A first examination of its biology, ecology and fisheries: What is the role of European Hake (*Merluccius merluccius*) in the waters of the northern North Sea and along the Norwegian coast?

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By

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Abstract

Based on the results from the annual stock assessment of the European hake (*Merluccius merluccius*) by the International Council for the Exploration of the Sea, a fourfold increase of the spawning stock biomass can be observed over the last decade. As a leading country in fisheries research, Norway has as of yet contributed surprisingly little to the research to hake. In this study I present first attempts to describe the distribution, abundance as well as spawning and nursery areas, and prey spectrum of the European hake in the North Sea and along the Norwegian coast. Survey data from the Institute of Marine Research from 2006-2014 and landing records obtained from the Norwegian Directorate of Fisheries from 2000-2014 as well as stomachs collected in 2014 were examined and analyzed. In the period analyzed catch data showed increasing landings from bottom trawl fisheries in the North Sea and to a lesser extent in the gillnet fisheries along the Norwegian mid-west coast. Concurrently abundance index of hake (CPUE) increased in the North Sea, the Skagerrak and along the coast, showing highest densities east of Shetland Islands in July. It appears that the increase in commercial hake landings can be related to the observed increase in spawning stock biomass. Fish in spawning condition were found along the slope west of the Norwegian trench. As a result of the current regimes in the North Sea hake egg and larvae may be transported from the spawning grounds on the south-west Norwegian trench into the Skagerrak. Smallest individuals <10.5 cm were mainly located in the Skagerrak, while individuals from 10.5-25.5 cm were caught in large numbers both east of the Shetlands and the Skagerrak. In terms of %F Norway pout was shown to be the most important prey species, followed by Atlantic herring and Atlantic mackerel. An overlap of the hake distribution with areas of highest abundance of Norway pout as well as feeding grounds for herring and mackerel may explain their dietary importance. Results from this study provide new and essential insights into characteristics of a commercially valuable and ecologically increasingly important species.

Abbreviations

CPUE	Catch per Unit Effort
IBTS	International Bottom Trawl Surveys
ICES	International Council for the Exploration of the Sea
IMR	Institute of Marine Research, Bergen
kg/nm	Kilogram per nautical mile
n/nm	Number per nautical mile
Q1	Quarter 1 (January – March)
Q2	Quarter 2 (April – June)
Q3	Quarter 3 (July – September)
Q4	Quarter 4 (October – December)
SSB	Spawning Stock Biomass
%F	Frequency of occurrence of prey species
%N	Percentage contribution of prey species to total diet

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1. Introduction

1.1. Motivation

For a country with a globally leading fishing industry and fisheries research community like Norway, European hake (*Merluccius merluccius*) has historically received little attention, especially considering how popular its fisheries and consumption are in the rest of Europe. Although the species has been caught for decades in Norwegian waters, it has both scientifically and commercially been of little or no interest. Landings of European hake in northern European waters show a steep increase over the past decade (Figure 1), underlining the necessity of more research effort. Two recent studies (Baudron & Fernandes, 2014; Cormon et al., 2014) show the growing biological and economic importance of this species east of the Shetland Islands, after a long period of European hake in the North Sea not being in the center of the focus of research.

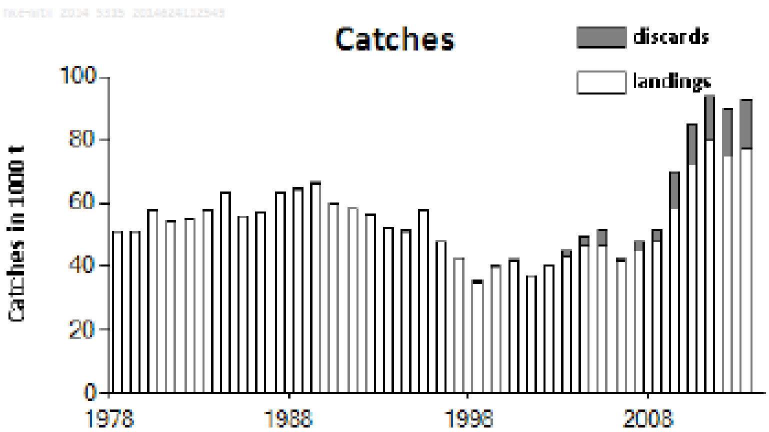


Figure 1: Trends of landings of European hake in the ICES northern Stock from 1978-2014 (Source: ICES Advice 2014, Book 9.)

Merluccius merluccius has been extensively studied in other areas of its distribution including the Mediterranean (Bartolino et al., 2008; Ferrer-Maza et al., 2013; Khoufi et al., 2014; Philips, 2014), the Bay of Biscay (Guichet, 1995; Sanchez & Gil, 1999; Poulard, 2001; de Pontual et al., 2003; de Pontual et al., 2006; Murua & Motos, 2006; Mahe et al., 2007; Dominguez-Petit et al., 2008), and the Celtic Sea (Du Buit, 1996; Poulard, 2001; Mahe et al., 2007).

Climate change has already caused a northwards shift in a number of North Sea fish species (Perry et al., 2005) and the steep increase in biomass of European hake suggests large scale changes in its spatial population dynamics. Reasons for that increase can be various, a warming of the oceans seems an obvious one, as well as the EU recovery plan from 2004 to reduce fishing mortality on European hake (EC, 2004), which was considered to have a positive impact on the stock development (Baudron & Fernandes, 2014). Additionally due to a changing fisheries and European hake being a non-managed species in Norway, detailed investigations are needed to monitor changes and to provide a biological and ecological knowledge level to base management procedures on. We are at a tipping point. To understand the necessity of the study, it is important to show the great possible commercial and ecological impacts of the species.

1.2. Global status and trends of hake fisheries in Norway

With a global catch of more than one million tonnes, the genus *Merluccius* with its 12 species (Appendix 1) (Murua, 2010) plays an essential worldwide ecological and commercial role (Alheit & Pitcher, 1995). The hake's high price and valuable flesh as well as its high annual catches underline its importance for global fisheries (Alheit & Pitcher, 1995). The large-scale fisheries began with a global catch of almost half a million ton in the beginning of the 1960s and had its peak about ten years later in 1973 with a landings of more than 2.2 million t. This development was supported by rapid technical improvements of global fishing fleets (Alheit & Pitcher, 1995). Catches afterwards declined and fluctuated from around 1 to 1.5 million t between 1980 and 2002. In 2012 the FAO considered the majority of the global hake as either fully, over-exploited or depleted (FAO, 2012).

Global catches of *Merluccius merluccius* displayed a steadily declining trend from 1950-2000, after which an increasing trend is visible. During the past five years landings have been stable at almost 100,000 t (Figure 2). Apparent is the increasing contribution (as seen in figure 1 + 2) of hake in the northern North Atlantic to the global landings of European hake (approximately 80 % in 2011).

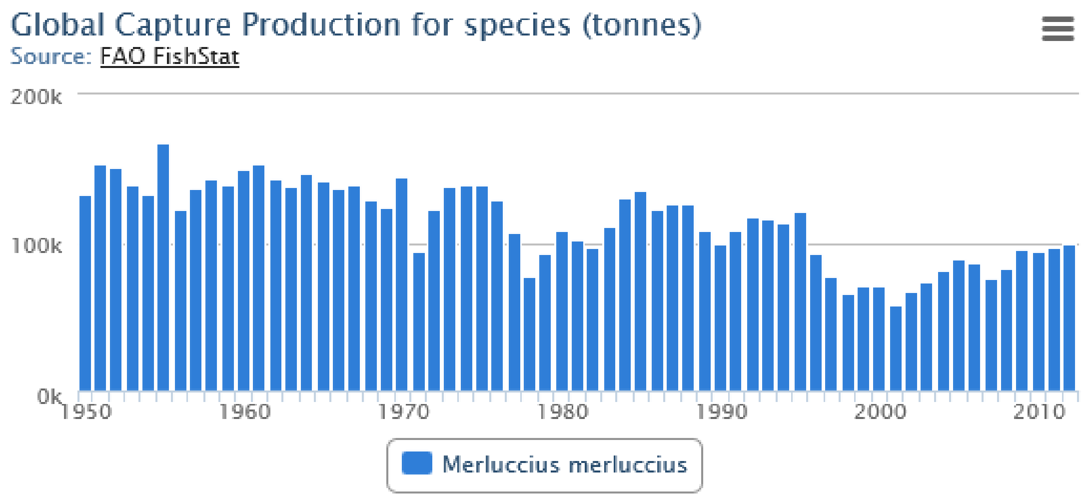


Figure 2: Global catches of European hake in tonnes (Source: FAO, 2014)

Different commercial fisheries as well as sports and recreational fishermen have been catching European hake along the Norwegian coast for decades, and yet basic investigations to support a development of the fisheries are lacking, due to historically low commercial catches. No stock assessments or quotas have been assigned to hake in Norwegian fisheries (Bakketeig et al., 2015). Along with the rapid increase in landings of European hake in more northern waters, landings in Norway have also increased (Figure 3). Until 2006 total catches were always below 1000 t, but more recently in 2014, fishermen caught about eight times more than in 2002 (4300 t). This may indicate either a change in the fisheries and the market, a change in the ecosystem with an increasing dominance of European hake, or both.

To further follow the potential impact of European hake on Norwegian fisheries and ecosystems, it is important to describe the biology and dynamics of its population and current understanding of the stock structure in North Atlantic waters. Basic biological knowledge is an essential tool for the sustainable long-term management of the European hake fishery in Norway and adjacent areas. An overview of available scientific hake studies will be useful when comparing the new findings from this study and also point out areas where more research is necessary in the North Sea and Norwegian coastal waters.

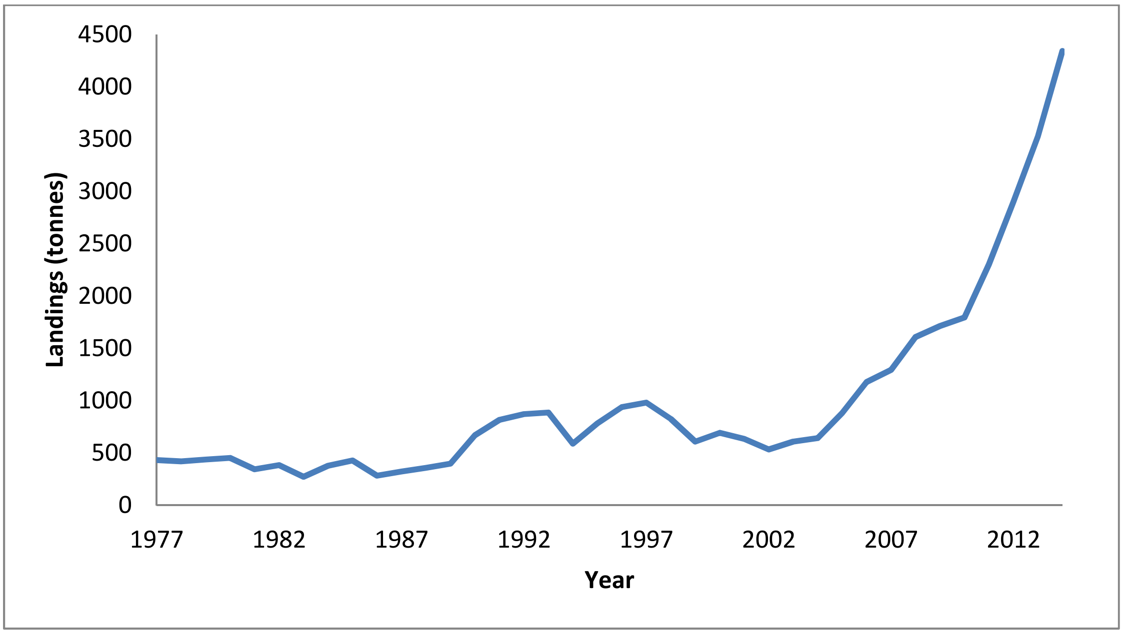


Figure 3: Trend of landings in tonnes of European hake in Norwegian waters from 1977 – 2014.

1.3. Biology of European Hake

1.3.1. Distribution

European hake is widely distributed over the North-east Atlantic and has its highest abundance from the British Isles to the south of Spain (ICES, 2013b). Its northern boundary is the northwest-coast of Norway and the waters south of Iceland. In the south it is present to the Gulf of Guinea Gulf off the West-African coast (Casey & Pereiro, 1995). Its distribution also extends easterly to Skagerrak and Kattegat and the Mediterranean and the Black Sea (Casey & Pereiro, 1995). Throughout their geographical range, European hake can be found at depths of between 30 and 500 m over sandy, muddy and rocky bottom (Casey & Pereiro 1995).

1.3.2. Spawning

Spawning activity of European hake occurs throughout 11 months of the year in the Bay of Biscay with a peak from January to March (Murua & Motos, 2006). In Atlantic waters around the Iberian Peninsula, European hake spawns from December to May with a peak in February (Pineiro & Sainza, 2003), and according to Costa (2012) individuals along the

Portuguese coast spawn all year around with peaks in March, May and August. The International Council for the Exploration of the Sea (ICES) assumes the peak of spawning activity to be from February to July (ICES 2013b), occurring along the shelf edge, with the main spawning grounds stretching from the Bay of Biscay in the south to the west of Ireland (ICES, 2013b). Spawning activity tends to be later in the year in more northern waters with spawning observed in August off Scotland (FAO, 2014). Groison et al. (2011) found spawners along the Norwegian west coast (61°34'N, 5°56'W) in August. In the Mediterranean, spawning peaks occur in January and July (Ferrer-Maza et al., 2013). Fishbase (Froese & Pauly, 2011) indicates that for approximately 25 % of spawning records, the activity took place throughout the whole year in Spain, Italy, France and Greece. The most important nursery grounds for European hake in the Atlantic are in the Bay of Biscay and off southern Ireland (ICESb, 2013). Spawning and/or nursery grounds in Norwegian waters have to be included here. European hake can reach a maximum total length of 140 cm and maximum total weight of 15.0 kg (Cohen et al., 1990). Fishbase (Froese & Pauly, 2011) indicates a length of 20 – 70 cm for length at first maturation. Off the Moroccan coast in the eastern Central Atlantic first maturity (L50) was estimated at 28.6 cm for males and 33.8 cm for females (Habouz et al., 2011) , while in Iberian Atlantic waters hake L50 was 32.8 cm for males and 45 cm for females (Pineiro & Sainza, 2003). Females in the Bay of Biscay matured at a length of 41.4 cm (Dominguez-Petit et al., 2008). Sources agree that males mature earlier and at a shorter length, and that the largest specimens are almost exclusively female fish.

Based on studies in the northwestern Mediterranean (Olivar et al., 2003) and the Bay of Biscay (Alvarez et al. 2001, Alvarez et al. 2004), eggs and larvae are found in high densities over the continental shelf, to where they are transported to after hatching. 0-group hake settle on the seabed at depths of more than 200 m and to more inshore shallower muddy substrates (75-120 m) by September (ICES, 2013b) after its larval pelagic life.

1.3.3. Growth

Estimations of European hake growth and subsequent von Bertalanffy growth parameters based on otolith analyses are a controversial topic. Studies by de Pontual et al. (2006) and Khoufi et al. (2014) show, that previous growth estimates for the Bay of Biscay hake (de Pontual et al., 2003) and the Gulf of Lions (Mellon-Duval et al., 2010) were biased due to an overestimation of age (or under estimation of growth). Especially the interpretation of otolith rings has still not been validated. Fishbase (Froese & Pauly, 2011) shows a wide spatial and from source to source variation for von Bertalanffy growth parameters for *M. merluccius.*

1.3.4. Stock structure

ICES has defined two stock units for management purposes of hake in the North Atlantic. The northern stock covers ICES Division IIIa, Subareas IV, VI and IIb and Divisions VIII a, b, d. The southern stock covers ICES Divisions VIII c and IX d (ICESb, 2013). In geographic terms, the northern stock extends from the Norwegian west coast in the north over the British Isles to the west and the Danish coast to the east and along the coast of France to the Bay of Biscay in the south (Figure 4). The southern stock is found south of the Bay of Biscay, along the Spanish and Portuguese coasts with the Gibraltar Strait as its southern boundary. This separation is somewhat controversial, since Lundy et al. (1999) showed that the management separation does not agree with the genetic structure of European hake and more recently Milano et al. (2014) showed that a high local genetic divergence between different populations exists. The Atlantic and Mediterranean populations are assessed by two separate bodies; ICES is responsible for the assessment of the Atlantic and GFCM (General Fisheries Commission for the Mediterranean) for the Mediterranean stock. This work focuses on the northern part of the northeast Atlantic stock, where Norwegian waters are located in.

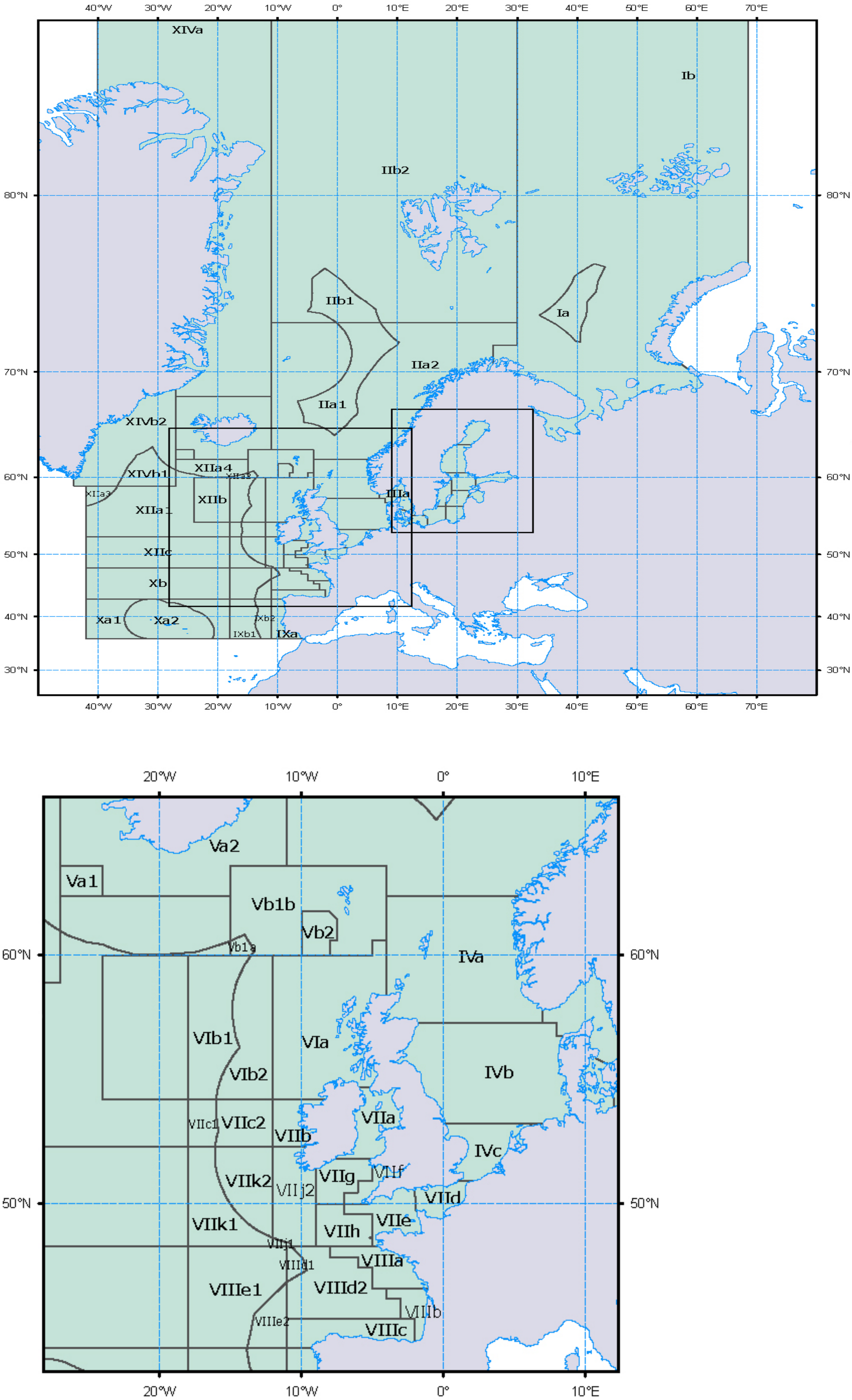


Figure 4: Maps of ICES Sub-areas and Divisions in the northeast Atlantic (Source: FAO).

1.4. Ecology

1.4.1. Prey spectrum

Prey spectrum from gut contents is a powerful and valuable method to estimate the influence of a predator in an ecosystem (Bowen, 1996; Du Buit, 1996; Baker et al, 2014). Not only essential ecological knowledge can be an outcome of a stomach content analysis, but it can also be used in stock assessments and for management purposes, such as in a multispecies virtual population analysis (MSVPA) (Bulgakova et al., 2001; Jennings et al., 2009). Extensive studies of hake diet exist for the Celtic Sea (Du Buit, 1996; Mahe et al., 2007), the Bay of Biscay (Guichet, 1995; Mahe et al., 2007) and the Gulf of Lions in the western Mediterranean (Bozzano et al., 1997). Combined, more than 10 000 stomachs were analyzed in these three studies, and the results demonstrate that as a predator, *M. merluccius* feeds primarily on fish, except for smaller individuals, which prefer crustaceans. Based on these studies the most important prey species in the Celtic Sea are Norway pout (*Trisopterus esmarki*), blue whiting (*Microsmesistius poutassou*), poor cod (*Trisopterus minutus*), but also the Clupeids (*Clupea harengus, Sprattus sprattus*) and Atlantic (*Scomber scombrus*) and horse mackerel (*Trachurus trachurus*). In the northern part of the Bay of Biscay, European anchovy (*Engraulis engrasicolus*) was an additional main prey species with a weight contribution to the diet of 19 % along with contributions, by weight, of 4 % from crustaceans and cephalopods. Data from the Gulf of Lions (Bozzano et al., 1997) suggest that prey selection is size dependent. Ontogenetic changes in hake diet were shown by Mahe et al. (2007) to occur in the Celtic Sea and the Bay of Biscay and by Abdellaoui et al. (2014) in the Morrocan part of the Atlantic, where hake >15 cm feed on Krill and adults mainly on fish. As European hake individuals grow larger, the percentage and the size of fish contributing to hake diet increase. Larger hake prey additionally on larger decapods and almost only fish.

Cannibalism apparently played a variable role in European Hake's diet choice. Guichet (1995) and du Buit (1996) described it as less important in the Bay of Biscay and the Celtic Sea, both arguing with a high degree of spatial separation between nursery grounds and adult individuals. Mahe et al. (2007) on the other hand described cannibalism in the same areas with a frequency of occurrence in all stomachs of 10 % as a "non-negligible" part of the diet, especially for larger fish (>30 cm), but also mention distribution patterns of juveniles and adults as a likely influencing factor. It was striking that the contribution of cannibalism to the prey spectrum in the Bay of Biscay and the Celtic Sea increased considerably between the beginning of the 1980s to the 2000s. Preciado et al. (2015) recently described i) a high inter-annual variability in cannibalism, ii) cannibalism as being most frequent in nursery areas and iii) cannibalism being related positively to abundance of juvenile conspecifics (<20 cm). They also found that 75 % of cannibalistic predators were 16-30 cm in length and that 75 % of prey-hake was 9-15 cm in length.

