

# Life history and spatial ecology of Skagerrak coastal cod (*Gadus morhua*)

*Ida Margrethe Aalvik*  
Master of Science Thesis  
2013

**CEES**  
Centre for Ecological and  
Evolutionary Synthesis



 **HAVFORSKNINGSINSTITUTTET**  
INSTITUTE OF MARINE RESEARCH

Centre for Ecological and Evolutionary Synthesis  
Department of Biology  
University of Oslo, Norway

*The sea, the great unifier, is man's only hope. Now, as never before, the old phrase has a literal meaning: we are all in the same boat.*

- Jacques-Yves Cousteau

# Life history and spatial ecology of Skagerrak coastal cod (*Gadus morhua*)



**Master of Science Thesis by Ida Margrethe Aalvik**

Supervisors:

Even Moland, Institute of Marine Research, Flødevigen

Esben Moland Olsen, Institute of Marine Research, Flødevigen

Nils Christian Stenseth, Centre for Ecological and Evolutionary Synthesis (CEES),  
Department of Biology, University of Oslo



# Preface

Grand thanks to everyone at Flødevigen Research Station, maybe especially the ‘oceanic dip crew’ which has helped me keep my cool throughout the year (phun intended). Big thanks to Jan Henrik Simonsen for teaching me about scales and Kate Enersen for teaching me about otoliths, and both for helping me around the lab. Über grateful for help with ‘elementary R’ issues, Carla Freitas and Anna Blix. Thanks heaps Maren Duus Halvorsen for being my blonde accomplice and for helping me stay focused. Thanks Even Moland for teaching me what real field work is all about (and boat etiquette) and Esben Moland Olsen for being a mountain of calm – and a billion thanks to the both of you for supplying me with endless knowledge and support.

Also would like to thank my parents for mixing their DNA and putting their heads together to shape such an extraordinary child.

And last but not least, thank you My Leiki for being supportive and patient and boosting my academic confidence.

*“So Long, and Thanks for All the Fish”*



# Abstract

Practically every Atlantic cod (*Gadus morhua*) stock have suffered from depletion and overfishing, placing the fish on IUCN's Red List as 'Vulnerable'. The Skagerrak Coastal Cod stocks are in no better shape, reported to be experiencing harvesting pressure comparative to the Canadian cod stocks prior to the collapse in the early 1990s. Sub-populations of coastal cod have been found to exhibit different behaviour and life-history strategies. This may cause the various populations to respond differently to fishing pressure indicating a need for localized ecosystem-based management, reflecting biologically meaningful population units. To improve the management of coastal cod, more knowledge and a better understanding of the various populations' fine-scaled behaviour and ecology is required. My study aspires to provide supplementary information to the knowledge base regarding the coastal cod's movement and behavioural ecology. By using a network of 44 moored acoustic receivers and tagging 80 codfish with transmitters, the spatial and behavioural ecology of 39 individuals was investigated over a three month period (June-July-August) during the summer of 2012. Home range sizes and vertical distribution was investigated by using acoustic telemetry, kernel density estimation and linear mixed-effect models. I predicted that the life history of the cod (e.g. body size) will affect the behavioural traits observed; that smaller fish will have a more constrained behaviour and that faster growing fish will exhibit elevated activity pattern and a bold behavioural type. I found that home range size varies with respect to month, as did cumulative distance travelled, vertical range, mean depth and max depth. Min depth was not found to be affected by any of the included variables. Body size (at age 1 =  $L_1$ ) was only found to influence vertical range, decreasing in parallel with a decrease in  $L_1$ . However, as  $L_1$  was based on age estimation from cod scales the results from these remains speculative. My results indicate that the spatial distribution of coastal cod in Sømuskilen is controlled more by environmental factors and their subsequent influence on behaviour, than life-history traits *per se*. Further, these findings support the notion that the meta-populations of coastal cod acts as localized entities and should be managed accordingly.





