reduced by food limitation (Scott & Fore, 1995). Studies of a natural population of Texan Side-Blotched Lizards *Uta stansburiana* Baird & Girard 1852 showed that low prey availability induced a trade- off between growth and reproduction (Tinkle, 1967).

In marine ecosystems the life history of fish has been shown to be food dependant (e.g. Shulman, 1999). The growth of the coral reef fish *Pomacentrus amboinensis* Bleeker 1868 is limited by food availability (Jones, 1986). In planktivorous fish large interannual variation in the lipid concentrations in the muscle are caused by varying abundance of plankton (Shulman, 1972; Luts, 1986 as cited in Shulman & Love, 1999). Comparing food regimes between habitats Shulman (1972 as cited in Shulman & Love, 1999) found that the fatness of red mullet *Mullus barbatus* L. 1758 and anchovy *Engraulis encrasicolus* (L. 1758) from areas prevailing high food abundances was higher than the fatness of their conspecifics sampled in areas with lower food availability. Atlantic cod *Gadus morhua* L. 1758 from the Faroe Bank, a highly productive area prevailing especially large quantities of food are in comparison to other Atlantic cod stocks, considerably more corpulent with especially large livers and white muscle tissue containing greater concentrations of protein (Love *et al.*, 1974). Thus, the profound influence of food on many species of marine fish has been well documented. However, studies within one ecosystem comparing different feeding regimes on a larger temporary scale are rather rare. An example of the drastic impact of a change in the feeding regime can be found in sprat sprat *Sprattus sprattus* (L. 1758) and anchovy in the Black Sea. During the 1980s the competition with jellyfish led to a decrease in the food availability for sprat and anchovy and caused a dramatic reduction in the individual fatness and the stock biomass. (Shulman, 1996 as cited in Shulman & Love, 1999; Minyuk *et al.*, 1997 as cited in Shulman & Love, 1999; Studenikina *et al.*, 1992).

In this study we investigate the influence of changing feeding regimes on a predator in the North Sea ecosystem. During the last four decades the North Sea communities experienced broad ecological changes: variations in hydrographical conditions, temperature, primary and secondary producers, as well as in higher trophic levels (Reid *et al.*, 2001; Beaugrand *et al.*, 2002; Weierman *et al.*, 2005). Likewise, the North Sea forage fish communities, feeding on zooplankton and being in turn preyed on by higher trophic levels (Alder *et al.*, 2008), have also underwent substantial changes during the last 40 years (Dickey-

Collas *et al.*, 2013; Engelhard *et al.*, 2014). Regarding the first half of the 2000s in the North Sea a number of forage fish species (sandeels *Ammodytes* spp. L. 1758, Norway pout *Trisopterus esmarkii* (Nilsson 1855), herring *Clupea harengus* L. 1758 and sprat) showed a marked decline in their spawning stock biomass and produced some of the smallest year classes on record. The spawning stock biomass of sandeels was low from 2000 to 2006, since 2002 herring and sprat produced below average year classes and the recruitment of Norway pout reached historic minima in 2003 and 2004. From 2007 onwards, the spawning stocks of sandeels, sprat and Norway pout increased again and Norway pout stock produced very strong year classes in 2009 and 2012 (ICES, 2013).

Whiting *Merlangius merlangus* (L. 1758) is widely spread and one of the dominating species in the demersal fish community of the North Sea ecosystem (Knijn *et al*., 1993; Greenstreet & Hall, 1996). The population of whiting reached an all-time high during the so called “gadoid outburst” in the 1960s and 70s and decreased continuously thereafter. Nevertheless, the population of whiting represents a substantial proportion of the piscivorous demersal predator community in the North Sea ecosystem, which is caught in large numbers in mixed demersal fisheries. Whiting is a highly selective feeder, which from a size of 25 cm on is almost exclusively piscivorous. Moreover, whiting relies mainly on few commercial important species, such as common brown shrimp *Crangon crangon* L. 1758 as a juvenile, and on sandeels, Norway pout, herring and sprat as an adult (Hislop *et al.*, 1991; Knijn *et al.*, 1993). With an annual consumption of approximately 700 000 tonnes sandeel, whiting consumes more biomass than the total annual landings of sandeel since 2003 accounted for (ICES, unpubl. data cited in Temming *et al.*, 2004). The predation of whiting on other fish focuses mainly on 0- and I - groups. Temming *et al.* (2007) showed that whiting in the North Sea is capable of wiping out a substantial fraction of a year class of cod within only a few days. Thus, whiting can be considered as highly sensitive to changes in the fish community regarding its few preferred prey species.

The aim of this study was to evaluate which influence the changes in the marine food web, in particular in the forage fish community in early 2000s had on whiting. The period from 2000 to 2007 was characterised by low prey availability while in contrast the years from 2008 onwards represent a period of sufficient food supply. Hence, we hypothesise that the shortages in forage fish have led to negative effects on condition and/ or growth of whiting.
Here, we evaluate the temporal development of:

- the length-at-age of North Sea whiting
- the prey abundance in the North Sea
- the stomach contents of whiting during different feeding regimes
- the condition of whiting during different feeding regimes

Moreover, we test the hypothesis of a lack of food induced decrease in the length-at-age of whiting by applying a bioenergetics model. Finally, we discuss possible alternative mechanisms (temperature, fishing) that could have led to the observed differences in whiting.

MATERIALS AND METHODS

DATA SOURCES AND SAMPLING

The present study is based on four different North Sea datasets:

(1) Data from the DAtabase of TRAwling Survey (DATRAS, downloaded on 25/11/2014) database containing data from the North Sea International bottom trawl survey (NS-IBTS) which is coordinated by the International Council for Exploration of the Sea (ICES). The IBTS is a large-scale survey which is based on 1–2 randomly located 30 minutes GOV (Grande overture vertical) trawl hauls in each of the statistical rectangles (30x 30 nm). A detailed survey description can be found in the Manual for the International Bottom Trawl Surveys (ICES, 2012).

(2) Data on stomach content masses from the German small scale bottom trawl survey (GSBTS) covering four 10 x 10 nm boxes in the North Sea. A total of 6-8 GOV trawl hauls each with approximately 30 minutes towing time within each box were carried out on each of three consecutive days per box. Detailed survey description can be found in Ehrich *et al.* (2007).

(3) Data on stomach content masses of whiting for the period 2004–2006 were derived from the integrated DAtabase and Portal for fish STOMach records (DAPSTOM) which is coordinated by the Centre for Environment, Fisheries & Aquaculture Science (Cefas). A detailed description of the data is given in Pinnegar (2014).

(4) Data on additional stomach content masses were derived from the ICES Year of the stomach data base. Fish stomachs were collected as part of an ICES initiative and detailed description of the data collection is given in the Manual for the ICES North Sea stomach sampling project in 1991 (ICES, 1991; Hislop, 1997).

Moreover, data from the output of an age-length structured Stochastic Multi-Species (SMS) model for the North Sea was used (Lewy & Vinther, 2004).

In addition, individual information on body lengths and masses, liver masses and stomach content masses of whiting was derived from two additional North Sea research cruises with the German IBTS standard vessel (Walther Herwig III) in 2007 and 2012. During both cruises the IBTS standard GOV trawl was deployed for 30 minutes, granting equal catchabilities. In 2007 fish stomachs were sampled during the German small scale bottom trawl survey (GSBTS) from four 10 x 10 nm boxes in July/ August (Ehrich *et al.,* 2007). From each haul, if possible, 5 fish of the length classes 20–24.9, 25–29.9, 30–34.9, 35–39.9 cm and >40 cm were immediately frozen at -40°C. In April 2012 whiting were caught during a research cruise in the frame of the EU-project VECTORS, covering a larger area of the North Sea, with a total of 69 trawl hauls. If possible, 10 fish of the same length classes as defined for the 2007 sampling were individually sampled and frozen immediately for later analysis. Additionally, if possible, 10 fish of the length classes <15 cm and 15–20 cm were sampled. In the laboratory from each individual fish total and standard length [1 mm] and body mass [0.01 g] were recorded, fish were sexed, gutted, internal organs were weighted [0.001 g] and empty body mass was determined [0.01 g]. Fish that showed signs of regurgitation were registered and the stomach contents were not analysed to reduce bias introduced by the fishing method. The mass [0.001 g] of the full and the empty stomach was recorded as well as the mass of the stomach content [0.001 g]. A summary of samples included in this analysis is given in table II-I.

LENGTH-AT-AGE OF WHITING

Data on the length-at-age of whiting from the 1st quarters 1990 to 2014 were derived from the DATRAS database. The mean length at a given year and roundfish area (RA) 1-7 was calculated to evaluate the trends over the period 1990 to 2014. To avoid problems with the correlation of lengths of the same cohort in consecutive years we used the length-at-age data without reference to cohorts for the analysis. To avoid seasonal bias we used only subsets of the first quarters for the analyses.

PREY ABUNDANCE

Data on prey abundance was derived from two sources. On the one hand catch (numbers) per unit effort (cpue) of forage fish species <15 cm in total length (sandeel, sprat, herring and Norway pout) in the 1st quarters 1990-2014 were extracted from the ICES DATRAS database. On the other hand numbers of forage fish (same species as above) at age one in 1st quarters were derived from the North Sea SMS model (Lewy & Vinther, 2004) output. Since the SMS model gives no spatially resolved output we calculated the sum of the numbers of forage fish. To estimate the prey abundance from the IBTS data the 1st quarter, mean cpue (numbers) was calculated for each prey species per roundfish area (RA) and year. Prey specific means for a given year were summed up per RA. The annual mean for the total North Sea was then calculated as the weighted mean over all RA weighted by to the number of rectangles each RA is composed of.

STOMACH CONTENTS & INDIVIDUAL FISH DATA

Since the ICES year of the stomach data were collected and analysed as pooled samples and since no information on individual stomach content masses is available it was decided to apply the same procedure for all other stomach data sets. Thus, for each haul and length class of whiting we calculated the average mass of the stomach content (M_{SC}) by pooling the individual samples: $M_{SC} = \frac{M_{TOT}}{N_F} \times \frac{(N_F+N_{SR}+N_R)}{N}$, where M_{TOT} is the total stomach content mass of all samples, N is the total number of whiting stomachs per haul and size class, N_F is the number of stomachs containing food, N_{SR} is the number of stomachs containing only skeletal remains and N_R is the number of stomachs regurgitated. We calculated mean M_{SC} for whiting for length classes between 25 cm and 40 cm because from 25 cm onwards whiting were considered to be predominately piscivorous (Hislop *et al.*, 1997) and < 40 cm because sample size decreased substantially in some subsets for whiting > 40 cm.

To be able to compare the data from the included size classes we calculated W_S as percentage of total body mass (M_{SCrel}). Due to the lack of information on the individual body masses of fish from the ICES subset, we calculated the average body mass of each predator size class for all datasets applying the length (L) mass (*M*) relationship $M(g) = a \times L\ (cm)^b$, where a = 0.0061 and b =3.067, calculated from research vessel surveys during the period 1997-2007 (Wilhelms, 2013). To assure the representativeness of samples we only included stomach samples with an N of 5 at the least for further analysis. If an ICES statistical rectangle was sampled more than once, M_{SCrel} was calculated weighted by the number of stomachs per haul. The average stomach content per RA was then calculated as the weighted mean M_{SCrel} of hauls within a given RA, weighted by the number of stomachs per haul. The year specific M_{SCrel} was compared on a quarter and area specific basis using a Kruskal-Wallis chi-squared test and the adjacent Wilcoxon rank sum test applying Bonferroni correction.

TABLE II-I. Number of North Sea whiting stomachs per year, quarter, roundfish area (RA) and dataset from included in the analysis.

Year	Quarter	RA	Dataset	total.N stomachs
1991	1	1	ICES_YoS	867
2012		1	IndDat	94
1991		3	ICES_YoS	313
2012		3	IndDat	200
1991		4	ICES_YoS	37
2012		4	IndDat	270
1990		6	ICES_YoS	114
1991		6	ICES_YoS	347
2012		6	IndDat	113
1991	2	4	ICES_YoS	409
2004		4	DAPSTOM	446
2005		4	DAPSTOM	428
2006		4	DAPSTOM	387
1991	3	1	ICES_YoS	2040
2007		1	IndDat	123
1991		2	ICES_YoS	764
2006		2	DAPSTOM	935
1991		3	ICES_YoS	823
1996		3	GSBTS	1402
1997		3	GSBTS	666
2007		3	IndDat	64
1991		4	ICES_YoS	534
1996		4	GSBTS	719
1997		4	GSBTS	471
2004		4	DAPSTOM	99
2006		4	DAPSTOM	1401
1991	4	2	ICES_YoS	469
2006		2	DAPSTOM	685
1991		4	ICES_YoS	138
2005		4	DAPSTOM	174
2006		4	DAPSTOM	1466

CONDITION OF WHITING

To analyse whether the condition of whiting decreased during period of low food abundance Fulton’s condition factor and the hepatosomatic index (HIS) were calculated. Fulton’s condition factor (k) was expressed as $k = 100 \times \left(\frac{W}{L^3}\right)$, where W is the somatic mass (g) and L is the total length (cm). Parameter k was calculated from 1st quarter IBTS data in the period 2000-2014 since before that time body mass was not recorded on an individual basis. A loess smoother (Cleveland, 1979; Cleveland, 1992) was fit to the annual mean k time-series for each length class to describe the variation in the condition of North Sea whiting.

Hepatosomatic index (HSI) was calculated from whiting sampled during the two research cruises in 2007 and 2012 since individual information on the liver masses were available from those fish. 2007 was considered as a year of low food abundance, 2012 as a year with sufficient food supply. *HSI* was estimated as *HSI* = 100 (LW/W), where LW and W

represent liver and somatic masses (g), respectively. Sex and length specific *HSI* were compared using Mann-Whitney Rank Sum Tests.

THE INFLUENCE OF THE FOOD CONSUMPTION ON THE GROWTH OF WHITING

To estimate the impact that decreased consumption may have had on the growth of whiting we used a simplified bioenergetics model (Temming & Herrmann, 2009). This model can estimate consumption from observed growth as described by a van Bertalanffy growth model. With the known relationship between stomach content and consumption the estimated consumption can then be transformed into the corresponding mean stomach content. This exercise was conducted to check, if the differences in the two data sets (growth and stomach content) can be related in an energetically consistent way. Hence, we tried to validate the assumption that the difference in consumed food alone can explain the observed differences in the growth of whiting. Therefore, a generalised van Bertalanffy growth function (Pauly, 1981; Temming & Herrmann, 2009) was applied to 1st quarter length-at-age data from the period 2000-2007, compared to length-at-age from the period 2008-2014, acquired from the IBTS dataset for females and males, respectively:

$$L_t = L_\infty \times \left(1 - e^{-KD(t-t_0)}\right)^{\frac{1}{D}},$$

where L_t is the total length of the fish at time t. L_∞ is the mean asymptotic total length, parameter K is the katabolic constant of the generalized van Bertalanffy function,, parameter D is related to the allometric scaling exponent (m) of anabolism/consumption as $D = b(1-m)$= 0.6 with growth exponent b=3 (Temming & Herrmann, 2009).

With parameter K fixed to 0.65, L_∞ and t_0 were estimated from the lengths at ages of whiting from the period of low prey abundance (2000-2007) in comparison to the period of sufficient food supply (2008-2014). The parameter L_∞ was converted into the mean asymptotic mass (M_∞) using a length-mass relationship: $M(g) = r \times L\ (cm)^b$, where r = 0.0061 and b =3.067, calculated from research vessel surveys during the period 1997-2007 (Wilhelms, 2013). Consumption (ΔC) per time interval Δt (month) was estimated as:

$$\Delta C = \frac{1}{K_3} bKM_\infty^{\frac{D}{b}} M_t^{\frac{a}{b}} \Delta t, \qquad (1)$$

where K_3 = 0.6 = net conversion efficiency sensu Temming & Herrmann (2009),

b = exponent of the length-mass relationship,

$D = b(1-m)$=0.6, with m=0.805 (Temming & Herrmann, 2009),

a = constant of the length- mass relationship $\frac{a}{b} = m$,

Δt = time interval in months,

M_t= mean mass of the fish during interval Δt.

The application of the model is fully described in Temming & Herrmann (2009).

The average daily consumption was then converted into the corresponding average stomach contents (S) using the relationship

$F = R\ S$^B (Jones, 1974, Temming & Herrmann, 2003), (2)

where F= feeding rate in g/h,

R = constant of the general gastric evacuation model (Jones 1974, Temming & Andersen, 1994, Andersen, 1999),

S = mean stomach content,

B = shape parameter of the general gastric evacuation model, here $B = 0.5$ (Mergardt & Temming, 1997, Andersen, 1999).

The equation above can be solved for S to allow for the conversion of the observed differences in consumption into the corresponding differences of daily average stomach contents:

$$S = \left(\frac{\Delta C}{24\,R'}\right)^{\frac{1}{B}} \tag{3}$$

RELATIONSHIP BETWEEN FORAGE FISH ABUNDANCE AND LENGTH-AT-AGE OF WHITING

To analyse the relationship between the forage fish abundance and the length-at-age of whiting, the annual numbers of age 1 prey fish from SMS model was plotted against the length-at-age of whiting age 3 to 6 from the IBTS data. Both, SMS prey abundance and whiting length-at-age were normalised $X_{norm} = \frac{X - \bar{X}}{s}$, where X is the annual mean prey abundance or length-at-age, $\bar{X}$ is the mean and s is the standard deviation over all years analysed. The 3-year running mean of normalised whiting length-at-age was plotted against the 3-year running mean of normalised prey abundance and a loess smoother (Cleveland, 1979; Cleveland, 1992) was fitted to describe the variation in the length-at-age of North Sea whiting with the prey abundance in the North Sea.

RESULTS

LENGTH-AT-AGE

In the period 2000-2007 the lengths-at-age of whiting from age 2 onwards were lowest, compared to earlier and later years. The time series of mean length-at-age of North Sea whiting showed a particular pattern for age 1 year, compared to all other ages. Besides large interannual fluctuations, the mean length-at-age 1 of whiting in the North Sea decreased substantially from 1990 to 2014. 1 year old females and males showed a steady decline in mean length with mean lengths below the long term average from 2001 onwards. The statistical comparison of the average length-at-age 1 year between 1990–1999, 2000–2007, and 2008–2014 resulted in significant differences between all three periods for females, where the mean length-at-age decreased from 17.9 cm in 1990-1999 to 16. 6 cm in 2008–2014. The average length-at-age 1 year of male whiting was significantly higher in 1990-1999, compared to 2000–2007, but between 2000–2007 and 2008–2014 no significant difference was found. The time series of ages 2 to 6 of North Sea whiting exhibited similar patterns between ages, but differed from the patterns for age class 1. The mean length-at-age 2–6 of both sexes showed mainly above average values in the period 1990 to 1999, followed by below average values from 2000 onwards until 2007. From 2008 to 2014 mean lengths at age increased again to above long term average values. The average lengths at age of whiting were significantly lower in the period 2000-2007, compared to 1990-1999 in all ages and both sexes. Female and male whiting from age 2 to 6 were on average 2.1 cm and 1.8 cm smaller in the period 2000–2007, compared to 1990–1998. The mean length-at-age 1 year of both sexes was about 1 cm lower in 2000–2007, compared to 1990–1999. This decrease was significant at the 99 % level (Fig. II-1; Table II-II).

In 2008-2014 compared to 2000-2007, the average length-at-age of 2–6 year old female and male whiting increased significantly by 3 cm and 2.2 cm respectively (pairwise Wilcoxon rank sum test; $P<0.001$). The mean length of females at age 1 decreased significantly - on average by 0.4 cm in 2008-2014, compared to 2000–2007. The comparison of the lengths at age between the periods 2008–2014 and 1990-1999 showed that female whiting had decreased by 1.8 cm at age 1, remained the same size-at-ages 2 and 3 years and had increased by 1, 2, and 2 cm at ages 4, 5 and 6 years, respectively. Males had decreased by 1.9 cm and 0.1 cm in ages one and two in 2008-2014, compared to 1990-1999, remained the same size in age 3 fish and increased by 0.8, 1 and 1 cm in individuals age 4, 5 and 6 years (Table II-III).

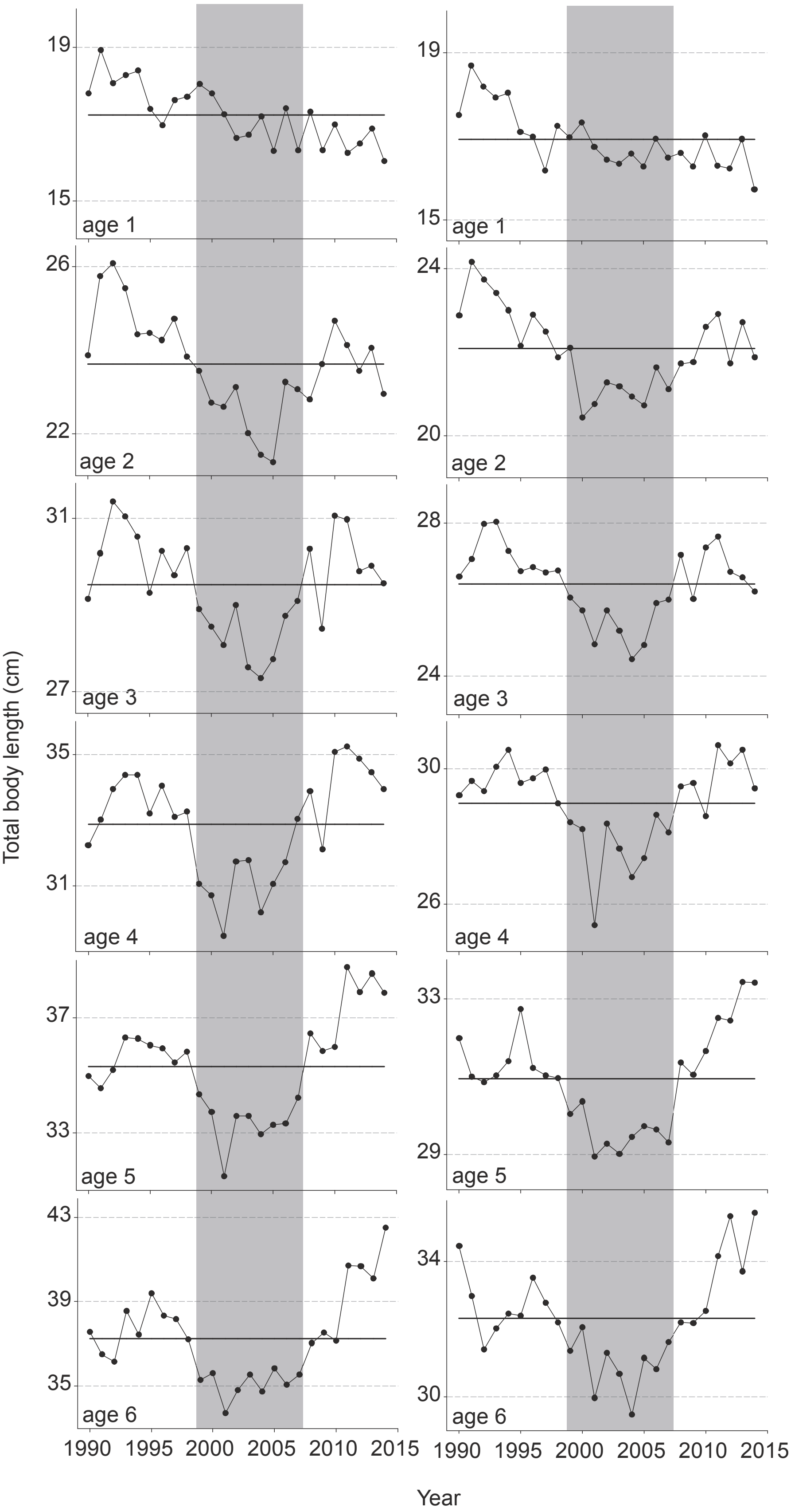

FIGURE II-1. Mean length-at-age of North Sea whiting derived from 1st quarter North Sea International Bottom Trawl Survey (NS-IBTS) dataset provided by the International Council for the Exploration of the Sea (ICES).