Seasonal variation is described by Bozzano et al. (1997) in the western Mediterranean and by Guichet (1995) in the northern part of the Bay of Biscay, where consumption rates for fish species and crustaceans varied throughout the year. Mahe et al. (2007) further discovered that selected prey does not correspond with the abundance of prey species in the Bay of Biscay and the Celtic Sea, but that European hake apparently has a preference for conspecifics and small pelagic species, such as Anchovy or Pilchard.

1.5. Objectives

In contrast to the amount of information on hake biology and ecology in areas such as the Mediterranean, the Bay of Biscay and around the Iberian Peninsula, relatively little is known about hake in Norwegian waters and the North Sea. Data on hake abundance is fragmentary, whether from fishery catch reporting or from scientific surveys. As part of annually and regularly conducted research cruises along the coast and in the North Sea, hake has been sampled as a "scientific bycatch" for decades. An increase in water temperature due to global warming might account for a northwards shift of the hake distribution (Perry et al., 2005) and strong recruitment success (Goikoetxea & Irigoien, 2013). As described earlier, an increase of European hake in the North Sea might already have had significant impacts on the fisheries. It is not unlikely that as a result of that increase the ecology of Norwegian coastal waters and the North Sea may be undergoing slow but visible changes. A central question thus is whether the European hake is on its way to become a keystone species along the coast of Norway and in the North Sea. A Keystone species (predator) is defined as:

> “a top predator that has an indirect beneficial effect on a suite of inferior competitors by depressing the abundance of a superior competitor. Removal of the keystone predator, just like the removal of the keystone in an arch, leads to a collapse of the structure. More precisely, it leads to extinction or large changes in abundance of several species, producing a community with a very different species composition and, to our eyes, an obviously different physical appearance” (Begon et al., 2006)

It is yet to be demonstrated that North Sea and Norwegian coastal hake belong to the same population or if they act independently from each other. This pilot study of the European hake’s biology and ecology is based on catch records as well as new survey data and will provide an important basis for further research. The major objective of this thesis is to answer the following questions:

1. What are the temporal trends in the commercial hake fishery in Norwegian waters? (Short description of Norwegian hake fishery)
2. Where does European hake have its major distribution areas along the Norwegian coast and in the North Sea and did it recently change?
3. Can spawning time as well as nursery grounds be indicated from biological survey data?
4. How does the diet of hake in Norwegian waters compare to that of hake in other areas?

2. Methodology

2.1. Survey design

All analyses were based on both landings and survey data. Survey data used and analyzed in this thesis were obtained on scientific research cruises, conducted by the Institute of Marine Research (IMR), Bergen. The results of four annually standardized surveys from 2006 – 2014 (Table 1) are used as the data source. Data in form of commercial catch data were obtained from the "Fiskeridirektoratet", the Norwegian fisheries ministry (website: http://www.fiskeridir.no/). Total landings of the Norwegian fleet in tonnes were obtained for the period 1977-2014. From 2000-2014 landings were divided by months and from 2005-2014 the landings by gear as well as ICES zone were further available. Due to discarding being forbidden in Norway by law (Gullestad, 2013), catches and landings are assumed to be equal. Landings were aggregated on a monthly basis and for the analysis and comparison purposes summarized to quarters (Q1: January-March; Q2: April-June; Q3:July-September; Q4: October-November)

Table 1: Dates of annual surveys used in this thesis, as conducted by the IMR (no data available for the IBTS Q3 2009). As a part of the IMR project on European hake I personally collected data at the IBTS Q3 survey 2014.

Year	Shrimp survey "Reketokt"	International Bottom Trawl Surveys (IBTS) Quarter 1 (Q1)	International Bottom Trawl Surveys (IBTS) Quarter 3 (Q3)	Coastal survey "Kysttokt" (Quarter 4)
2006	3.Feb-14.Feb	12.Jan-28.Jan	2.Jul-26.Jul	25.Okt-8.Dec
2007	7.Feb-19.Feb	16.Jan-4.Feb	21.Jun-19.Jul	16.Okt-19.Nov
2008	4.Feb-21.Feb	8.Jan-30.Jan	12.Jul-29.Jul	6.Nov-16.Dec
2009	24.Jan-12.Feb	5.Feb-22.Feb	No data	29.Sep-29.Okt
2010	14.Jan-31.Jan	6.Feb-24.Feb	1.Jul-31.Jul	29.Sep-9.Nov
2011	10.Jan-30.Jan	7.Feb-6.Mar	28.Jun-25.Jul	6.Okt-12.Nov
2012	9.Jan-27.Jan	15.Feb-14.Mar	25.Jun-25.Jul	2.Okt-13.Nov
2013	12.Jan-29.Jan	23.Jan-22.Feb	4.Jul-4.Aug	3.Okt-2.Nov
2014	9.Jan-28.Jan	14.Jan-19.Feb	30.Jun-29.Jul	26.Sep-1.Nov

All procedures and gear specifications for the IBTS surveys are summarized in the "Manual for International Bottom Trawl Surveys" (ICES, 2012). The shrimp and coastal surveys are according to IMR standardizations, coverage and design of the individual surveys are listed in Table 2.

Table 2: Survey design and specifications for the shrimp, IBTS Q1 + Q3 and coastal survey.

	Shrimp survey	IBTS Q1 + Q3	Coastal survey
Survey coverage	Southwest coast and Skagerrak	Central-northern North Sea	Norwegian coast north between Ålesund and Kirkenes
Survey design	Stratified with fixed bottom trawl stations	Stratified random (30*30 nautical miles ICES rectangles)	Fixed bottom trawl stations
Trawl net	Campeplen 1800 trawl	36/47 GOV survey trawl	Campelen 1800 trawl
Cod end mesh size	20 mm	20 mm	20 mm
Groundgear	Rockhopper gear	Groundrope with rubber discs	Rockhopper gear
Sampling time	Day and night trawling	Shooting not before 15 mins after sunrise/ Hauling completed 15 mins before sunset	Day and night trawling

2.2. Data collection

Length frequency data have been collected since 2006 on every cruise for every individual per haul. Weight and maturity recording was conducted on the IBTS Q1 and Q3 surveys between 2010 and 2014, on the coastal survey from 2012-2014 and on the shrimp survey in 2014. Data from all surveys except the IBTS Q3 2014, where I personally participated in, were electronically received from the IMR. On board, large predatory, commercially valuable fish within the catch, such as cod (*Gadus morhua*), saithe (*Pollachius virens*), monkfish (*Lophius piscatorius*) or European hake, were individually measured. Total length of European hake was taken with an electronic measuring board, weight with a scale. Maturity was taken according to five stages maturity key of the IMR handbook (Table 3; Mjanger et al., 2013).

Table 3: General 5-stages maturity key of the IMR (Source: Mjanger et al., 2013).

Stage	Description
1	**Immature** Gonads are small. No visible eggs or milt.
2	**Maturing** Gonads are larger in volume. Eggs or milt are visible but not running
3	**Spawning** Running gonads. Light pressure on the abdomen will release eggs or milt.
4	**Spent/Resting** Gonads small, loose and/or bloody. Regeneration starting, gonads somewhat larger and fuller than stage 1. No visible eggs or milt.
5	**Uncertain** Use only when difficult to distinguish stages 1 and 4.

2.3. Stomach collection and identification of prey

In 2014 a total of 200 stomachs were taken and frozen on board during the IBTS Q1 and Q3, the Norwegian coastal survey, the shrimp survey in the Skagerrak, the Shetlands-teaching cruise in November and during field work for the University of Bergen on Askøy, right outside Bergen. I collected stomachs on the IBTS Q3 survey, others I received. All stomachs which were not everted were collected and individually frozen on board after sampling. Stomach analysis was conducted in the laboratory from September - December 2014. Before analysis stomachs were defrosted, blotted and wet weight including stomach content to the nearest milligram was taken. The analysis of the stomach content was done mainly according to Bowen's manual on the quantitative description of diet (Bowen, 1996). Fish identification was either conducted visually, or by examination of the otoliths and species' specific otolith shape (Whitfield & Blaber, 1978). Stomachs which only contained well-digested material and without identifiable prey items, were searched for otoliths. When no otoliths could be found, the whole stomach including the content was rinsed through sieve with a 1 mm mesh size to flush out any remaining otoliths. A careful handling of the stomachs and the prey items is necessary in order not to miss any otoliths. The bag a stomach was stored and frozen in was also rinsed and flushed through a sieve after removing the contents, in order to ensure that no otoliths were retained in the bag. When it was impossible to use otoliths for certain species identification, especially to separate gadoid species with similar otolith characteristics, anatomical characteristics such as the shape of the mouth or the size of muscle segments were used to identify prey species.

As recently discussed by Baker et al. (2014), there are several different methods of analyzing and interpreting stomach contents and diet. According to their outcome, our study was carried out on the base of a quantitative approach by frequency of occurrence (%F), which is considered to be the most robust method. The unit %F stands in that context for the percentage of analyzed stomachs, in which the certain prey species was found. Additionally, percentage composition (%N) was calculated, where the number of individuals of the different prey species is divided by the total number of prey items. No extrapolations or calculations utilizing gravimetric or volumetric methods were conducted in order to avoid misinterpretations. Stomachs collected on Askøy were added to the coastal survey data due to a very low number and a geographically similar origin.

2.4. Data handling and analysis

All data collected on the cruises were stored in the Institute of Marine Research (IMR) database and for analyses purposes exported into Microsoft Excel format. For every trawl haul station information including position coordinates, fishing depth, trawl duration and distance were recorded. Due to different trawl durations, all catch weights (kg) and numbers (n) were standardized to Catch per Unit Effort (CPUE) values (kg/nm).

For mapping and statistical analysis the software program R version 3.1.2 (R Development Core Team) with the RGeostats package (version 10.0.8) was used. In order to identify and demonstrate changes in abundance, CPUE data in numbers (n/nm) and weight (kg/nm) were plotted. For this purpose, an average CPUE per year per station was calculated by dividing the total CPUE by the number of stations. To monitor distribution and possible changes, CPUE data in numbers were mapped. Additionally, the center of gravity, defined as "the mean location of the population" – taking catch size and location into consideration - (Woillez et al., 2007), was calculated. To identify a trend or shift in distribution, Centres of gravity (lat and long) were plotted over time with Microsoft Excel 2010 and tested for significance with a linear regression with R (Perry et al., 2005). In a linear regression the best fit for slope and intercept by minimizing the sum of squares of all data points, is calculated.

The R coefficient indicates in this context how well the regression describes the observed data points. Trends of landings and survey CPUEs were plotted with Microsoft Excel 2010. Additionally standard errors were calculated for each year of the four surveys. For this purpose, the number of stations, the average CPUE per station and the standard deviation for each survey were computed by Microsoft Excel 2010. Afterwards the standard error for each survey and each year was calculated by dividing the standard deviation by the square root of the number of stations.

When mapping CPUE values for each survey the maximum CPUE value for each of the four surveys over the entire time period was used as a reference value. This means that the maximum bubble size for each year was proportional to the highest value in order to make a visual comparison of changes in abundance possible. CPUE plots of the station data of the coastal survey were all plotted over the same geographical range from 62°-69°5'N and 4°-16°E for a more suitable visual comparison. That was done due to a very far north-eastwards range of the cruise in the Barents Sea without any presence of European hake, which would have made a visual comparison more difficult. Due to different annual coverage areas during the shrimp survey the range of CPUE stations was also standardized and 59° north defined as northernmost station for every year, since station data were available up to that point for the whole period.

In order to identify potential spawning sites individual maturity data was plotted by position. For every available station with data from 2010-2014, the number of spawning (ripe and running gonads) fish (maturity stage = 3) was divided by the total number of fish at that station to calculate a probability of a caught fish to be in a spawning condition. For identification of potential nursery grounds, small individuals from 4.5-10.5 cm (4.5 cm represents the smallest fish caught during all surveys) and specimens between 10.5 - 25-5 cm were selected and mapped. Due to difficulties and earlier underestimations of European hake growth, the definition and critical length of juvenile or 0-group European hake is controversial. In 2003, Maynou et al. considered individuals under 10 cm as juveniles belonging to the 0-group. Later studies revealed a much higher mean length of 0-group fish, respectively 23.8 cm in the Bay of Biscay and Celtic Sea (Kacher & Amara, 2005) and 24.3 cm in the Bay of Biscay (de Pontual et al., 2006). The most recent paper on growth of European hake from the eastern Mediterranean (Pattoura et al., 2015) showed a length of 28.3 cm for females and 26.5 cm for males at the end of their first year. 10 cm is furthermore assumed to be a critical value when it comes to ageing of fish. Above 10 cm it becomes uncertain if these individuals all belong to the same age group, or if variations of growth rate between individuals caused overlaps between different year classes (personal communication Richard Nash).

3. Results

3.1. Trends of Norwegian landings of European hake

As visualized in Figure 3, between 1977 and 2005, landings of European hake in Norway fluctuated stably between 500 and 1000 tonnes annually. Within the available time series, catches exceeded 1000 tonnes a year the first time in 2006 (1179 t), increased slowly until 2010 (1794 t), from when they soared with an annual increase of 500 – 800 t to a total catch of 4342 t in 2014.

3.1.1. Intra-annual variations

In addition to the increase in total landings (Figure 3), there was also a striking trend in intra-annual variation in landings of European hake in Norway. The contribution of quarters one and two (Q1 and Q2) to the whole annual catch was low (less than 30 %) until 2008, after which it increased up to more than 60 % in 2011 (Figure 5). At the same time, percentage landings during quarter three (Q3) decreased from about 70 % in 2000 to 30 % in 2014, while landings during quarter four (Q4) remained stable at around 20 %.

Total landings during all four quarters increased during the period 2000-2014 (Figure 6). The steepest rise can be found in Q2, where landings increased steadily from 75 t in 2000 to 1400 t in 2014. Although percentage contribution of Q3 decreased over time, its total catches remained stable at around 500 t between 2000-2012, after which landings increased to 1300 t in 2014. Landings during Q1 and Q4 increased as well, with a recent sharp decline in Q1, and a sharp upswing in Q4.

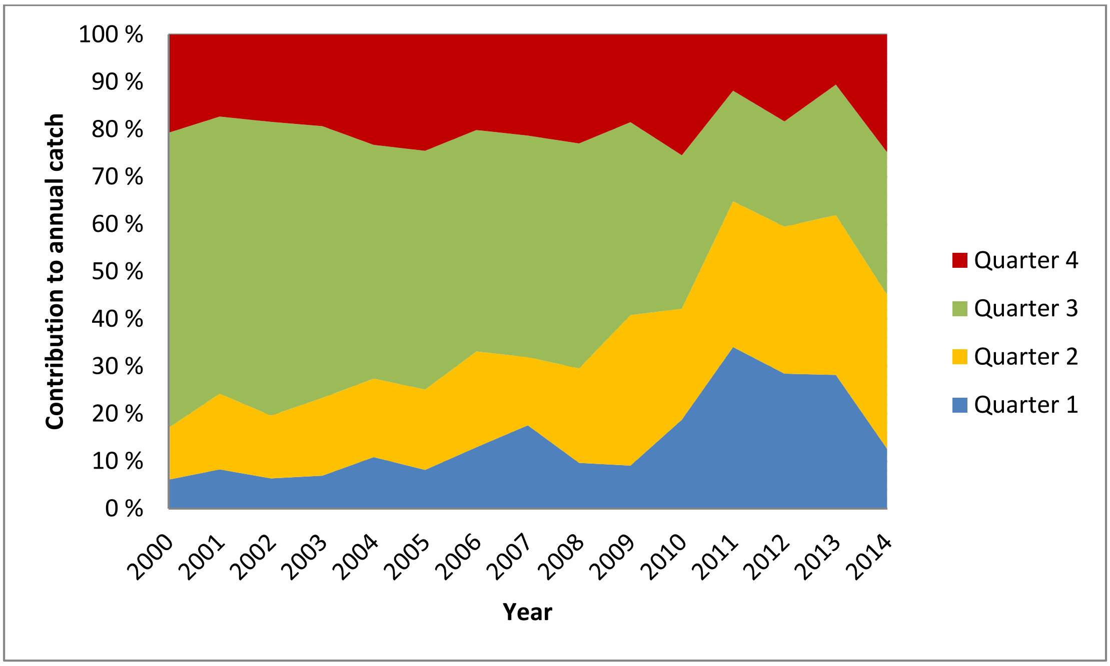


Figure 5: Percentage contribution of quarters to total landings of European hake in Norway from 2000-2014.

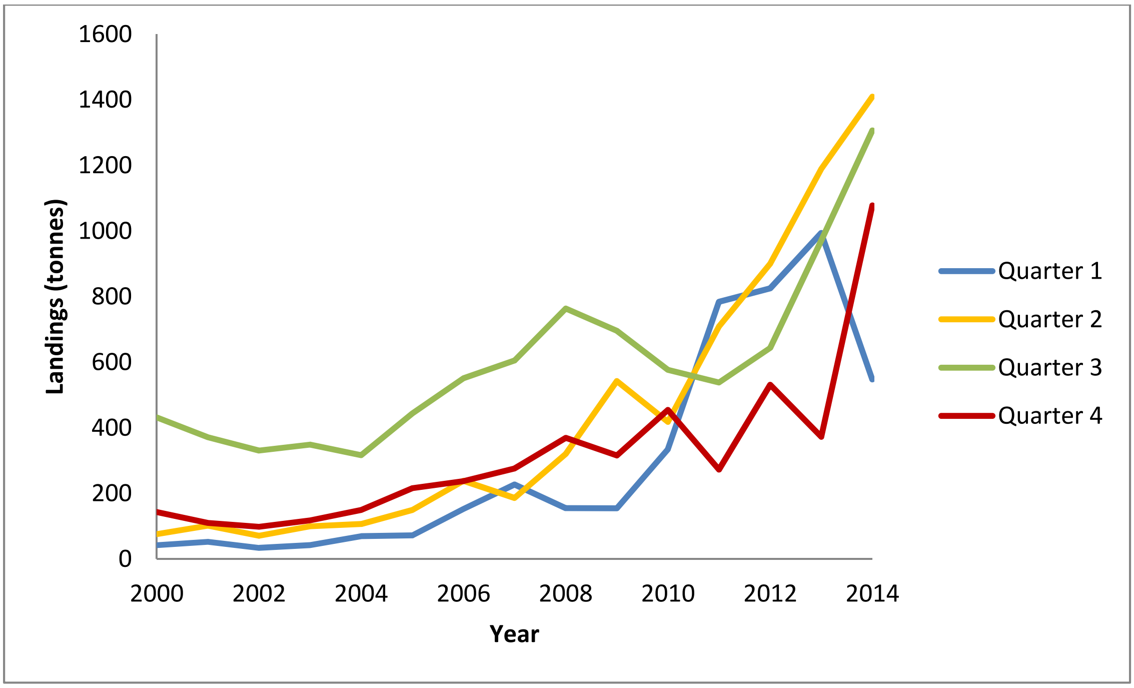


Figure 6: Total landings in tonnes of European hake in Norway from 2000-2014 divided into quarters.

3.1.2. Spatial dynamics

With a visible increase in contribution of the ICES subdivision IVa (Figure 4) to the total catch, the spatial dynamics showed a clear trend during the period analyzed (Figure 7). In

2005, at the beginning of the time series, subdivision IIa2 accounted for almost 60 % of landings in Norway. Throughout the following ten years its contribution decreased by more than half, and the contribution of IVa more than doubled. At the same time, contributions of the minor important subdivisions IIIa and IVb declined to a negligible level. Landings from subdivision IVc were 0 for eight years and represented less than 0.1 % and were therefore excluded from the plots. Most recently, in 2014, 98 % of all landings came from subdivisions IIa2 and IVa. This increase in landings in the northernmost areas of European hake can indicate a northwards movement of the species, but conclusions have to be drawn with caution.

The major increase of contributing landings in subdivision IVa was also observed in the total catches (Figure 8). Landings in subdivision IIa2 increased steadily throughout the whole time series from about 500 t to 1000 t. Catches obtained in subdivision IVa increased by more than twelve times from 250 t in 2005 to 3150 t in 2014. Between 2010 and 2014, landings increased by approximately 500 t every year. Total catches in subdivisions IIIa and IVb do not show a visible trend, but remained low at no more than 100 t.

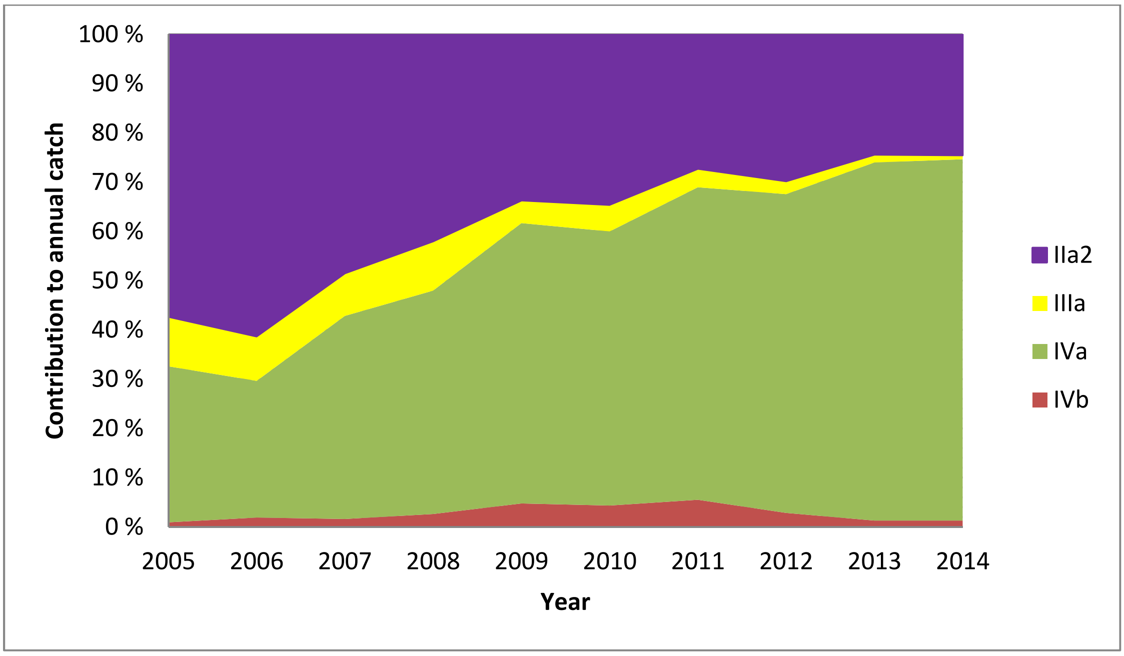


Figure 7: Percentage contribution of ICES subdivisions IIa2, IIIa, IVa and IVb to total landings of European hake in Norway from 2005-2014.