# Table of Contents

1	Introduction.....	1
2	Material and methods.....	7
2.1	Study area.....	7
2.2	Study species .....	8
2.3	Acoustic telemetry.....	9
2.4	Sampling methods.....	9
2.4.1	Capture.....	9
2.4.2	Tagging procedure.....	10
2.4.3	Cod body size and parasites.....	11
2.4.4	Age estimation from scales.....	11
2.5	Behavioural analyses.....	13
2.5.1	Pre-analytical data processing.....	13
2.5.2	Model selection.....	15
3	Results.....	17
3.1	Cod body size and parasites.....	17
3.2	Age estimation from scales.....	18
3.3	Home range sizes.....	19
3.4	Cumulative distance.....	23
3.5	Vertical selection.....	24
3.5.1	Mean depth.....	25
3.5.2	Min depth.....	25
3.5.3	Max depth.....	26
3.5.4	Vertical range.....	27
4	Discussion.....	28
4.1	Horizontal activity patterns.....	28
4.2	Vertical activity patterns.....	32
4.3	Unknown and un-included variables.....	34
4.4	Evaluating study design uncertainties and potential sources of error.....	34
5	Conclusion and conservation incentives.....	37
6	References.....	39

Appendix 1..... 51  
Appendix 2..... 53  
Appendix 3..... 54  
Appendix 4..... 55  
Appendix 5..... 1

# 1 Introduction

Atlantic cod (*Gadus morhua*) is considered to be one of the most commercially important marine species in the world (FAO, 2010), and has even been referred to as “the beef of the sea” (Kurlansky, 1997). Atlantic cod is a commodity which has been sought after for centuries, but it is not until the last couple of decades that the impact the fishing industry has had on the affected fish stocks and the marine ecosystems have received noteworthy attention from fisheries scientists and managers. Atlantic cod is predominately harvested using bottom trawls. Bottom trawling is one of the most disruptive and widespread human-induced physical disturbances inflicted on seabed communities and have become a global concern (Cryer, Hartill & Shea, 2002; Watling & Norse, 1998). This mobile benthic fishing gear disturbs the benthos both directly and indirectly by removing the biogenic structure of the seabed, stirring up sediment plumes and subsequently changing the habitat complexity and the species community inhabiting the trawled areas (Cryer et al., 2002; Frank, Petrie, Choi & Leggett, 2005; Watling & Norse, 1998). A prime example of how bottom trawling has influenced the ecosystem balance can be found off the Gulf of Maine. Here intensive fishing pressure directed at ground fish led to a substantial decrease in the harvested fish stocks (i.e. Atlantic cod), something that resulted in an ecosystem shift where the large predatory fish keeping urchin (and other bottom-dwelling species) populations stable, were replaced by smaller fish not able to fill the niche left by vital dominant fish species. This led to a dramatic decline in kelp forest distribution as the increasing urchin population devoured all kelp within their vicinity (Jackson, Alexander & Sala, 2011). The previous example is not a unique one; concomitant evidence for restructuring of food webs by means of overfishing has been found all over the globe. In the large eastern Scotian Shelf ecosystem off Nova Scotia, Canada, overharvesting has brought about severe changes in cod abundance (which previously existed as the primary predatory species), resulting in substantial increases in prey species abundances (esp. shrimp and crabs) now dominating the system (Frank et al., 2005).

The practice of fishing started as a simple mean of providing for own consumption and fish was caught using rudimentary gears. The introduction of the first steam and otter trawlers to the North Sea at the end of the 19<sup>th</sup> century marked the start of the industrial

revolution for the fisheries sector in Europe (Russell, 1943). Following this there has been a continuous advancement in technology, fishing gear and fishing practices which have led to a substantial intensification of fishing effort and catch rate. Nets in synthetic materials, electronic devices deployed to assist in locating fish, more space for storing catch on boats (and so increasing time spent at sea; boat days) have all contributed to a landing boom (Garcia & Grainger, 2005; Kesteven, 1996; Thurstan, Brockington & Roberts, 2010). With all this increase in fishing efficiency, practically every Atlantic cod stock have experienced overfishing and depletion (Committee on the Status of Endangered Wildlife in Canada, 2003; Jackson et al., 2011; Kesteven, 1996; Thurstan et al., 2010), and are today only shadows of once prosperous populations.