TABLE II-II. Results of the Kruskal-Wallis rank sum test of the length at different ages and time periods of North Sea whiting.

Age	Sex	Period	MEAN length (cm)	MEDIAN length (cm)	N fish	χ^2-value	df	*P*
1	F	1990-1999	17.9	18.0	1495	123.6	2	<0.001
		2000-2007	17.0	17.0	1697			
		2008-2014	16.6	16.2	2475			
2	F	1990-1999	24.7	24.0	1758	173.6	2	<0.001
		2000-2007	22.5	23.0	2027			
		2008-2014	23.7	24.0	2478			
3	F	1990-1999	30.1	30.0	1571	153.0	2	<0.001
		2000-2007	28.3	28.0	1578			
		2008-2014	30.0	30.0	2416			
4	F	1990-1999	33.2	33.0	1260	319.8	2	<0.001
		2000-2007	31.1	31.0	1189			
		2008-2014	34.3	34.0	1847			
5	F	1990-1999	35.4	35.0	707	384.0	2	<0.001
		2000-2007	33.2	33.0	902			
		2008-2014	37.7	37.0	1154			
6	F	1990-1999	37.4	37.0	425	373.8	2	<0.001
		2000-2007	35.1	34.6	1035			
		2008-2014	39.7	39.0	1018			
1	M	1990-1999	17.5	18.0	1707	105.7	2	<0.001
		2000-2007	16.7	17.0	1959			
		2008-2014	16.4	16.1	2928			
2	M	1990-1999	23.0	23.0	1504	207.6	2	<0.001
		2000-2007	21.0	21.0	1938			
		2008-2014	22.2	22.9	2677			
3	M	1990-1999	27.0	27.0	1158	140.7	2	<0.001
		2000-2007	25.3	25.2	1196			
		2008-2014	26.8	27.0	1633			
4	M	1990-1999	29.5	29.0	839	183.5	2	<0.001
		2000-2007	27.4	27.2	815			
		2008-2014	29.9	29.8	1053			
5	M	1990-1999	31.2	31.0	543	154.5	2	<0.001
		2000-2007	29.5	29.0	595			
		2008-2014	32.4	32.0	562			
6	M	1990-1999	32.5	32.0	453	206.6	2	<0.001
		2000-2007	30.9	31.0	959			
		2008-2014	33.6	33.0	885			

TABLE II-III. Results of the Wilcoxon rank sum test of the length-at-age data of female (f) and male (m) whiting sampled in different periods. *P*-values of the pairwise comparisons were adjusted using the Bonferroni correction.

Sex-age (years)		***W*-value**			***P***	
f-1		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	1465067		**2000-2007**	<0.001	
	2008-2014	2231958	2221866	**2008-2014**	<0.001	<0.01
f-2		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	2215938		**2000-2007**	<0.001	
	2008-2014	2372091	2130808	**2008-2014**	<0.001	<0.01
f-3		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	1489594		**2000-2007**	<0.001	
	2008-2014	1880150	148995	**2008-2014**	1	<0.01
f-4		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	932677		**2000-2007**	<0.001	
	2008-2014	1001143	677932	**2008-2014**	<0.001	<0.01
f-5		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	403048.5		**2000-2007**	<0.001	
	2008-2014	302136	263390.5	**2008-2014**	<0.001	<0.01
f-6		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	281745		**2000-2007**	<0.001	
	2008-2014	170931	267836	**2008-2014**	<0.001	<0.01
m-1		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	1915826		**2000-2007**	<0.001	
	2008-2014	2937197	2966371	**2008-2014**	<0.001	0.12
m-2		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	1855992		**2000-2007**	<0.001	
	2008-2014	2189343	2120382	**2008-2014**	<0.001	<0.01
m-3		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	857708.5		**2000-2007**	<0.001	
	2008-2014	952220.5	747853	**2008-2014**	1	<0.01
m-4		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	442345.5		**2000-2007**	<0.001	
	2008-2014	415660	280589	**2008-2014**	0.08	<0.01
m-6		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	203155.5		**2000-2007**	<0.001	
	2008-2014	127211	97951.5	**2008-2014**	<0.001	<0.01
m-6		**1990-1999**	**2000-2007**		**1990-1999**	**2000-2007**
	2000-2007	260226.5		**2000-2007**	<0.001	
	2008-2014	164556.5	259710	**2008-2014**	<0.001	<0.01

PREY ABUNDANCE

The amount of small prey fish, available for whiting, was on average 334 numbers per hour (n/h) in the IBTS time series and 396 million recruits estimated for the North Sea in the SMS model output. The prey abundance calculated from both time series showed similar patterns. In both time series the 3 - year running mean was below long term average for several consecutive years from 2003-2008. From 1990-2002 the mean forage fish abundance was 373 numbers of forage fish per hour (n/h) calculated from the IBTS data and 336 million recruits calculated from the SMS model for the total North Sea. In 2003-2008 the mean prey abundance was 211 n/h and142 million recruits in the IBTS data and the SMS model respectively. In the years after 2007 the mean prey abundance was 353 n/h (IBTS) and 382 million recruits (SMS model) (Fig. II–3).

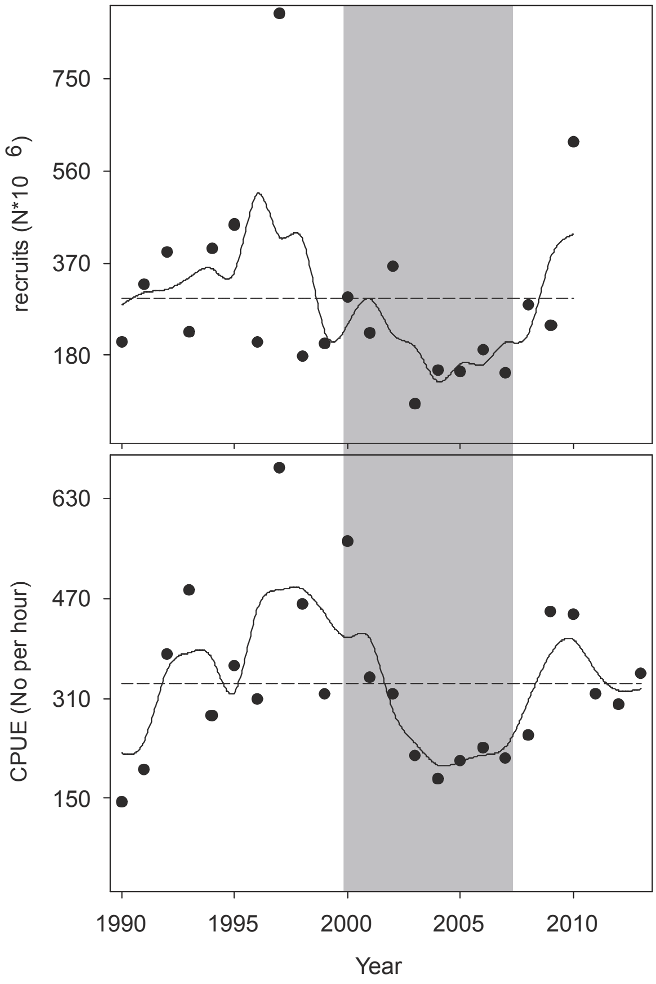

FIGURE II–2. Forage fish (*Ammodytes* spp., *T. esmarkii*, *S. sprattus*, *C. harengus*) abundance in the North Sea, calculated from the SMS model (a) and the IBTS data (b). Dots represent the annual means. The solid lines are the 3yr running means and the dashed line is the mean over from 1990 to 2010 (a) or 1990 to 2013 (b).

STOMACH CONTENT MASSES

The comparison of the average stomach content masses of whiting bigger than 25 cm in total body length showed that on average all stomach contents sampled in the period of low prey abundance and low mean length-at-age of whiting (2000–2007) were lower compared to samples from the periods of high prey abundance and higher mean length-at-age (1990–1999 & 2008–2014).

The initial analysis of the influence of the quarter and the RA on the stomach content masses in 1991 showed significantly lower stomach content masses in the first quarter, compared to the others (χ^2= 132.5998, df = 3, P< 0.001; pairwise Wilcoxon rank sum test with Bonferroni correction Q 1 vs Q 2-4: P<0.001) and significantly different stomach content masses between the areas sampled (χ^2= 21.7971, df = 6, P<0.01). Thus, to account for the effect of quarter and area, all subsequent comparisons between the different years were done separately for each area and quarter.

First quarter samples were only available for 1990, 1991 and 2012. In all RAs sampled, except for RA 4, where no significant difference was detected, the average stomach content mass was significantly higher in 2012 compared to 1990 and 1991.

In the second quarter the mean stomach content mass of samples from RA 4 from 2004, 2005 and 2006 were 0.63, 1.33, and 1.85% and hence generally lower, compared to the mean stomach content mass of 2.47% in 1991 samples. The pairwise Wilcoxon- tests indicated significant differences between 1991 and 2004 (W=1361.5, P< 0.001), 1991 and 2005 (W=1765.5, P< 0.001), but not between 1991 and 2006 (W=1364, P =0.08). The stomach content mass found in 2004 was also significantly lower compared to 2005 (W=1205.5, P< 0.05) and 2006 (W=798.5, P< 0.001).

In 3rd quarters in all RAs the mean stomach content mass of samples from years where mean length-at-age of whiting and forage fish abundance was low (2000–2007) was lower, compared to years, where length-at-age and prey abundance was high (1990–1998 & 2008–2012). In RA 1 the mean stomach content mass in 1991 was 2.1% and significantly higher compared to 2007 mean stomach content mass of 0.48% (W=2501, P< 0.001). Mean stomach content mass of 0 % found in 2006 in rounfish area 2 was significantly lower, compared to 2.1 % in 1991 (W=1450, P< 0.001). 3rd quarter samples in RA 3 showed significantly lower stomach content masses in 2007, compared to 1991 (W= 614, P< 0.001), 1996 (W=312, P< 0.05) and 1997 (W=426, P< 0.01). In RA 4 stomach content masses found in 2004 and 2006 were significantly lower, compared to 1991, 1996 and 1997 (P<0.001).

4th quarter samples were available for RA 2 and 4. In RA 2 the stomach content masses found in 2006 were significantly lower compared to 1991 (W=825, P<0.001). In RA 4 the mean stomach content masses found in 2005 and 2006 were lower compared to 1991, but only the differences between 1991 and 2006 were significant (W=359, P<0.001). (Fig. II–3; Table II–IV & II–V).

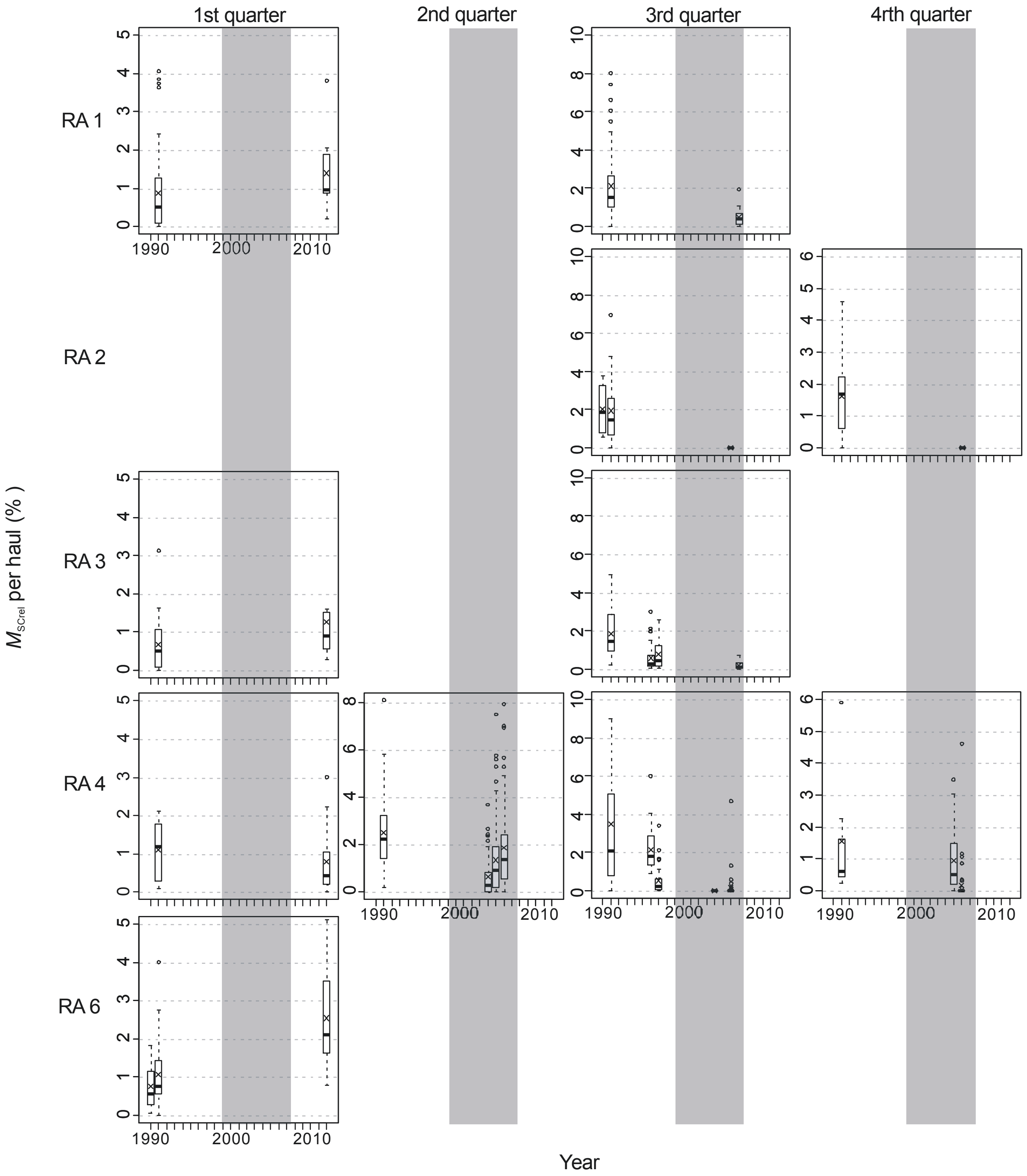

FIGURE II–3. Average stomach content masses as percentage of total body mass (M_{SCrel}) per haul of whiting per quarter and ICES roundfish area (RA) sampled. The edges of the dark grey lines in the upper box of each panel indicate significant differences between groups at the 0.05 level from the pairwise comparisons using Wilcoxon rank sum test with Bonferroni correction.

TABLE II–IV. Results of the Wilcoxon rank sum tests of the stomach content masses as percentage of the total body massess (M_{SCrel}) of North Sea whiting sampled per quarter, Roundfish Area (RA) and year. P-values of the pairwise comparisons were adjusted using the Bonferroni correction.

Quarter	**RA**	**Year**	$\boldsymbol{M_{SCrel}}$	**N hauls**	**χ^2-value**	**df**	***P***
1	1	1991	0.87	81	5.0	1	<0.05
		2012	1.39	10			
1	3	1991	0.68	30	4.4	1	<0.05
		2012	1.26	16			
1	4	1991	1.10	5	0.4	1	0.54
		2012	0.80	20			
1	6	1990	0.76	13	8.9	2	<0.05
		1991	1.07	39			
		2012	2.54	6			
2	4	1991	2.47	32	40.9	3	<0.001
		2004	0.63	48			
		2005	1.33	73			
		2006	1.85	65			
3	1	1991	2.10	128	33.7	1	<0.001
		2007	0.48	22			
3	2	1991	1.94	59	50.3	1	<0.001
		2006	0	25			
3	3	1991	1.84	53	53.6	3	<0.001
		1996	0.57	34			
		1997	0.77	44			
		2007	0.18	12			
3	4	1991	3.46	27	119.6	4	<0.001
		1996	2.13	28			
		1997	0.53	35			
		2004	0	18			
		2006	0.15	50			
4	2	1991	1.61	38	41.3	1	<0.001
		2006	0	22			
4	4	1991	1.55	7	50.0	2	<0.001
		2005	0.94	32			
		2006	0.17	55			

TABLE II–V. Results of the Kruskal-Wallis rank sum test for interannual differences of North Sea whiting stomach content masses per quarter (Q) and Roundfish Area (RA).

Q	RA		***W*-value**					***P***			
1	1		**1991**					**1991**			
		2012	228				**2012**	<0.05			
1	3		**1991**					**1991**			
		2012	149				**2012**	<0.05			
1	4		**1991**					**1991**			
		2012	59				**2012**	0.56			
1	6		**1990**	**1991**				**1990**	**1991**		
		1991	207				**1991**	0.99			
		2012	6	40			**2012**	<0.01	<0.05		
1	4		**1991**	**2004**	**2005**			**1991**	**2004**	**2005**	
		2004	1361				**2004**	<0.001			
		2005	1765	1206			**2005**	<0.001	<0.05		
		2006	1364	799	1931		**2006**	0.08	<0.001	0.36	
3	1		**1991**					**1991**			
		2007	2501				**2007**	<0.001			
3	2		**1991**					**1991**			
		2006	1450				**2006**	<0.001			
3	3		**1991**	**1996**	**1997**			**1991**	**1996**	**1997**	
		1996	1548				**1996**	<0.001			
		1997	1840	641			**1997**	<0.001	1		
		2007	614	312	426		**2007**	<0.001	<0.05	<0.01	
3	4		**1991**	**1996**	**1997**	**2004**		**1991**	**1996**	**1997**	**2004**
		1996	388				**1996**	1			
		1997	818	906			**1997**	<0.001	<0.001		
		2004	477	504	630		**2004**	<0.001	<0.001	<0.001	
		2006	1289	1368	1608	369	**2006**	<0.001	<0.001	<0.001	0.57
4	2		**1991**					**1991**			
		2006	825				**2006**	<0.001			
4	4		1991	2005				**1991**	**2005**		
		2005	136				**2005**	1			
		2006	359	1550			**2006**	<0.001	<0.001		

CONDITION OF WHITING

The condition of whiting was analysed for the period 2000–2014, using Fulton's *k*, calculated from the IBTS length-body mass data. The condition factor was lower in the period 2000–2007, where likewise length-at-age, prey abundance and stomach content masses of whiting were low, compared to 2008–2014. The differences in Fulton's *k* in the length classes 25–29.9, 30–34.9 and 35–39.9 cm were on average 0.03 g cm^{-3}. This would account for a small difference in mass in for example a 33 cm fish of 12 g in body mass (286 g vs. 298 g).

In the length class 40–49.9 cm the difference between 2000–2007 and 2008–2014 was 0.1 g cm^{-3} corresponding to a mass difference of 60 g at a body length of 44 cm (Fig. II–4).

As an alternative condition indicator the *HSI* from 2007, a year of low length-at-age, prey abundance and stomach contents was compared to the respective values in 2012, a year of high length-at-age, prey abundance and stomach contents. The comparison revealed that from a size of 30 cm onwards for both sexes, the median *HSI* was significantly higher in 2012, compared to 2007. The *HSI* of females and males of a length of 30–34.9 cm in 2012 was 23% and 15% higher compared to 2007. The differences in *HSI* between 2012 and 2007 fish increased up to 44% in male whiting of a length of 35–39.9 cm and 54% in females of a length of 40–49.9 cm (Table II–VI).

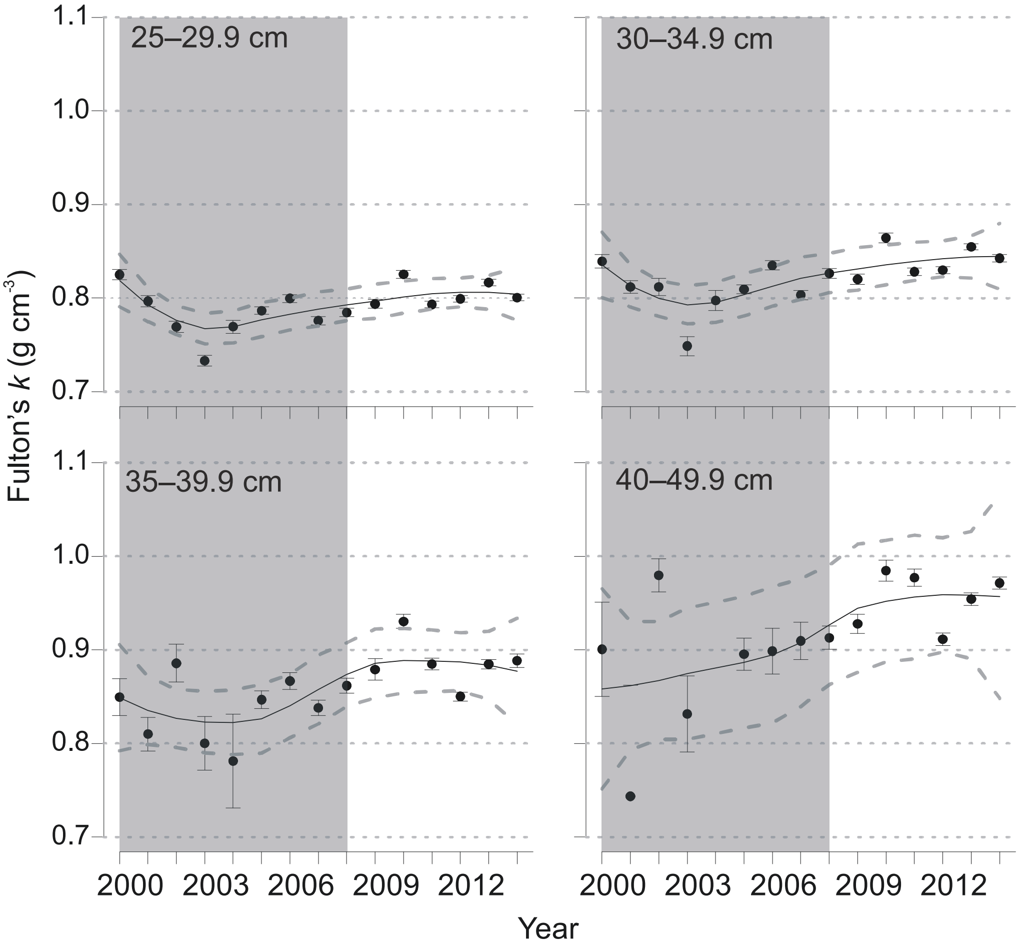

FIGURE II–4. Annual mean Fulton's *k* of whiting, calculated from the ICES NS-IBTS dataset of the first quarters 2000–2014. Black lines are the fitted loess smoothers and dark grey dashed lines show the confidence intervals of the fit.