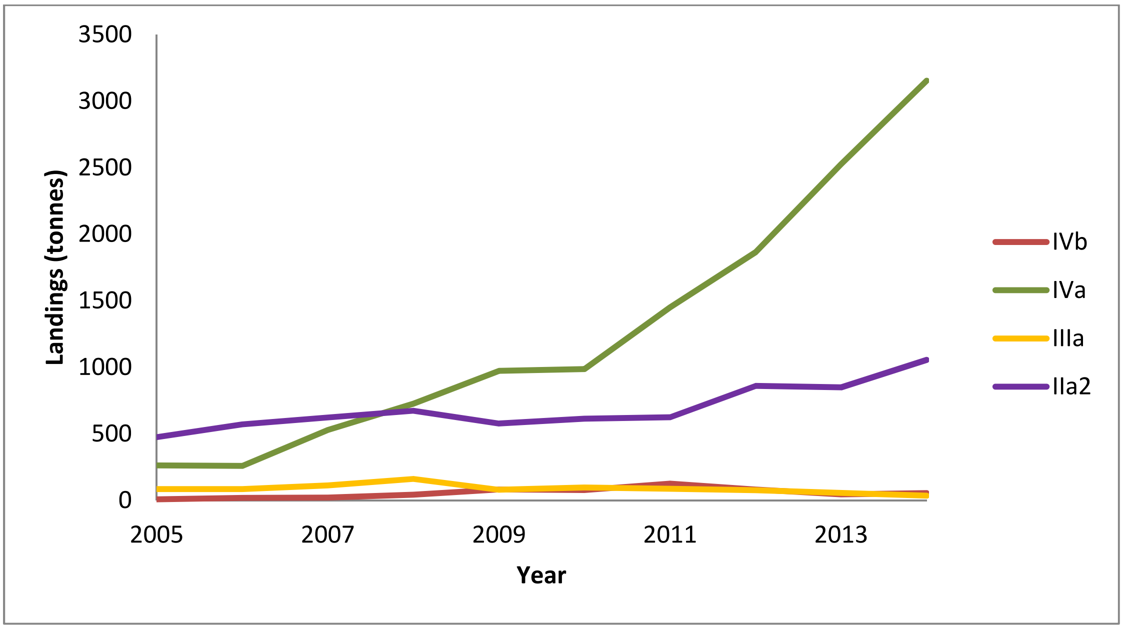


Figure 8: Total landings in tonnes of European hake in Norway from 2005-2014 of ICES subdivisions IIa2, IIIa, IVa and IVb.

3.1.3. Fishery

Data obtained from the Ministry of Fisheries were divided into seven fishery / gear types, purse seine, gillnet, hook & line, longline, seine, bottom trawl and “others”. Purse seine, hook & line, longline and “others” accounted together for less than 1 % of the total landings, and bottom trawl, seine and gillnet for the remaining 99 % (Appendix 2). Between 2005 and 2014, the contribution of bottom trawl landings increased from 25 % to almost 70 % and at the same time gillnet landings declined from over 60 % to 25 % (Figure 9). Percentage landings contribution by the seine fishery decreased from almost 12 % in 2005 to about 1 % in 2010 and afterwards increased again to about 5 % in 2014.

Total landings from the bottom trawl fishery showed a substantial increase from 200 t in 2005 to almost 3000 t in 2014 (Figure 10). Catches with gillnets doubled between 2005 and 2008 and remained stable at around 1000 t after this period.

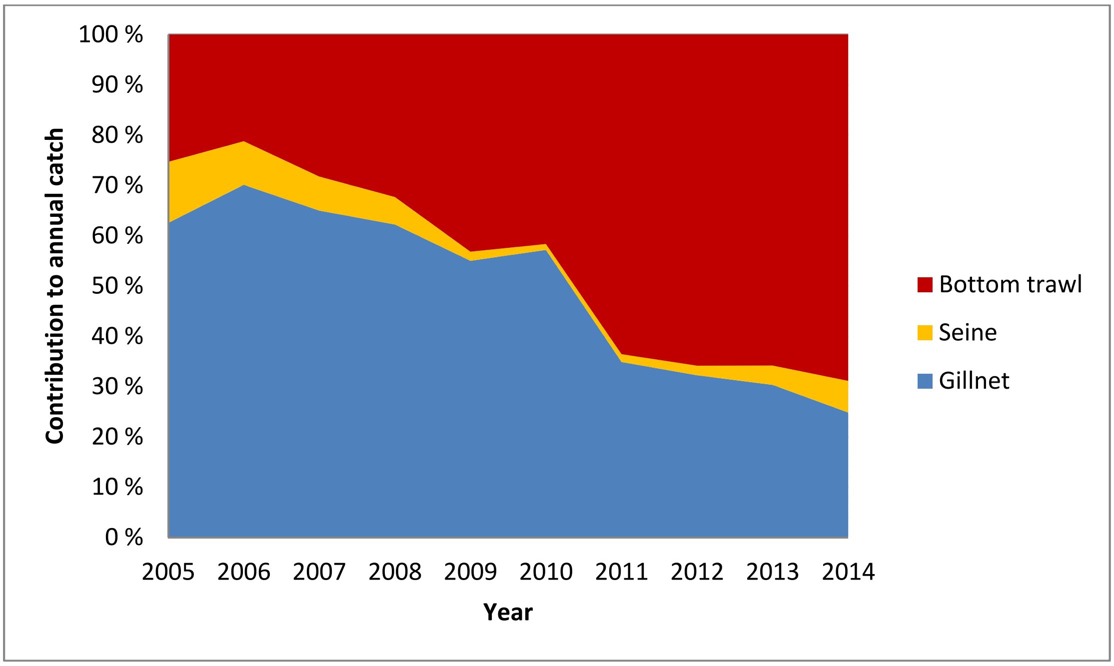


Figure 9: Percentage contribution of trawl, gillnet and Danish seine to total landings of European hake in Norway from 2005-2014.

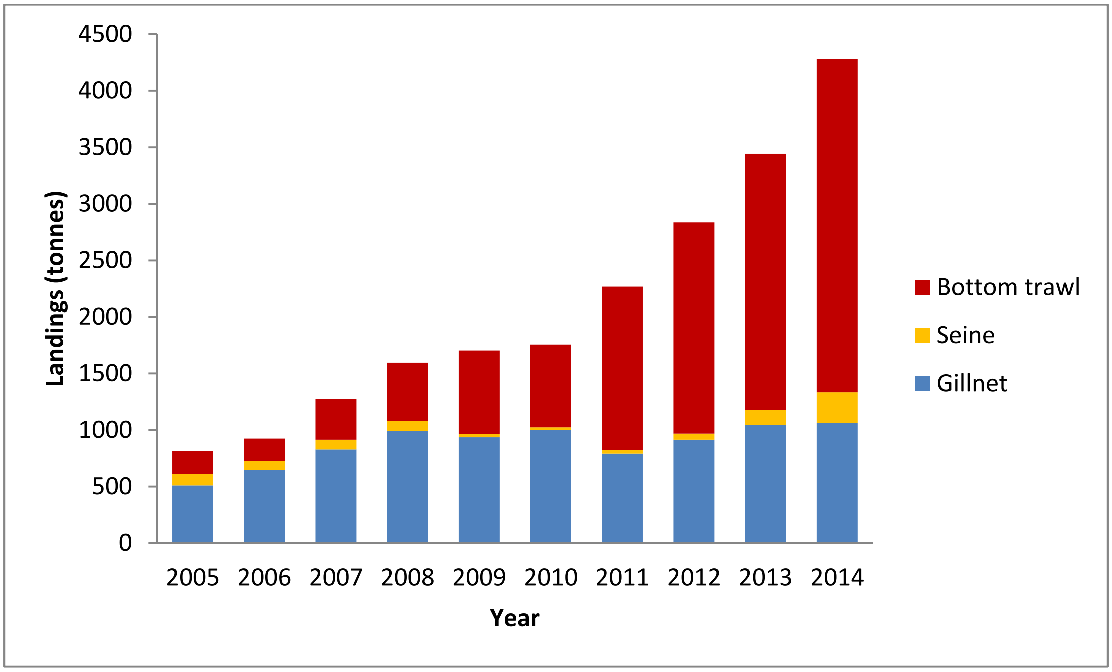
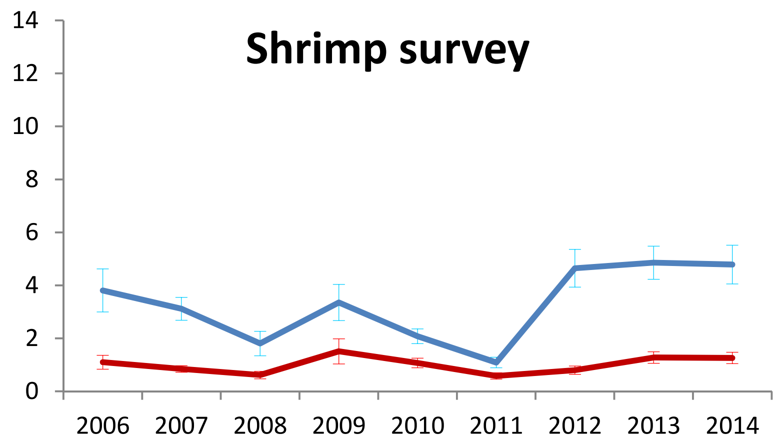


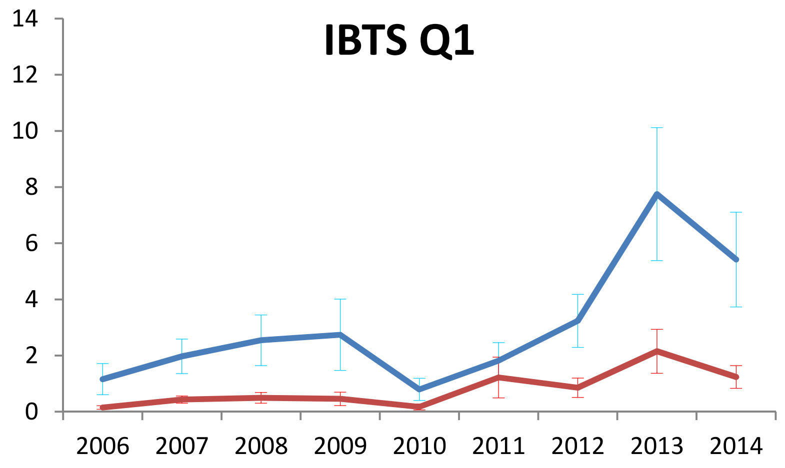
Figure 10: Total landings in tonnes of European hake in Norway from 2005-2014 of trawl, Danish seine and gillnet.

3.2. Biology

3.2.1. Abundance

Throughout all four surveys an increasing trend in CPUE in numbers (blue line) is visible, and throughout all surveys except for the shrimp survey, the CPUE in weight (red line) increased clearly as well (Figure 11). The generally highest CPUE was found on the IBTS Q3 survey in the summer in the North Sea, with maximum values of an average CPUE 11.5 n/nm and 9 kg/nm per station in 2013. On the shrimp survey, the IBTS Q1 and the IBTS Q3 the years 2012-2014 showed an especial increasing trend in CPUE in numbers, the CPUE on the coastal survey was rather stable, with exceptionally high values in 2012. Striking is furthermore a constant and strong divergence between CPUE in numbers and weight in Q1 on the shrimp and IBTS Q1 surveys, where numbers were every year visibly higher. This trend was partially seen on the IBTS Q3 as well, but not during the coastal survey, where CPUE in weight recently, in 2013 and 2014, outgrew numbers.





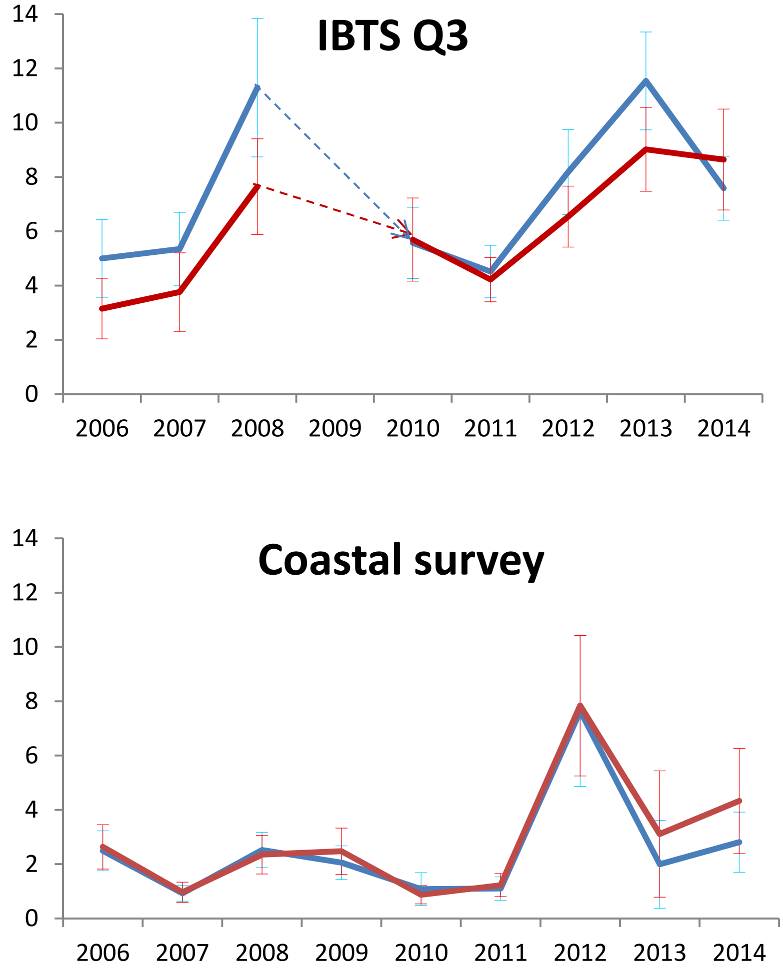
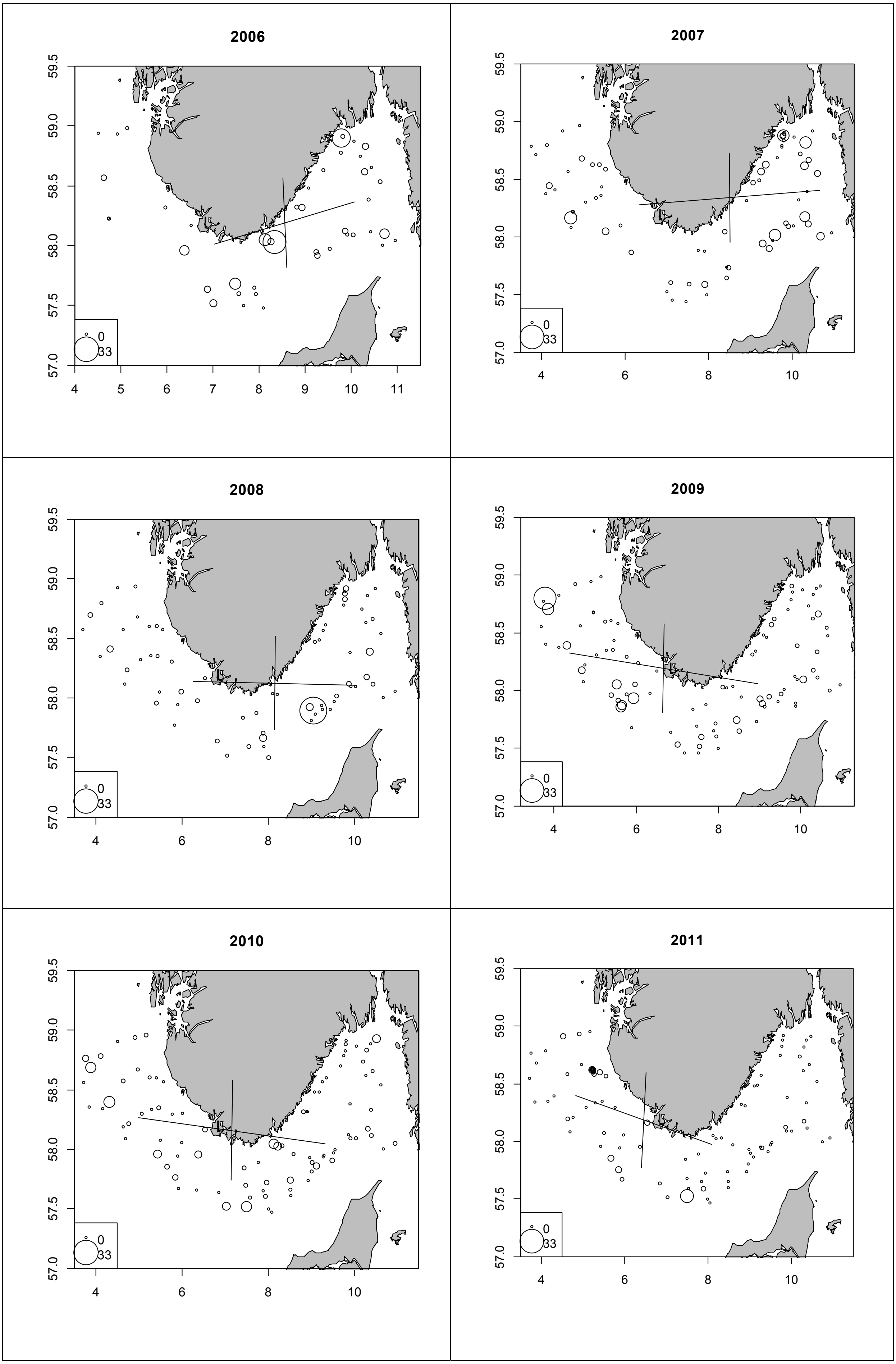


Figure 11: Average CPUEs in n/nm (blue line) and kg/nm (red line) with standard error bars for every year from 2006-2014 (no data for the IBTS Q3 survey in 2009; dotted lines represent unknown transition from 2008-2010).

3.2.2. Distribution

3.2.2.1. Shrimp survey

Despite a standardization of survey coverage, stations in 2006 and 2014 are missing along the south-west Norwegian coast between Egersund and Mandal, because stations were not sampled due to unfavorable weather conditions (Figure 12). Along with an increasing CPUE from 2012-2014 (Figure 11), stations with high catches visibly increased as well. Abundance especially increased in the Skagerrak along the coast from Kristiansand to the entrance of the Oslofjord and the southern shelf edge of the Norwegian trench towards Denmark. The year with the highest number of large catches was 2013 with a peak catch rate of 33/nm.


2006
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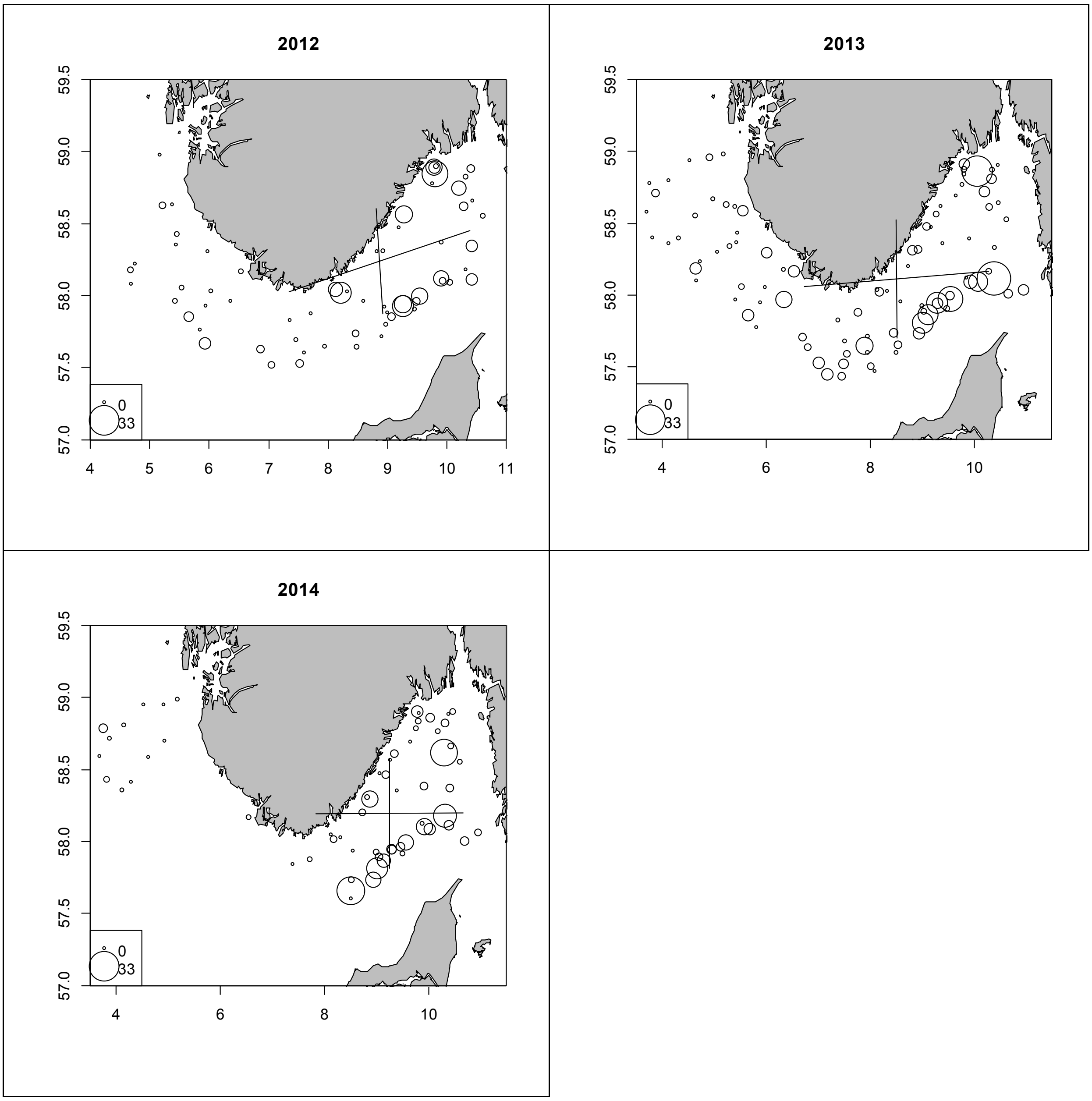
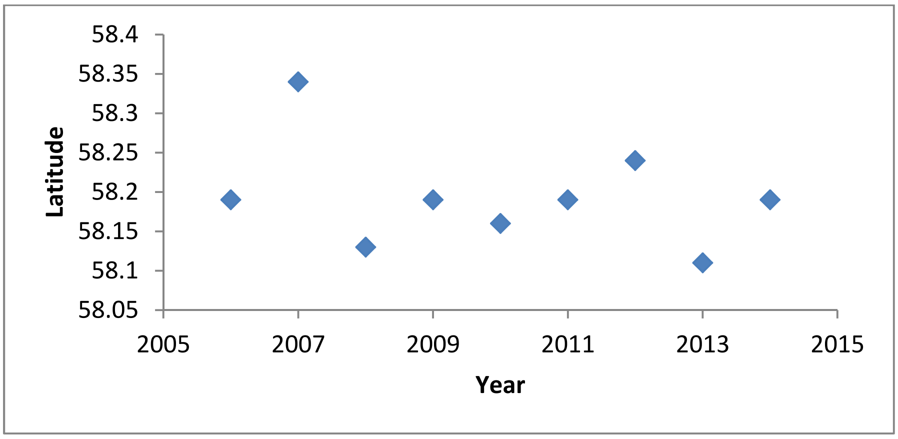


Figure 12: CPUE (n/nm) plots of European hake on the shrimp survey from 2006-2014 (maximum CPUE throughout the period = 33/nm), 2013).