The Atlantic cod is a dominant large predatory fish, displaying social behaviour, and pose as an important demersal (bottom-dwelling) species in the North Atlantic continental shelf ecosystems (Rose, 2007). With its clear ontogenetic shifts in diet, cod populations influence and maybe even regulate the population dynamics of its prey species, in all stages of its life (Casini et al., 2008; Van Leeuwen, De Roos & Persson, 2008). Changing population abundance and distribution of a dominant predator in a system can lead to devastating cascading effects on the trophic dynamics (Baum & Worm, 2009; Casini et al., 2008; Heithaus, Frid, Wirsing & Worm, 2008). Alternations inflicted on an ecosystem can result in a decline in intra-species variation and a concurrent loss of biodiversity, something that can reduce the durability and overall resilience of the affected system (the diversity-stability hypothesis) (Elton 1958; Tilman 1996; Loreau et al. 2001; Frank et al. 2005; Worm et al. 2006; Hutchings et al. 2012). On a species level, genetic diversity (heterozygosity) is directly correlated with population fitness, by conserving intra-population genetic diversity inbreeding depression is averted (Reed & Frankham, 2003). "Diversity is directly related to persistence" (Hutchings et al. 2012), when more genetic variation is retained within a system the better equipped it will be to respond favourably to potential threats (Worm et al., 2006), this means that species will have a higher adaptive potential necessary to evolve and persist (McNeely, Miller, Reid, Mittermeier & Werner, 1990). However, ecosystem changes and loss of species will not just have implications for marine life; it will affect the social and economic well-being of coastal communities by altering the services provided by the marine ecosystem (Hutchings et al. 2012).

The ocean provides ever changing habitats for its residents, and in some ecosystems the inhabitants gain from being plastic in their responses to their surrounding environment in order to survive. Studies on animal behaviour have shown that fish exhibit high inter-individual variation in behaviour, meaning that fish display a range of personalities (behavioural differences that are maintained through time and across contexts, Wolf & Weissing 2012) just like other animal taxa (Gosling, 2001). The term 'behavioural syndromes' was recently presented by Sih et al. (2004) to explain a consistency in behaviour on an individual level. 'Behavioural syndrome' as defined by Sih et al. (2004) refers to "a suite of correlated behaviours reflecting between individual consistency in behaviour across multiple (two or more) situations. A population or species can exhibit a behavioural syndrome. Within the syndrome, individuals have a behavioural type (e.g. more aggressive versus less aggressive behavioural types)". In order to investigate behaviour with uniformity, Réale et al. (2007) proposed a standardized framework consisting of five broad axes of animal personality; (1) *shyness–boldness*, (2) *exploration–avoidance*, (3) *activity*, (4) *aggressiveness* and (5) *sociability*. The concept of behavioural syndromes pose highly relevant to ecology and evolution seeing that it indicates that plasticity in behavioural traits are limited (Sih et al., 2004). The intrinsic behavioural types show an intra-individual stability, meaning that individuals do not always exhibit an optimal behaviour in a given situation. This is relevant information when investigating how behavioural ecology interacts with movement ecology. The behavioural types which have received a lot of attention in studies on fish are aggressiveness and shyness-boldness, and their positive relationship (e.g. Huntingford 1976; Huntingford et al. 1990; Wilson et al. 1993; Wilson et al. 1994; Coleman & Wilson 1998; Bell & Stamps 2004; Sih et al. 2003; Ward et al. 2004; Sih et al. 2004; Bell 2005; Jones & Godin 2010).