TABLE II–VI. Average liver masses as proportion of the total fish body mass (*HSI*) of North Sea whiting, sampled in 2007 and 2012 and results of the Mann-Whitney Rank Sum Tests.

Sex	Fish Length (cm)	2007 median HSI	2012 median HSI	*U*	N small / N big	*P*
F	25–29.9	3.76	3.13	5274	99/147	<0.001
F	30–34.9	2.88	3.72	4261	65/219	<0.001
F	35–39.9	2.58	4.36	416	18/120	<0.001
F	40–49.9	2.80	6.10	8	3/42	<0.05
M	25–29.9	2.41	2.44	7208	91/161	>0.05
M	30–34.9	2.10	2.48	2390	45/135	<0.05
M	35–39.9	2.04	3.67	17	8/15	<0.01

ESTIMATED CONSUMPTION AND CORRESPONDING STOMACH CONTENTS

The modelled average stomach content massess for 2000–2007, the period of low length-at-age and low prey abundance displayed clearly lower values compared to 2008–2014, the period of high length-at-age and low prey abundance. The magnitude of these differences that would account for the observed growth differences between the periods was even smaller compared to the differences in the stomach content masses found in the North Sea between 2007 and 2012.

The generalised von Bertalanffy growth model fitted to length-at-age data from the North Sea IBTS resulted in an L_∞ of female whiting of 37.6 cm in the period 2001–2007 and of 42.5 cm in 2008–2014. Estimated L_∞ of male fish was 32.6 cm in 2001–2007 and 35.8 cm in 2008–2014. The growth models showed for both sexes that up to an age of 2 years the length-at-age was similar in both, the high and the low prey periods. From age 2 onwards the mean length-at-age modelled was higher for the period 2008–2014 compared to 2001–2007 and the differences increased with age. At age 6 the model predicted a 4.1 cm higher body length for females and a 2.8 cm longer body length for males.

The estimated consumption based on the K3-model and the respective von Bertalanffy growth parameters for the period 2001–2007 was 1.38 g per day in a 3 year old female and increased to 2.81 g per day in a 6 year old fish. The consumption of male whiting for the corresponding ages was as 0.99 g day^{-1} and 1.84 g day^{-1}. 2008–2014 the consumption of 3 year old female and male whiting was 1.80 g day^{-1} and 1.23 g day^{-1}. 6 year old females and males from that period consumed 4.01 g day^{-1} and 2.44 g day^{-1}, respectively. The daily consumption of female and male whiting at age 2 to 8 in the period 2008–2014 was on average 27 and 22% higher compared to 2001–2007, respectively.

The corresponding theoretical mean stomach content masses (*S*), calculated with eq. 3, for a female whiting within the size range of 25–40 cm were on average 0.37% of fish body mass in 2001–2007 compared to 0.44% of fish body mass in 2008–2014. Males within this size range had an average theoretical stomach content mass of 0.31% of the body mass in 2001–2007 and of 0.35% of the fish body mass in 2008–2014. This means on average a 14 and 11% lower average stomach content during 2001–2007 for females and males, respectively.

The actual mean stomach content masses of whiting within a size range of 25–40 cm sampled in the North Sea were in 2007 0.69% of the body mass in females and 0.43% of the body mass in males. In 2012 whiting stomach contents masses were on average 1.39 and 0.56% of the fish body mass for females and males, respectively. This implies for females 50 and for males 24% lower stomach content masses in 2007 compared to 2012 (Fig II–5; Table II–VII.).

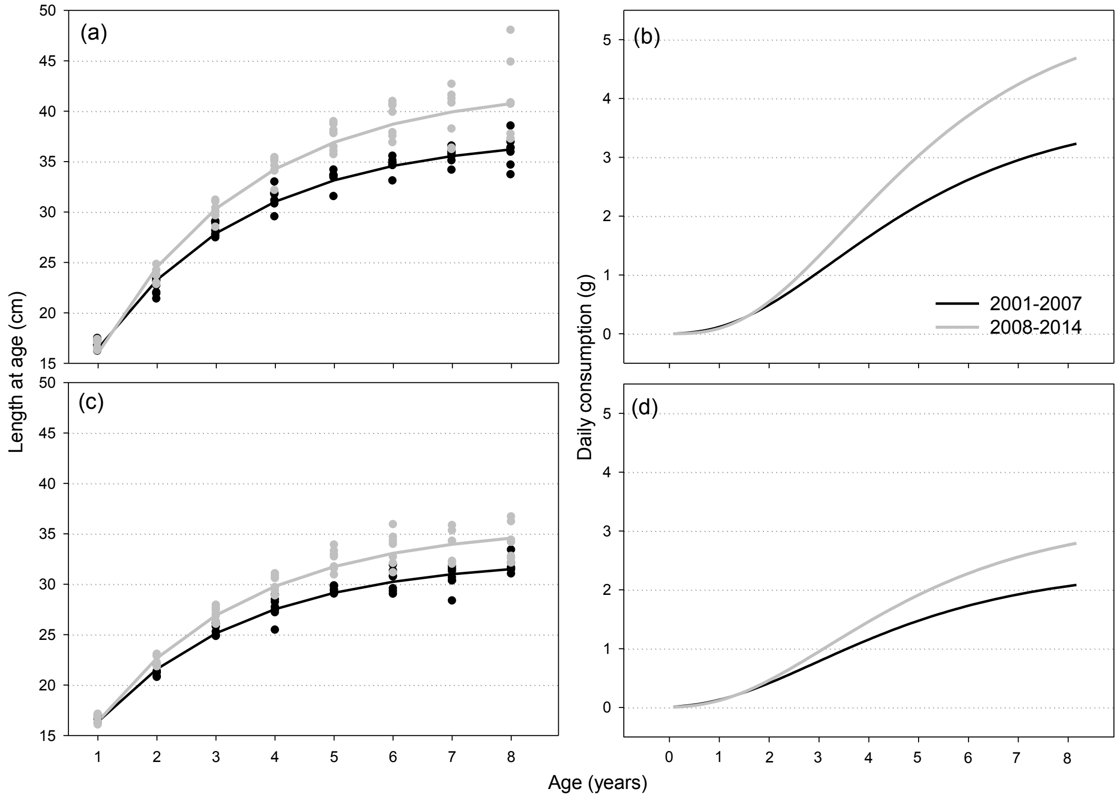

FIGURE II–5. Length-at-age of whiting and estimated von Bertalanffy growth curves (a and c) of female (a) and male (c) whiting. Estimated Consumption (b and d) of female (b) and male whiting (d) from the K3 model for the period 2001–2007 (black) and 2008–2014 (grey).

TABLE II–VII. Average stomach content masses (S) expressed as percentage of fish body mass calculated from the K3-model and observed mean stomach content masses (% body mass) of North Sea whiting of total lengths of 25 - 40 cm.

	model output		**field data**	
	S (% BM) 2001–2007	S (% BM) 2008–2014	Stomach content mass (% BM) 2007	stomach content mass (% BM) 2012
females	0.37	0.44	0.69	1.39
males	0.31	0.35	0.43	0.56

RELATIONSHIP BETWEEN FORAGE FISH ABUNDANCE AND LENGTH-AT-AGE OF WHITING

The loess smoother fitted to the normalised mean length-at-age of whiting in relation to the normalised forage fish abundance indicated an increase in length-at-age of whiting with increasing forage fish abundance up to a certain level where a further increase of prey fish abundance does not cause a further increase in the length-at-age of whiting (Fig. II–6).

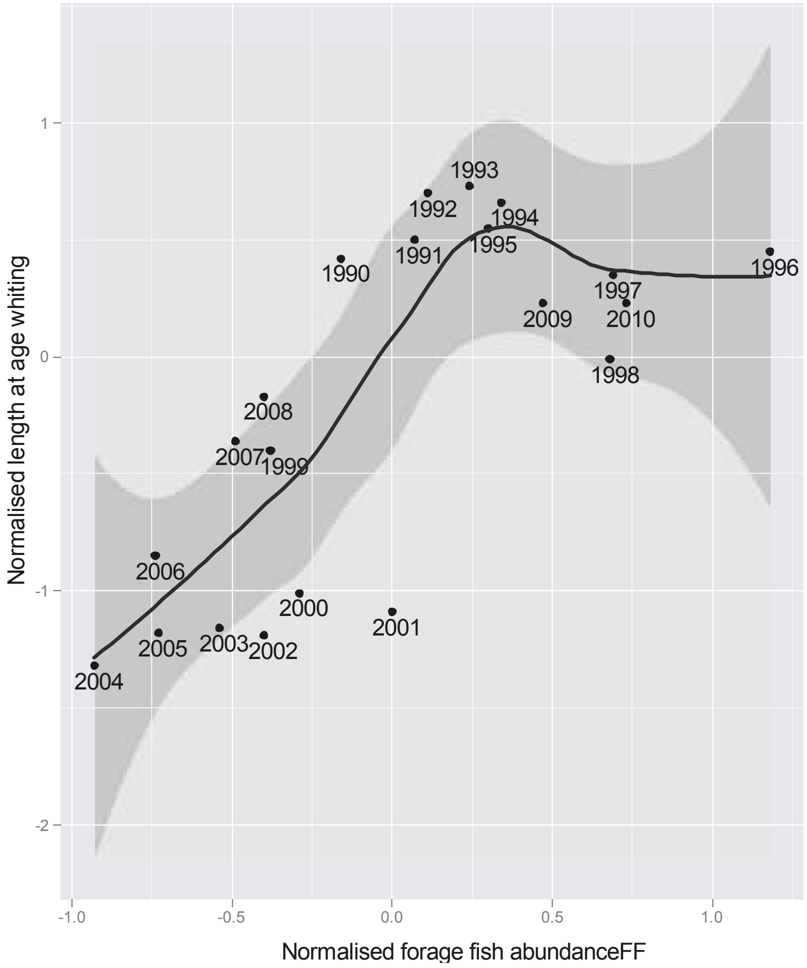

FIGURE II–6. Normalised length-at-age of North Sea whiting vs normalised forage fish abundance. Black line is the fitted loess smoother. Dark grey zone represents 95% confidence level interval.

DISCUSSION

LENGTH-AT-AGE OF ADULT WHITING

The decline in the length-at-age two and older North Sea whiting during the period 2000 to 2007, and the subsequent increase in mean length-at-age from 2008 onwards, coincided with changes in several factors that have been shown to influence mean length-at-age. Changes in such factors were observed for (i) size selective mortality (e.g. Jennings *et al.*, 1999), (ii) water temperature (e.g. Burrows *et al.*, 2011) and (iii) food resources (e.g. ICES, 2013). All these factors could have had, in theory contributed to the observed changes in the mean length-at-age of whiting.

THE INFLUENCE OF SIZE-SELECTIVE MORTALITY

A possible explanation for a smaller mean length-at-age in the period 2000 to 2007 could be a change in the size-selective mortality. For adult whiting, the fishery is the main cause of mortality (ICES, 2013). Fishing gears used in mixed demersal fisheries, in which whiting is caught, are size-selective. In combination with the large variability in growth rates of fish of the same cohort, the necessary requirements for removing selectively the fast growing individuals and decreasing the population mean length-at-age are given (e.g. Sinclair *et al.*, 2002a). In addition, a high fishing mortality can lead to a smaller first spawning size by harvesting selectively the large individuals which have a higher risk of being caught premature (e.g. Rijnsdorp, 1993; Sinclair *et al.*, 2002; van Walraven *et al.*, 2010). In gadoids, Neuheimer and Taggart (2010) found that size- selective fishing mortality is responsible for the decrease in length-at-age and age at maturity in Scotian Shelf haddock *Melanogrammus aeglefinus* (L. 1758) and Sinclair *et al.* (2002b) found the same for the Gulf of St. Lawrence cod stock.

In the North Sea whiting has a minimum landing size of 27 cm and is mainly caught in the mixed demersal roundfish fishery and as bycatch in the Norway lobster *Nephrops norvegicus* (L. 1758), sandeel, Norway pout, and flatfish fishery (ICES, 2012). The mortality of adult whiting might be more influenced by the targeted demersal roundfish fishery and small individual might be restrained due to discards. Thus, fishing and discard mortality might be relevant to the observed growth changes of whiting in the North Sea. However, the assessment of whiting from 1990 to 2012 shows that the fishing mortality (F) of age groups two to six has actually declined in the period 1990 to 2000 and increased again, afterwards. Moreover the total mortality (Z) of whiting in the North Sea has decreased from 1990 to 2012 (ICES, 2012). The pattern in the mortality time series of whiting is contrary to what would be expected if fishing mortality would have determined the mean length-at-age of the stock. Thus, changes in the fishing effort cannot be the cause of the observed decline in the mean length-at-age of whiting.

THE INFLUENCE OF TEMPERATURE

Temperature is the most important abiotic factor affecting the physiology and the behaviour of ectotherms (e.g. Fry, 1971). The influence of temperature on growth processes in fishes has been subject in numerous studies and in most fishes under ad libitum feeding conditions, the growth rate increases with temperature to an optimum, beyond which growth decreases (e.g. Hutchison & Maness, 1979; Beitinger & Fitzpatrick, 1979).

Globally, the North Sea is amongst the most rapidly warming continental shelf seas (Burrows *et al.*, 2011). From 1990 to 2007 the annual mean surface temperature in the North Sea increased continuously by about 0.5°C per decade, whereas in the years after 2007 the temperature decreased again (Meyer *et al.*, 2011; Emeis *et al.*, 2015). Due to the varying hydrographical conditions, the temperatures in the North Sea show a spatially distinct pattern. Highest temperatures reaching easily 18°C in summer with fastest warming during the past decades were observed in the shallow waters of the German Bight, whereas deeper waters in the central and northern North Sea remained colder and showed slower warming (Meyer *et al.*, 2011).

The growth of North Atlantic cod has been shown to increase linearly with increasing temperatures, within the species natural range of experienced temperatures of 2–13°C. Below or above those temperatures, growth is reduced (Jobling, 1988). Several studies (e.g. Olsen *et al.*, 2010) argued that the growth of cod in the southern North Sea decreased during recent decades as a result from increasing temperatures, since the southern North Sea marks the most southerly boundary of the species distribution and the temperatures lie at the upper margin of the temperature range that is optimal for cod growth.

However, in contrast to Atlantic cod, for whiting the North Sea is not at the southern boundary of its distribution range, which reaches in the south to the Mediterranean and the Black Sea. Within the Black Sea the average experienced temperatures of whiting range from 9°C to 20°C (Shulman & Love, 1999). In the summer, temperatures in the coastal regions of the southern North Sea regularly exceed 18°C and average annual surface temperatures in the North Sea increased from 10.3°C in 1990 to 11.3°C in 2007 (Emeis *et al.*, 2015). Moreover, fish are not stationary and can behaviourally thermoregulate by spatial displacement (Beitinger & Fitzpatrick, 1979). Adult whiting might avoid the high summer temperatures in the respective areas by moving to colder water bodies (Temming & Hufnagl, 2015). Thus, temperatures in the North Sea lie well within the natural range of occurrence of this species and a negative impact of temperature on the growth of whiting is unlikely. This is supported by the finding that the length-at-age of whiting from the Irish Sea was not temperature dependant (Gerritsen *et al.*, 2003). In addition, our findings show that the mean length-at-age of adult North Sea whiting has increased between the period 2008–2014 and 1990–1999. If the increasing temperature would have a negative impact on whiting one would expect contradictory development of the length-at-age. Thus, the observed reduction in the length-at-age of whiting in the North Sea in the period 2000–2007 is most likely not resulting from a direct effect of temperature on growth.

WHITING LENGTH-AT-AGE 1 YEAR

The length-at-age 1 year, like all other ages classes, was smaller in the period 2000–2007, compared to 1990–1999. While all older age groups show an increase in the mean length-at-age from 2008 onwards, the mean length-at-age 1 has further decreased from 17.7 cm to 16.5 cm by the end of the time series. This indicates that the mean length-at-age of 1-group whiting is influenced by other or additional factors than the older age groups. There are two possible explanations for the observed pattern; either a real decrease in growth of 0-group whiting or a shift in the timing of the spawning of whiting recruits. The principle factors resulting in a decrease in growth would be the same as for adult whiting: water temperature, selective mortality or food resources. The temperature in the North Sea increased from 1990 to 2007 and subsequently decreased (Emeis *et al.*, 2015), whereas the length-at-age 1 of whiting remains low until 2014. Thus, it is unlikely that the temperature directly caused the slower growth in juveniles.

Selective mortality of fast growing 0 - groups might theoretically lead to the observed decrease in mean length-at-age 1. Size-selective mortality in juvenile fish typically favours bigger individuals, since they tend to be more resistant against starvation and less vulnerable to predation (Peterson & Wroblewski, 1984). Van der Veer *et al.* (1997) found that the size-selective mortality in juvenile flatfish in the Wadden Sea can actually favour smaller individuals due to bird predators and age 1 cod preying selectively on the larger individuals of the age 0-cohort. Juvenile whiting are important prey for adult gadoids and if these would prefer larger 0 -groups this might have led to a decrease in the size at age 1. However, size-selective mortality requires relatively high predation mortality in the population (Sogard, 1997). The stock biomass of cod and whiting in the North Sea is decreasing (ICES, 2012), leading to lower predation pressure on age 0-group whiting. Thus, size-selective mortality by predation is unlikely to be the cause of the observed decrease in length-at-age 1.

The diet of whiting smaller 15 cm is dominated by crustaceans and gobies (Hislop *et al.*, 1991). These prey items are unlikely as a growth limiting factor since both are rather increasing in abundance in the North Sea due to a release of the predation pressure of gadoids (Temming & Hufnagl, 2015).

Alternatively, the smaller size of the age 1–group in the first quarter of the IBTS could be explained with a dominating contribution of late season cohorts since the beginning of the 2000s. Changes in the zooplankton community can severely influence the survival of larvae and thus recruitment, as was shown for cod. Temperature induced changes in the spatio - temporal distribution of the zooplankton occurred in the mid 1980s and led to lower survival of cod larvae (Beaugrand *et al.*, 2003). Hence this remains as a likely explanation also for whiting, although no specific studies have been conducted so far.

PREY ABUNDANCE IN THE NORTH SEA

So far, the most likely explanation for the observed decrease in growth of whiting in age groups 2 to 6 is a change in the prey abundance in the North Sea ecosystem. Whiting is a highly selective feeder, which from a size of 25 cm on, is almost exclusively piscivorous, having less than 20 % of non-fish prey in its diet (Hislop *et al.*, 1991). Additionally, *M.merlangus* relies only on few species, such as sandeels, Norway pout, herring and sprat (Knijn *et al.*, 1993; Temming *et al.*, 2007). Thus, changes in the abundance of forage fishes should most likely influence the growth rates of whiting in the North Sea. The analysis of the abundance of forage fishes revealed below average values in the period 2000–2007, representing a period of low forage fish abundance in the North Sea, lasting for seven consecutive years. Regarding the first half of the 2000s in the North Sea all forage fish species (sandeels, Norway pout, herring and sprat) showed a marked decline in their spawning stock biomass and produced some of the smallest year classes on record (ICES, 2013). The spawning stock biomass of Sandeels was low from 2000 to 2006, since 2002 herring and sprat produced below average year classes and the recruitment of Norway pout reached historic minima in 2003 and 2004. From 2007 onwards, the spawning stocks of sandeels, sprat and Norway pout increased again and Norway pout stock produced very strong year classes in 2009 and 2012.

STOMACH CONTENTS OF WHITING

The amount of prey available in an ecosystem should be reflected by the stomach contents of a predator (Fahrig *et al.*, 1993). As expected, lower values were observed in the period between 2001 and 2007, when compared to same quarters and roundfish areas in earlier and later years, respectively. Thus, with respect to whiting, we consider the period from 2001 to 2007 as an era characterised by low prey availability in the field reflected in low stomach contents of whiting,. The years from 2008 onwards represent again a period of sufficient food supply. Hence, the shortages in forage fish should lead most likely to negative effects on growth or condition of whiting.

CONDITION OF WHITING

The Fulton's condition factor of a fish has been shown to reflect its fitness and well-being (e.g. Bolger & Connolly, 1989). Thus, a change in the condition of whiting in the period of low prey availability could be expected. However, the condition of whiting during the period 2001 and 2007 showed only a small decline, compared to 2008-2014. Lambert & Dutil (1997) found that Fulton's K of Atlantic cod decreased by 0.3 in 30 - 39 cm specimens during the collapse in the northern Gulf of St Lawrence stock. Likewise, for Baltic cod the Fulton's K was shown to decrease by 0.2 during unfavourable environmental conditions (Eero *et al.*, 2014). Compared to the magnitude of change in the mentioned gadoids we consider the change in Fulton's condition Factor by 0.1 of whiting in the North Sea during the period of low food availability as relatively minor.

Another measure of the condition of a fish is the liver mass, expressed as percentage of the total body mass. The so called hepatosomatic index (*HSI*) or liver condition index (*LCI*) is especially suitable to describe the condition in gadoids, where the prime organ for energy storage is the liver (e.g. Marshall *et al.*, 1999). In 2012, the HSI was on average higher in both sexes compared to 2007. This indicates that the nutritional condition of whiting during the period of poor food supply was lower, compared to a year where sufficient prey was available, even though this was hardly visible in the Fulton condition factor.

In 2012, whiting was sampled in March, which is within the spawning period of that species in the North Sea which may last from January until July. In 2007, whiting was sampled in the third quarter, which is at the end, or after the spawning period. Therefore, a proportion of the livers, sampled in the first quarter of 2012 might consist of vitellogenin, which is a phospholipoglycoprotein, produced by the liver to be embedded in the eggs of spawning female fish. Thus, higher *HSI* in female whiting 2012 might be partly due to the sampling season. However, in male fish the *HSI* was also higher in 2012 compared to 2007. Since male fish do not produce vitelologenin the effect of higher *HSI* in 2012 is considered to be more likely an effect of the year rather than of the season. Thus, the *HSI* was lower in a year where prey abundance was low compared to a year where more prey was available.

ESTIMATED CONSUMPTION AND CORRESPONDING FIELD DATA

In our analysis of field data we found poor growth in a period, which was also characterized by low stomach content values. It remains unclear, however, if the two observations correspond also in quantitative terms. In other words: does the lower mean stomach content, if maintained over long periods translate into a lower consumption such, that this leads to observed slower growth rates? To answer this question, we used the simple consumption model of Temming & Herrmann (2009), which relates consumption and growth based on the parameters of a generalized von Bertalanffy growth equation (GBGE) via the net conversion efficiency K_3. Practically we fitted the generalized fitted the GBGE to the whiting length-at-age data from the two contrasting periods 2000–2007and 2008–2014. We then calculated the respective consumption per age class applying the same value of K_3 in both cases. The resulting consumption estimates were then converted into the respective mean stomach contents.