The centers of gravity were located between 58°11'N and 58°34'N as well as 6°46'E and 9°25'E (Figure 13). No significant linear relationship between year and latitude (r^2-value: 0.1028; p-value: 0.400) as well as year and longitude (r^2-value: 0.03379; p-value: 0.636) was observed.



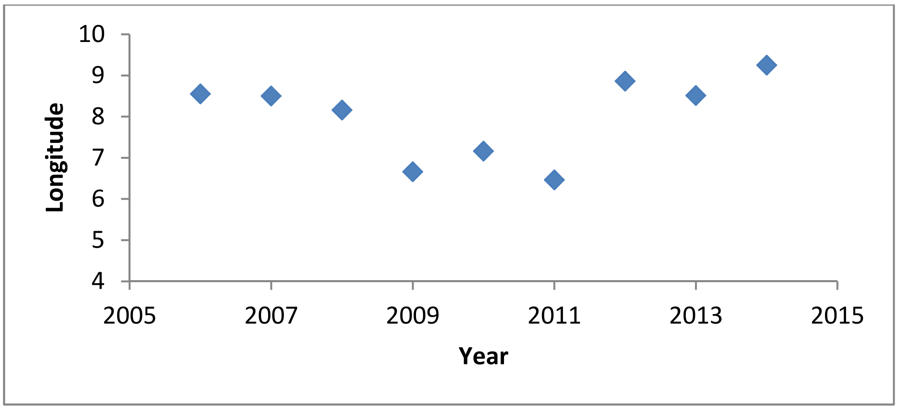
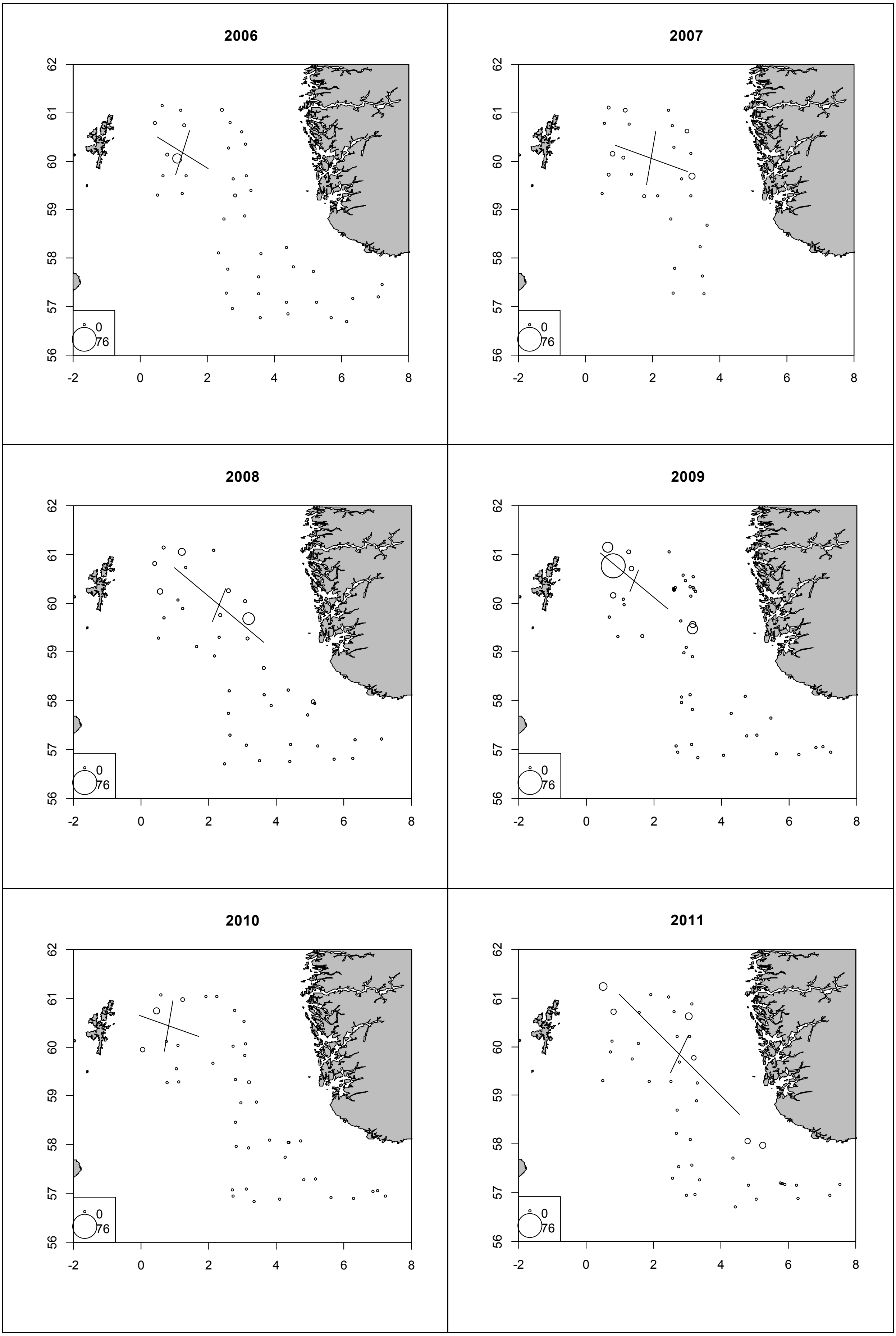


Figure 13: Plots of latitude and longitude of centres of gravity from 2006-2014 of European Hake catches on the shrimp survey.

3.2.2.2. IBTS Q1 survey

The main distribution area of European Hake in the North Sea throughout the IBTS Q1 survey in January/February was found in an area between the Shetland Islands and the Norwegian west coast (Figure 14) with a striking increase in number and dispersion of high catches from 2012-2014.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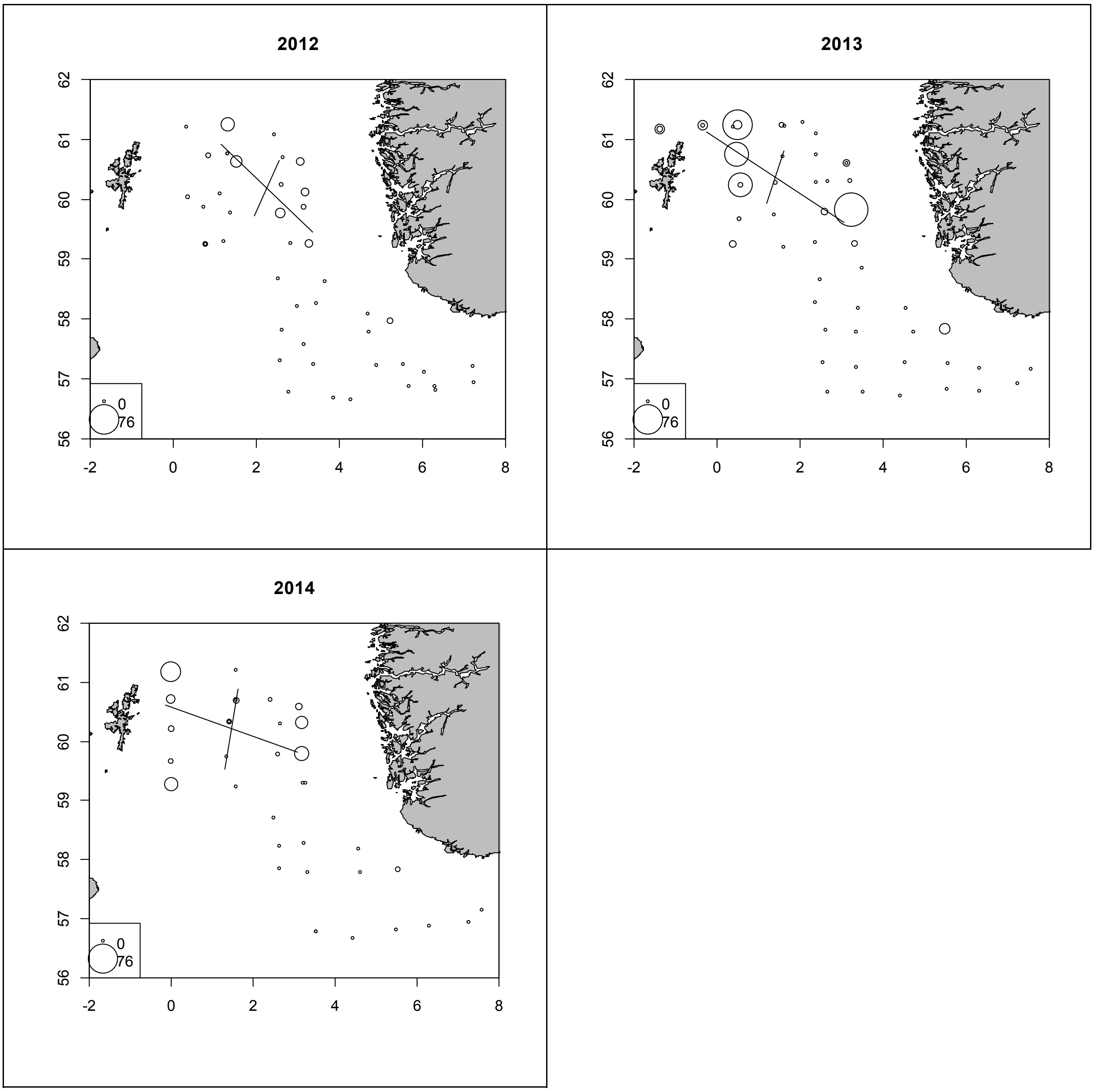
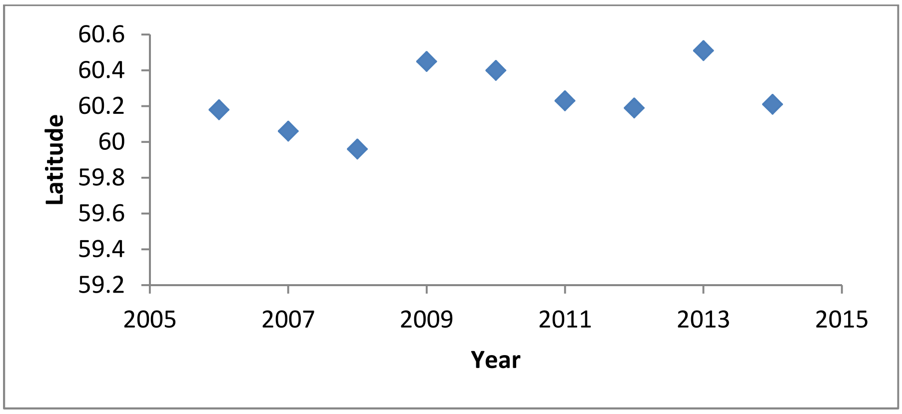


Figure 14: CPUE (n/nm) plots of European hake on the IBTS Q1 survey from 2006-2014 (maximum CPUE throughout the period = 76/nm), 2013).

The centers of gravity were found between 59°96’N and 60°51’N as well as 1°26’E and 2°95’E (Figure 15). The linear regressions between year and latitude (r^2-value: 0.2094; p-value: 0.254) as well as year and longitude (r^2-value: 0.0109; p-value: 0.806) were found not to be significant. Available data for 2010 did not allow a calculation of coordinates for the center of gravity for 2010 and but an estimate would locate it at 60°4’N and 1°1’E.



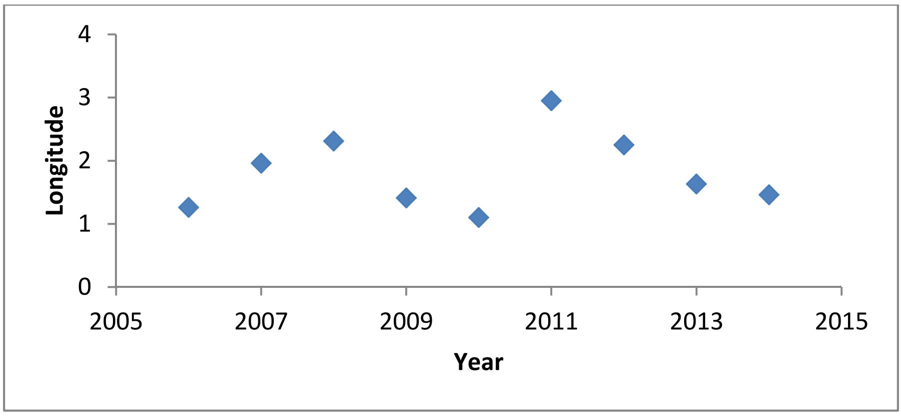
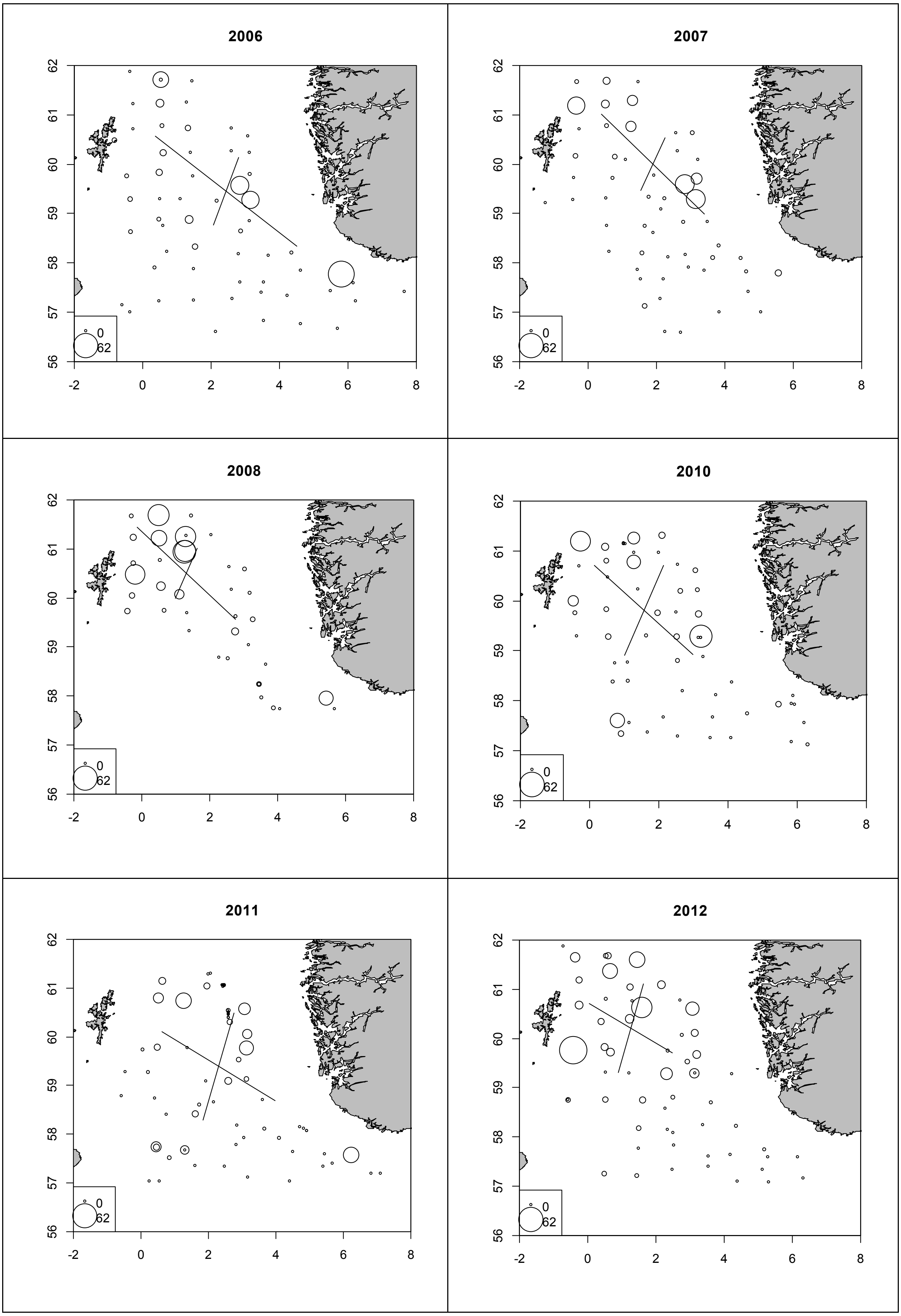


Figure 15: Plots of latitude and longitude of centres of gravity from 2006-2014 (coordinates for 2010 were guessed) of European Hake catches on the IBTS Q1 survey.

3.2.2.3. IBTS Q3 survey

During the IBTS Q3 survey from 2006-2014 hake was found throughout the whole North Sea and a range from the most northern to the most southern station of the survey (Figure 16). For 2009, no catch records were available. As well as on the IBTS Q1 survey, an increase and a higher dispersion in stations with high catches of European hake were striking. Missing stations in 2008 were not sampled because of unfavourable weather conditions.

The centers of gravity were found between 59°39’N and 60°51’N as well as 1°26’E and 2°44’E (Figure 17). The linear regressions between year and latitude (r^2-value: 0.004875; p-value: 0.870) as well as year and longitude (r^2-value: 0.1398; p-value: 0.362) did not show a significant result.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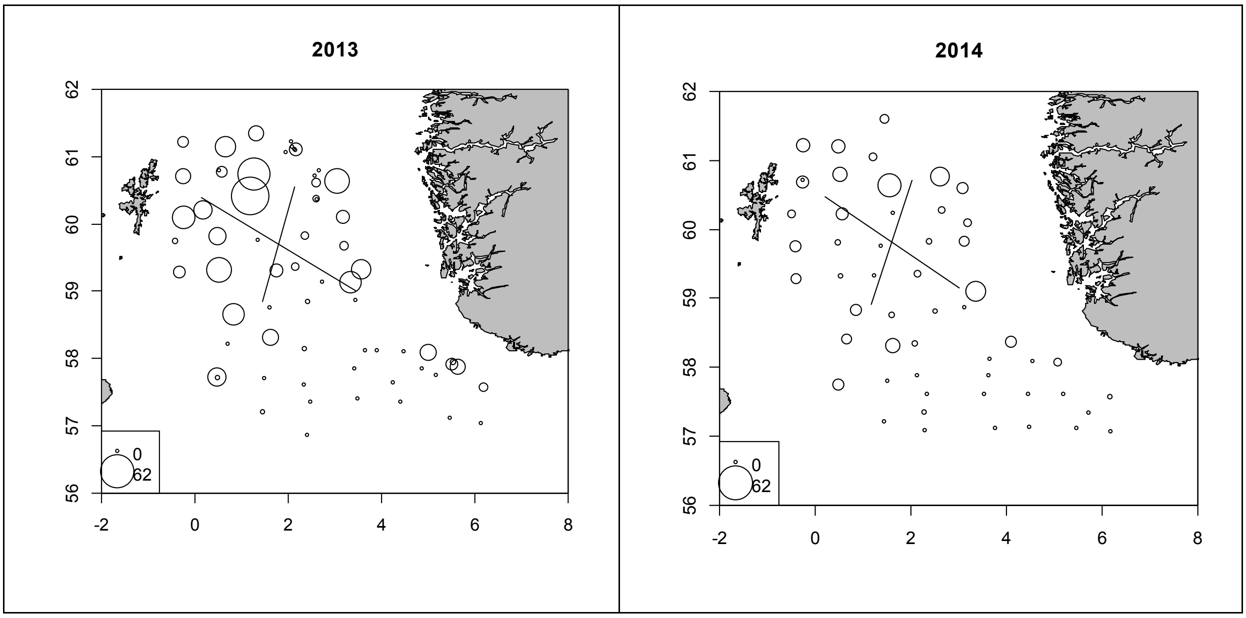
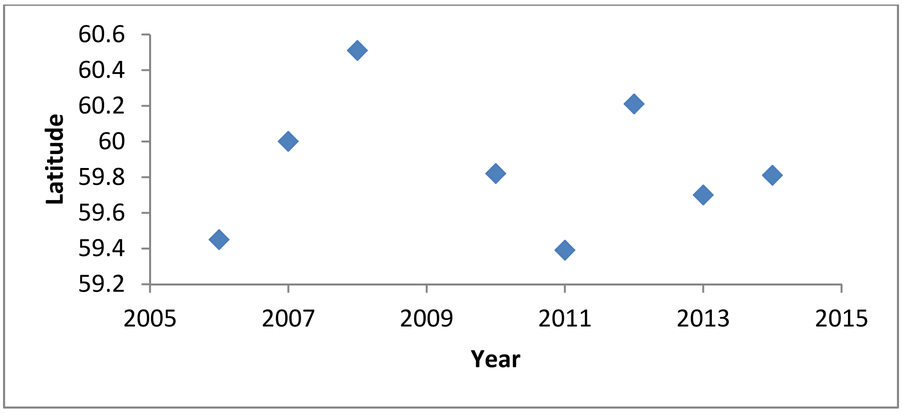


Figure 16: CPUE (n/nm) plots of European hake on the IBTS Q3 survey from 2006-2014 (exclusive 2009; maximum CPUE throughout the period = 62/nm), 2013).