Obtaining knowledge on fine scale ecology and behaviour which underlie observed movement patterns in animals is key when mapping the spatial ecology of a species. The more information one has on a given species, the better are the chances of effectively and sustainably managing the species in question. There is an increasing awareness of the cumulative effects that human activities inflict on ecosystems, and the need to create and implement holistic management plans for fisheries. There are many potential human generated threats facing our fish stocks, such as unsustainable fishing practices and

overfishing, pollution and habitat destruction related to oil and gas extraction and projected future climatic changes, to mention a few (Ottersen, Olsen, Van der Meeren, Dommasnes & Loeng, 2011). One of the major impact factors is anthropogenic fishing pressure which seems to be the main source of mortality in many fish stocks and may even exceed natural mortality by more than 400% (Mertz & Myers 1998). Today over half of the world's fish stocks (53%) are estimated to be fully exploited and 32% are estimated to be overexploited, depleted or recovering, while 15% are estimated to be underexploited or moderately exploited (FAO, 2010). One species that is experiencing an exceedingly high fishing pressure is the Atlantic cod (*Gadus morhua*). The Atlantic Cod is one of the most valuable marine resources of the entire northern Atlantic. Along the Norwegian Skagerrak coast the coastal Atlantic cod have historically been one of the most important fish species, representing great socio-economic importance to the communities relying on the harvested stocks. The Skagerrak coastal cod is sub-divided into multiple local, genetically differentiated, cod populations distributed over a small geographic area, sometimes found as little as 30 km apart, creating genetically different fjord populations (Knutsen et al. 2003; Jorde et al. 2007). Such highly stationary local cod populations are in danger of being eradicated. The populations are seen to experience a varying decline in cod abundance and if the current harvesting pressure continues (targeting larger and more fecund individuals) the spawning stock might not be sufficiently large enough to rebuild the populations. This is what happened along the Swedish Skagerrak coast, where overfishing severely depleted the local cod populations resulting in a dramatic decline in cod abundance leaving the populations nearly depleted (Svedäng & Bardon 2003; Cardinale & Svedäng 2004; Svedäng 2003).

Over the past two decades the coastal cod populations have experienced a decrease in stock size, but it is also seen that the fishes' life-history traits have changed; reduction in size at maturation and size-at-age has been documented for these populations (Rowell 1993; Olsen et al. 2004; Hutchings 2005; Olsen et al. 2005). A depleted stock size has led to a decrease in the cod fishery, but harvesting is still going strong contradictory to the fact that Olsen & Moland (2011) reported that the Skagerrak coastal cod populations are being overharvested; they stated that the stocks were experiencing harvesting pressure comparative to the Canadian fish stocks prior to the stock collapse in the early 1990s, something that led to the enforcement of a fishing moratorium. The Atlantic cod has since

1996 been listed as 'Vulnerable' on the IUCN Red List (IUCN, 2012), this is a listing resulting from mismanagement which has led to unsustainable anthropogenic fishing pressure causing overexploitation of mature cod, and subsequently leading to inadequate recruitment of juveniles to the fishery (Hutchings & Myers 1994; Hutchings 1996; Walters & Maguire 1996; Myers et al. 1997; Hutchings 2000; Fu et al. 2001; Smedbol et al. 2002). According to ICES (2012) the current state of the Atlantic cod stock in and adjacent to the North Sea is "outside of safe biological limits", despite the fact that the stocks have experienced a steady recovery from its historical low in 2006. The spawning stock biomass (SSB) remains just below the critical spawning stock ( $B_{lim}$ ) providing reduced reproductive capacity, with fishing mortality currently remaining below the precautionary mortality ( $F_{pa}$ ) which is still estimated to be above  $F_{MSY}$  (fishing mortality supporting MSY) (ICES, 2012). Consequently, ICES advises that cod landings in 2013 should not exceed 25 441 tonnes (compared to estimated landings in 2012: 35 000 tonnes).

The Skagerrak Coastal cod display different genetic composition, growth rates, age and size at maturity as well as dissimilar movement and migration patterns from the offshore cod stocks (Fromentin et al. 2000; Knutsen et al. 2003; Olsen et al. 2004). Conversely, Skagerrak coastal cod is not managed separately from other Norwegian cod stocks. However, the Fisheries authorities have introduced a number of protective measures in order to regulate the coastal cod fishery. Set quotas, sorting grids, minimum legal size (MLS), bycatch and gear restrictions, area and period constraints are some of the implemented regulations in this fishery (Gjørseter et al. 2009). A suggested protective measure is to establish marine protected areas (MPAs) in order for the coastal cod populations to rebuild themselves. A study undertaken by Moland et al. (2013) concluded that even partial protection of coastal cod led to an increase in population density and body size. In 2012 Norway's first no-take marine reserve was established on the Skagerrak coast, in the municipality of Tvedestrand.