These theoretically derived average stomach contents were on average 14% higher in female and 11% higher in male fish from the period with high growth. This implies that 14 and 11% lower average stomach contents would have led to the observed growth depression in the period 2000–2007 alone, not including effects of temperature or any other factor. The actual stomach content masses found in the stomachs of whiting 25–40 cm from field samples in the 3rd quarter of 2007 were on average 50% in females and 24% in males lower than in fish sampled in 1st quarter 2012. This shows that the calculated decrease in the amount of food consumed that would theoretically have led to the observed decrease in growth, is not only realised, but exceeded. The samples from 2007 were sampled in the 3rd quarter contrary to the 1st quarter samples from 2012. The effect of the season might have contributed to the differences in the amount of food eaten by whiting. However, when considering the impact of the quarter on the stomach content mass, the samples from 1981 and 1991 can serve as a reference since all four quarters were sampled. In 1981 whiting within a size range of 25–40 cm had on average 1.3 times higher stomach content masses in the 3rd quarter compared to the first quarter (Hislop *et al.*, 1991). Thus, higher stomach content masses found in 2012 can be considered as an effect of the year, rather than of season. This finding is reinforced by the comparison of the median stomach content masses 2007 and 2012 towards 1991 samples from the respective quarters and ICES statistical rectangles. Whiting in 2007 had significantly lower stomach content masses compared to the 3rd quarter stomachs in 1991, whereas whiting in 2012 had equal or higher amounts of food in their stomachs as specimen from the 1st quarter 1991. Additionally, the comparison of 1991 stomach masses from the sampling areas of 2007 and 2012 data revealed that in 1991 the samples form first quarter covering the sampling area of 2012 had significantly lower stomach content masses, compared to third quarter data covering the same area sampled in 2007. In summary, the fact that stomach content masses found in 1st quarter whiting stomachs 2012 were higher compared to the 2007 3rd quarter samples is most likely an effect of the year, rather than of the region or season sampled. Thus, whiting stomachs sampled from a period of low prey abundance in the North Sea verified low prey availability for whiting in the North Sea by showing that fish had less prey in its stomachs compared to a time where more prey was abundant.

RELATIONSHIP BETWEEN FORAGE FISH ABUNDANCE AND LENGTH-AT-AGE OF WHITING

The relationship between the normalised forage fish abundance and the normalised length-at-age of adult whiting was described by a sigmoid function. This implies (i) that if prey abundance drops below a certain level, the growth of whiting decreases with prey abundance and (ii) if prey abundance has reached a certain level, the growth of whiting is not increasing any further with more available food. In 2001 this relationship does not hold. Whereas the growth of whiting is rather low, forage fish abundance is on an average level. This might be due to additional effects of temperature, a density effect or an untypical low overlap of the predator and its prey (Temming *et al.*, 2007). However, increasing metabolic costs due to higher temperatures cannot explain the discrepancy in 2001 since the temperature was comparably high to for example 1990 with equal prey abundance (Emeis *et al.*, 2015). Competition caused by high densities of whiting seems to be an unlikely explanation since in 2001 the relation between spawning stock biomass of whiting and forage fish abundance was not outstanding (ICES, 2013). Data on spatial overlap between whiting and its prey are not available. Thus, this hypothesis cannot be evaluated. However, in the period 1990–2010 the abundance of forage fish rather well explained the growth of whiting in the North Sea. The sigmoid shape of this relationship is biologically meaningful and gives a good basis for an interpretation of the relationship between predator growth and prey abundance. Food is the driving force of fish growth, whereas temperature controls the growth rate and fish age scales the growth (Brett & Groves, 1979). Thus, if forage fish abundance increases the growth of whiting is increasing to an optimum after which a further increase in growth is limited by temperature or/and ontogeny.

We found a clear link between the length-at-age of whiting and the abundance of forage fish in the North Sea. This observation might lead to serious consequences for the stock recruitment relationship of whiting on the one hand and for multispecies modelling of the North Sea ecosystem on the other. The growth and the size at age of female fish influence the reproductive output. Although fishing mortality had decreased since the 1990s and management actions were taken to preserve the stock, the North Sea whiting stock was on historical low level in 2005–2008 (ICES, 2013). Smaller females produce less offspring and lower growth rates affect the rate at which immature individuals recruit to the spawning stock. This might severely influence the reproductive output of the spawning stock (Marshall & Frank, 1999). Thus, lower food availability might have contributed to the observed minimum in recruitment between 2003 and 2007 (ICES, 2013), which in turn might be the cause for the decreased stock.

Considering multispecies models of the North Sea ecosystem our findings emphasise that an isolated view of a fish population, uncoupled from the interacting species in the ecosystem might be dangerously misleading. It might be an opportunity to incorporate the length-at-age of whiting as a function of the prey abundance to enhance the model predictions. Thus, it is of urgent need to understand take into account predator prey interactions in management plans or ecosystem modelling.

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Chapter III

Influence of fishing mortality, temperature and prey abundance on the length-at-age and individual growth of North Sea cod Gadus morhua

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ABSTRACT

The Atlantic cod *Gadus morhua* used to be one major component of the North Sea ecosystem and an important exploited food fish. In the course of large-scale ecosystem changes and due to commercial use the stock has decreased dramatically since the 1960s. For sustainable management decisions and to preserve a resource for the commons it is of major interest to asses to which extend natural or anthropogenic changes led to the observed decrease in the North Sea cod stock. In this study we analysed the population structure using data from the International Bottom trawl survey in addition to growth rates inferred by otolith macrostructures of North Sea cod. We found divergent growth parameters between the southern and the northern stock components with faster growth in the south. Changes in the mean length-at-age of North Sea cod arouse from a negative influence of the fishing mortality. Additionally, decreasing shares of the southern stock-component led to a decrease in the total mean length-at-age. Both effects are probably miscellaneous since the fishery mortality causes the reduction of the fast growing proportion of the southern North Sea cod stock. Moreover, the temperature was negatively correlated with the mean length-at-age of North Sea cod. Otolith macrostructure analysis showed that no general depression in growth of North Sea cod occurred in the period 1975–2005. However, cod growth in the southern part of the North Sea appeared to be distinctively temperature dependant.

INTRODUCTION

Ecosystem health - i. e. the functioning and resilience of a food web is influenced by bottom-up processes such as the availability of resources, as well as by predatory top-down control (Holt, 1977; Berlow *et al.*, 2004). Although there is disagreement to which extend both forces contribute to the composition of populations and communities most studies agree that both work together simultaneously (e.g. Hunter & Price, 1992). In addition, if a perturbation is introduced in an ecosystem both forces are determining the reaction of a community to these changes (Montoya *et al.*, 2009). Therefore, it is crucial to understand the links between the species in an ecosystem to evaluate how this system will respond to perturbations. Marine ecosystems are of particular interest because they are facing both natural (e.g. changes in temperature, hydrography, abundance of predator or prey species) and anthropogenic (e.g. fishing; pollution; construction activities) perturbations and currently conservation concerns arouse due to changes in commercial important resources (Worm *et al.*, 2006; Levin & Lubchenco, 2008; Kirby *et al.*, 2009).

The Atlantic cod *Gadus morhua* L. 1758 is amongst the most important commercially exploited fish species and a major component of many ecosystems worldwide (Link *et al.*, 2009). However, trends in the world fisheries production indicate that Atlantic cod, that used to be the second most important fish species in 1970, descended to the sixth most important in 1989, to being only the tenth most important in 1992, is facing drastically changes in its abundance (Garcia & Newton, 1995). The decline in abundance has been ascribed to overexploitation by humans on the one hand and to biotic and abiotic ecosystem changes on the other hand (e.g. Myers *et al.*, 1996).

One example, where both natural and anthropogenic factors worked together to provoke an appreciable distortion are the Atlantic cod stocks in Canadian coastal waters. In the beginning of the 1990s many stocks simultaneously collapsed and despite a temporary moratorium on commercial fishing and reduced quotas the cod stocks remained at minimum levels (Hutchings & Myers, 1994). This was ascribed to high natural mortality, poor condition and growth rates together with recruitment failure (Myers *et al.*, 1997; Lambert & Dutil, 1996; Lambert, 2011). Likewise, in European waters the population dynamics of the Baltic cod stock were influenced by multiple interrelated factors. During the late 1980s and early 90s cod stock decreased dramatically and remained low for about two decades (Köster & Möllmann, 2000). Increasing fishing mortality together with high natural mortality depleted the stock and recruitment failure was ascribed to hydrographical conditions, clupeid predation on cod eggs and a decrease food items (Köster *et al.*, 2009). Moreover, the recovery of the stock was retarded due to shortages in clupeid food causing lean cod (Eero *et al.*, 2012).

In the North Sea cod was historically widely distributed and one of the most important commercially exploited species within this ecosystem. During the so called ‘gadoid outburst’ in the 1960s and 1970s some very strong year classes led to a capacious spawning stock. This era ended in the mid 1980s when a marked decline in recruitment was observed reaching historical minimum in the 2000s (Olsen *et al.*, 2011). The North Sea community went through pronounced ecological changes during the last five decades. Alterations were documented in hydrographical conditions, temperature, primary and secondary producers, as well as on higher trophic levels (Reid *et al.*, 2001; Beaugrand *et al.*, 2002; Weierman *et al.*, 2005). In addition, the North Sea forage fish communities, feeding on zooplankton and being in turn preyed by higher trophic levels (Alder *et al.*, 2008), have also underwent substantial changes during the last 40 years (Dickey-Collas *et al.*, 2013; Engelhard *et al.*, 2013). At the beginning of the 2000s a number of forage fish species, namely sandeels *Ammodytes* spp. L. 1758, Norway pout *Trisopterus esmarkii* (Nilsson 1855), herring *Clupea harengus* L. 1758 and sprat Sprattus sprattus (L. 1758) showed a marked decline in their spawning stock biomass and produced some of the smallest year classes on record (ICES, 2013). Thus, together with an extensive and unsustainable fishery North Sea cod is facing both pronounced natural and anthropogenic perturbations (Cook *et al.*, 1997; Olsen *et al.*, 2011).

The aim of this study was to evaluate the influence of temperature, prey availability and fishing mortality on the length-at-age of North Sea cod. Spatial differences in the length-at-age were assessed. A more precise analysis of the growth history of cod from the southern North Sea based on otolith macrostructure analysis should give further insights into the influence of these effects in the former main territory of North Sea cod.

MATERIALS AND METHODS

DATA SOURCES AND SAMPLING

Data and material used in this study originate from 4 different sources.

(1) To be able to describe the temporal and spatial development of the length-at-age and the abundance of North Sea cod datasets were obtained from the DAtabase of TRAwling Survey (DATRAS, downloaded on 24/04/2015) provided by the International Council for the Exploration of the Sea (ICES). Those data were collected in the North Sea during the 'North Sea International Bottom Trawl Survey' (NSIBTS) in 1^{st} quarters of each year between 1975 and 2015 (ICES, 2012) (Fig. III–1). Two types of datasets were extracted. The lengths at age of cod were derived from Sex-Maturity-Age–Length Keys (SMALK's) which were recorded individually on a Roundfish Area (RA) basis. Secondly, Catch Per Unit Effort (CPUE, in numbers per hour of hauling) data to provide a proxy for the abundance of cod at given age per RA. Detailed description of the survey designs and sampling procedures can be found in the Manual for the International Bottom Trawl Surveys (ICES, 2012).

(2) The spatial and temporal development of the growth-at-age of North Sea cod was described using annual increment widths of otoliths. Fish were sampled in the North Sea during scientific and commercial fishery cruises between 1980 and 2010. Otoliths used in this analysis originated from two sources. German otoliths were sampled, transversally thin sectioned, embedded and stored by the Johann Heinrich von Thünen Institute of Sea Fisheries in Hamburg, Germany (TI). Images of those otoliths were taken and kindly provided by Petra Jantschick. The other part of the analysed otoliths in this study were whole dissected and stored Danish otoliths provided by the archive of the National Institute of Aquatic Resources in Charlottenlund and Hirtshals, Denmark (DTU Aqua).

(3) Spatially resolved (0.25° latitude, 0.5° longitude) monthly mean North Sea bottom temperatures were derived from the NORWegian ECOlogical Model system (NORWECOM) downloaded at http://www.imr.no/~morten/wgoofe/ (Skogen *et al.*, 1995, Skogen & Soiland, 1998; Hjollo *et al.*, 2009). Annual mean temperatures between December and January (winter) and between August and October (summer) were calculated for the total North Sea as well as for RA 6 separately. These temperatures were selected since the onset of the formation of the opaque zone (indicating good fish growth) and the onset of the translucent zone (ascribed to poor fish growth) on the otolith of North Sea cod occur during those periods (Pilling *et al.*, 2007; Millner *et al.*, 2011).

(4) Time series of the prey abundance and fishing mortality (F) were derived from the Working Group on Multispecies Assessment Methods (WGSAM) 2011 key run of the Stochastic Multi Species (SMS) model presented by Lewy & Vinther (2004). Prey abundance was estimated using the numbers of recruits of North Sea fish species (sandeel, sprat, Norway pout, herring, whiting, cod, haddock, plaice, sole) possibly serving as cod prey (Hislop *et al.*, 1997). We decided not to use IBTS based catches of small individuals of these species because the catchability of small and pelagic fish species in the GOV bottom trawl net is highly variable in that survey and especially poor for sandeel (Fraser *et al.*, 2007). We used the annual average F of cod, sole and plaice from the SMS model as a proxy for the fishing effort in the North Sea. Additionally, to the F of cod, the F caused by the flatfish fishery also affects cod due to large proportions of cod in the by- catches of this fishery.

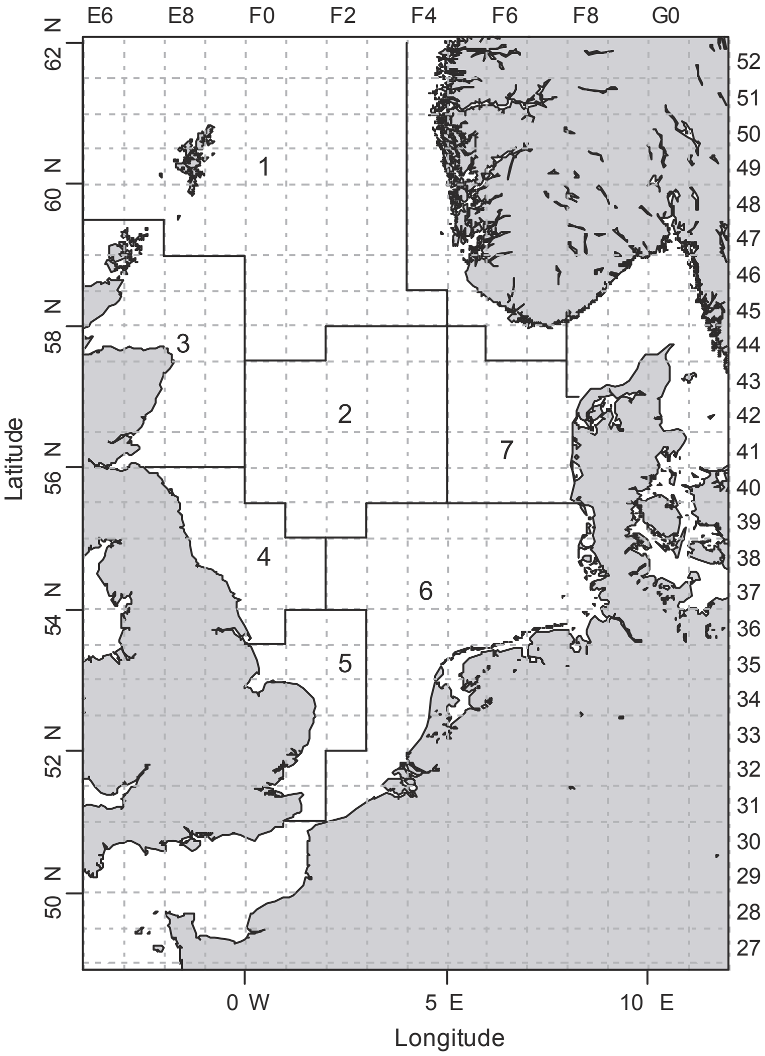

Figure III–1. Map of the study area. Black lines indicate North Sea Roundfish Areas (1–7) and the grey dashed lines delineate ICES statistical rectangles.

MEAN LENGTH-AT-AGE

The annual mean length-at-age of male and female North Sea cod was estimated by first calculating the average length of a given age, sex and year per RA weighted by the number of fish per record in the SMALK dataset. The mean length-at-age in a year of female and male for the total North Sea was then estimated as the mean length weighted according to the CPUE (numbers per hour of hauling) of cod for a given age, year, sex and RA. Since the CPUE data from the DATRAS database does not contain information about the sex of the fish a year, age and RA specific sex-ratio based on the SMALK data was used to calculate sex-specific CPUEs of cod for a given age, year, sex and RA. Local polynomial regression (LOESS) smoothers with a span of 0.5 (n= 41) were fitted to the mean length-at-age 1–6 years time series to investigate for trends in the length-at-age of North Sea cod.

SPATIALLY RESOLVED MEAN LENGTH-AT-AGE AND ESTIMATION OF GROWTH PARAMETERS

The annual mean length-at-age per RA of male and female cod was estimated by calculating the average length of a given age, sex and year per RA weighted by the number of fish per record in the SMALK dataset. Kruskal-Wallis rank sum tests with adjacent pairwise comparisons by Wilcoxon rank sum tests were performed to assess differences between the mean lengths at age of RAs 1 to 7. Significance was adjusted by sequential Bonferroni correction.

To assess spatial differences in growth von Bertalanffy growth functions were fitted to the length-at-age data for a given RA:

$$L_t = L\infty \times \left(1 - e^{-K(t-t_0)}\right),$$

where L_t is the length of the fish (cm) at time t (age), $L\infty$ is the mean asymptotic body length and growth coefficient K determines how quickly a certain percentage of $L\infty$ is reached. t_0 is the age at which L_t is 0. Parameter t_0 was set to 0 since the age when fish length is 0 should be close to 0 and thus negligible information arises from this parameter for adult fish (Johnson *et al.*, 2005). To be able to compare the model parameters we estimated only one parameter ($L\infty$ or K) at a time while fixing the other to avoid the interaction between both parameters.

SPATIALLY RESOLVED ABUNDANCE INDEX OF NORTH SEA COD

An index of the abundance of cod in RA 1 to 7 was estimated by multiplying the CPUE (number of cod/30min) for a given age and RA with the number of ICES statistical rectangles the concerning RA contains. The proportion of each RA from the total North Sea abundance index was calculated for each year from 1975 to 2015. To account for differences in the mean length-at-age between cod caught in RA 5 and 6 and the rest of the North Sea also the proportion of cod from RA 5 and RA 6 was analysed separately. Time series of the shares of the CPUES of RA 5 and 6 were grouped according to 4 time periods (1975–1984, 1985–1994, 1995–2005, 2006–2015) and Kruskal-Wallis rank sum tests with adjacent pairwise comparisons by Wilcoxon rank sum tests were performed to assess differences between the proportion of cod caught in RA 5 and 6 between different time periods. Significance was adjusted by sequential Bonferroni correction.

OTOLITH-BASED ASSESSMENT OF ANNUAL GROWTH

Only the otoliths of cod age 5 and age 6 years were selected for increment measurements to minimise possible errors introduced by size-selective mortality. The Danish otoliths were treated according to the ‘crack & burn method’ described by Christensen (1964) and Pentilla and Dery (1988). After breaking the anterior part of the otolith was burnt and the protruding material at the breakage was ground (Struers LaboPol-5, polishing disc grain size 800 µm) to the core plane of the otolith ensuring that the polished surface plane was aligned perpendicular to the ventral edge of the otolith. The polished anterior end was embedded in plasticine on a microscope slide aligning the surface parallel to the surface of the microscope slide and photographed at a magnification of 16x using a stereo microscope (Leica MZ12.5®) connected to a digital camera system (Olympus DP50®/analySIS 3.2®). To minimize interferences by grinding scratches the section was wetted with oil.

Both, pictures of the German otoliths and of the Danish otoliths were measured using image analysis software (ImageJ1.43u® or Image-Pro Plus® 6.0.). The widths of the annual increments were measured all by one experienced reader along the distal radius of the otolith in the ventral lobe. According to Pentilla and Dery (1988) one increment was defined as the distance from the start of an opaque to the end of the following hyaline zone and each measurement along the measuring axis was conducted perpendicular to the increment 3 times. The mean of the three measurements was used for further analyses.

For the growth analysis we used the original increment width measurements instead of back-calculated fish length from otolith growth to avoid possible bias introduced by back-calculation methods (Campana, 1990; Francis, 1990; Bolle *et al.*, 2004). In general, otolith increment growth reflects the body growth of cod (e. g. Dannevig, 1933; Trout, 1954; Blacker, 1974). The opaque zone of one annual otolith increment is deposited during December and July, reflecting faster growth in cod. The translucent part of the increment is formed between August and December and is associated with lower metabolism and poor growth of cod (Righton, 2001; Pilling *et al.*, 2007; Millner *et al.*, 2011).

Otolith growth declines with age as fish length growth declines with age. Thus, to compare the otolith growth at different ages amongst the individuals a normalised (standardised) increment size IW_{az} was calculated using the following equation:

$$IW_{az} = \frac{(\mathrm{IW_a} - \mathrm{IW_{a\bar{x}}})}{\mathrm{IW_{a\sigma}}},$$

where $IW_{a\bar{x}}$ is the overall mean increment width for the specific age a subtracted from the measured individual increment width (IW_a), divided by the standard deviation of total measured increment width of a given age ($IW_{a\sigma}$).

The standardised increment widths were assigned to the corresponding year of formation and then grouped according to 4 time periods (1970–1984, 1985–1994, 1995–2005, 2006–2010). The increment growth was tested for differences between the RAs and the time period by applying Kruskal-Wallis rank sum tests and adjacent pairwise Wilcoxon comparisons with Bonferroni correction. The representation of a growth chronology i.e. time series of the increment growth at age class 1-5 was only possible from otoliths sampled in RA 6 due to smaller sample sizes in the other RAs. All analyses were performed using the software R version 3.2.0 (R core Team, 2015).