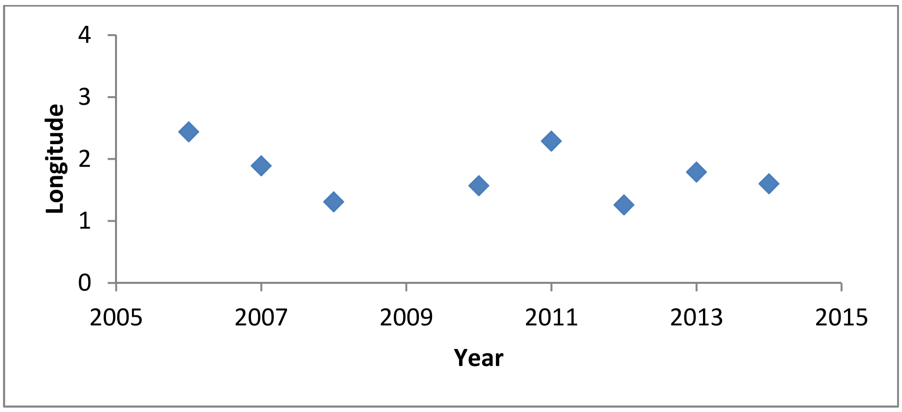


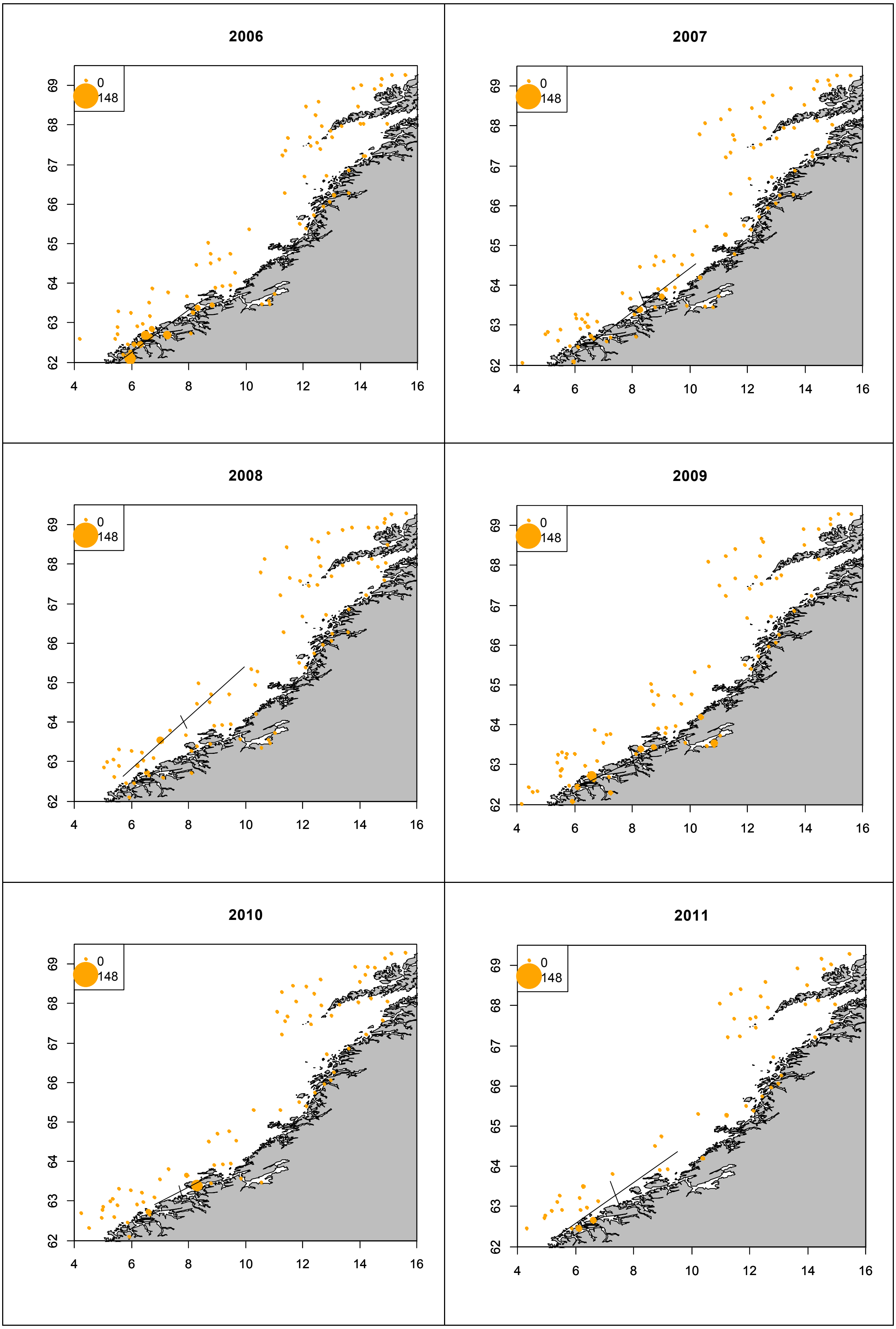
Figure 17: Plots of latitude and longitude of centres of gravity from 2006-2014 (exclusive 2009) of European Hake catches on the IBTS Q3 survey.

3.2.2.4. Coastal survey

Throughout the coastal survey with a survey range from the very east of the Norwegian part of the Barents sea south-westwards to Ålesund, European hake was mainly caught from Ålesund in the south up to the Lofoten Islands in the North (Figure 18).

In 2011, one very small catch (CPUE = 0.28 kg/nm) was recorded at 71°39'N and 26°04'E, which represented an exceptionally far north-eastern point for the presence of European hake. This station was left out in the CPUE map for 2011 to retain geographic proportions and visual interpretability of the plots.

The centres of gravity were located between 62°76'N to 64°01'N and 6°69'E to 8°03'E (Figure 19). The linear regressions between year and latitude (r^2-value: 0.1015p-value: 0.403) as well as year and longitude (r^2-value: 0.09941; p-value: 0.409) were found not to be significant.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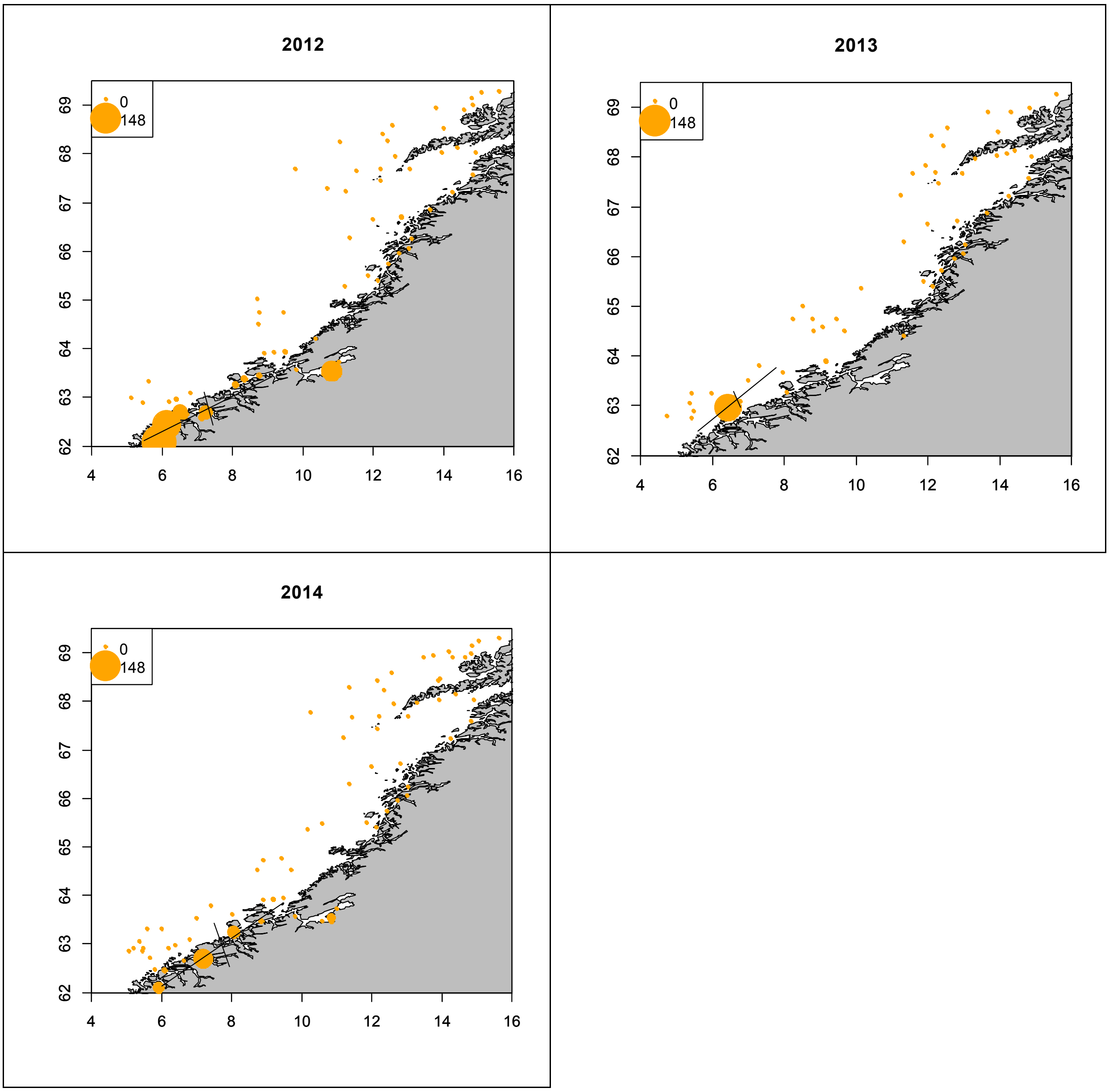


Figure 18: CPUE (n/nm) plots of European hake catches on the coastal survey from 2006-2014 (maximum CPUE throughout the period = 148/nm), 2013).

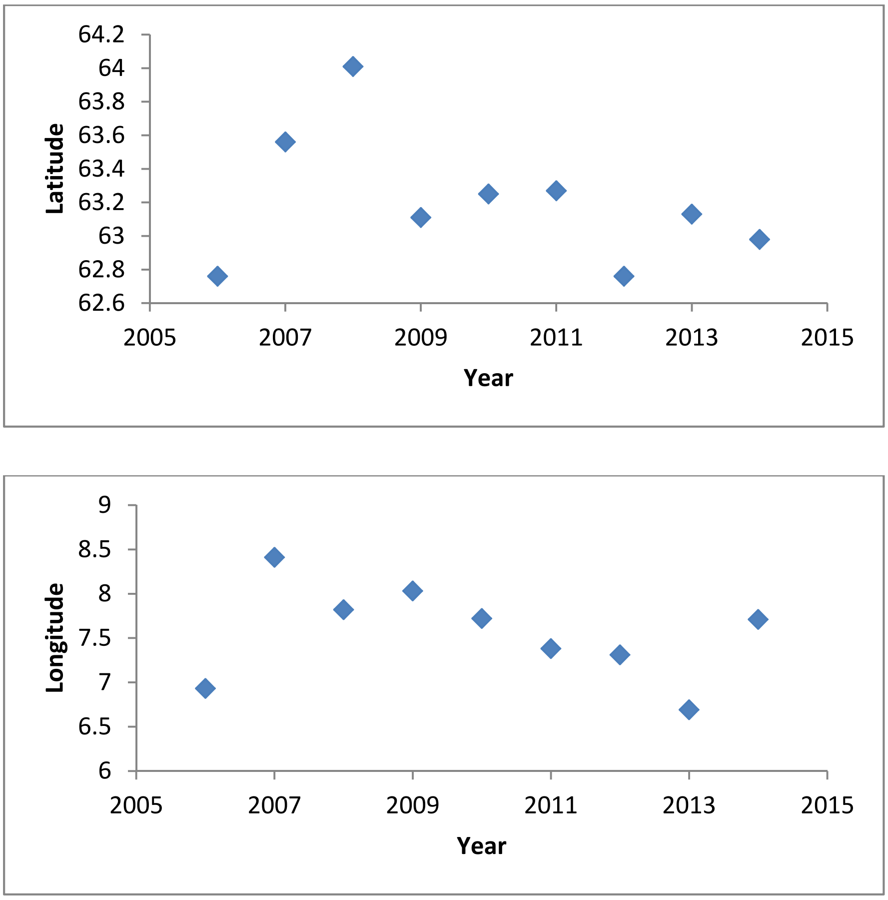


Figure 19: Plots of latitude and longitude of centres of gravity from 2006-2014 of European Hake catches on the coastal survey.

3.2.3. Spawning

Maturity data were available for 2935 individuals of which 86 were identified as fish in spawning condition. Total length of spawning fish ranged from 35-100 cm with a mean of 65.7 cm. Male to female sex ratio of spawning fish was 2.3 : 1. Length range of spawning females was 58-100 cm with an average of 77.7 cm and of spawning males 35-83 cm with an average of 60.4 cm. Spawners were found on the IBTS surveys in the North Sea in Q1 and Q3 and on the Norwegian coastal survey in Q4. Data show a large numerical dominance of spawners throughout Q3 in July (Appendix 3). The shrimp survey in the Skagerrak showed exclusively immature individuals.

3.2.3.1. Quarter 1

Spawning fish in Q1 were caught west of the Norwegian trench between 60°3’N and 61°3’N (Figure 20) at a depth of 128-173 m. Numerically, there were only a few stations with spawning individuals in the winter with a maximum probability of a fish being in spawning condition of 0.33.

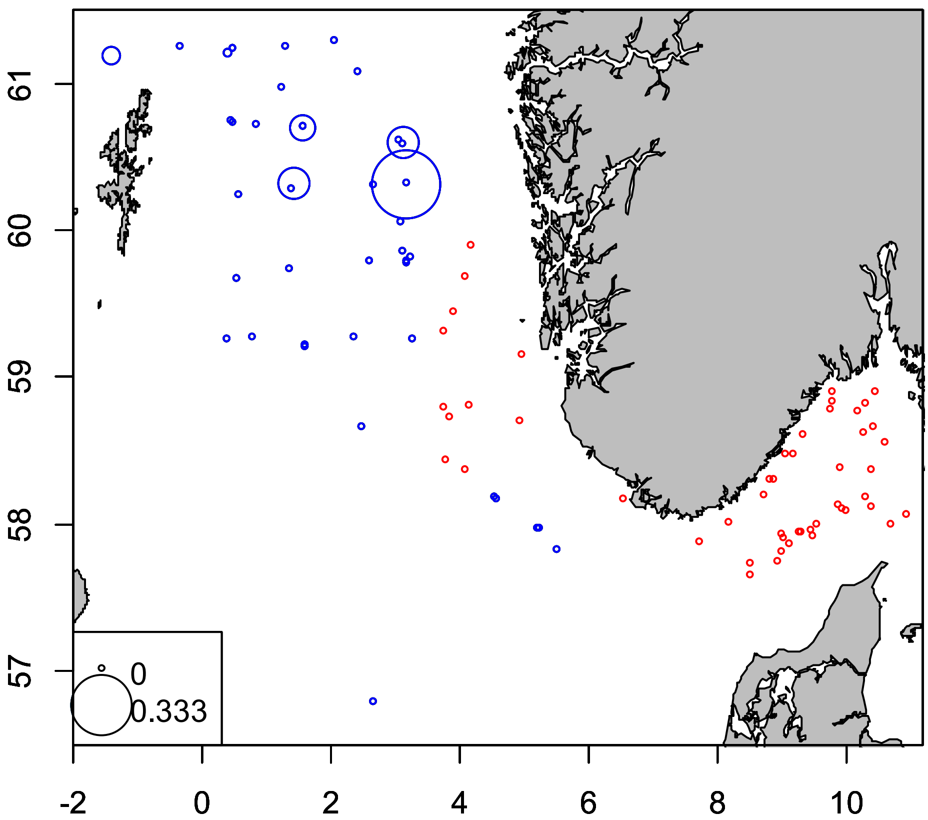


Figure 20: Probability of an individual fish being in spawning condition during the IBTS Q1 (blue) and shrimp (red) survey from 2010-2014. Maximum value at a station during that period = 0.33 (=33 % of the fish caught were in spawning condition).

3.2.3.2. Quarter 3

The maximum proportion of spawners was found in Q3 and, they were further south than in Q1, between 57°03'N and 61°60'N (Figure 21) in a depth range of 68-176 m. There was a noticeable tendency of spawners to be on the offshore side of the Norwegian trench, along the slope of the shelf edge. The maximum probability of a fish being in spawning condition during that time was 1. Stations with probabilities of 0.5 and higher were exclusively found south of 59°14'N and east of 1°60'E.

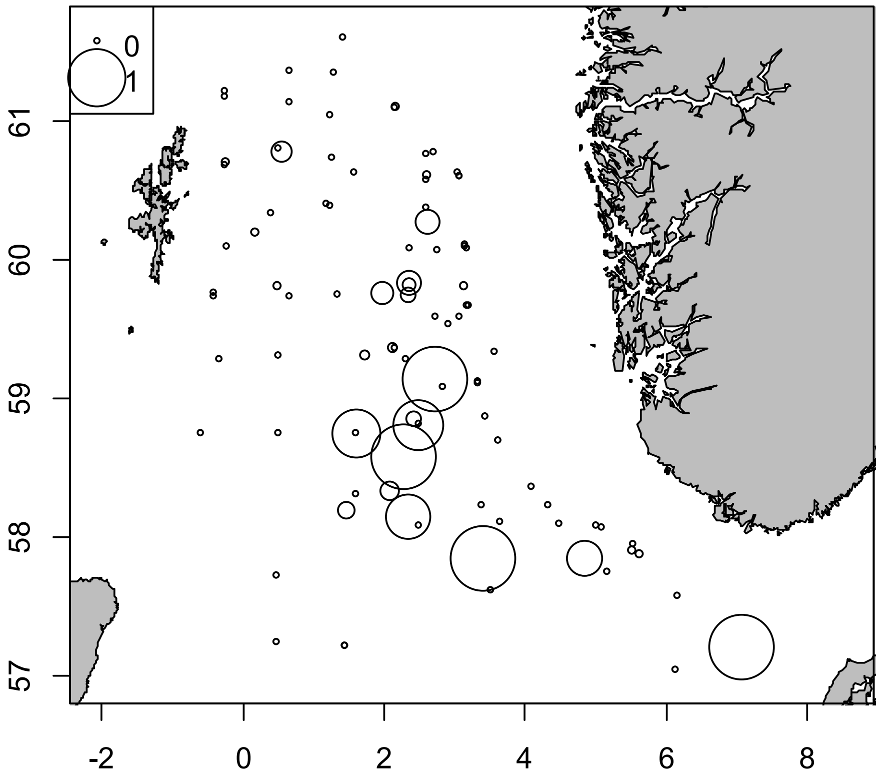


Figure 21: Probability of an individual fish being in spawning condition during the IBTS Q3 survey from 2010-2014. Maximum value at a station during that period = 1 (=100 % of the fish caught were in spawning condition).

3.2.3.3. Quarter 4

During the Norwegian coastal surveys in Q4, spawning fish were caught either close to the coast or inshore between 62°68'N and 63°55'N (Figure 22), which is the northernmost point of spawning records of European hake. The maximum probability of a fish being in spawning condition was 0.5 during that survey.

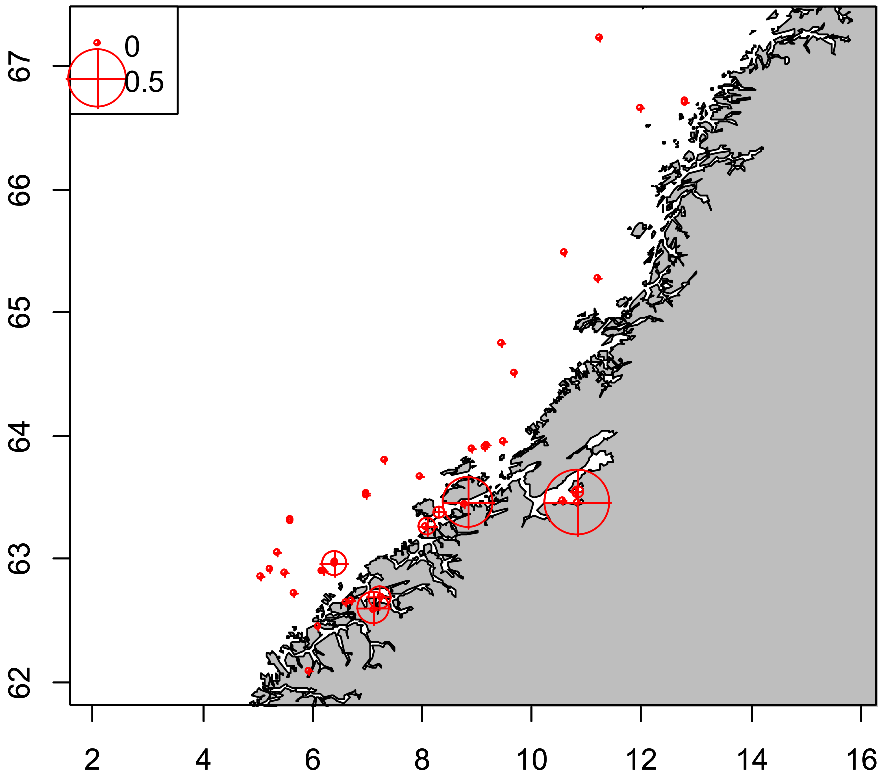


Figure 22: Probability of an individual fish being in spawning condition during the coastal survey from 2012-2014. Maximum value at a station during that period = 0.5 (=50 % of the fish caught were in spawning condition).

3.2.4. Nursery grounds

0-group fish from 4.5-10.5 and 10.5-25-5 cm were found on all four surveys. In total, 257 individuals from 4.5-10.5 (mean: 9.65 cm) and 2453 from 10.5-25.5 cm (mean: 18.67 cm) were caught and their distribution plotted. The highest number (~59 %) of small specimens from 4.5-10.5 cm was caught on the shrimp survey in Q1. Together with the IBTS Q1, Q1 accounted for 77 % of all juveniles found throughout the time period. From 2471 individuals in between 10.5 and 25.5 cm, most specimens (1010) were caught during the IBTS Q3 surveys in Q3, and fewest during the coastal surveys in Q4 (213).

3.2.4.1. Quarter 1

In Q1, specimens from 4.5-10.5 cm were caught in high densities in the Skagerrak and around the south-west coast of Norway along both onshore and offshore shelf edges of the Norwegian trench with batches south-west of the Oslofjord and close to the shore off the city of Kristiansand (Figure 23a). The distribution in the North Sea showed a more randomly dispersed pattern with a few loose batches mainly east of the Shetland Islands. The number of small individuals caught per station ranged from 1-9.

Specimens from 10.5-25.5 cm were caught in high numbers during the IBTS Q1 survey with especially high catches on the plateau east of the Shetland Islands and west of the Norwegian trench (Figure 23b). During the shrimp survey, juveniles between 10.5 and 25.5 cm show a very similar distribution to the smaller ones, with patches outside Kristiansand, south-west of the Oslofjord and along the shelf edges of the Norwegian trench.