Species level information on behavioural traits and habitat utilization is valuable for conservation purposes such as effective marine reserves. When we identify the areas most important for the fish, its 'critical habitat' (or 'essential fish habitat' (EFH)) and the fishes' spatial ecology, its home range ("the spatial expressions of the behaviours animals do to survive and reproduce", Burt 1943), we can work towards creating ecologically meaningful

marine reserves where the fish can thrive (Lindholm, Auster, Ruth & Kaufman, 2001).

In light of the (conservation) status of some Atlantic cod stocks, now depleted and red listed, action needs to be taken to protect and restore all cod stocks in order for the populations to persist into the future (Wroblewski, Neis & Gosse, 2005). In order to implement a sustainable management approach, more information on coastal cod's ecology is required. However, fish are not easily observed stationary entities and their populations consist of a heterogeneous assemblage of individuals. In order to observe and continuously monitor marine animals, acoustic telemetry has become a widely recognized tool for scientists all over the globe (Heupel, Semmens & Hobday, 2006; Heupel & Simpfendorfer, 2002). Acoustic telemetry is appropriate as a monitoring technology as long as the animal is sufficiently large enough to have a transmitter attached or implanted, without influencing the animal's behaviour or life quality (Heupel et al., 2006). This monitoring method makes it possible to identify the fine-scale movements of each tagged animal, as the acoustic tag transmits a unique signal which is picked up by a surrounding network of moored receiver stations.

By using acoustic telemetry, the objective of this study is to obtain new knowledge on the fine scale spatial ecology of coastal Atlantic cod on the Skagerrak coast. Further, my aim is to go beyond a descriptive approach and quantify the behavioural traits underlying the movement patterns observed. I investigate how these traits vary temporally through three summer months and whether they are correlated with fish life histories (e.g. body size).



## 2 Material and methods

### 2.1 Study area

The study was undertaken in Sømskilen and adjacent waters on the Norwegian Skagerrak coast on the border between Arendal and Grimstad municipalities (Figure 1). Sømskilen is a semi-sheltered basin holding numerous small islands and skerries, covering an area of approximately 3 km<sup>2</sup>. In total, the study area covers approximately 5 km<sup>2</sup>. Sømskilen is predominantly a shallow water basin with an average depth of 10-15 m, but areas included in the north-eastern part of the study area reaches maximum depths >30 m. The dominant substrate type from 5-10 m depth is hard bottom creating macro-algae habitats. In basins and flat areas the substrate is dominated by sand or mud with patches of eel grass (Espeland et al. 2010; Olsen & Moland 2011). Sømskilen is influenced by the river Nidelva which has three outlets; one of which enters the study area in the northern part of the basin.