ANALYSIS OF FACTORS DETERMINING LENGTH-AT-AGE AND GROWTH-AT-AGE

To determine the influence of external factors on the length-at-age of North Sea cod and the otolith growth of cod from RA 6 temperature, prey abundance and size-selective mortality were used since all 3 factors have been shown to influence the growth and/or the length-at-age of Atlantic cod (Brander, 2000; Rindorf *et al.*, 2008; Sinclair *et al.*, 2002b). Two separate redundancy analyses (RDA) were performed to determine the degree to which the factor variables influence the length-at-age or the otolith growth-at-age of cod. RDA is a type of reduced rank regression and represents a special form of the principal component analysis (PCA) (Van Den Wollenberg, 1977, Ter Braak, 1994). The principal components of the standardised response variables and the standardised explanatory variables are extracted simultaneously, in such way as to maximise the correlation between the components (Braak & Looman, 1994). To test for significance of the derived canonical axes of the RDA the results were compared against random expectation creating 9999 random ordination configurations (full model) and regression relationships using Monte Carlo significance test applying the F-statistic (Ter Braak, 1986). We used cross-correlations and Variance inflation factor (VIF) values in order to detect possible co - linearity between the explanatory variables. VIF values >5 were excluded from the RDA. Marginal effects and conditional effects were estimated. Marginal effects represent the variability explained by using only one explanatory variable without considering the others. Conditional effects estimate the variability explained by one explanatory variable after removing the effects of the others. A Forward selection of the explanatory variables according to their conditional effect was applied.

To describe the time series of the mean length-at-age of cod in age classes 1–6 between 1975–2010 in the RDA the annual mean North Sea winter and summer temperature, prey abundances (number of recruits of sandeel, sprat, Norway pout, herring, whiting, cod, haddock, plaice, sole), the annual proportion of cod from RA 5 and RA 6, and the fishing mortality were used as explanatory variables.

The RDA of the increment growth of cod otoliths in RA 6 between 1975 and 2005 used the annual mean winter and summer temperatures in RA 6, the prey abundance (number of recruits of sandeel, sprat, herring, whiting, cod, plaice, sole) and the fishing mortality as explanatory variables. RDA analyses were performed using Brodgar software package 2.7.4 (www.highstat.com).

RESULTS

LENGTH-AT-AGE OF NORTH SEA COD

The mean body length of North Sea cod in age classes 1–5 years of both sexes showed a decreasing trend between 1975 and 2005 after which the lengths-at-ages increased again and remained high until 2015. Between the periods 1975–1984 and 1985–1994 the mean length of cod in age classes 1 to 5 decreased on average by 4 cm (8%). Cod in the age classes 1–5 decreased again on average by 4 cm (8%) smaller in 1995–2005 compared to 1985–1994. From 1995–2005 to 2006–2015 the mean length of cod of age classes 1 to 5 increased again on average by 5 cm (12%). In age 6 cod the average length of females decreased steadily from 1975 to 2015 by 7 cm (7%) at the end of the time series. Mean body length of male cod at age 6 years decreased by 9.6 cm (10%) in the period 1995–2005 compared to 1985–1994 and remained at this level until the end of the time series (Fig. III–2).

SPATIALLY RESOLVED LENGTH-AT-AGE

The mean length-at-age was significantly different between RAs in which the fish were caught in all age groups and both sexes. Cod caught in RA 5 and 6 were in general larger compared to their conspecifics from the other RAs. At age 1, cod from RA 5 and RA 6 was on average 3 cm and 1 cm bigger compared to cod from the remaining RAs. Compared to the remaining RAs the mean length-at-age 2 was 10 cm and 6 cm bigger in RA 5 and RA 6 respectively. In age 3, the difference in size between RA 1–4 and 7 and RA 5 and RA 6 increased to 13 cm and 11cm. In age classes 4-6 cod from RA 5 and RA 6 were on average 5 cm and 6 cm larger than their conspecifics from the remaining North Sea (Kruskal-Wallis rank sum tests; $P<0.001$; Table III–I).

The fit of the von Bertalanffy growth models to the length-at-age of the RAs 1–7 showed a large variability in L_∞ and K between the RA examined. In RAs 5 and 6 males and females showed highest estimates for K, whereas lowest were found in RAs 3 and 4. With fixed K and t_0, L_∞ of fishes from RA 5 and RA 6 was on average 19 cm (11%) larger compared to the remaining North Sea. Growth parameter K in RA 5 and RA 6 was on average 0.03 (16%) higher than of the other RAs (Table III–II).

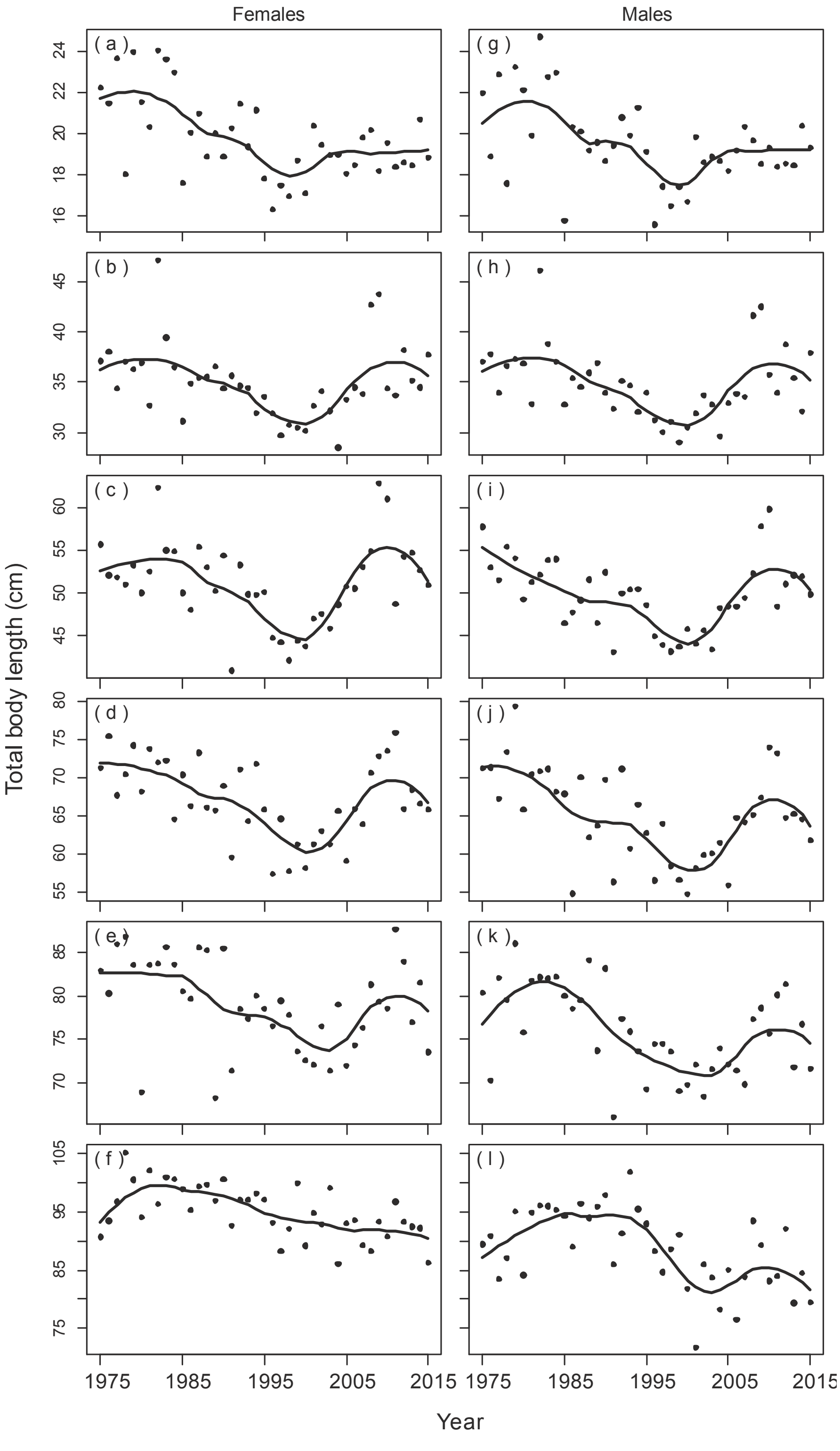

Figure III–2. Time series of the mean length-at-age 1 to 6 years of North Sea cod (upper panels age 1, lowest panels age 6). Left panels show female fish length and right male fish length-at-age. Dots represent annual means and solid black line shows loess smoother fitted to the annual mean length-at-age (loess span 0.5).

Table III–I. Mean length-at-age of North Sea cod caught in Roundfish Area (RA) 1 to 6. Results of the Kruskal-Wallis rank sum test for spatial differences between the lengths-at-ages.

Age	**RA**	**Females**					**Males**				
		MEAN length (cm)	**N fish**	χ^2	**df**	***P***	**MEAN length (cm)**	**N fish**	χ^2	**df**	***P***
1	1	20.2	306	62.7	6	<0.001	19.7	374	56.7	6	<0.001
	2	19.0	852				18.1	1089			
	3	20.1	909				19.8	1003			
	4	21.1	785				20.4	862			
	5	22.8	637				22.0	574			
	6	21.1	3068				20.2	3083			
	7	18.6	750				18.2	873			
2	1	33.9	6027	128.2	6	<0.001	34.2	5801	131.6	6	<0.001
	2	31.5	2694				31.4	2731			
	3	34.0	1566				34.6	1570			
	4	33.8	1812				33.2	1780			
	5	43.5	829				44.4	744			
	6	40.8	4222				40.5	4131			
	7	31.4	2027				31.8	1940			
3	1	50.8	3937	178.4	6	<0.001	50.4	4019	153.3	6	<0.001
	2	42.6	815				43.2	1056			
	3	51.8	679				51.6	784			
	4	45.6	635				45.8	607			
	5	64.6	492				61.4	326			
	6	62.2	1147				60.5	1374			
	7	49.0	593				49.1	677			
4	1	67.5	1684	88.8	6	<0.001	66.0	1563	64.4	6	<0.001
	2	67.5	260				63.9	331			
	3	72.2	279				66.8	283			
	4	61.7	196				63.6	235			
	5	76.7	138				74.1	105			
	6	77.1	585				75.3	667			
	7	67.7	240				68.0	339			
5	1	78.2	757	70.7	6	<0.001	75.6	637	73	6	<0.001
	2	84.1	284				82.5	308			
	3	83.4	138				82.0	104			
	4	79.1	99				78.6	89			
	5	87.9	49				87.1	23			
	6	89.4	320				87.3	479			
	7	81.7	175				77.7	201			
6	1	91.9	525	64.5	6	<0.001	87.4	407	44.4	6	<0.001
	2	98.1	441				95.5	445			
	3	96.1	84				93.3	54			
	4	98.6	121				94.5	116			
	5	100.4	69				96.7	23			
	6	102.8	497				95.9	448			
	7	98.9	205				91.8	154			

TABLE III–II. Von Bertalanffy growth parameters estimated from the lengths-at-ages 1-6 of cod caught in Roundfish Area (RA) 1–7 in the North Sea. Left part of the table shows model estimates for parameter L_∞ with fixed t_0 and K. Right part of the table shows estimated parameter K with fixed L_∞ and t_0.

Sex	**RA**	**L_∞ (cm)** K_{fixed}=0.146; $t_{0\ \text{fixed}}$= 0	**K** $L_{\infty\ \text{fixed}}$= 157.1; $t_{0\ \text{fixed}}$= 0
F	1	151.4	0.138
	2	154.6	0.140
	3	158.7	0.147
	4	148.7	0.134
	5	173.5	0.168
	6	173.7	0.168
	7	156.0	0.143
M	1	146.8	0.132
	2	149.9	0.135
	3	153.0	0.140
	4	146.9	0.132
	5	169.5	0.162
	6	167.2	0.159
	7	149.6	0.135

ABUNDANCE SHARES OF THE RAS IN THE TOTAL NORTH SEA COD AGE GROUPS

The analysis of the spatial pattern of the composition of the abundance index of cod at age within the North Sea showed a change in the relative importance of the RAs for the total North Sea stock over the period 1975 to 2015. The proportion of cod at age 1 in RA 6 represented up to 80% of the total cod within the North Sea from 1975 to the end of the 1980s. After 1990 the shares of cod at age 1 from RA 6 in the total North Sea stock was hardly 20%. The majority of cod of age class 1 in the post 1990s was found in RA 7 off the Danish coast and in RA 3 and RA 4 along the English coast. The shares of cod from RA 1 in the total North Sea age class 1 had increased until 2015. The proportion of cod abundant in RA 6 of the total North Sea cod age class made up to 40% until the beginning of the 1990s and decreased to hardly 5–10% after 1991. During the 1990s large shares in cod at age 2 were found in RA 4 whereas in the 2000s the shares in cod age class 2 shifted to mainly RA 7 and 1. After 2005 the shares of cod from RA 5 increased from about 10% to more than 30%. The composition of the shares of each RA in age class 3 showed that from 1975 to the end of the 1980s 25% of the age cohort was contributed by RA 5 and RA 6. In the 1990s and the beginning of the 2000s shares of both RAs together in cod at age 3 made hardly 15%. After 2003 the percentage of the total cod age 3 cohort from RA 5 & 6 increased again to 70%. The shares in RA 1 increased from 30% to more than 50% from 1975 to 2015. The shares of RA 1 in cod at age 4 increased from 1975 up to 70% after 2007. From the beginning of the 1990s increasing shares in cod were abundant in RA 7 and from around 2004 onwards almost no cod were found in RA 4. The shares of RA 1 in age 5 cohort were largest compared to the remaining RAs with increasing proportions from 1975 to 2015. Until the mid-1990s the shares of cod at age 6 in RA 1 was on average around 25%. From 1995 onwards the shares in RA 1 increased to almost 80% in 2007, followed by a decrease afterwards. From the beginning of the 2000s no cod were caught in RA 4 Generally in all ages and both sexes the importance of cod in RA 6 had decreased dramatically while RA 7 off the Danish coast and RA 1 in the northern North Sea gained importance for age 3 + cod and RA 3 and RA 4 off the English coast for juvenile cod. RA 2 is not as prominent as other RAs in the North Sea stock composition (Fig. III–3A).

The cumulative share of RA 5 and RA 6 in the total cod stock was considerably lower in the period 1995–2004, compared to 1975-1984. In age 1 cod the proportion decreased from over 50% to only 20% in 2005–2015. Age 2 North Sea cod consisted of more than 30% fish caught in RA 5 and RA 6 in 1975–1984. In age classes 3, 4 and 5 shares of RA 5 and 6 decreased in the period 1995–2005 with subsequent increase. The shares of RA 5 and RA 6 in age 6 cod decreased by half from the period 1975–1984 to the period 2006–2015 (Fig. III–3B).

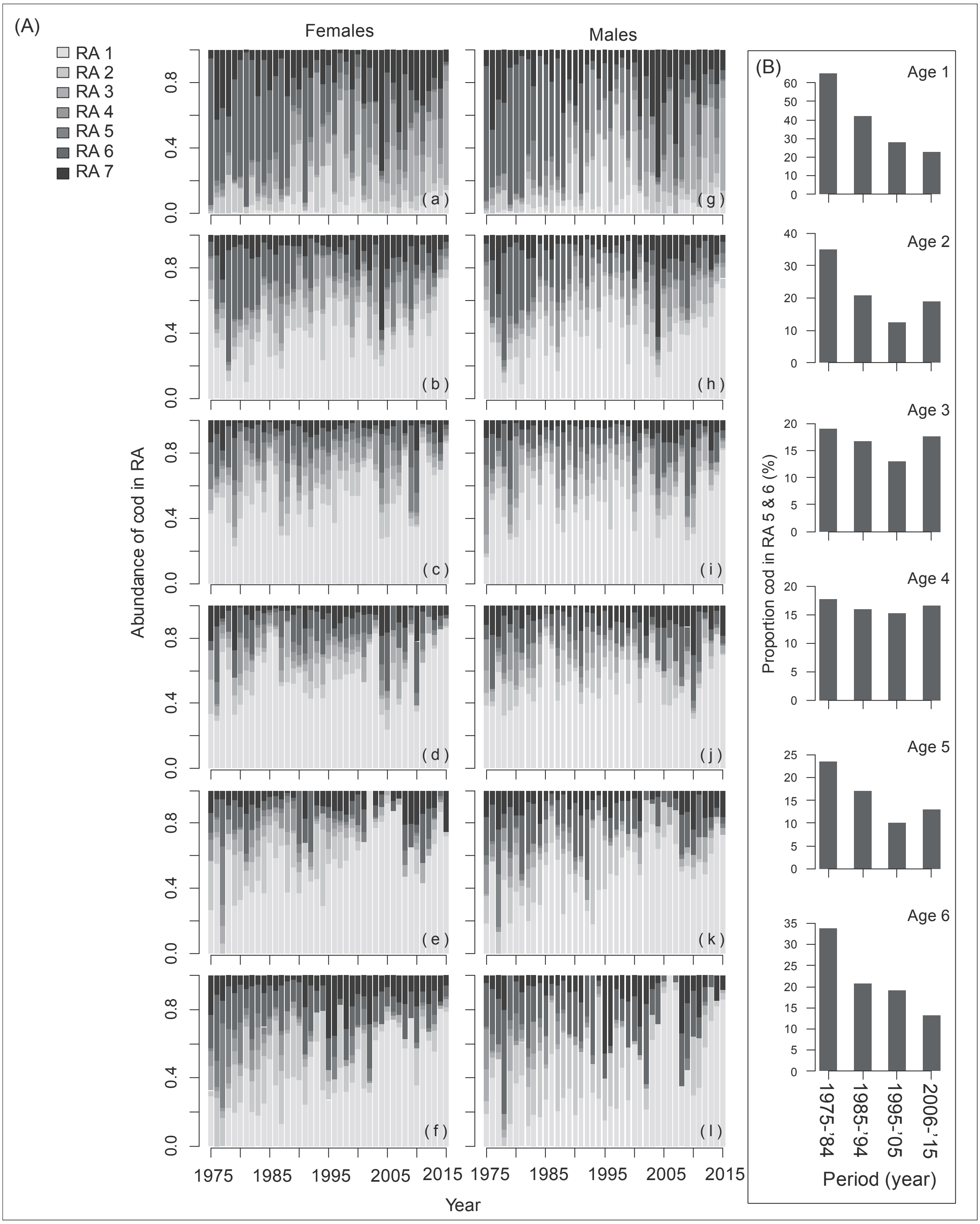

FIGURE III–3. 1st quarter IBTS CPUE in numbers per hour of cod. (A) age 1–6 years female (A-F) and age 1–6 years male (G–L) North Sea cod between 1975 to 2015 in Roundfish Areas (RA) 1–7. (B) Cumulative proportion of cod caught in RA 5 and 6 of the total cod catches in the North Sea.

OTOLITH INCREMENT GROWTH OF NORTH SEA COD

The standardised otolith increment width was significantly different between the RA (χ^2= 27.826, df = 6, P<0.001). The comparison of the increment width between the time periods 1970–1984, 1985–1994, 1995–2005 and 2005–2010 showed that in RA 2 and RA 3 increments were significantly smaller in 1995–2005 compared to periods before (Wilcoxon rank sum tests; P<0.05). In RA 1, RA 4, RA 6 and RA 7 no significant difference was found in the increment width between the periods (Fig. III–4).

The growth chronologies of increments formed at ages 0–5 years in RA 6 cod otoliths revealed no common trend for all age classes. The growth of increments at age 0 increased over the period 1975 to 2005 whereas the increment growth-at-age 1 year decreased over the observed time period. Otolith growth-at-age 2-4 showed large inter-annual variability with no clear trend between 1975 and 2005. The increment growth-at-age 6 showed no clear trend until the beginning of the 1990s after which increment growth declined (Fig. III–5).

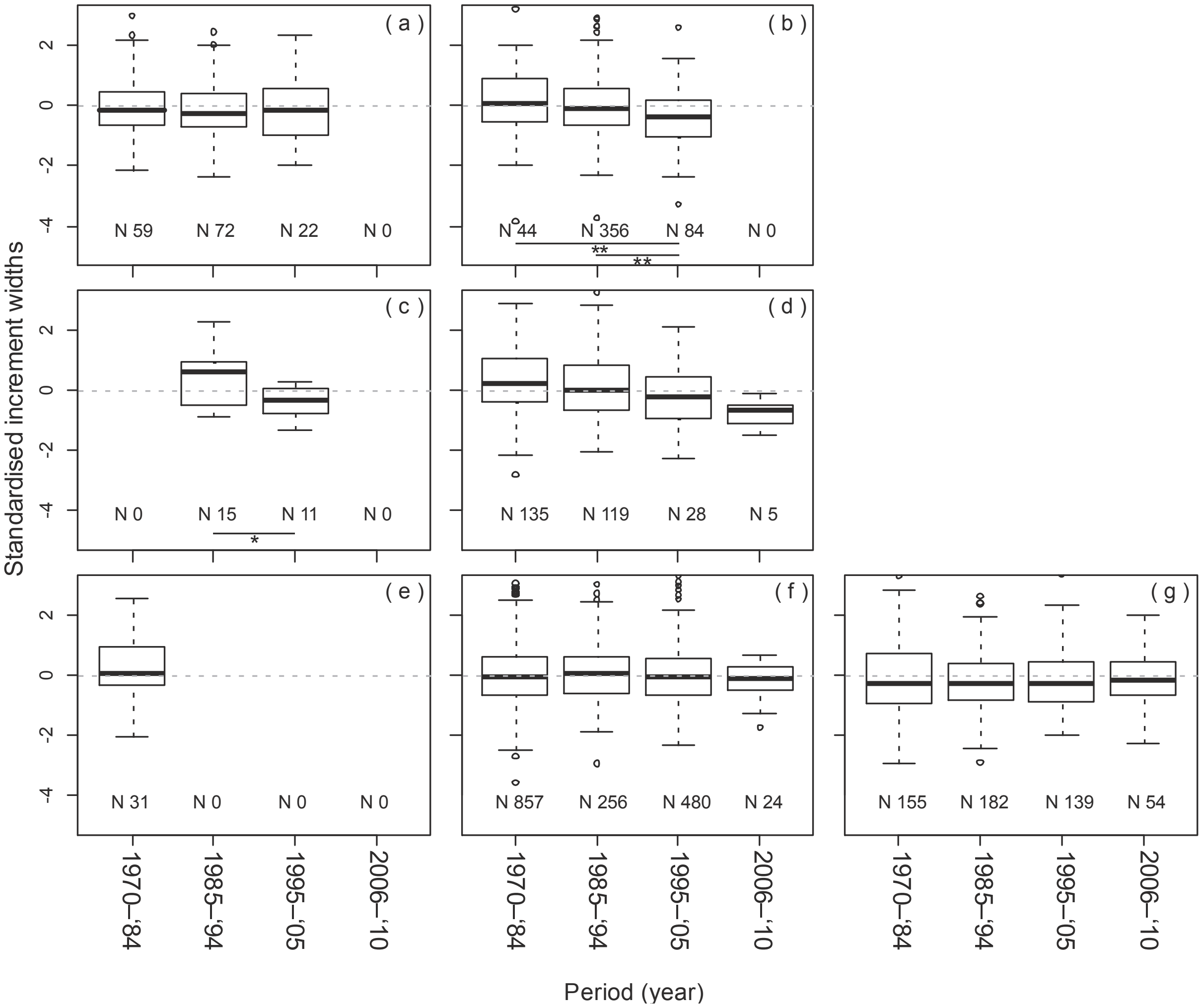

FIGURE III–4. Standardised otolith increment widths formed at ages 1–6 years in time periods between 1970 and 2010 of cod caught in North Sea roundfish areas 1–7 (a–g).