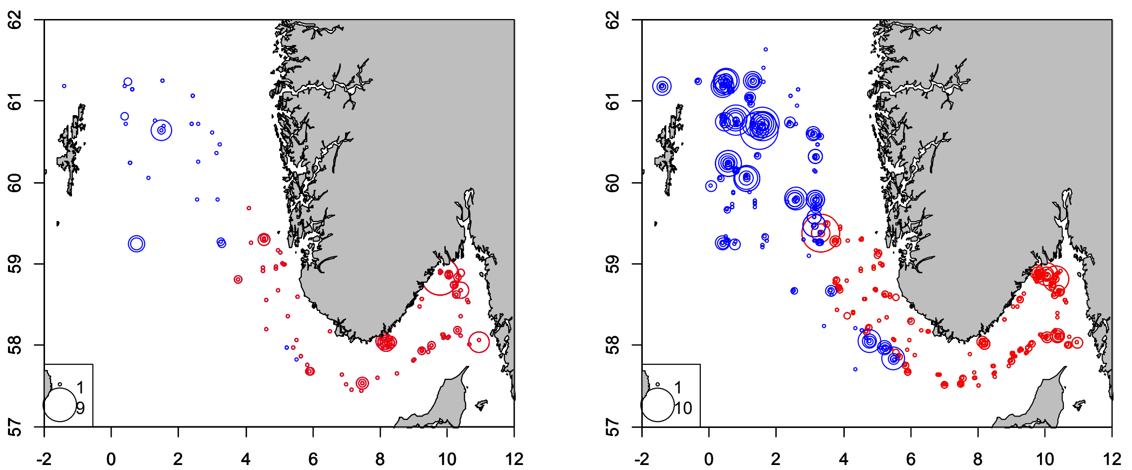


Figure 23 a+b: Distribution of stations with catches (numbers/station) of European hake from 4.5-10.5 cm (a; left; maximum number = 9) and 10.5-25.5 cm (b; right; maximum number = 10) during the IBTS Q1 (blue) and shrimp (red) survey from 2006-2014.

3.2.4.2. Quarter 3

In the summer, at the beginning of Q3, a small amount of small fish was caught in the North Sea with a range of 1-7 individuals per station. These fish were widely dispersed in the western part of the North Sea from 57°67'N in the south up to 61°55'N in the north (Figure 24a).

Larger specimens from 10.5-25.5 cm were caught over a wider range of distribution with a striking patch at one station south-east of Shetland Islands (59°76'N, -0°41'W; Figure 24b). Other areas with high number of catches were generally on the plateau east of the Shetland Islands and on the offshore side of the slope along the Norwegian trench. The maximum number of European hake individuals between 10.5 and 25.5 cm during the whole period caught at one station was 32.

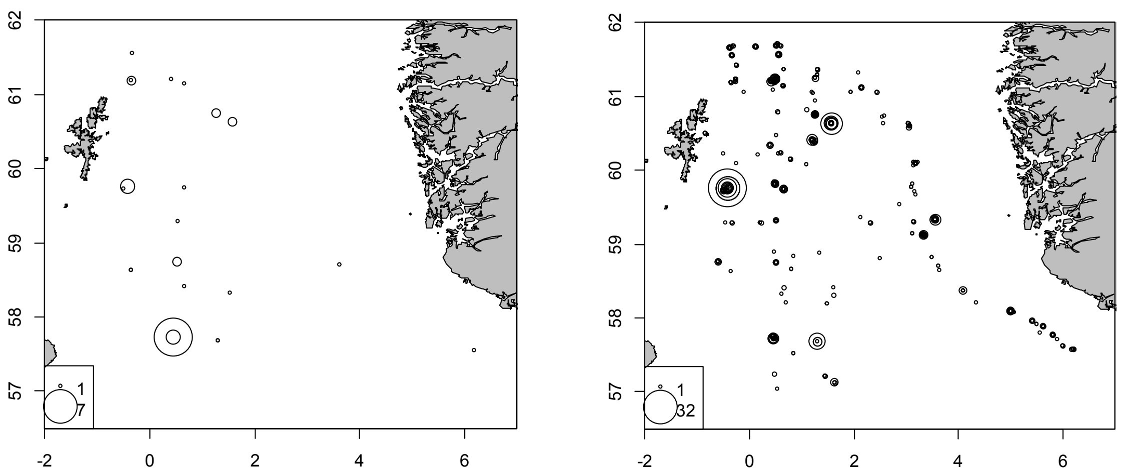


Figure 24 a+b: Distribution of stations with catches (numbers/station) of European hake from 4.5-10.5 cm (a; left; maximum number = 7) and 10.5-25.5 cm (b; right; maximum number = 32) during the IBTS Q3 survey from 2006-2014.

3.2.4.3. Quarter 4

During the Norwegian coastal survey, two specimens between 4.5 and 10.5 cm were caught at two stations inshore, one inside the Trondheimfjord and the other right outside the city of Ålesund (Figure 25a). The majority of individuals from 10.5-25.5 was caught in an area between Ålesund and the Trondheimfjord, between 62° and 64°N (Figure 25b). At a few stations north of 64°N up to the Lofoten (69°3'N) small catches were made as well. The highest number of specimens between 10.5 and 25.5 cm at one station was 14.

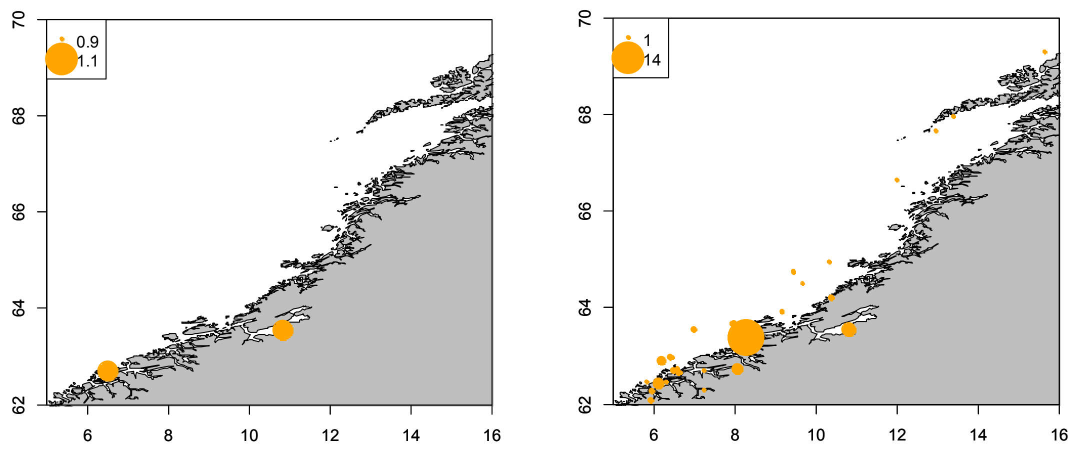


Figure 25 a+b: Distribution of stations with catches (numbers/station) of European hake from 4.5-10.5 cm (a; left; maximum number = 1) and 10.5-25.5 cm (b; right; maximum number = 14) during the coastal survey from 2006-2014.

3.3. Ecology

3.3.1. Prey spectrum

3.3.1.1. Diet composition

Of 200 analyzed stomachs 114 (57 %) contained prey items and 86 (43 %) were empty. The amounts collected on the different cruises and the proportion of full and empty stomachs varied from survey to survey (Appendix 4). In total fourteen fish, two crustacean and one species of starfish were found and identified (Appendix 5). Due to different stages of digestion not all organisms could be identified down to species level, but were assigned to higher level taxonomic categories. By occurrence fish was the most frequent group with 84 %F in all stomachs, followed by crustaceans with 13 %F. In 5 % of all stomachs pieces of brown algae were found. The most important fish species in the diet were Norway pout (44 %F), Atlantic herring (14 %F), Atlantic mackerel (10 %F) and blue whiting (5 %F) (Figure 26).

In the percentage composition (%N) of all identified prey items, fish accounted for 79 %, crustaceans for 17 % and others for 5 % (Appendix 5). Cannibalism was evident in 1 %F in all stomachs, suggesting that it played a minor role.

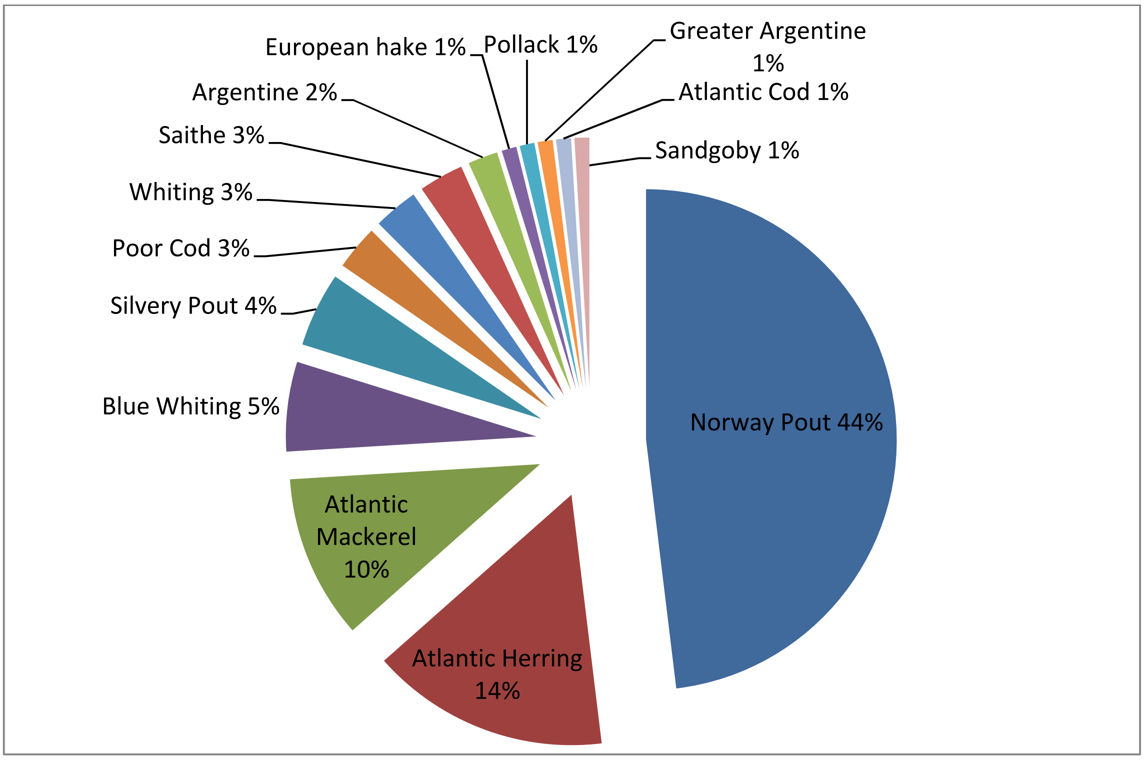
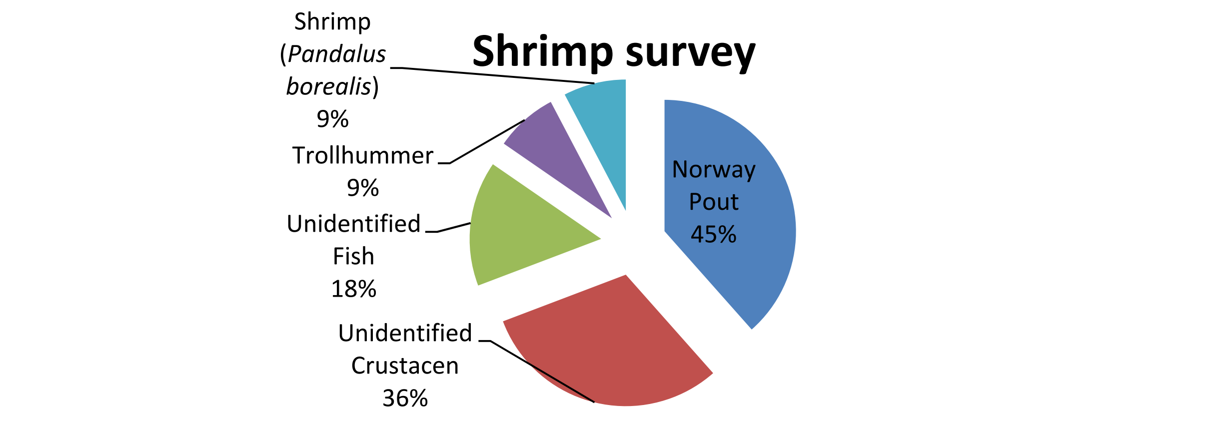


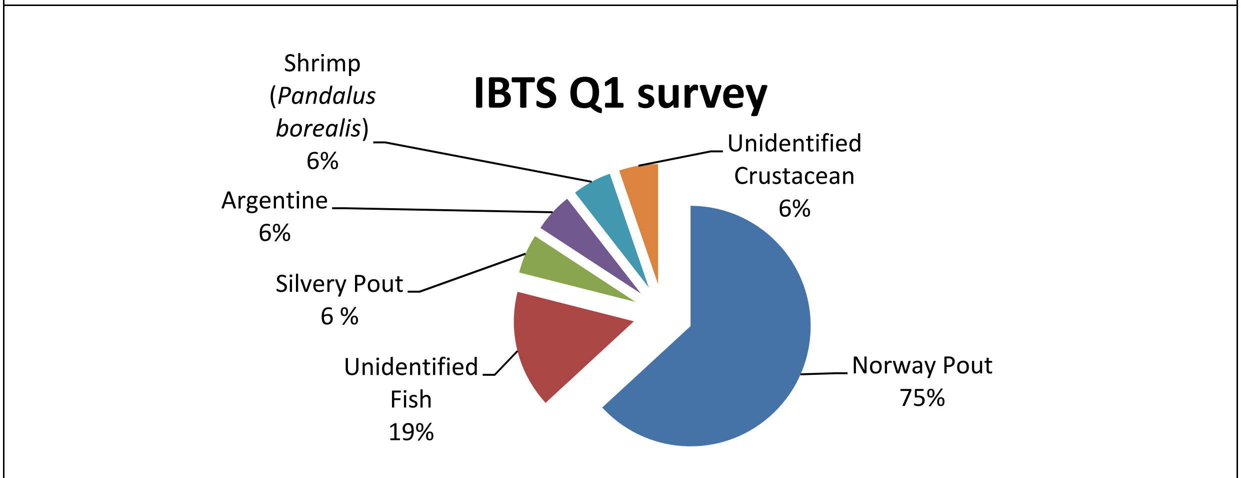
Figure 26: Distribution of frequencies of occurrence of identified fish species of all stomachs analyzed 2014.

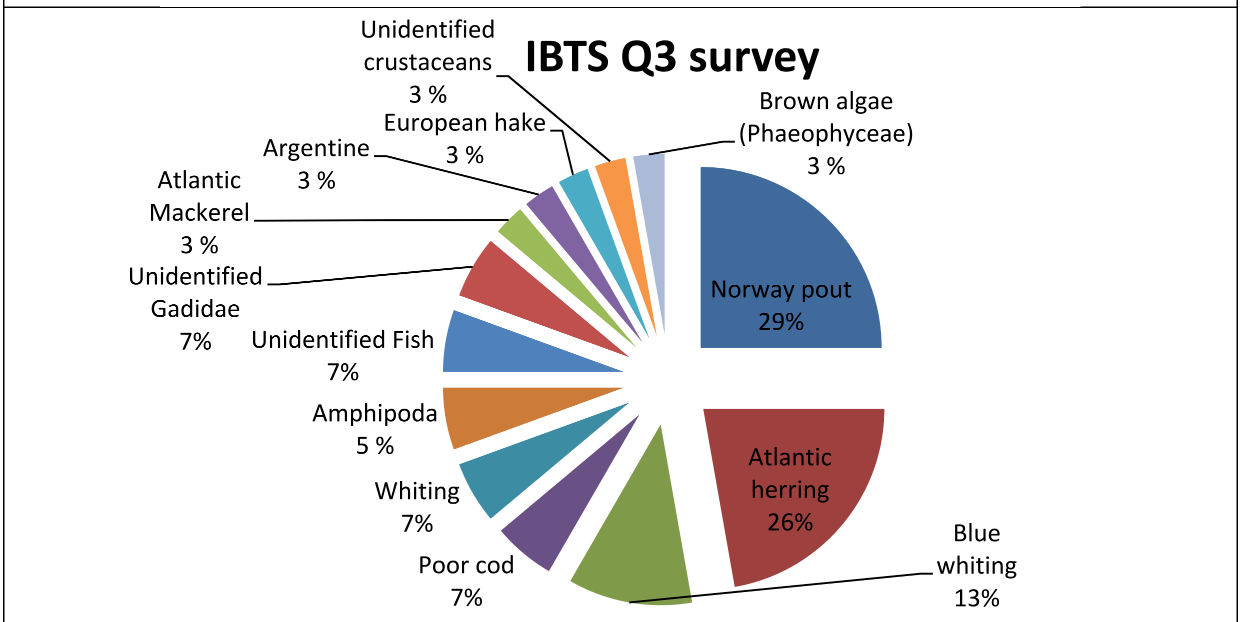
3.3.1.2. Variation between surveys

One striking difference when looking at the frequencies of occurrence is the diversity of prey between the surveys (Figure 27). With only 4 and 5 different prey groups the Shetland and shrimp surveys showed the least diversity in the diet spectrum. Fish collected on the IBTS Q1 (13) and the coastal survey (18) showed the highest number of different preys. On the shrimp survey in the Skagerrak an exceptionally high percentage (54 %F) of all crustaceans was found in the diet, which was a difference of 42 %F to the second highest appearance (IBTS Q1; 12 %F). Norway pout was the dominant fish species in the diet spectrum on every survey, except for the Shetland cruise, where Atlantic mackerel was with 53 F% the most important prey item. Atlantic herring, the overall second most important diet species contributed strikingly on the IBTS Q3 (26 %F) and the coastal survey (21 %F). The top three most frequently occurring prey groups were exclusively fish on the IBTS Q1, IBTS Q3 and

Shetland cruise, on the shrimp survey crustaceans and on the coastal survey brown algae were as well important.







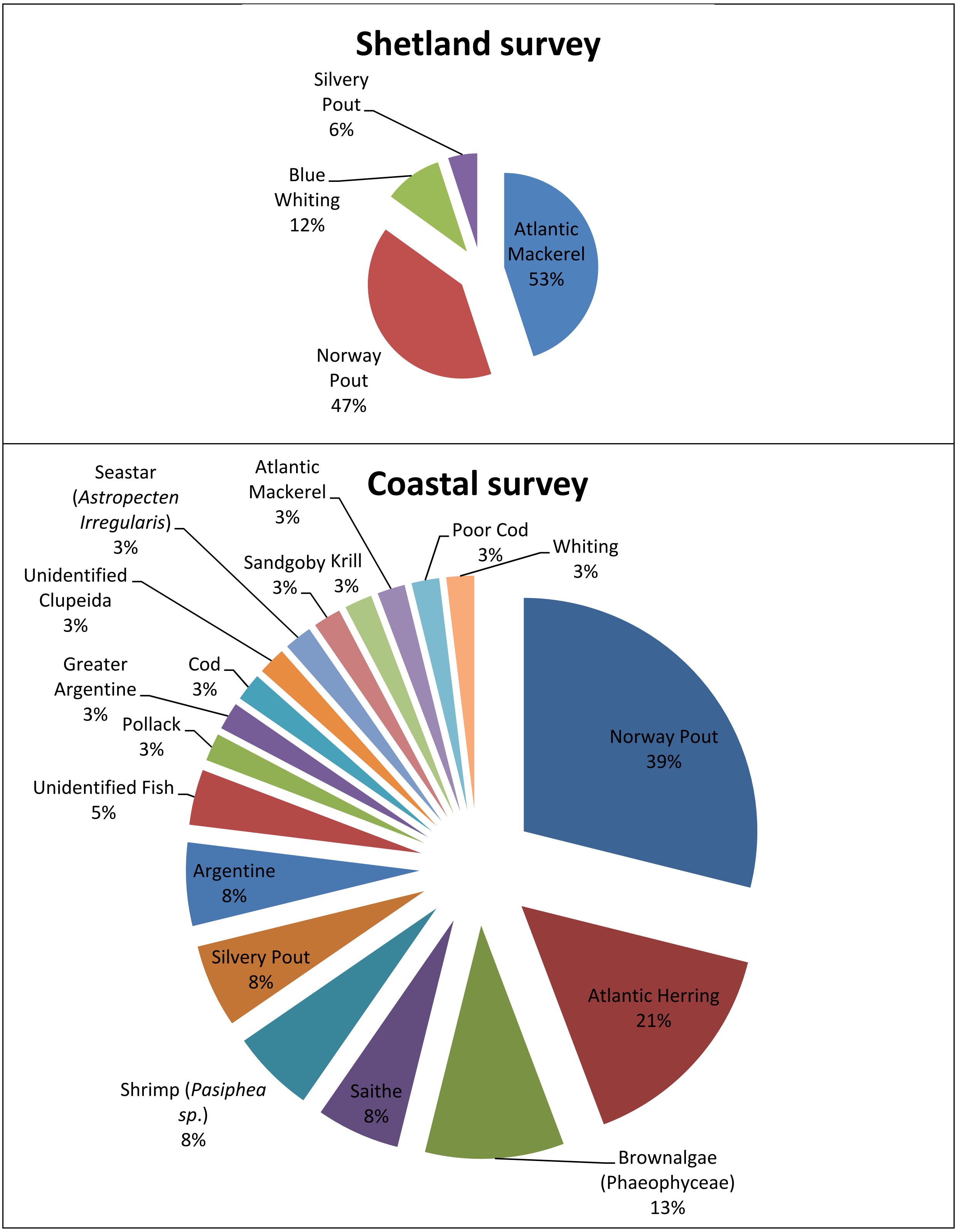


Figure 27: Distributions of frequencies of occurrence (total %F for each survey) of identified fish species of all surveys 2014.

3.3.1.3. Seasonal variation

Norway pout was a major prey species on all surveys throughout the whole year (Table 4). Especially on the winter surveys IBTS Q1 and the shrimp survey, Norway pout was discovered in over 60 %F. Crustaceans also played a major role during the winter with a %F of 29.6 with a dominance of northern shrimp, *Pandalus borealis*. Atlantic herring and Atlantic mackerel were both only found in stomachs collected during cruises from June-November. Atlantic herring shows a strong occurrence in Q3, Atlantic mackerel in Q4. Blue whiting was mainly preyed upon in July in Q3. The large gadoidae cod, saithe and pollack were exclusively found in stomachs collected during the coastal survey in October.

Table 4: Seasonal separation of hake prey into 2014 quarters by frequency of occurrence (%F). Results which are considerably striking or show strong seasonal deviation from the %F throughout the whole year, were highlighted.