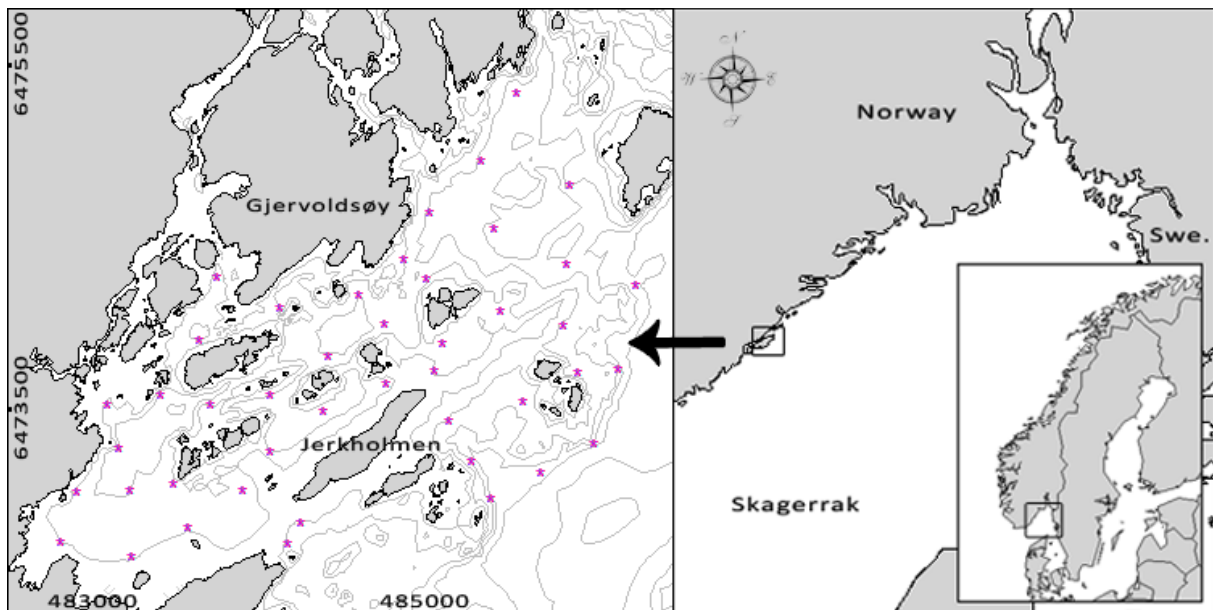


Figure 1 Left panel: the study area (Sømskilen). Light grey lines are the 5, 10, 15, 20, 30, 40, 100 and 150 m depth contour; pink asterisks: position of acoustic receivers (n=44); coordinates are presented in Easting and Northing. Right panel: location of the study area on the Norwegian Skagerrak coast. Insert in right panel: the Scandinavian Peninsula (Norway and Sweden), Denmark and the location of the Skagerrak Sea.

## 2.2 Study species

Atlantic cod is found in both coastal waters and offshore shelf habitats, distributed in the eastern and western North Atlantic Ocean. The Atlantic cod situated in Skagerrak belongs to the group of cod referred to as Norwegian Coastal Cod (NCC) (Møller, 1969), and several local populations of coastal cod can be found along the Skagerrak coast (Knutsen et al. 2003), only geographically separated by approximately 30km (Jorde et al. 2007). The Norwegian Coastal Cod inhabits fjords and near-shore areas where they subsist as stationary populations throughout their lifespan (Jakobsen, 1987).

Atlantic cod is an exceedingly fecund broadcast spawning species, having females that carry an average of 1 million eggs per year which is distributed over multiple spawning events taking place in sheltered coastal basins during February – April (Olsen et al. 2008; Knutsen et al. 2011). Depending on temperature, cod eggs hatch into larvae within 3 weeks. After this the larvae remain as pelagic zooplankton feeders until they reach 3 – 5 cm during early summer months (May – June), when they undergo metamorphosis to become demersal (bottom-dwelling) juveniles and settle in shallow waters in fjords and bays (Gjørøseter et al. 2007; Knutsen et al. 2011). Growth rate and age (size) at maturation may vary within and among populations (Olsen et al. 2004). Olsen et al. (2008) found that the majority of individuals in the coastal Skagerrak population will, on an average, grow 10-15 cm per year and mature when they are approximately 2-3 years measuring 30-50 cm in length. Fishing mortality is exceedingly high in these populations (75%; Olsen & Moland 2011), and few fish are found to be older than 5 or 6 years of age (Olsen et al. 2010), with the maximum recorded age of 12 (Gjørøseter et al. 1996). From this we can see that the coastal cod has a substantially shorter lifespan than historical cod data suggests, describing individuals >130 cm in length, >30 kg in weight with fish surpassing 20 years of age (Olsen et al. 2010).

The minimum legal size for cod is currently 40 cm for both commercial and recreational harvest (south of 62° North). Cod is harvested using a wide variety of gear including bottom trawl, gill net, longline, seine, traps and hand line (Julliard et al., 2001), but the majority of the fish is caught by the mixed demersal fisheries primarily using towed gears.