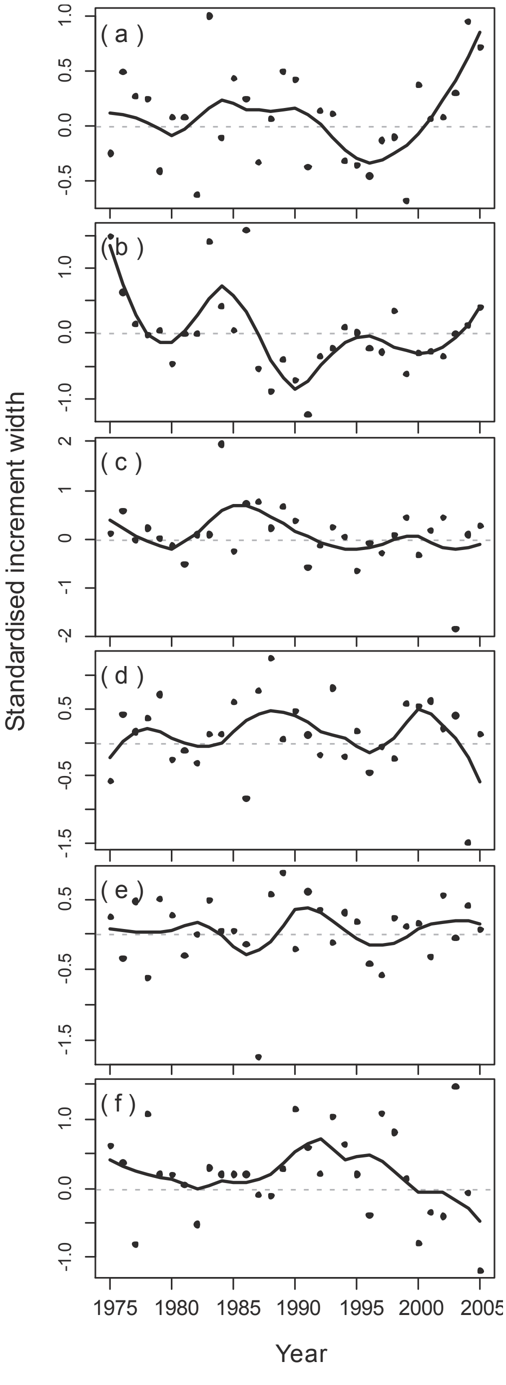

FIGURE III–5. Annual mean standardised increment width at ages 1 to 5 or 6 years (a–f) of cod caugth at age 5 or 6 in RA 6. Black lines are loess smoothers fitted to the mean annual increment width with a span of 0.4.

FACTORS DETERMINING THE LENGTH-AT-AGE

The RDA model explained 62.1% of the variability in the annual mean length-at-age 1–6 years of cod between 1975 and 2010 (*F*=2.8; *P*<0.001). The mean F of cod, plaice and sole was the most important explanatory variable and highly correlated with axis 1. F was negatively correlated with the average annual mean length-at-age 1–6 years. The marginal effect of fishing mortality explained solitarily 31% of variation in the length-at-age of cod and 50% of the explained variation in the RDA (*F*=15.1; *P* <0.001).

The conditional effect of the summer temperature explained 12% of the variation and was negatively correlated with the length-at-age of cod. After excluding the effects of the other variables temperature accounted for 21% (marginal effect) of the variation in the length-at-age data. Conditional effects of all other variables tested were not significant. However, marginal effects indicated also a distinct isolated effect of the cumulative share of cod from RA 5 and RA 6 on the total North Sea stock which explained 28% of the variation in the length-at-age and was negatively correlated with the fishing mortality (F). Nonetheless, after excluding the effects of the other explanatory variables conditional variance explained decreased to 3% and was no longer significant (Fig. III–6; Table III–III).

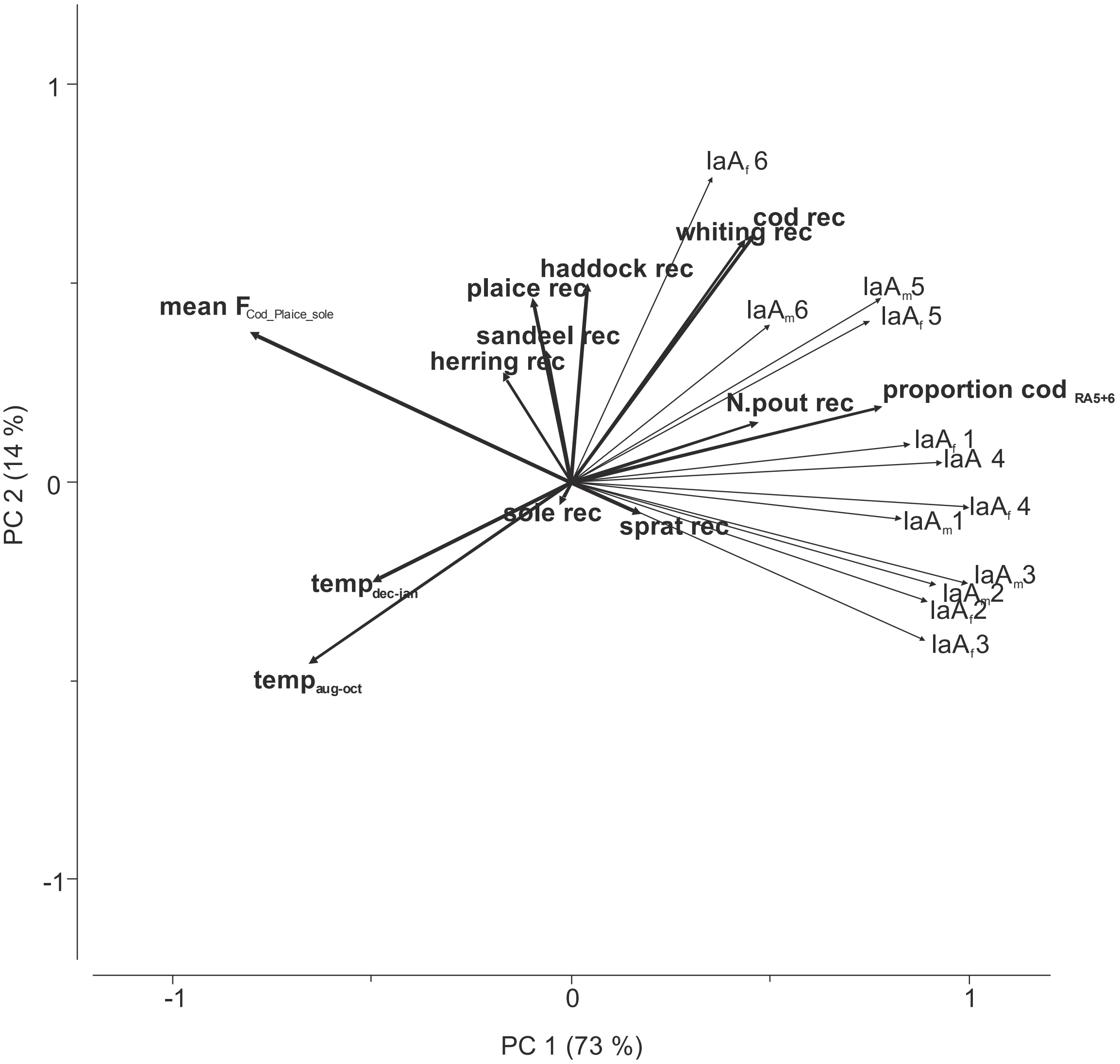

FIGURE III–6. Ordination of length-at-age (LaA) 1–6 years of cod (thin arrows) in relation to the explanatory variables (bold arrows) after forward selection. Suffixes indicate m= male and f = female. Note that ankles between explanatory and response variables indicate the correlation between them (ankle <90° positive correlation; ankle >90° negative correlation).

TABLE III–III. Results of Redundancy analysis performed on the standardised length-at-age of North Sea cod age 1–6 years as response variables and different explanatory variables.

RDA model *Monte Carlo significance test of all canonical axes*			**explanatory variables**	**VIF**	**Marginal effects**		**Conditional effects**		
% explained variation	*F*	*P*			% of total variation	% of explained variation	% of explained variation	*F*	*P*
62.1	2.8	<0.001	mean $F_{\text{Cod Sole Plaice}}$	1.9	31	50	31	15.1	<0.001
			mean temp aug–oct	3.2	21	35	12	7.0	<0.001
			proportion $\text{cod}_{\text{RA 5 + 6}}$	3.4	28	45	3	1.9	0.1
			N. pout recruits	2.3	11	18	2	1.5	0.2
			sandeel recruits	2.8	2	3	2	1.2	0.3
			sprat recruits	2.0	2	3	2	1.2	0.3
			whiting recruits	3.0	12	19	2	1.4	0.2
			cod recruits	4.0	13	21	1	0.9	0.5
			haddock recruits	1.9	3	4	1	0.8	0.5
			herring recruits	2.3	2	4	1	0.5	0.8
			plaice recruits	3.5	3	4	1	0.6	0.7
			sole recruits	1.5	1	1	1	0.9	0.5
			mean temp dec–jan	2.4	12	19	1	0.7	0.6

GROWTH-AT-AGE IN RA 6 AND FACTORS DETERMINING GROWTH-AT-AGE

The RDA model explained 37% of the variability in the mean increment width at age 0–5 years of cod in RA 6 between 1970 and 2005 (F=1.6; P<0.05). The annual mean summer temperature in RA 6 was the most important factor influencing increment width (F=2.7; P<0.05) explaining conditionally 8% of the variability explained by the RDA. Summer temperature was negatively correlated with the increment width at age 1 and 2 years and uncorrelated with age 0, age 3 to 5 years increment widths. The annual mean winter temperature was significantly determining increment growth (F=2.6; P<0.05). The otolith increment growth time series at age 0 and age 4 years were positively correlated with the mean winter temperature. Conditional effects of all other variables tested were not significant (Table III–IV; Fig. III–7).

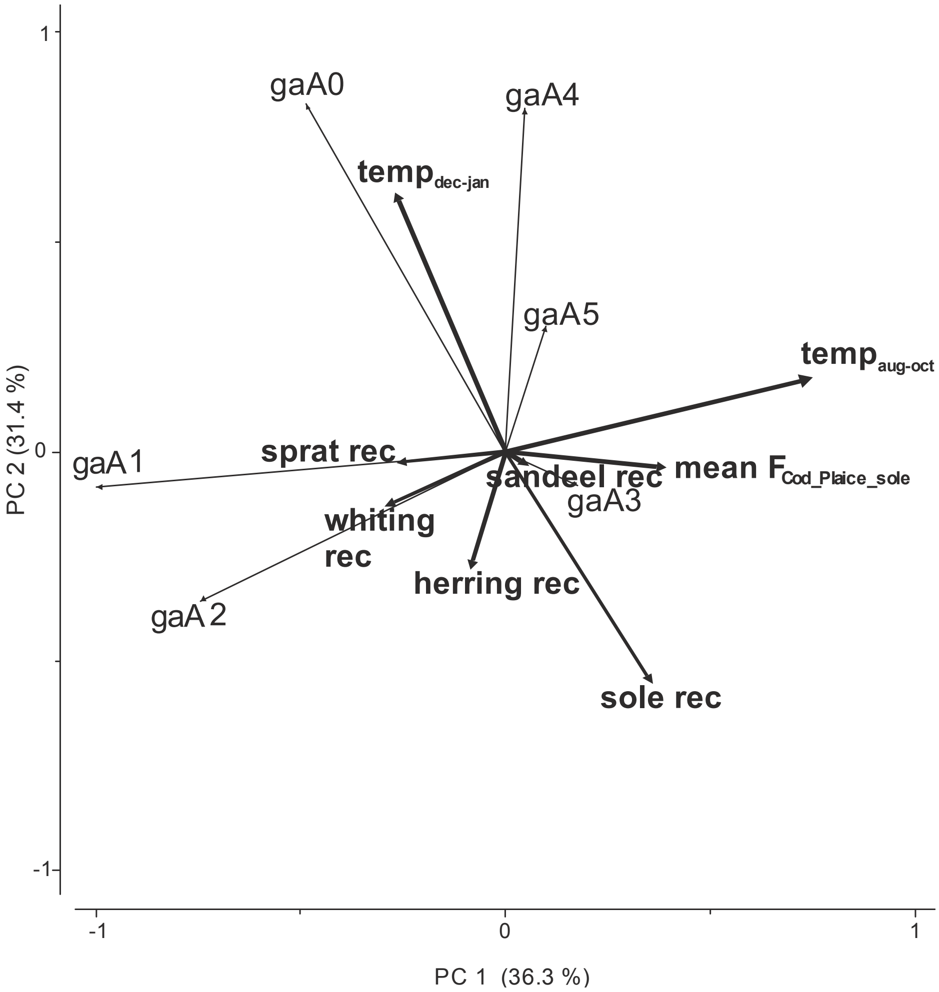

FIGURE III–7. Ordination of growth-at-age (gaA) 0–5 of cod (thin arrows) in relation to the explanatory variables (bold arrows) after forward selection. Note that ankles between explanatory and response variables indicate the correlation between them (ankle <90° positive correlation; ankle >90° negative correlation).

TABLE III–IV. Results of the standardised redundancy analysis (RDA). Marginal and conditional effects of the biotic and abiotic explanatory variables on the of growth-at-age 0–5 years of North Sea cod.

RDA model *Monte Carlo significance test of all canonical axes*			**explanatory variables**	**VIF**	**Marginal effects**		**Conditional effects**		
% explained variation	*F*	*P*			% of total variation	% of explained variation	% of explained variation	*F*	*P*
0.37	1.6	<0.05	mean temp $_{\text{aug–oct}}$	1.9	8	22	8	2.7	0.01
			mean temp $_{\text{dec–jan}}$	1.1	8	22	8	2.6	0.02
			sole recruits	1.3	7	20	6	2.0	0.07
			herring recruits	1.6	2	6	4	1.3	0.24
			sprat recruits	1.8	4	12	3	1.1	0.38
			whiting recruits	2.2	3	9	3	1.2	0.32
			sandeel recruits	1.3	1	2	2	0.7	0.61
			mean $F_{\text{Cod Sole Plaice}}$	2.8	2	7	2	0.7	0.63

DISCUSSION

TEMPORAL TRENDS IN THE LENGTH-AT-AGE OF NORTH SEA COD

The average length-at-age of North Sea cod decreased in the period 1975 to 1994 by 16% remained at a low level in the following years between 1995 and 2005 and increased again after 2005. These results agree with other studies identifying a decline in the length-at-age of North Sea cod (Rindorf *et al.*, 2008; Marty *et al.*, 2014). However, these time series ended in 2005 until when no recovery in the mean length-at-age was observed. Multiple other cod stocks in the North Atlantic showed a decline in the average size-at-age since the 1970s (Brander, 2007; Sinclair *et al.*, 2002).

MECHANISMS CONTROLLING THE POPULATION MEAN LENGTH-AT-AGE

Regarding the following discussion it should be borne in mind that on an individual basis growth is equivalent to the length-at-age. However, on a population basis the average length-at-age is not necessarily equivalent to the individual growth. Generally, temporal changes in the mean size-at-age in a population might arise from two different mechanisms: (i) changes in the growth of fish in an age class or (ii) changes in the composition of the individuals representing an age class of a population.

The growth of fishes is in general determined by multiple intrinsic (e.g. sex & maturity) and extrinsic (e.g. temperature & food) factors (Fry, 1971). If the growth of most fish in an age class decreases the mean length-at-age is reduced. In turn, if growth increases the mean length-at-age increases.

The second possible mechanism altering the mean length-at-age is a change in the composition of the population. The influence of the composition of the population on the mean size-at-age requires a priori that individual variability in this trait exists within the population. Within population variability in the length-at-age might arise either from different genotypes of the individuals or from phenotypic plasticity. As any other trait the size-at-age shows phenotypic plasticity. This leads to different expressions of the size-at-age depending on the environmental conditions the individual is facing. Thus, if the population inhabits an area with divergent environmental stimuli, different sizes at a given age are exhibited. Additionally, size-selective mortality is required to change the composition of the individuals that represent the population. If individuals with a lower size-at-age (slow growers) are selectively removed from an age class the mean size-at-age of the population increases. On the other hand if individuals with a large size-at-age (fast growers) are eliminated from an age class the size-at-age of the population decreases.

TEMPORAL TRENDS IN REGIONAL GROWTH-AT-AGE OF NORTH SEA COD

The growth of otolith increments of cod was lower only in RA 2 and 3 during the period of low length at age (1995–2005) compared to earlier periods. Individual growth of fish caught in RAs 1, 4, 6 and 7 did not differ significantly in the period of low length-at-age compared to the periods before and after. Thus, we found no evidence for a general decline in the growth of North Sea cod. Therefore this cannot be the cause of the length at age depression.

In the German Bight (RA 6) it was possible to reconstruct a growth chronology for each age class separately. The increment growth in age 0 cod increased between 1975 and 2005. This increase either implies that 0 group cod actually grew faster at the end of the observed time series or that the length of the growth period increased.

Growth of age 0 cod might have increased between 1975 and 2005 if juvenile cod benefited from the ecological and physiological changes in the German Bight. Better growth might result from increasing temperatures assuming sufficient food supply. Juvenile cod in the southern North Sea feeds mainly on invertebrates such as the brown shrimp (*Crangon crangon* L.) and on small fish such as sand gobies (Daan, 1973). Sand gobies as well as brown shrimp are aplenty abundant in the southern North Sea (Temming & Hufnagl, 2014). Thus, increasing temperatures might have led to an increase in age 0 cod growth, as food shortage is unlikely.

A prolonged growth period of age 0 cod might result from a shift of the spawning period of adult cod towards earlier in the year or from a seasonal shift in the window of survival of the cod offspring in RA 6. Large inter-annual variation, as well as a shift of the spawning season have been documented for several cod stocks (Hutchins & Myers, 1994a; Wieland *et al.*, 2000). In the southern North Sea the spawning of the sole (*Solea solea* L.1758) stock shifted towards earlier in the season (Fincham *et al.*, 2013). Thus, a shift in the spawning season of cod in the southern North Sea might have occurred. In the 1960s spawning of cod in the southern North Sea took place between January and April (Brander, 1994). Although there is evidence that the location of the spawning grounds of cod within the North Sea did not change since the 1960s (Fox *et al.*, 2008) information lacks on the present spawning seasonality of cod in the southern North Sea. Therefore, a shift in the spawning period cannot be verified.

The survival of cod larvae and juveniles is highly dependent on seasonal feeding conditions (Fry, 1971; Cushing, 1990; Gotceitas *et al.*, 1996). The timing and the composition of zooplankton that cod preys upon has changed substantially between 1960 and 2000 (Beaugrand *et al.*, 2003), which might favour the survival of early seasonal cohorts. Thus, an earlier window of survival of cod offspring might have led to the observed increase in otolith increment width from 1975 to 2005.

Nonetheless, without further investigations, it is neither possible to determine which of the possible explanations is responsible nor to distinguish to which extend each theory contributes to the observed increase in otolith increment width of age 0 cod.

The otolith increment growth-at-ages 2 to 5 altered more or less arbitrary with no clear trend except for age class 5 where growth declined between 1990 and 2005. Thus, the individual growth of cod older than 2 years in RA 6 did not change within the observed time period.

SPATIAL PLASTICITY OF THE LENGTH-AT-AGE & THE GROWTH

Our results show distinct spatial variability in the mean length-at-age of cod. The comparison of the mean length-at-age of fishes between RA 1 to 7 showed that in general, fish from the southern North Sea (RA 5 and RA 6) were larger at a given age compared to their conspecifics from the central and northern parts of the North Sea. In addition, von Bertalanffy growth parameters varied between the RAs. Assuming equal time at fish length 0 cm (t_0) and identical growth coefficients (*K*) fish from the southern North Sea showed on average an 11% larger mean asymptotic length (L_∞) compared to fish from the remaining North Sea. With a given L_∞ fish from the southern North Sea had on average a 16% higher *K* compared to fish from the remaining North Sea. Likewise, the cod growth inferred from otolith increment width differed between the RAs.

Although early studies showed stock homogeneity within the North Sea based on haemoglobin typing (Sick, 1965) and the North Sea cod stock is managed as one unit (ICES, 2013) other studies alluded to population sub-structuring within the North Sea stock (e.g. Wright *et al.*, 2006). Spatial variability in otolith growth increments have been documented with largest growth in the southern and smallest in the northern North Sea (Bolle *et al.*, 2004). Daan (1974) found that growth rates of southern North Sea cod started off faster and slowed down earlier compared to northern North Sea cod. Moreover, molecular genetic studies identified 4 genetically divergent populations inhabiting North Sea waters off Bergen, within the Moray Firth, off Flamborough and within the Southern Bight (Hutchinson *et al.*, 2001). Otolith isotope composition revealed isolation between juvenile cod from the Moray Firth and Buchan indicating spatial separation of spawning aggregations and recruits (Gibb *et al.*, 2007). Consequently, trends in the spawning stock biomasses were significantly different between different areas of the North Sea (Holmes *et al.*, 2008). Thus, there is evidence that North Sea cod is not one panmictic population. Our results confirm these findings and imply that North Sea cod is an agglomeration of spatially divergent sub-populations.

PREY ABUNDANCE

No effect of the abundance (N recruits) of selected prey species was detected neither on the length-at-age of North Sea cod nor on the otolith increment growth of cod in RA 6. These results seem a bit counterintuitive considering the observed simultaneous decline in the spawning stocks of several important prey species of cod (sandeels, Norway pout, herring and sprat) in the beginnings of the 2000s (ICES, 2013). Moreover, Rindorf *et al.* (2008) found that growth of age 1 cod depended on a sandeel biomass index and the growth of older North Sea cod increased significantly with increasing demersal prey fish biomass index. However, the authors stated that the sandeel biomass index was highly correlated with the cod density index that was also significantly correlated with the growth of age 1 cod and that it is not possible to disentangle both effects. Moreover, considering that the demersal prey biomass only accounted for 6% of the variation in the growth data the influence of single prey species on North Sea cod as in our analysis might be too weak to be detectable. Cod growth in other regions is highly influenced by prey abundance (Mehl & Sunnanå, 1991; Jørgensen, 1992; Krohn *et al.*, 1997; Mello & Rose, 2005). However, those cod stocks largely depend on the abundance of one single prey species that is dominating the cod diets (Lilly, 1987; Mehl, 1989). In the North Sea cod is a carnivorous generalist that is feeding on a variety of species. Cod diets directly reflect the abundance of a certain prey indicating that cod feeds more or less non-specific, making an influence of the availability of a given food species unlikely (Floeter & Temming, 2003; Link *et al.*, 2009). Moreover, the diet of cod includes distinct proportions of non-fish prey. Especially in the southern North Sea depending on season and size the diet of cod consists of up to 80% of invertebrates (Daan, 1973). For this reason together with the declining abundances of cod a limitation of the growth of North Sea cod introduced by a limitation of forage fish seems to be fairly unlikely.