	Q1 (%F)	Q2 (%F)	Q3 (%F)	Q4 (%F)
No. of full stomachs	27	0	31	56
Fish total	85.19	0	87.10	85.71
Norway pout (*Trisopterus esmarkii*)	**62.96**	0	**29.03**	42.86
Atlantic herring (*Clupea harengus*)	**0.00**	0	**25.81**	14.29
Atlantic Mackerel (*Scomber scombrus*)	**0.00**	0	3.23	**17.86**
Blue whiting (*Micromesistius potassou*)	0.00	0	**12.90**	3.57
Silvery Pout (*Gadiculus argenteus*)	3.70	0	0.00	7.14
Poor cod (*Trispoterus minutus*)	0.00	0	6.45	1.79
Whiting (*Merlangius merlangus*)	0.00	0	6.45	1.79
Saithe (*Pollachius virens*)	0.00	0	0.00	3.57
Argentine (*Argentina sphyraena*)	3.70	0	3.23	0.00
European hake (*Merluccius merluccius*)	0.00	0	3.23	0.00
Pollack (*Pollachius pollachius*)	0.00	0	0.00	1.79
Greater argentine (*Argentina silus*)	0.00	0	0.00	1.79
Atlantic cod (*Gadus morhua*)	0.00	0	0.00	1.79
Sand goby (*Pomatoschistus minutus*)	0.00	0	0.00	1.79
Unidentified Fish	18.52	0	6.45	3.57
Unidentified Argentine (*Argentina* sp.)	0.00	0	0.00	5.36
Unidentified Gadidae	0.00	0	6.45	0.00
Unidentified Clupeidae	0.00	0	0.00	1.79
Crustaceans total	**29.63**	0	9.68	7.14
Pandalus borealis	**7.41**	0	0.00	0.00
Galatea strigosa	3.70	0	0.00	0.00
Pasiphaea sp.	0.00	0	0.00	**5.36**
Krill (*Euphausiacea* sp.)	0.00	0	0.00	1.79
Amphipoda	0.00	0	6.45	0.00
Unidentified crustaceans	18.52	0	3.23	0.00
Others total	0.00	0	3.23	10.71
Sand sea star (*Astropecten irregularis*)	0.00	0	0.00	1.79
Brown algae (Phaeophyceae)	0.00	0	3.23	**8.93**

4. Discussion

4.1. Impact of Methodology

4.1.1. Survey design and data collection

4.1.1.1. Survey catch rates

Fisheries surveys are conducted to collect information on species abundance and distribution for stock assessment purposes (Gundersen, 1993), as well as biological information for certain species and hydrographical and environmental data (ICES, 2012). Although research on survey design constantly improves, underlying assumptions for abundance estimations from trawl surveys can be violated (Gundersen, 1993; Charles 1998; Cordue, 2007). The survey data used for this study contains information about the abundance and distribution (CPUE per station), the biology (length frequencies and gonad maturity), and the ecology (stomach collection from 2014).

Research vessel noise (Ona & Godø, 1990; Engås & Løkkeborg, 2002), fish density (Godø et al., 1999; Kotwicki et al., 2014), diel behavior and geographic distribution (Petrakis et al., 2001), escapement beneath the trawl (Ingólfsson & Jørgensen, 2006), fish size (Kotwicki et al., 2015), light intensity (Kotwicki et al., 2009; Bradburn & Keller, 2015), environmental conditions (Queirolo et al., 2012) and gear performance (Engås & Godø, 1986; Bertrand et al., 2002; Politis et al., 2012) are all factors that can influence catch rates of demersal fish species such as cod, haddock, saithe or walleye pollock during bottom trawl surveys. As a large demersal predator, European hake inhabits a similar ecological habitat to cod, haddock or saithe and exhibits similar behaviors, e.g. diel vertical migrations. All these factors are also likely to have an impact (Michalsen et al., 1996) on the data forming the basis of this project. The factors which may influence catchability during bottom trawl surveys act on a species, individual and abundance level. That in turn affects CPUE and length frequencies as well as composition of specimens for biological sampling and stomach collection.

4.1.1.2. Landings

The quality of commercial catch data depends heavily on the correct reporting by fishermen, and as such can be subject to uncertainties caused by misreporting (Pitcher et al., 2002;

Bousquet et al., 2010), which can have serious consequences for stock assessments (Walters & Maguire, 1996; Hentati-Sundberg et al., 2014). A discard ban has been in place in Norway since the mid 1990s, and the strict enforcement of the rules coupled with high sanctions have resulted in a decrease in discarding (Gullestad, 2013). Another source of uncertainty in landings data is the lack of catch data from recreational fishermen (Zeller et al., 2011). This may be especially applicable in Norway, where tourist fishing is popular (Vølstad et al., 2011) and hake catches are known to occur.

4.1.1.3. Biological data

A last aspect which has to be mentioned when looking at collected data from scientific surveys is the underlying objectivity when identifying maturity stages. Although there are clearly defined stages (Table 3), the final decision of the stage can vary from person to person, dependent on general experience of staff and experience with the certain species. The most critical distinction of maturity stages is between stage one (immature) and four (spent), where mistakes can be easily made. Only data from stage three (spawning) were used to identify spawning fish, and identification and separation from stage two (maturing) and stage four is rather clear.

Still, scientific cruises with their survey designs are subjected to continuous improvements and besides data from the reference fleet, the most important source of information for a representative insight into the North Sea and Norwegian coast ecosystems. Catch data from commercial fisheries need to be seen and treated with caution to avoid stock collapses due to misinterpretations (Hutchings & Myers, 1994; Harley et al., 2001). Their validity can be improved with data from scientific surveys (Walters & Maguire, 1996), but can also be useful to try and understand the spatial components of landings (Booth, 2000). To conclude, the scientific cruises conducted by the IMR are, despite uncertainties surrounding the quality of data collected, the most reliable data source and are, when treated carefully and with awareness for possible biases, a very valuable data source.

4.1.2. Stomach analysis and identification of prey

As recently discussed by Baker et. al (2014), evaluating fish diet by the frequency of occurrence of different prey items is the most robust method to avoid misinterpretations, and was therefore chosen for analysis purposes in this study. The results depend highly on the correct identification of prey species as well as the detection of all items in the stomach in order to obtain the right number of correctly identified items. One decisive factor influencing the accurate identification of prey is the state of digestion (Hyslop, 1980; Bowen, 1996), which depends on the prey type and the time after ingestion (Legler et al., 2010) as well as on the time between capture and freezing (Haywood, 1995). Stomachs personally collected for this study were always removed from the hake as soon as possible after capture. However, the frozen stomach samples collected on other surveys may have been subject to delayed removal and freezing. Due to high workloads on scientific surveys, is it likely that it took 2-3 hours after capture and before samples were frozen. According to Haywood (1995), the flesh of shrimps is almost completely digested already 60 minutes after ingestion, and it is therefore likely that especially small diet items, such as small crustaceans and juvenile fish are subject to underestimation. For larger items there was less identification uncertainty, since prey objects could be positively identified based on anatomical characteristics or otolith shape.

To conclude, a safe and very careful handling of the stomachs and the prey items was assured and I believe that the results are, with minor restrictions I mentioned, correct. When looking at how representative they are, it has to be considered that everted stomachs were not sampled, and the occurrence of fish with everted stomach was high at certain stations where sampling was conducted very deep. Diet at these stations might consequentially vary from my results.

4.2 Consideration of Results

4.2.1. Norwegian hake fisheries

This is the first analysis of commercial and survey data on hake along the Norwegian coast, since this species has not been listed for assessment or monitoring by the Norwegian fisheries directorate. This has limited the data to a shorter time series which restricts analysis and conclusions of historical landings. The lack of attention hake received also limited the quality of available data with the result that these conclusions are based on the available landings as well as other, not directly related sources.

The catch equation C = f * q * B (Deriso, 1980), where C=catch, f=effort, q=catchability and B=biomass describes the relationship between catches and biomass. An increase in catches (as observed in the Norwegian hake fishery) can thus have different reasons: i) either an increase in effort, ii) an increase in catchability, iii) an increase in biomass, or iv) a combination of all or some of the factors. When looking at the recent striking increase in Norwegian landings, it is apparent that it occurs concurrently with an increase in SSB of the Northern hake stock (Figure 28).

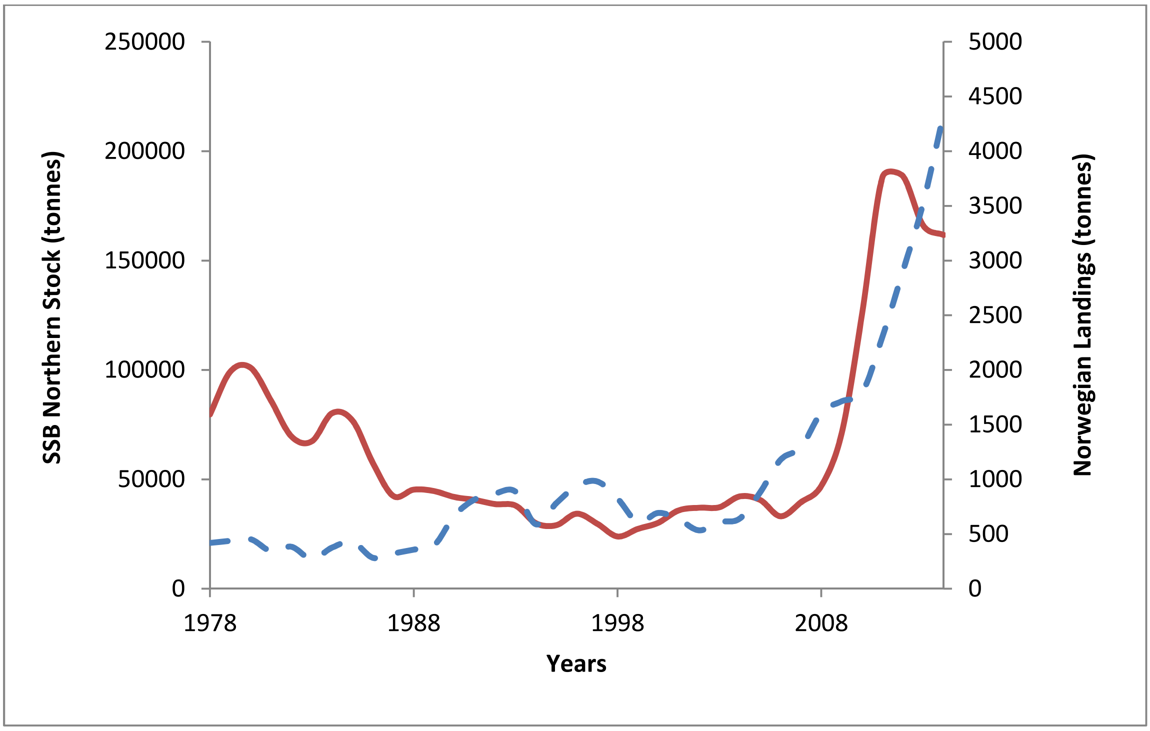


Figure 28: SSB of the Northern stock (tonnes; red line) and Norwegian landings (tonnes; dotted blue line) of European hake from 1978-2014.

A closer look at the Norwegian landing, reveals that the increase in catches comes from one source mainly – the bottom trawl fisheries in ICES area IVa (Figure 29), which includes the North Sea between the Shetland Islands and the west coast of Norway. The landings from IVa developed almost parallel to total Norwegian hake landings from 2005 – 2014, especially during the rapid increase between 2010 and 2014. Gillnet landings from area IIa2, which covers the mid-west Norwegian coastline, can be identified as the second largest fishery. Since there is not a targeted fishery on European hake in this area, and Norway does not have a quota (TAC; Total Allowable Catch) for European hake in the North Sea, the question is which targeted fisheries contribute to the steep increase. In the North Sea, hake is caught as part of a mixed demersal fishery along with haddock, cod or whiting (Baudron & Fernandes, 2014). According to the "Havforskningsrapporten" (Bakketeig et al., 2015), which summarizes Norwegian landings and quotas for the most relevant commercial species, the saithe fishery with a Norwegian share of 52 % (= 34.323 t) of the total quota, is the largest and most important Norwegian fisheries in the North Sea. This is followed by haddock with 23 % (= 9.634 t), cod 17 % (4.962 t). As recently discussed by Cormon et al. (2014), saithe and hake inhabit very similar parts of the ecosystem, feed on similar prey species and will most likely increase their spatial overlap with an increasing biomass of hake. Taking additionally the Norwegian hake landings from ICES area IVa into account, it allows the conclusion that hake is mainly caught as a bycatch in Norwegian saithe and mixed demersal North Sea fisheries along with cod or haddock.

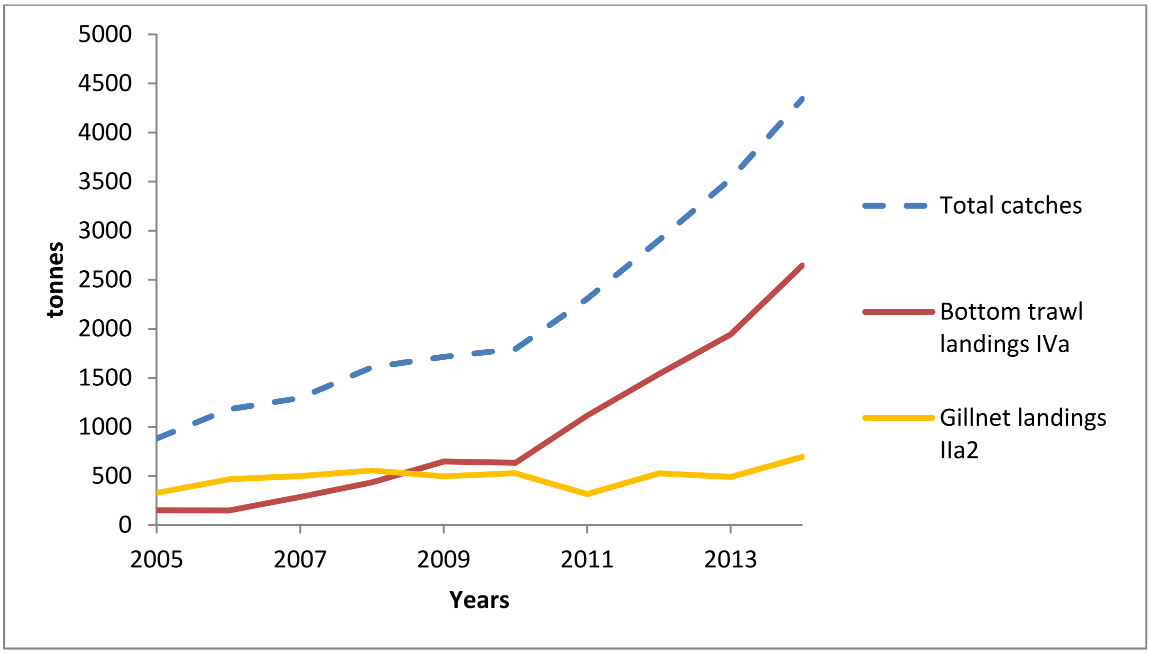


Figure 29: Total catches, bottom trawl landings (tonnes) from ICES area IVa and gillnet landings from ICES area IIa2 of the Norwegian fleet from 2005-2014.

Gillnet landings from ICES area IIa2 did not experience a similar rapid increase as observed for ICES area IVa, but fluctuated around 500 t annually with a recent increasing trend, resulting in a total catch of almost 700 t in 2014. These landings are mainly limited to the coastal areas outside Møre og Romsdal (Bakketeig et al., 2015), a county in the northern part of western Norway. Also striking is the steep increase in bottom trawl landings from that area from 62 t in 2010 to 289 t in 2011, after which they remained at ~ 300 t annually. Additionally hake can account for up to 49 % of the total catch weight in bottom trawl fisheries for Norwegian lobster (*Nephrops norvegicus*) outside Møre og Romsdal (Rønneberg & Larsen, 2006). Over the time period of sampling (week 26-52 in 2005 + four weeks in 2006) this bycatch represented a total catch of ~ 38 t, which in turn can be considered as a major proportion of trawl landings from area IIa2 (42 t in 2005; 29 t in 2006).

Developments in the gillnet fisheries along the Norwegian coast and the bottom trawl fisheries in the North Sea are also visible in the changed seasonal pattern in the landings. From 2000-2006 the majority of catches was made during Q3. According to two newspaper articles from July 2007 (Nordpoll, 2007) and August 2010 (Seljehaug, 2010), these months appear to be the most important period where fishermen target hake along the Norwegian coast, which would explain the high landings during Q3. When analysing the total catches throughout the year, it is apparent that from 2006, when total catches exceeded 1000 t for the first time and SSB began to steeply increase (Figure 28), landings started to increase during all four quarters as well (Figure 6). That development supports the temporal trend of gillnet fisheries dominating the landings until the SSB increased and catches consequentially increased along the coast and in the North Sea.

The Norwegian fisheries and landings of European hake have experienced some major changes throughout the last decade, which can be especially seen in total catches as well as spatial and temporal variations. The main reason for the rapid changes is most likely the increase in SSB, which has an undeniable influence on catches. Still, effort data are missing and catchability is a somewhat unknown parameter in the catch equation and due to that uncertainties about the increasing landings remain. In spite of these uncertainties, landings can be a valuable addition for analysing changes in abundance and distribution, what will be discussed in the next section.

4.2.2. Biology

4.2.2.1. Distribution and abundance

The increasing trend in the SSB of European hake, as shown in the recent ICES advice (2014), is reflected in the CPUE data from the North Sea and the Norwegian coast. Additionally, a slight recent decline in 2014 is as well visible in survey data from the IBTS Q1 and Q3 surveys in the North Sea. CPUE data from the IBTS Q3 survey in 2008 have to be approached with caution. A number of missing stations in the southern survey area, where hake catches are usually low, will most likely have resulted in an average CPUE which is not representative and thus comparable with the CPUE in other years, and would be expected to be lower if all stations had been sampled.

Baudron & Fernandes (2014) recently assessed the stock size of European hake in the North Sea from 2001-2011 based on survey data and showed a striking increase especially during the second half of the year. SSB was more than three times as high as in the first half of the year (Figure 30). This trend can be seen in our CPUE data as well and continues after 2011, when the study of Baudron & Fernandes (2014) ended.

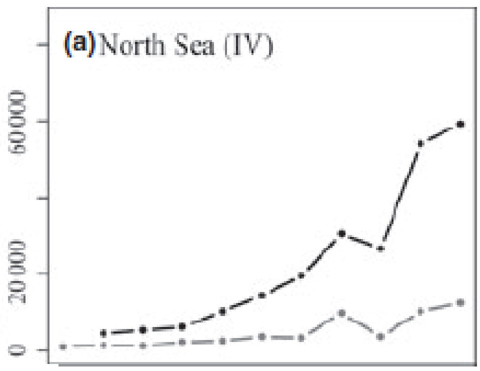


Figure 30: Spawning Stock Biomass (tonnes) estimations of European hake in the North Sea in the first half of the year (grey line) and the second half of the year (black line) from 2001-2011 (Source: Baudron & Fernandes, 2014).

When critically assessing observed trends in Baudron & Fernandes (2014) and comparing these with results from this study of Norwegian data, two visible aspects have to be considered. Firstly, In Q3 we observed a CPUE (biomass) about five times as high as in Q1, but in terms of numbers (abundance) only 1.5-2 times more were caught. This can be explained by an intra-annual variation in the size composition of the hake stock in the North Sea, with many fish of small size caught during IBTS Q1 in the winter and a higher percentage of large fish caught in the summer during IBTS Q3. An explanation for this seasonal variation in size composition could be an inflow of large fish in the summer to feeding / spawning grounds in the North Sea. Secondly, when taking Norwegian landings from the North Sea (ICES IVa) throughout the year into account, the large increase in biomass during the second half of the year must be questioned. As discussed before, the catch equation includes the somewhat unknown parameters effort (f) and catchability (q), which makes a direct connection between catches and biomass difficult. In contrast to Baudron and Fernandes's (2014) biomass estimation for 2011, Norwegian landings show a visibly increasing trend in the first half as well, seen in catches during Q1 and Q2 being both higher than in three and four. Analyses of our survey data, along with the results presented in Baudron & Fernandes (2014) show a clear dominance of biomass in the second half of the year. Fisheries data do not indicate this trend. On the other hand, landings have to be treated with caution due to unknown parameters of the catch equation. Landings can certainly increase due to an increased effort. An increased effort during the first half of the year seems to be unlikely, when considering that especially small specimen are present, which are less valuable commercially than large individuals. Furthermore, although surveys are designed to be representative in spatial and temporal distribution and changes, biases can occur. Bottom trawls during surveys are restricted to trawlable grounds, in most case sandy or soft bottoms, but hake individuals might be allocated over rocky, hard bottom as well, where they might be caught be commercial fishermen, using different gear. Still, most commercial vessels use similar gear in the North Sea as on the IBTS, which reduces the possibilities to fish over hard bottoms.

The main area of distribution of European hake in the North Sea is located in an area east of the Shetland Islands and west of the Norwegian trench. This overlaps to a large extent with high densities of Norway pout adults and juveniles (Nash et al., 2012; Johnsen, 2014). Along with Norway pout accounting for the most important prey species of hake in the North Sea and along the Norwegian coast, the presence of Norway pout seems likely to be a reason for the high densities of hake.

Summarizing all trends of the centers of gravity, there is no significant change or common development visible for all the different areas. Still, one visible trend can be identified on both North Sea surveys in Q1 and Q3 between 2006 and 2008; over the period of the first three years of the time series a clear south-eastwards trend during the IBTS Q1 and a north-westwards trend during the IBTS Q3 is visible. The trends can only be seen until 2008, when the rapid increase of SSB started. This increase probably caused the observed increase of stations with high catches, indicating an expansion of the stock, which in turn, affects the calculated centers of gravity. That expansion in distribution, along with an increase in abundance, makes it difficult on the one hand to see a significant movement of the stock in one direction, but on the other hand, as expected when SSB rises, the stock expands and its area of occupation increases (Baudron & Fernandes, 2014).

Along the Norwegian coast north of Ålesund the main area of distribution outside the coast of Møre and Romsdal overlaps with the gillnet and Norwegian lobster fisheries. The distribution during the coastal survey raises the question of what the status of European hake in the coastal areas between Ålesund and Egersund is, where no survey coverage exists. Highest densities of hake at the southernmost range of the coastal cruise suggest an extended area with hake further south, where fishermen target them as well (Nordpoll, 2007).

4.2.2.2. Spawning grounds

Throughout all three quarters with survey coverage (no survey data was collected in Q2), data from the IBTS Q3 surveys in July show both the largest number of stations and the highest probability of fish being in spawning condition at one station. It is furthermore visible that spawning individuals were found in each quarter, in the North Sea in Q1 and Q3 and along the mid-west Norwegian coast in Q4. Although survey data only represent a snapshot of a constantly changing environment, our results suggest that European hake may spawn over several months with a peak in July. That peak in July is later than in Iberian Atlantic waters (Pineiro & Sainza, 2003) and in the Bay of Biscay (Murua & Motos, 2006). The data confirms spawning activity in July along the shelf edge (ICES, 2013b); Figure 21). A separation of distinct spawning grounds in the North Sea is supported by the fact that the main distribution throughout the IBTS Q3 survey (Figure 16) is further north, which indicates that fish in spawning condition actively assemble separately from the majority of the population. The visible presence of spawning individuals in July along the off shore edge of the Norwegian trench suggests that spawning activity of the Northern stock is not necessarily restricted to only the Bay of Biscay and off Ireland (ICES, 2013b), but also occurs in the North Sea and likely along the Norwegian coast.

Spawning described for more southern areas (Pineiro & Sainza, 2003; Murua & Motos, 2006; Ferrer-Maza et al., 2013) occurred mainly offshore. Fish in spawning condition during Q4 between 62° and 64°N as well as in inshore areas have not been described before, although the FAO (2014) mentions spawning activity of European hake further north later in the year, which would match with previous observations (Bjelland & Skiftesvik, 2006; Groison et al. 2011). To confirm these findings, more survey data would be necessary along the west coast of Norway to identify distinct spawning periods throughout the year or an egg survey. Our results furthermore confirm the questioning of genetic unity of the Northern stock of European hake. Milano et al. (2014) already proved a high genetic divergence between local populations, an investigation of genetic exchange between Norwegian coastal populations and North Sea hake to get further insight in its population dynamics is needed at this point (Westgaard et al., 2014).