TEMPERATURE

The mean winter and summer bottom temperatures had a significant negative impact on the mean length-at-age of North Sea cod. Generally, temperature might determine the length-at-age in two ways: via its influence on the spatial distribution of cod or through its influence on the growth of fish.

Increasing temperatures led to decreasing abundances of cod in the southern North Sea (Hedger *et al.*, 2004; Perry *et al.*, 2005). Cod in the northern North Sea grows slower and has a lower length-at-age (Daan, 1974). Thus, the decreasing abundance of cod in the southern North Sea could have altered the composition of the cod population with higher proportions of slow growers from the North leading to the observed depression in the population mean length-at-age.

Temperature influences metabolic rates and consumption and thus might control the growth of fishes (e.g. Jobling, 1988; 1995). Growth increases with temperature to an optimum after which growth decreases again (Brett, 1969). Optimum temperature for the growth of cod determined in laboratory experiments ranged between 17°C in early juveniles to 9°C in adults (e.g. Pedersen & Jobling, 1989; Björnsson & Steinarsson, 2002; Björnsson *et al.*, 2007). However, tagging studies from the North Sea revealed that the majority of adult cod inhabited temperature regimes that were considered as superoptimal for growth without seizing the opportunity to move into colder waters (Neat & Righton, 2007).

The otolith increment growth of cod in RA 6 was significantly determined by the average winter and summer bottom temperatures. Earlier studies found no significant effect of temperature on the growth of adult cod (e.g. Sinclair *et al.*, 2002b; Rindorf *et al.*, 2008). However, multiple other studies indicated a distinct effect of temperature on adult cod growth (e.g. Björnsson & Steinarsson, 2002; Brander, 2007). Brander (1995) stated that temperature differences experienced within one stock tend to be fairly small and commonly are difficult to separate from other factors like migration which leads to a failure of the detection of the influence of temperature. Moreover, temperature explained more than 90% of the variation in growth between different North Atlantic cod stocks whereby higher temperatures led to higher growth. The lack of an effect of temperature on growth might arise from using the inappropriate temperature (Brander, 2000).

Growth of age 0 cod was positively correlated with winter temperature. As winter temperatures in the southern North Sea lay well below the thermal optimum for juvenile cod growth it is reasonable to conclude that with increasing winter temperatures growth is enhanced as long as enough food is supplied. Moreover, other studies found a positive relationship between temperature and the growth of juvenile Atlantic cod (Armstrong *et al.*, 2004; Mello & Rose, 2005; Rindorf *et al.*, 2008). On the other hand temperature might have caused a prolongation of the growth period of age 0 cod. As discussed above a shift of the window of survival of cod offspring or the spawning period of adults might have been associated with temperature.

In general, the onset of the opaque (indicating good body growth in fish) as well as the translucent (indicating poor body growth in fish) zone formation on a cod otolith is temperature dependent (Pilling *et al.*, 2007). The negative relationship between the growth of age 1 and age 2 cod and the summer temperature might arise from an earlier onset of the period of poor growth initiated by higher temperatures, that results in a reduction of the total annual growth. Nonetheless, in age 3 to 5 cod no relationship with temperature was detected.

One might speculate that cod of these ages broaden their area inhabited and might regulate the temperature behaviourally.

SPATIAL COMPOSITION OF THE INDIVIDUALS REPRESENTING AN AGE CLASS OF THE COD POPULATION

The proportion of the southern stock component (RA 5 & RA 6) of the total North Sea cod stock declined between 1975 and 2005. Whereas the share of the total stock that is present in the southern North Sea increased again in age class 2 to 5 after 2005, the shares of the ages 1 and 6 inhabiting the southern North Sea declined steadily between 1975 and 2015. This is consistent with other studies on the distribution patterns of cod. The North Sea cod stock declined dramatically since the 1970s and the distribution area within the North Sea has shifted to the central and northern North Sea (Hedger *et al.*, 2004; Perry *et al.*, 2005; Rindorf & Lewy, 2006; ICES, 2013). Thus, the proportion of fast growing cod from the southern North Sea decreased. Accordingly, viewed as an isolated factor the proportion of fish caught in the southern North Sea accounted for 24% of the variation in the length-at-age of cod. However, this effect is annihilated when including the fishing mortality in the RDA. The proportion of cod from the southern North Sea was negatively correlated with the fishing mortality which had a marginal effect of 31%. Thus, the influence of the fishing mortality is overpowering the influence of the shares of the southern stock component in the North Sea cod stock. Both effects are miscellaneous since fishing mortality causes a reduction in the proportion of the southern stock component and thus encompasses most of the effect. An additional effect of the fishing mortality on the length-at-age seems likely.

SIZE-SELECTIVE MORTALITY

The length-at-age was significantly negatively affected by the fishing mortality. Similar negative correlations between fishing mortality and size-at-age were found in the southern Gulf of St. Lawrence (Sinclair *et al.*, 2002b) and the West Greenland (Riget & Engelstoft, 1998) cod stocks. Fishing mortality as one major source of size-selective mortality in an exploited fish stock can affect the length-at-age both, indirectly and directly.

Indirect effects

Fishing mortality as an indicator of the fishing effort might influence the length-at-age indirectly via the influence on prey items of cod. Generally, invertebrates such as crustaceans and larger polychaetes are an essential component of the nutrition of North Sea cod. Highest shares are found in cod over a size range of 10 cm to 100 cm from the southern North Sea during summer with about 80% of invertebrates in their diets. The proportion of invertebrates in the diet of cod is lower in other seasons and decline with increasing size and latitude (Daan, 1973). Fishing (especially beam trawling) affects prey items of cod i.e. the benthic communities by ploughing chains through the sediment (e.g. Kaiser *et al.*, 2000, Reiss *et al.*, 2009). Beam trawls as well as otter trawls cause mortalities up to 39% in some prey species of cod (Bergman & van Sandbrink, 2000). Moreover, Tillin *et al.* (2006) showed that trawling caused large-scale shifts in the composition of functional groups in parallel with a decrease in the biomass of parts of the benthic community in the North Sea. Additionally, the impact of fishing on the bottom habitat might have increased due increasing trawling speeds and heavier trawling chains of otter and beam trawls since the 1970s (Bergman & Hup, 1992). Thus, the impact of trawling on the growth rates of cod via the influence on the benthic community might be negative. On the other hand trawling might enhance the prey availability for cod because it was shown to have the potential to increase the abundance of important prey species (Jennings *et al.*, 2001; Hiddink *et al.*, 2008). Higher growth rates in plaice and sole were shown to result from trawling intensity (Rijnsdorp & Van Leeuwen, 1996; Millners & Whiting, 1996). Moreover, Daan (1975) suggested that cod feeds heavily on discarded flatfish in the southern North Sea. However the effect of a lack of food would have been present in the growth-at-age otolith information. Since we did not find a significant effect of the fishing mortality on growth, an indirect effect of the fishing seems to be unlikely.

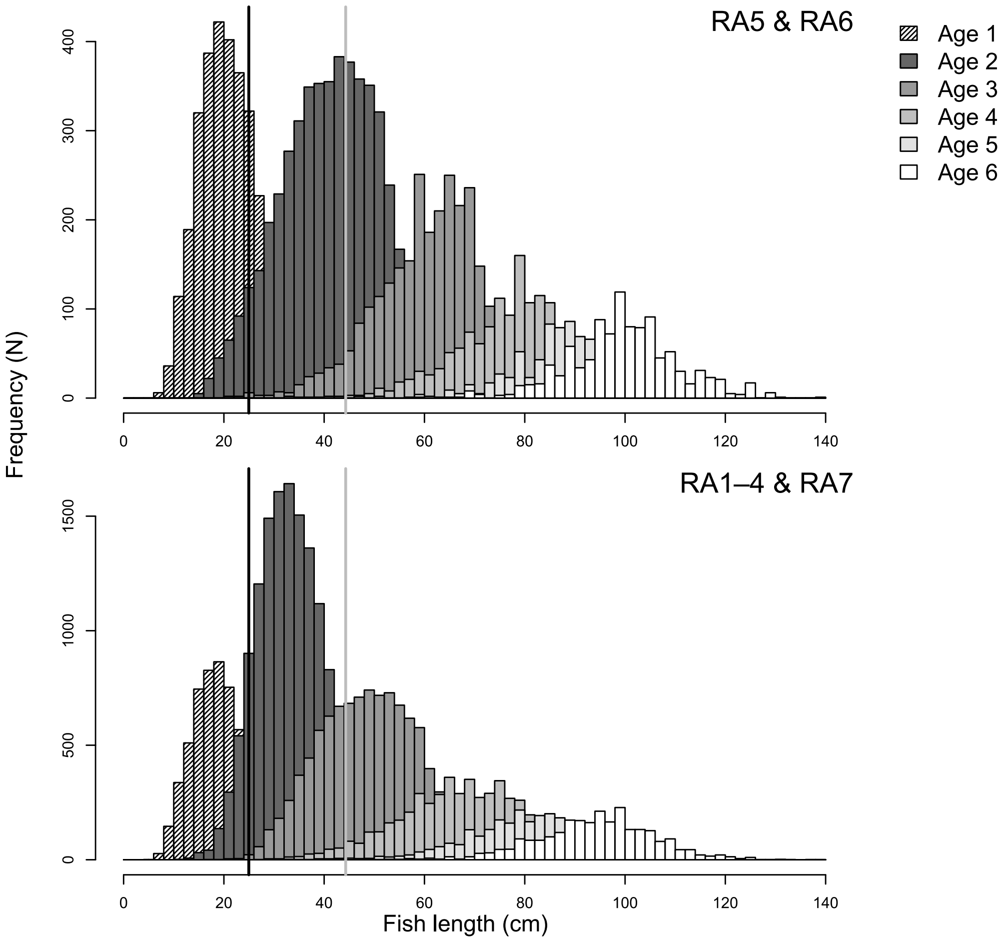

FIGURE III–8. 1st quarter length-at-age histograms of North Sea cod caught in RA 5 and RA 6 (upper panel) and in RA 1–4 and RA 7 (lower panel). Lines show the L_{50} of cod calculated using the size selection equation given by Halliday et al 1999 for a diamond mesh. The black line represents the 50% selection length (L_{50}) for a diamond mesh of 80 mm (flatfish fishery south of 56°; ICES 2013) and the grey line represents L_{50} for a mesh size of 120 mm (cod recovery plan north of 56°;EU regulation 2056/2001). L_{50} was estimated from the Mesh size using the relationship proposed by Halliday *et al.* (2013).

Direct effects

A direct effect of the fishing effort is caused by the selective removal of fast growing fish from the stock by targeted cod fisheries on the one hand. On the other hand size-selective removal of the slow growing proportion of an age class might arise from by-catches in fisheries targeting other species. Size-selective mortality results from the combination of growth variability in an age class and the size-selective characteristics of most fishing gears (Hanson & Chouinard, 1992, Sinclair *et al.*, 2002a). An additional long-term effect might arise from the removal of the fast growing genotypes from the population since the growth potential of the remaining smaller individuals might be lower (Sinclair *et al.*, 2002b).

North Sea cod is caught by virtually all demersal gears, either as a target species or as by-catch with mesh sizes ranging from 70 mm in the French whiting fishery to 219 mm in some targeted cod and plaice fisheries (ICES, 2013).

In the central and northern part of the North Sea the EU cod recovery plan implemented a minimum mesh size of 120 mm (EU regulation 2056/2001). This results in a 50% selection length (L_{50}) of 44 cm in cod (Halliday *et al.*, 1999). Cod in this area reach a length of between 12 cm and 59 cm at age 2. The length frequency distributions at ages 3, 4 and 5 start with 17 cm, 28 cm and 33 cm. Thus, cod of the age classes 2 to 5 are selectively caught when they are relatively larger compared to their conspecifics.

In the southern North Sea a mesh size of 80 mm is commonly used in the sole and plaice fishery (ICES, 2013) leading to an L_{50} of about 25 cm in cod (Halliday *et al.*, 1999). This affects already the age 1 cohort where lengths range from 7 cm to 50 cm with a selective removal of the larger individuals. The length frequency distribution of cod ages 2 and 3 starts with 16 cm and 20 cm, respectively. Thus, these age classes are directly affected by selective mortality of large fish within an age class. From age 4 onwards cod in the southern North Sea are caught over the full length range in the fishery. Thus, size-selective mortality might have contributed to the length-at-age depression in age 1 to 3 animals but has no size-selective effect for older age classes that are caught over the full length range in the fishery. However, the effect of the size-selective mortality might have cumulated through the older age classes as has been shown for the Gulf of St. Lawrence cod. The growth potential of an age cohort was reduced by selectively removing the fast growing fish (Sinclair *et al.*, 2002b).

However, as North Sea cod from the southern North Sea (RA 5 and RA 6) is relatively fast growing and larger compared to the rest of the North Sea, a selective removal of that stock component leads to a depression in the mean length-at-age of North Sea cod. In turn, if the fishing mortality decreases as seen in the first half of 2000s where effort reductions in the plaice and sole fishery were introduced by the EU (ICES, 2013) the mean length-at-age increases again.

Thus, size-selective mortality is the major cause of the observed length-at-age depression in North Sea cod. However, it is not possible to quantify the overall influence of the main anthropogenic factor affecting for this fish stock since numerous fisheries with other mesh sizes and technical measures additionally control the mortality of cod. Moreover, spatially specific fishing intensity might cause divergent reactions in the sub unit stocks considering the spatial heterogeneity of the population dynamics of the North Sea cod.

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GENERAL DISCUSSION

TEMPORAL DEVELOPMENT OF THE SIZE-AT-AGE

The temporal development of the length-at-age of both cod and whiting in the North Sea showed a depression during the analysed time periods. Nevertheless, the patterns, the timing, magnitude and duration of the length-at-age depression varied between both species. While whiting showed a clear drop of 6 % in the length-at-age in the period 2000–2007 with an adjacent increase of 7% in the length-at-age (**chapter II**), the length-at-age of cod decreased from 1975 to 1994 by 16 %, remained at a low levels between 1995 and 2005 and increased again after 2005 by 12 % (**chapter III**).

The span of the analysed length-at-age time series differed between cod and whiting: while for cod the scientific survey data from the period 1975–2015 were analysed, the years between 1990 and 2015 were used for whiting. This was due to the questionable scientific survey data available for whiting. During the 1980s the catch data and the scientific survey data were inconsistent and showed contradictory trends (ICES, 2009). Therefore, it was decided not to evaluate the development of the length-at-age of whiting during the disputable period. Thus, it is not possible to compare the length-at-age of cod and whiting in the period before 1990. The depression pattern of the length-at-age of North Sea cod is consistent with earlier studies although, due to the analysed time period, they did not describe the increase in the length-at-age after 2005 (Rindorf *et al.*, 2008; Marty *et al.*, 2014). Aside from the assessment report (ICES, 2013), in North Sea whiting the depression in the length-at-age has not been reported so far.

The observed differences between the temporal development of the length-at-age of North Sea whiting and cod confirm the initial hypothesis that both species in the same habitat show divergent temporal changes in the length-at-age patterns. Thus, these differences support the assumption that these two gadidae differ in their physiological ecology. Moreover, it can be assumed that cod and whiting living both in the North Sea ecosystem and thus are exposed to the same environment, are influenced by divergent factors and/or react in different ways to the same factors that led to the observed temporal development of the length-at-age.

MECHANISMS AFFECTING THE SIZE-AT-AGE

The mean length-at-age of a natural fish population is generally controlled by two different mechanistic processes: (i) the growth of fish in an age class or (ii) the composition of the individuals representing an age class. The individual growth rate of a fish is affected by multiple intrinsic (e.g. sex & maturity) and extrinsic (e.g. temperature & food) factors that influence the metabolism of a fish. If the individual growth rates of most fishes in an age class decline, the mean length-at-age in the population decreases and vice versa. The size composition of an age class is mainly determined by size-selective mortality. Usually, fishes show relatively high variation in the individual size-at-age, which leads to a wide range of sizes that fishes of the same age exhibit within one population. The selective removal of individuals with a lower size-at-age (slow growers) leads to an increase in the mean length within the age class. In turn, removing selectively individuals with a large size-at-age (fast growers) causes a decrease in the mean length-at-age of the population.

INTRINSIC FACTORS AFFECTING FISH—SEX

One powerful intrinsic factor that might affect the growth of fish is the sex. In the **1st chapter** of the present thesis, sex was revealed as a significant force affecting the life history, physiology, and ecology of whiting. Female North Sea whiting were larger in body length and heavier in body mass compared to males of the same age. Moreover, the sex-specific differences in body length increased with age up to about 6 cm in 7 year old fish (Fig. 4). Whiting, as most other roundfish species, does not display outer dimorphism other than these growth differences and has not been sampled sex-related. Therefore, nowadays sex-specific growth is not considered in studies and management decisions regarding whiting. In contrast, earlier publications on whiting growth and morphology described and considered sexual size dimorphism. Regarding North Sea whiting size differences of 4.3 cm in 7 year old fish were described (Messtorff, 1959). In whiting from the Isle of Man waters females at age 7 years were 10.5 cm larger compared to males of the same age (Bowers, 1954). Female whiting from the French Atlantic coast were 13 cm larger than males of the same age (Desbrosses, 1948). To summarise, female whiting grow faster than males of the same age, but this was somehow forgotten.

Compared to whiting, in Atlantic cod sexual size dimorphism is far less pronounced. Although there is published evidence for sexual size dimorphism in cod (Lambert, 2003; Marshall *et al.*, 2006; Keyl *et al.*, 2015), the differences in the length-at-age between females and males become only slightly visible from a size of approximately 100 cm onwards and hardly before the fish reach an age of 9 years (Fig. 4). In the North Sea the cod stock is exposed to a relatively high total mortality (Z). Assuming an average mortality (Z) of 0.8 (ICES, 2012), only 0.07 % of a cohort reaches the age of 9 years (Table 1). Likewise, regarding the survey based catch per unit effort data (ICES NS-IBTS, unpublished data) the number of cod bigger than 100 cm makes only about 0.1 % of the total number of cod in the North Sea. Therefore, the proportion of the North Sea cod population that reaches the age and size where sexual size dimorphism becomes relevant is very small. In summary, sexual size dimorphism in cod theoretically exists but is not very meaningful to the actual North Sea population and thus is not addressed in the present study.

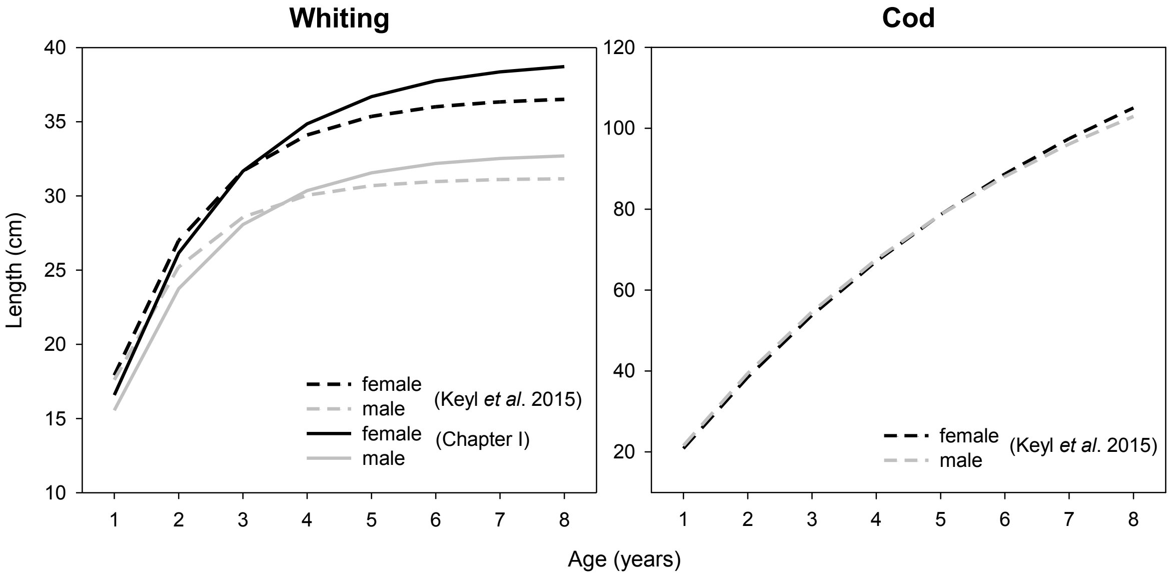

FIGURE 4. Length-at-age of female (black dotted and solid lines) and male (grey dotted and solid lines) North Sea whiting and cod predicted from von Bertalanffy growth parameter estimates. Solid lines in the left panel represent estimates from the von Bertalanffy growth function fitted to the 2012 1st quarter ICES NS-IBTS data (Chapter I). Dotted lines represent model estimates from the von Bertalanffy growth function fitted to scientific survey data from quarters 1–4 in the period 1970–2011 (Keyl *et al.*, 2015).

TABLE 1. Percentage of a hypothetical cod cohort surviving until age 9 years exposed to different total mortalities (Z). Average Z for age classes 2–6 years is extracted from the ICES North Sea cod working group report (ICES, 2012). Equal Z is applied to age classes 0–8 years.

Z (2–6)	**% of cohort reaching age 9 years**
0.60	0.45
0.80	0.07
0.90	0.03
1.00	0.01
1.20	0.00

Sex-specific physiology & ecology of Whiting

The consequence of sexual size dimorphism in whiting is, that corresponding differences in the physiology or ecology between females and males must exist, which account for the excess energy resulting in higher growth of females. Generally, three different mechanisms could be responsible: (i) divergent metabolic costs, (ii) different energy allocation patterns or (iii) unequal food intake between female and male whiting. In **chapter I** the role and the contribution to the length-at-age differences of the aforementioned mechanisms was disentangled.

Metabolic costs

Higher metabolic costs could be the cause of the lower growth in male whiting. Differences in the metabolic costs in turn could result from differences in the routine or activity related metabolism (Fry, 1971). Differences in the activity levels have been shown to result in growth dimorphism in numerous animals mainly resulting from mating competition or higher parental care of one sex (Clutton-Brock & Vincent, 1991; Henderson *et al.*, 2003). In addition, higher activity levels can be related to higher routine metabolic rate, as has been shown for male spiders (Shillington, 2005) but this has not been investigated in fishes.