Noticeable is the low total number of fish in spawning condition (86) of all available specimens with maturity recorded (2395), which means that all results and conclusions are basedon 86 individuals in the period from 2010-2014. This might have several reasons; firstly maturity stage three (spawning) is, compared to the whole life cycle as well as the annual cycle of a mature individual, a very short period. That limits the number of individuals which can theoretically fall in category three during a short survey snapshot to a considerable degree. Secondly, as discussed by Botha (1973) for South African Cape hakes (*Merluccius capensis, Merluccius paradoxus*), hake spawn off the bottom, further up in the water column. This reduces their susceptibility to bottom trawls during spawning activity. Since all data for our study come from bottom trawl surveys, the missing availability of spawning individuals to bottom gear can further explain the low sampling size. Thirdly, as described by Alvarez et al. (2004), hake eggs and larvae have a temperature preference of 12-12.5 °C and around 15 °C in north-east Atlantic waters, which might extend temperatures in the North Sea (Becker, 1996).

It also has to be considered that the number of collected maturity data differed between surveys from 2010-2014. Data for the coastal survey were only available for 2012-2014, for the IBTS Q1 and IBTS Q3 surveys in 2010-2014. Given a similar coverage for all surveys a higher number especially in Q4 during the coastal survey would be expected. On the shrimp survey maturity was only recorded in 2014, which limits its comparability to other surveys a lot. Still, due to a lot of small fish and a generally low CPUE the expected number of spawners during Q1 in the Skagerrak would be expected to be low.

4.2.2.3. Nursery grounds

Two striking trends are visible when summarizing the occurrence of juvenile (0-Group) fish; specimen ranging 4.5–10.5 cm in length were almost exclusively found in the Skagerrak during the first quarter, and specimens 10.5–25.5 cm in length mainly in the North Sea west of the Shetland Islands during Q1 and Q3. When looking at previous studies of North Sea fish, it is not surprising that especially the smallest individuals were caught in the Skagerrak. Based on Knutsen et al. (2004), who studied the transport of cod larvae from the North Sea into the Skagerrak and Corten (1990) who described the variability in recruitment of pelagic fish stocks in relation to the inflow of Atlantic water into the North Sea, it seems likely that small individuals as well as larvae of European hake are transported from their spawning grounds, which are along the shelf edge of the Norwegian trench, into the Skagerrak. Atlantic water coming from the North and entering the North Sea east of the Shetland Islands can either circulate or flow along the Norwegian trench as well as with other currents into the Skagerrak (Figure 31). The smallest hake may be transported into the Skagerrak, as proposed for cod larvae (Knutsen et al., 2004). At this point it has to be considered though, that Knutsen et al.'s (2004) study was based on cod larvae spawned between January and April and in a likely shallower depth than hake. That might expose them to different current regimes than in the late summer and autumn, when spawning hake were found. My results correspond as well with the findings of Munk et al. (1999) who found larvae of cod, haddock and saithe along the shelf edge and the Norwegian coast of the Skagerrak, which appears to fulfill the role of a somewhat "universal" nursery ground. A high number of small individuals in the Skagerrak seems also plausible when considering the time difference between time of spawning in the North Sea during Q3 and the appearance of juveniles in the Skagerrak in the beginning of the following year. Occasional presence of small individuals in the North Sea (Figure 23a & 24a), in Q1 and Q3 becomes plausible as well, taking the circulating currents between Scotland and Norway into account, which do not carry eggs and larvae into the Skagerrak.

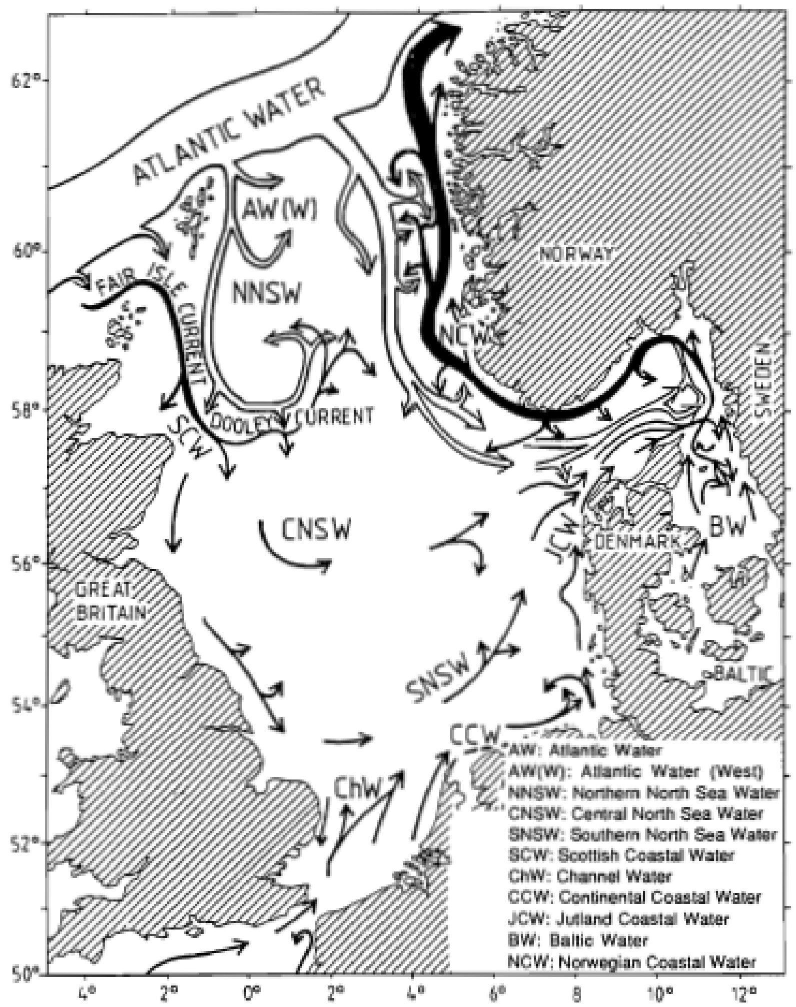


Figure 31: System of North Sea currents (Source: Svendsen et al., 1995).

The presence of juveniles (6.5 and 10.5 cm) off the Møre and Romsdal coast (caught during the coastal survey) raises the question of their origin. Throughout the whole survey period only two individuals were caught (Figure 24a), and there are several possible explanations for this. According to Sætre et al. (2002), who described displacement and residence of Norwegian spring-spawning herring larvae along the Norwegian mid-west coast, larvae hatching between 62° and 65°N, where hake in spawning condition were found, mainly drift northwards or remain in retention areas, both further off the coast. That increases the chance of European hake larvae being transported out of the survey range. Another potential explanation is, if spawning occurs in October/November, that juveniles might have outgrown our size limit of 10.5 cm in the following year and cannot be caught anymore during the survey, what would explain the high numbers of individuals from 10.5-25.5 cm.

A high concentration of 0-group individuals (10.5-25.5 cm) east of the Shetland Islands during Q1 and Q3 matches the general trend of high CPUEs of European hake, as well as Hislop's (1984) and Nash et al.'s (2012) descriptions of 0-group Norway pout and haddock in high densities in that area. Throughout the coastal survey, fish from 10.5-25.5 cm were as well in highest proportions in areas with a generally high adult? CPUE. It is still notable that a non-negligible number of 0-group fish is found in the Skagerrak during Q1, whose origin is more uncertain and open for discussion.. These fish can either represent individuals which outgrew the 4.5-10.5 cm category hatched during Q3 in the year before, or individuals who hatched for example in the winter, drifted into the Skagerrak and remained there, or individuals who have another origin, such as coastal or more southern areas. Still, there is a clear visible trend, that habitats of individuals from 4.5-10.5 cm and from 10.5-25.5 cm are separated. Another obvious reason may be physical swimming advantage of larger fish. The concluding hypothesis would be that small fish are mainly transported by the currents and as they grow bigger, they actively swim to search for more suitable feeding habitats, for example off the Shetland Islands.

4.2.3. Ecology

4.2.3.1. Prey spectrum

Compared to results from diet studies in the Celtic Sea (Du Buit, 1996; Mahe et al., 2007), two differences are apparent; the domination of Norway pout as by far most important prey item (Appendix 5), and the minor importance of cannibalism, especially compared to findings of Mahe et al. from 2007. The diet of hake described for the northern North Sea and Norwegian coast is different to the Bay of Biscay (Guichet, 1995) and the western Mediterranean as well (Bozzano et al., 1997) – as may be expected from such a geographic distance.

A main reason for cannibalism is the overlap of feeding and nursery areas (Mahe et al., 2007; Guichet (1995). The absence of such overlap may be a likely explanation for very low cannibalism in the North Sea. As this study shows, juveniles are mainly transported into the Skagerrak, but areas of highest CPUEs are in the northern North Sea east of Shetland Islands, which explains the lack of geographic overlap. Compared to the latest study by Preciado et al. (2015), it is still somewhat surprising that not more cannibalism occurred in the

Skagerrak, where juveniles were found as well as individuals from 16-30 cm in length, which were shown to account for 75 % of all cannibalistic predation. Preciado et al. (2015) mentioned as well that the degree of cannibalism can be due to spatial patterns of resources. Along with their suggestions, it is possible that hake mainly preyed on Norway pout in the Skagerrak instead of conspecifics, which may reduce competition for shrimps, which might be a key prey for both. Bozzano et al. (1997) claim that cannibalism is a survival mechanism, when resources (prey items) are scarce. It seems also plausible that hake prefer other species with a higher nutritional value, such as mackerel or herring, even if conspecifics are available.

At the same time, two reasons likely impact the high ingestion rates of Norway pout; a high overlap of the survey areas with the main areas of distribution of Norway pout, especially east of the Shetlands (Nash et al., 2012; Johnsen, 2014) and very high predation throughout the winter months during Q1, when other alternatives are rare. As shown in Figure 27, Norway pout is especially important as fish prey item during the period of the shrimp and the IBTS Q1 survey, where neither herring, mackerel, nor blue whiting were preyed upon. These three species have a large scale migratory behavior in common, which limits their geographical overlap with hake in the North Sea and along the Norwegian coast seasonally, restricted to the summer and autumn. It also has to be considered that European hake has a higher degree of habitat overlap with Norway pout – both are demersal species - to herring or mackerel, which mainly live in the pelagic zone. Compared to a study from 1927 (Hickling) it stands out that Norway pout played no role as a prey species during that time, which indicates a long term change in the diet.

Variability in availability of different prey species due to migratory behavior, as mentioned above, is a likely factor to explain seasonal diet variations, which is also reflected in the variations between the different surveys. Guichet (1995) described seasonal variation of hake diet in the Bay of Biscay, with a dominance of European Anchovy in Q1 and Q2, and horse mackerel in Q3 and Q4. The paper lacks an adequate discussion of the observed seasonal variation for an appropriate comparison with the Norwegian and North Sea data. A striking observation during Q1 is the high frequency of occurrence of crustaceans (29.63 %) found in the Skagerrak and the North Sea hake stomachs. As shown in Figure 27, the main part of crustaceans comes from the shrimp survey samples, less from the IBTS Q1. A possible reason for a higher predation on crustaceans might be the high availability of shrimps in the Skagerrak and differences in diet may thus be a reflection of availability of different species. Another aspect, which appears when results from the nursery grounds are taken into account is that a large number of small fish (4.5–25.5 cm) was caught in the Skagerrak. That indicates a size dependent predation, as a higher proportion of crustaceans is ingested by small, immature individuals. This observation corresponds to findings by Bozzano et al. (1997), Mahe et al. (2007) and Abdellaoui et al. (2014). It would also explain the high number of unidentified crustaceans, due to difficulties with identification down to species level because of very small and far digested items in the stomach. At this point, a quantitative length related analysis would give further insight into possible ontogenetic changes of diet, but requires a broader size range of sampled individuals for representative results.

The variation in diet between surveys is also reflected in the dominance of Mackerel throughout the Shetland cruise, which is the only survey where Norway pout was not the most frequent prey species. During the survey fishermen targeting mackerel were observed close to the survey area. Mackerel was also identified in the survey catches and unexpected amounts of dead mackerel, as a result of the nearby fishing activity were observed (personal communication Frank Midtöy, BIO, UiB). The occurrence of dead mackerel left by the fishermen, which have been afterwards ingested by hake individuals, might partially explain the high proportion of mackerel in the stomach. Hake might also have preyed upon mackerel by migrating vertically off the bottom, which is supported by Hickling (1927), who described that hake are independent of the seabed for their feeding.

Unexpected is as well the high frequency of occurrence of brown algae, observed on the coastal survey, where it accounted for the third most important prey item (13 %F; five individuals). Three possible hypotheses why brown algae are ingested in a high proportion are presented: i) it might be accidentally taken up while feeding on something else, such as snails, ii) brown algae might fulfill the role of an “emergency diet”, in situations when alternatives are rare, or iii) they may have ended up in the stomach without a purpose but consumed during the trawling process in the net. Brown algae as part of the diet of European hake has not been described before, estimation why they have been ingested is difficult at this point. The presence of algae has not been mentioned in other studies on European hake diet (Guichet, 1995; Du Buit, 1996; Bozzano et al., 1997; Mahe et al., 2007).

In summary, the hakes' main prey species - Norway pout, herring, mackerel and blue whiting - are also of commercial interest. Additionally commercially valuable gadoids, such as saithe and cod, were preyed upon in coastal waters. These results give valuable insight in the ecosystem and in predator-prey relations of European hake, which are in turn important information for MSVPAs and stock assessment purposes.

4.2.3.2. Hake's Role in the Ecosystem

The overall objective of this study is to analyse and discuss if European hake is about to become or is already a keystone species in the North Sea and Norwegian waters. Defining a keystone species in an ecosystem is a controversial issue with different approaches. Power et. al (1996) identified a keystone species to have a large impact on the ecosystem, disproportionate to its abundance. Used by Vandermeer & Maruca (1998) and Libralato et al. (2006), this definition appears to find increasing consensus. Begon et al. (2009) adopted that criterium as well, arguing with a low biomass making the process of identifying a keystone species more challenging and at the same time excluding trivial, dominant examples of the ecosystem. Jordan et al. (2009) introduced a method based on the interactive structure in an ecosystem and a consequential importance of one species for identifying a keystone species, disregarding its biomass. Despite these differences, Goeden (1982), Vandermeer & Maruca (2006) and Begon (2009) agree that a keystone predator is mainly characterized by its superior competition towards other large species, as well as the direct consumption of these, both resulting in a direct and depressing impact on the other predator's abundances. Libralato et al. (2006) and Begon (2009) mentioned furthermore that a keystone species can have strong impacts on several species, but not only competitive predators. Thus, including competition and abundance of competitors as well as other species in the ecosystem, the definition allows the further conclusion that a keystone predator might be dependent on its impact, which is related to its biomass. It seems apparent that this impact of a species always has an influence on its "keystoneness". Included should be at this point as well the possible indirect impacts, such as a decreased availability of prey for competitors due to a high predation of a keystone species.

Considering the results of our project and differences between definitions, arguments for and against considering European hake as a keystone predator can be identified (Table 5). European hake especially fulfills the criteria for a keystone species in Norwegian coastal areas, but evidence is weaker for its impact in the North Sea. In spite of everything, an ultimate classification is difficult and more data as well as observations over a longer time period are necessary to answer this question. It is furthermore often difficult to make ecological assessments on species, for which there is primarily fisheries data, rather than ecological studies.

Table 5: Overview of evidence for designating European hake a keystone species in the North Sea and along the Norwegian coast.

	Pro-arguments	Contra-arguments
North Sea	- Increasing abundance indicates competitive success - High impact on Norway pout stock due to predation - Obvious indirect impact on competitors by heavily reducing available prey, especially Norway pout	- Degree of impact seemingly dependent on stock biomass - No direct predation on competitors - Apparent high abundance of prey species, food competition to other predators low
Norwegian mid-west coast	- Direct predation on competitors - Apparently higher impact disproportionally to abundance - Increasing abundance indicates competitive success - High impact on Norway pout stock due to predation - High variety of prey species in diet indicates manifold impacts of the ecosystem	

4.3. Conclusion & Outlook

The rapid increase of European hake in northern European waters is certainly an impressive example how quick a commercially heavily exploited fish stock can recover, although hake are known to be robust to high fishing pressure (Alheit & Pitcher, 1995). Various attempts have been made to explain this phenomenon, temperature was mentioned as well as a reduced fishing mortality due to the EU recovery plan (Baudron & Fernanes, 2014). Still, an ultimate and single reason has not been proven yet and maybe many factors have to be included at this point. Fish stocks do underlie strong natural fluctuations without anthropogenic influences, together with a cautious management and a supporting temperature development an increase like seen for European hake in northern waters is possible. IMR recently published (Arneberg et al. 2015) data showing that 2014 was an especially warm year in the North Sea and the Skagerrak throughout the whole water column. On the IBTS Q1 survey 2015 a single station north-east of the Shetland Islands showed a hake catch of 2.15 tonnes (IMR, unpublished), which is more than thirteen times as high as the highest catch in the data series used for this analysis (0.16 tonnes) and indicates as well a steeply increasing biomass during the first half of the year. Many indications show that things change rapidly these days, and it is up to us to keep track of that. To progress our knowledge about European hake in the North Sea and along the Norwegian coast, more research is urgently needed. An egg and larvae survey would be helpful to confirm the suggested spawning and nursery areas, survey methods in cooperation with recreational fishermen have the great potential to give us new insight into coastal hake populations and a detailed investigation of physical parameters, such as temperature and salinity, might give new background information on the stock development.

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Appendices

Appendix 1: Recognized species of the genus *Merluccius*, their common name and their distribution (Murua, 2010).

Scientific name	Common name	Distribution
Merluccius albidus	Offshore hake	North-west, Central-west Atlantic
Merluccius angustimanus	Panama hake	North-Central east Pacific
Merluccius australis	Southern hake, Austral hake	South-east and South-west Pacific
Merluccius bilinearis	Silver hake	North-west Atlantic
Merluccius capensis	Cape hake, Shallow-water hake	South-east Atlantic
Merluccius gayi	Chilean hake, Peruvian hake	South-east Pacific
Merluccius hubbsi	Argentine hake	South-west Atlantic
Merluccius merluccius	European hake	North-east Atlantic
Merluccius paradoxus	Deepwater Cape hake, Deepwater hake	South-east Atlantic
Merluccius polli	Benguela hake	South-east Atlantic
Merluccius productus	Merluza nortena, North Pacific hake, Pacific hake, Pacific whiting	North-east Pacific
Merluccius senegalensis	Senegalese hake	South-east Atlantic

Appendix 2: Landings in tonnes of European hake in Norway divided by gear type and year.

	2005	2006	2007	2008	2009	2010
Annet	2.6	0.6	1.0	0.3	0.4	0.7
Garn	510.6	648.2	828.7	992.5	936.8	1003.3
Juksa	1.8	2.0	1.0	0.5	1.6	5.3
Line	6.7	3.1	6.5	5.8	4.4	10.1
Not	0.8	0.9	0.0	0.0	0.0	0.1
Snurrevad	99.2	80.2	86.5	87.2	30.8	20.6
Trål	206.6	196.1	360.0	515.3	735.6	731.0
Grand Tot	828.4	931.0	1283.7	1601.6	1709.6	1771.1
	2011	2012	2013	2014	Total	
Annet	4.4	3.3	11.1	6.9	31.2	
Garn	791.4	914.5	1044.3	1062.9	8733.3	
Juksa	1.0	1.7	4.3	2.2	21.3	
Line	11.0	33.2	16.4	20.7	117.7	
Not	0.8	5.7	0.2	0.1	8.8	
Snurrevad	34.8	54.6	132.2	270.4	896.4	
Trål	1442.2	1867.9	2266.1	2948.1	11269.0	
Grand Tot	2285.6	2880.8	3474.6	4311.3	21077.7	

Appendix 3: Number of spawning fish (maturity stage=3) by survey and year.

	IBTS Q1	IBTS Q3	Norwegian coastal survey
2010	0	3	0
2011	0	1	0
2012	0	19	6
2013	7	26	0
2014	3	12	9
Total	10	61	15

Appendix 4: Summary of dissected stomachs separated by survey and content 2014.

Survey	No analyzed	No full	No empty	% full	% empty
IBTS Q1	26	16	10	61.54	38.46
IBTS Q3	46	31	15	67.39	32.61
Shetland cruise	25	17	8	68.00	32.00
Coastal survey	74	37	37	50.00	50.00
Shrimp survey	24	11	13	45.83	54.17
Askøy	5	2	3	40.00	60.00
Total	200	114	86	57.00	43.00

Appendix 5: Results of prey species identification 2014 separated into total frequency (Total F), frequency of occurrence (%F), total number found (Total N) and percentage composition (%N).

	Total F	%F	Total N	%N
Fish total	96	84.21	153	78.87
Norway pout (*Trisopterus esmarkii*)	50	43.86	72	37.11
Atlantic herring (*Clupea harengus*)	16	14.04	20	10.31
Atlantic Mackerel (*Scomber scombrus*)	11	9.65	12	6.19
Blue whiting (*Micromesistius potassou*)	6	5.26	7	3.61
Silvery Pout (*Gadiculus argenteus*)	5	4.39	7	3.61
Poor cod (*Trispoterus minutus*)	3	2.63	3	1.55
Whiting (*Merlangius merlangus*)	3	2.63	3	1.55
Saithe (*Pollachius virens*)	3	2.63	3	1.55
Argentine (*Argentina sphyraena*)	2	1.75	2	1.03
European hake (*Merluccius merluccius*)	1	0.88	1	0.52
Pollack (*Pollachius pollachius*)	1	0.88	2	1.03
Greater argentine (*Argentina silus*)	1	0.88	1	0.52
Atlantic cod (*Gadus morhua*)	1	0.88	1	0.52
Sand goby (*Pomatoschistus minutus*)	1	0.88	1	0.52
Unidentified Fish	9	7.89	12	6.19
Unidentified Argentine (*Argentina* sp.)	3	2.63	3	1.55
Unidentified Gadidae	2	1.75	2	1.03
Unidentified Clupeidae	1	0.88	1	0.52
Crustaceans total	15	13.16	32	16.49
Pandalus borealis	2	1.75	2	1.03
Galatea strigosa	1	0.88	1	0.52
Pasiphaea sp.	3	2.63	6	3.09
Krill (*Euphausiacea* sp.)	1	0.88	2	1.03
Amphipoda	2	1.75	12	6.19
Unidentified crustaceans	6	5.26	9	4.64
Others total	7	6.14	9	4.64
Sand sea star (*Astropecten irregularis*)	1	0.88	1	0.52
Brown algae (Phaeophyceae)	6	5.26	8	4.12