The routine metabolism has been shown to be affected by the size of the organs, with a changing relative effect due to allometric growth. Amongst others, the mass of the gut has been shown to substantially influence the metabolic costs in fish (Goolish & Adelman, 1988). Therefore, the sex-specific mass of the empty stomach, assuming that this parameter can serve as an approximation to sex-specific differences in metabolic costs, was compared. From a size of 30 cm onwards, female whiting had a higher empty stomach mass compared to males of the same length. In addition, the differences increased with fish length. Thus, it is reasonable to hypothesise that the metabolic costs approximated by the stomach mass are higher in female whiting. Similar results were detected in dab *Limanda limanda* (L. 1758) where the mass of the total gut was larger in females compared to males of the same length (Temming & Hammer, 1994). This is contradictive to what would be expected since lower growth cannot result from lower metabolic costs. However, a higher mass of the gut does not only bring along additional metabolic costs, but it also might increase gastric evacuation speed and assimilation efficiency since a larger digestive surface leads to higher turnover rates. As a result, the additional metabolic costs caused by the larger gut might be over-compensated by a faster food passage and increased assimilation efficiency resulting in higher consumption rates (Temming & Hammer, 1994). This is consistent with the finding that faster growth in female walley *Sander vitreus* (Mitchill, 1818) was caused by higher food consumption and higher food conversion efficiencies (Rennie *et al.*, 2008) (**chapter I**).

Energy Allocation Patterns

Sex-specific differences in the energy allocation patterns could be caused by the earlier sexual maturation in male whiting. While 16% of males are sexually mature at age 1 year and 73% at age 2 years, only 43% of females mature at age 2 years. Expressed in body length, 50% of males mature at a body length of 19.3 cm compared to 22 cm in females (Bowers, 1954; Messtorff, 1959). The energy loss that is caused by gamete production in addition with potential increasing activity levels during mating might result in somatic growth reduction in male fish (Roff, 1983). However, the differences in the size-at-age between female and male whiting are not restricted to the age and size range where the sex-specific reproductive investment might differ but in fact increase with age. Therefore, the earlier sexual maturation of males cannot explain the different growth rates in adult whiting.

Another difference in energy allocation patterns might be reflected in sex-specific condition factors: gadoid length growth and body mass growth can be decoupled during unfavourable conditions with continuing length growth without gaining mass (Pedersen & Jobling, 1989). If males invest energy into gaining mass instead of length at an earlier point during life history, the body mass-length relationship would differ between the sexes with better condition in male fish. However, this hypothesis was not verified: the condition of male whiting was not higher but in fact lower, compared to females of the same length.

Sex-specific differences in energy allocation patterns could be manifested by different liver masses between females and males. In gadoids the surplus energy is primarily stored in the liver and therefore the mass of the liver is a good indicator for the individual energetic status of a fish (Lambert & Dutil, 1997). If males would allocate their energy into liver growth instead of body growth, they would have higher liver masses compared to females of the same length. However, female North Sea whiting had higher liver masses compared to males of the same length. This shows that females did not only have higher growth rates but also had larger amounts of energy stored in their liver compared to males of the same length. Therefore, the allocation of energy into liver growth instead of body growth in male whiting cannot be responsible for the higher growth in females, but rather supports the hypothesis that a sex-specific difference in the energy acquisition or uptake through food intake exists (**chapter I**).

Energy uptake

Sex-specific feeding habits and resulting adaptations are common in nature and the selection for niche divergence might account substantially for the evolution of sexual dimorphism (Darwin, 1871). Therefore, the most likely cause of the observed growth differences between female and male whiting is a sex-specific energy uptake level, which in turn could be caused by differences in the amount of food ingested or differences in the quality i.e. the energy content of the prey. Sex-specific diets have been described for many mammals, reptiles and birds (e.g. Houston & Shine, 1993) but studies comparing the diets of female and male marine teleosts are rare. Nevertheless, in whiting the diet composition did not differ between females and males of the same length. This result implies that the food quality is not the cause of sexual size dimorphism in North Sea whiting.

As a consequence, the total amount of food is most likely the explanation for the observed sexual dimorphism in growth rates. In whiting larger than 25 cm, females had generally lower percentages of empty stomachs and the feeding proportion had an overall higher total stomach content mass compared to males of the same length. The results are consistent with other field studies on sex-specific food intake in fishes showing sexual size dimorphism (Lozán, 1992; Temming & Hammer, 1994) and with a bioenergetics modelling approach determining lower food consumption in males as the cause of sexual size dimorphism in percids (Rennie *et al.*, 2008). Lower amounts of food and higher amounts of empty stomachs in male whiting could be a result of an evolutionary developed behavioural aspect: males that reduce their investment in feeding time, increase their reproductive success by spending more time on searching for, and spawning as close as possible to, a female and thus are evolutionary favoured (Parker, 1974). This theory is supported by sex-specific spawning behaviour of whiting. While males are continually active, display extensive territorial aggression and show an active courting behaviour, females do not show an increase in the activity level during spawning period (Hawkins, 1970) (**chapter I**).

EXTRINSIC FACTORS AFFECTING FISH—TEMPERATURE

Temperature is one momentous abiotic factor affecting the growth of fish. Being ectothermic, fishes are directly influenced by temperature via its influence on the physiology (e.g. metabolic rates and consumption) and on the behaviour (Fry, 1971; Shulman & Love, 1999). In general, assuming ad libitum feeding conditions, the growth rate increases with increasing temperature to an optimum beyond which growth is reduced due to species-specific optimal temperature range of metabolic processes (Brett, 1969). The North Sea is one of the fastest warming shelf seas worldwide (Burrows *et al.*, 2011). In the period between 1990 and 2007, the annual average surface temperature increased continuously by 0.5°C per decade. After 2007, the surface temperature decreased again (Emeis *et al.*, 2015). Due to varying hydrographical conditions, temperature shows a spatially very heterogeneous pattern within the North Sea: while in the shallow southern parts large annual temperature extremes are typical (with summer temperatures exceeding 18°C) the deeper parts of the central and northern North Sea are not exposed to these extremes and show slower overall warming (Meyer *et al.*, 2011).

In the **2nd chapter**, temperature was excluded as the main source of the observed decrease in the length-at-age of North Sea whiting between 2000 and 2007. The global distribution range of whiting expands southwards to the Mediterranean and the Black Sea where average experienced temperatures range between 9°C and 20°C (Shulman & Love, 1999). Although summer temperatures in the southern North Sea regularly exceed 18°C, and the average annual surface temperatures in the North Sea increased from 10.3°C in 1990 to 11.3°C in 2007 (Emeis *et al.*, 2015), the temperature range of the North Sea lays well within the natural range of occurrence of whiting. Moreover, fish are not stationary and can behaviourally thermoregulate by spatial displacement (Beitinger & Fitzpatrick, 1979). Adult whiting can avoid high summer temperatures in parts of the North Sea by moving into colder waters (Temming & Hufnagl, 2015). Therefore, a negative impact on growth and thus length-at-age of whiting caused by increasing temperatures is unlikely. Likewise, the length-at-age of Irish Sea whiting was not temperature dependant (Gerritsen *et al.*, 2003). Moreover, the mean length-at-age was higher in the two periods 1990–1999 and 2008–2014 compared to 2000–2007. If increasing North Sea temperatures would have negatively affected the growth of whiting, a contrary temporal development of the length-at-age would have been expected. Therefore, one conclusion of the **2nd chapter** is that observed length-at-age depression was not caused by a direct effect of the temperature on the growth of North Sea whiting.

In the **3rd chapter** the influence of temperature on the length-at-age of North Sea cod was evaluated. The natural range of occupied temperatures lies between -1 and 19°C (Sundby, 2000). In contrast to whiting, Atlantic cod's upper global thermal boundary is reached in the southern North Sea. In the present study, temperature was shown to have a significant negative impact on the mean length-at-age of North Sea cod. The influence of the temperature might arise either from a direct affect on the growth or from the influence on the spatial distribution of the fish. The growth of cod could have been reduced due to increasing temperatures (Olsen *et al.*, 2010). In laboratory experiments the optimum temperature for cod growth ranged between 17°C in early juveniles, to 9°C in adult cod. Below or above these temperatures growth is reduced (Jobling, 1988; Pedersen & Jobling, 1989; Björnsson & Steinarsson, 2002). As these temperatures are easily exceeded in the North Sea a negative effect on growth might be feasible.

On the other hand, decreasing abundance of cod in the southern North Sea has been suggested to be caused by rising sea temperatures (Hedger *et al.*, 2004). Likewise, a northwards shift of the cod population in the North Sea co-occurring with rising temperatures between 1977 and 2001 has been documented (Perry *et al.*, 2005). As cod in the northern North Sea grow slower and have a lower length-at-age (Daan, 1974; **chapter III**), the spatial composition of the cod population might have been altered by the temperature in such a way that higher proportions of the slow growing northern component led to an overall decrease in the population mean length-at-age. However, contradicting signals in the North Sea cod stock have also been documented: while it has been suggested that in the southern North Sea especially large cod might be struggling with rising temperatures, an egg survey conducted in 2004 revealed that highest densities of cod eggs, indicating high abundances of adult spawners, were found in the southern and German Bights (Fox *et al.*, 2008). Heessen & Daan (1994) found no evidence for a temperature related abundance pattern in the North Sea cod stock. Moreover, individual tagging studies showed that the majority of adult cod inhabiting areas with warm temperatures, that were considered as superoptimal for growth, did not chose to migrate into cooler waters nearby, that were thought to be of more virtue (Neat & Righton, 2007). Therefore, it remains unclear how temperature affects the distribution of cod in the North Sea—whether a northwards shift is caused or whether the southern stock component is endangered to go extinct because of unfavourable temperatures.

EXTRINSIC FACTORS AFFECTING FISH—FOOD AVAILABILITY

Fish rely on sufficient supply of food to be able to maintain, grow and reproduce. Considering that at the beginning of the 21st century in the North Sea a number of forage fish species produced some of the smallest year classes on record (ICES, 2013), it was hypothesized that whiting as well as cod respond to these changes with a decrease in the length-at-age.

Therefore, in the **2nd chapter** the influence of the prey abundance i.e. the food availability, defined as the abundance of four major forage fish species in the North Sea ecosystem (sandeel, sprat, herring and Norway pout) on the growth of whiting was evaluated. The analysis of the prey abundance in the North Sea between 1990 and 2013 showed that in the period 2000–2007 the prey abundance was below average for seven consecutive years. Before and after that period the prey abundance was markedly higher. As whiting is a highly specialised predator of selected forage fish species the low prey abundance between 2000 and 2007 was expected to have affected the amount of food in the stomachs of whiting, as well as the condition and the length-at-age. The length-at-age of North Sea whiting was considerably lower between 2000 and 2007 compared to before and after. As expected, the stomach content masses of whiting sampled during the period of low prey abundance were significantly lower compared to a period of high prey abundance. Moreover, a modelling approach revealed that the magnitude of the observed difference in the stomach contents could have had not only bioenergetically caused the observed depression in the length-at-age, but were ample enough to account for even larger differences. Likewise, the hepatosomatic index (relationship between the liver mass and the body mass) was considerably lower in a year of low prey abundance (2007) compared to a year of high prey abundance (2012). The length-at-age of North Sea whiting was determined by the prey abundance following a sigmoid function. This means that decreasing prey abundance below a certain threshold leads to a depression of the length-at-age. However, Fulton's condition factor *K* of whiting did not show a distinct depression between 2000 and 2007. This is contrary to Atlantic cod where studies from other regions found a marked decline in the Fulton's *K* during periods of unfavourable conditions (Lambert & Dutil, 1997; Eero *et al.*, 2012). Although those ecosystems are very different from the North Sea, these findings show that the observed physiological reaction patterns differ between the two species: while in whiting unfavourable conditions i.e. low prey abundance lead to an overall depression in growth (i. e. length, mass and energy storage tissue), cod reacts—at least initially—with no reduction in length growth but rather with a reduction in condition.

In **chapter III** the influence of selected prey species on the length-at-age of North Sea cod was evaluated. In contrast to whiting, in North Sea cod no effect of the abundance (N recruits) of prey species was detected on the length-at-age. This disagrees with the initial hypothesis and with studies on Atlantic cod from other regions that detected a pronounced dependence of cod size-at-age on prey abundance (e.g. Mehl & Sunnanå, 1991; Jørgensen, 1992). Likewise, multiple other studies found a significant effect of food availability on life history traits of cod (Godø & Moksness, 1987; Steinarsson & Steffásson, 1996; Krohn *et al.*, 1997; Eero *et al.*, 2012). However, in those ecosystems predator-prey interactions and trophic linkages differ conspicuously from the North Sea. In the Barents Sea as well as in Icelandic and Newfoundland waters cod is feeding very selectively and relying almost exclusively on capelin (Mehl, 1989; Magnússon & Pálsson, 1989; Lilly, 1987). Similarly, in the Baltic Sea which is generally very limited in species richness compared to the North Sea, cod depends largely upon only two prey species: sprat and herring (Eero *et al.*, 2012).

In contrast to that, in the North Sea cod can be considered as an omnivorous generalist that feeds on a broad variety of prey items and the diets of cod directly reflect the abundance of a certain prey (Link *et al.*, 2009). In addition, the diet of cod includes distinct proportions of non-fish prey. Especially in the southern North Sea the diet of cod may consist of up to 80 % of invertebrates (Daan, 1973). Therefore, and due to the declining abundances of cod, a food-induced limitation of the growth of North Sea cod seems to be fairly unlikely.

EXTRINSIC FACTORS AFFECTING FISH—SIZE-SELECTIVE MORTALITY

Changes in the mean length-at-age of whiting and cod could be a result of changes in the size-selective mortality. The main cause of adult mortality in whiting and cod is the fishery (ICES, 2013). A direct effect of the fishing mortality on the mean length-at-age could be caused by the targeted cod and whiting fisheries that selectively remove fast growing fish from the stock causing a decrease in the length-at-age. On the other hand, by-catches in fisheries targeting other species could cause size-selective removal of the slow growing proportion of an age class increasing the average length-at-age in the population.

In the **2nd chapter** the influence of fishing on North Sea whiting was evaluated leading to the conclusion, that fishing did not cause the depression in the length-at-age. Whiting in the North Sea is mainly caught in the mixed demersal roundfish fishery and in large numbers as by-catch in the Norway lobster, Sandeel, Norway pout and flatfish fishery (ICES, 2013). Therefore, adult whiting fishing and discard mortality might have affected the life history of North Sea whiting. However, the time series of the mortality of North Sea whiting is contrary to the observed time series of the length-at-age, showing larger lengths-at-ages before and after the period 2000–2007. The fishing mortality (F) of whiting in age classes 2-6 years has declined in the period 1990–2005 and increased again afterwards. In addition, the total mortality (Z) decreased steadily between 1990 and 2012, indicating that the fishing mortality cannot be the cause of the observed decline in the mean length-at-age of whiting.

In contrast to that, in the **3rd chapter** of the present thesis it was revealed that fishing has dramatically affected North Sea cod. The length-at-age was significantly negatively correlated with the fishing mortality, supporting the findings of Sinclair *et al.* (2002) and Riget & Engelstoft (1998), who found that size-at-age was determined by fishing mortality in other cod stocks. North Sea cod is caught by virtually all demersal gears, either as a target species or as by-catch with mesh sizes ranging from 70 mm in the French whiting fishery to 219 mm in some targeted cod and plaice fisheries (ICES, 2013). Two phenomena were found in cod regarding the effect of size-selective mortality: on the one hand the aforementioned effect of the size-selective removal of larger individuals occurred in the age classes 2–5 years in the central and northern North Sea, which could have contributed to the observed length-at-age depression; on the other hand size-selective mortality affected the spatial composition of the total North Sea cod population. Regional differences exist in the length-at-age of cod within the North Sea, with the fastest growing stock component inhabiting the southern North Sea (**chapter III**). In the southern North Sea cod are caught over the full age range from age 1 year upwards. This might result in the almost complete removal of the southern stock component reflected in a depression of the total North Sea cod population mean length-at-age. In accordance with that, the abundance of cod in the southern North Sea decreased distinctively between 1970 and 2015 (**chapter III**). Moreover, when fishing mortality decreased to the extent that it did in the first half of the 2000s due to effort reductions in the plaice and sole fishery introduced by the EU (ICES, 2013), the southern stock component and the mean length-at-age increased again.

In addition, a long-term effect might be induced by the selective removal of the fast growing genotypes from the population since the growth potential of the remaining smaller individuals might be lower (Sinclair *et al.*, 2002). Besides phenotypic plasticity of individuals with an identical gene pool, there is growing evidence that genetic variation within fish stocks leads to divergent expressions of life history traits, such as growth. Thus, the heritability of growth rates in Atlantic cod is very likely (Stokes & Law, 2000). If individuals with fast growing genotypes are selectively removed by the fishery they will not reproduce and hence no recruits are produced that inherit fast growth genes. Only the slow growing genotypes will reproduce and pass their genes to the next generation. This might result in recruits that have a smaller growth potential and in the long term the fast growing genotypes might go extinct. However, the role and the influence of genetic or non-genetic phenotypic plasticity on life history traits in fish is widely debated and needs further investigation to be able to conclusively assess these effects (Rijnsdorp, 1993; Law, 2000; Stokes & Law, 2000; Naish & Hard, 2008).

CONCLUSIONS & PERSPECTIVES

In summary, this thesis showed that North Sea whiting and cod differ in their physiological ecology, life history and population dynamics. This leads to species-specific implications and consequences in the assessment and management decisions considering both stocks in the North Sea. In contrast to cod, whiting exhibits distinct sexual size dimorphism in the North Sea. The **1st chapter** showed that higher somatic growth rates accompanied by larger energy reserves in female whiting compared to males of the same length result from higher energy intake levels, indicated by the amount of food in the stomachs. In addition, the higher empty stomach masses of females suggest higher gastric assimilation capacity and evacuation rates in females. This hypothesis needs to be tested in further physiological studies on whiting, where the sex should be considered explicitly. Moreover, the findings in **chapter I** have implications for the stock assessment and management decisions considering North Sea whiting. One fundamental paradigm in fisheries management is the avoidance of growth overfishing (Beverton & Holt, 1957). Currently, the assessment does not consider sex explicitly and reference data such as the size- and maturity- at-age is not sex-specific. Likewise, model outputs such as mortality at age are not separated by sex (ICES, 2013). In addition, assessment models do not incorporate size-at-age keys separately for by-catch: on the one hand, faster growing females grow earlier into the selection range of commercial gears which results in a higher fishing mortality and a higher risk of being growth overfished compared to males of the same age and on the other hand, total mortality induced by natural mortality, as well as by by-catch could be higher in males because they are growing slower and might therefore represent a higher proportion in the discards and in the predation mortality, compared to females of the same age. The differences in mortalities could also have affected the reproductive output of the stock since in gadoids larger females produce more and larger eggs that have the potential to result in a higher number of offspring with an elevated fitness (Trippel, 1999). In addition, average size-at-age in the stock and thus total allowable catches (TAC) could be biased due to changing sex ratios in North Sea whiting stock, as seen in North Sea plaice (Kell & Bromley, 2004). Finally, the pronounced sex-specific differences in consumption and growth rates could have biased the multispecies assessment if possible changes in sex ratios since 1991 remain unaccounted for.

In the **2nd chapter** of the present thesis, a clear linkage between the prey abundance and the length-at-age of whiting in the North Sea was revealed. A simultaneous decrease in forage fish abundance and whiting length-at-age in the period 2000–2007 and a subsequent parallel increase in prey abundance and whiting length-at-age after about 2008 was discovered. The findings from **chapter 2** might have consequences for the stock-recruitment relationship of North Sea whiting, as well as for multispecies modelling of the North Sea ecosystem. The size-at-age of female fish affects the reproductive output of a stock because smaller females produce less offspring. Additionally, lower growth rates affect the rate at which immature individuals recruit to the spawning stock. If food is limited, spawning may even be skipped completely (e.g. Skjæraasen *et al.*, 2012). This might severely influence the reproductive output of the spawning stock (Marshall & Frank, 1999). The North Sea whiting stock showed historically low levels between 2005 and 2008 (ICES, 2013), despite decreasing fishing mortality since the 1990s. This might have resulted from the observed minimum in recruitment between 2003 and 2007 (ICES, 2013), which in turn might have been caused by the lower length-at-age and limited food supply induced by lower prey abundances in the North Sea.

Regarding ecosystem conservation and multispecies modelling, the results from **chapter II** emphasise that an isolated view of a fish population, detached from the interacting species in the ecosystem might be dangerously misleading. The conservation and sustainment of fish stocks within an ecosystem do not only have implications regarding the respective stock but should also consider the sustainment of other species on other trophic levels in the ecosystem that contribute to the well being of a stock. The predator-prey relationship for whiting detected in the present thesis provides an opportunity to incorporate the length-at-age of whiting as a function of the prey abundance to enhance the multispecies model predictions and improve the status of the North Sea ecosystem. Moreover, whiting has proven to be an indicator species for the status of the North Sea ecosystem which is highly sensitive to changes in forage fish stocks.

The **3rd chapter** evaluated the influence of temperature, prey availability and fishing mortality on the length-at-age of North Sea cod. The observed decrease in the mean length-at-age of North Sea cod was mainly caused by the fishing mortality caused by the flatfish and cod fishery. In addition, the temperature had a negative impact on the length-at-age. In contrast to whiting (**chapter II**), cod growth is determined by anthropogenic top-down effects from selective removal of the large specimens (**chapter III**). Since the status of the cod stock is well below save biological limits in the North Sea, these results emphasise the urgent need of a revision and changes in the management actions to be able to sustain the North Sea cod stock.

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Individual contributions to chapters with multiple authors

Chapter I Sex-specific food intake in whiting *Merlangius merlangus*

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All analyses, text writing and graphical illustrations were performed by R. A. M. Lauerburg under the supervision of A. Temming who critically reviewed the chapter. F. Keyl helped to develop the idea for this study. P. Kotterba provided stomach content data. F. Keyl, P. Kotterba and J. Floeter critically reviewed the text of this chapter.

Chapter II Forage fish controlling population dynamics of North Sea whiting – evidence from field data and bioenergetics modelling

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All analyses, text writing and graphical illustrations were performed by R. A. M. Lauerburg under the supervision of A. Temming who critically reviewed the chapter. A. Temming and J. Floeter helped to develop the idea for this study. J. Floeter, P. Kotterba and J. K. Pinnegar provided data included in this study.

Chapter III Influences of fishing mortality, temperature and food on the length-at-age and individual growth of North Sea cod *Gadus morhua* L.

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All analyses, text writing and graphical illustrations were performed by R. A. M. Lauerburg under the supervision of A. Temming who critically reviewed the chapter. P. Grønkjær and C. Möllmann helped to develop the idea of this study. J. Floeter provided data included in this study. G. Kraus and T. Brey provided otolith material included in this study.

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift „Governing factors for the size-at-age: the influence of sex, food availability, temperature and fishery on the growth performance of North Sea whiting *Merlangius merlangus* and cod *Gadus morhua*“ selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, Februar 2016

Rebecca A. M. Lauerburg

Certification of Written English Quality

I hereby confirm that the thesis by Rebecca A. M. Lauerburg entitled "Governing factors for the size-at-age: the influence of sex, food availability, temperature and fishery on the growth performance of North Sea whiting *Merlangius merlangus* and cod *Gadus morhua*" has been prepared according to excellent written English language standards.
Sincerely,

Keith MacPherson
Founder
MacPherson Language Institute