## 2.3 Acoustic telemetry

In order to track cod movement a system of moored acoustic receivers (VR2W, Vemco Divison, Amirix Systems Inc., Halifax, Canada) was utilized. The receivers (n=44) are distributed all throughout the study area (Figure 1), where they are attached to subsurface buoys anchored to the seabed and positioned 3 meters below the surface. The omnidirectional hydrophones are distributed so that there is an overlapping detection range in order for each signal to be received by multiple receivers (>3) at approximately the same time. The hydrophones record of presence/absence information on animals within the study area can be used to estimate their movement. By using the weighted means of number of recorded signals received by each hydrophone during a set period of time, the individual fish's short-term centre of activity can be calculated (Simpfendorfer et al. 2002). This information can further be used when exploring fish's movement ecology; including home range and behavioural patterns.

## 2.4 Sampling methods

### 2.4.1 Capture

The sampled cod were captured in Sømskilen during May 2012. Capture was carried out utilizing fyke nets left for a maximum duration of 6 days. All fish captured were recorded and classified according to species and measured to the nearest cm. A total of 80 individual cod were selected for tagging according to length and capture location, where the aim was to sample roughly an equal number of cod throughout the available size range and area of capture (Figure 3).

All 80 codfish were tagged with an external T-bar anchor tag (TBA1, 30 x 2 mm, Hallprint Pty. Ltd, Holden Hill, South Australia) attached in the musculature below the dorsal fin with a standard tag applicator. The tags held information regarding a reward, contact information to the Institute of Marine Research Flødevigen and the specific animal's identification number. Two types of tags were used posting a high (NOK 500) or low (NOK 50) reward when returned to the Institute of Marine Research Flødevigen. High reward tags were attached to 20 % (one in five cod) to enable estimation of reporting rate. In addition, all cod

equipped with an acoustic transmitter (see below) received a high reward T-bar tag in order to maximise tag return.

#### ***2.4.2 Tagging procedure***

Tagged cod were equipped with a V9P-2L transmitter (9x38 mm, <3g weight in seawater, Vemco Division, Amirix Systems Inc., Halifax, Canada). These tags have a built in pressure sensor and are programmed to emit an acoustic pulse train at random intervals every 110 to 250 seconds (mean: 180 seconds). Tags thus transmit depth and location information to the nearest receiver(s) together with the fish's unique identification number.

The tag implanting surgery was carried out in the field at a suitable location. Here, the cod were anesthetized in a clove oil solution (as described in Munday & Wilson 1997). Clove oil is an effective anaesthetic causing minimal stress to the animal as well as having other favourable traits, such as antimicrobial, antifungal and antiviral effects (Chaieb et al., 2007; Tort, Puigcerver, Crespo & Padros, 2002). The animal was left in the anaesthetic bath for approximately 2 minutes (depending on fish size and wanted response: belly up, slow ventilation by opercular movement), after which it was taken out of the clove oil solution and placed on a clean and wet wood surface. A small incision (10-12mm) was made posterior to the pelvic fins, through which the V9P-2L acoustic transmitter was gently inserted in the animals body cavity.

The wound was then closed using absorbable sutures (Dexon\* II™, Tyco Healthcare Group, Mansfield, MA, USA) and the fish was placed in a tub filled with aerated sea water in order to regain full consciousness. The process was sped up by stimulating respiration and helping the fish clean its gills from residual anaesthetic by moving it back and forth in the tub, as well as giving it a gentle massage. The time elapsed from anesthetization to the fish regained full health was between 5 – 30 minutes.

During surgery, a scale sample and a small tissue sample (from the caudal peduncle) was taken from each individual. The tissue samples were fixed in 1 ml vials containing 100% ethanol for DNA profiling. Scale samples were placed in small coin envelopes for later age estimation in the lab.

### 2.4.3 Cod body size and parasites

In order to document as much information as possible on each fish, numerous measurements were taken, which could also provide useful for creating a detailed assessment of the individuals health condition. Each fish was handled exactly the same way; we measured total length to the nearest cm, measured weight, colour of the fish was noted (red/brown/grey or combinations of the three), caudal peduncle height and width was measured using vernier callipers, and presence/absence of three species of ectoparasites was noted; black spot disease (*Cryptocotyle lingua*), gill parasites (*Lernaeocera branchialis*) and fish lice (*Caligus elongates*)(see Appendix 1; Table 8).

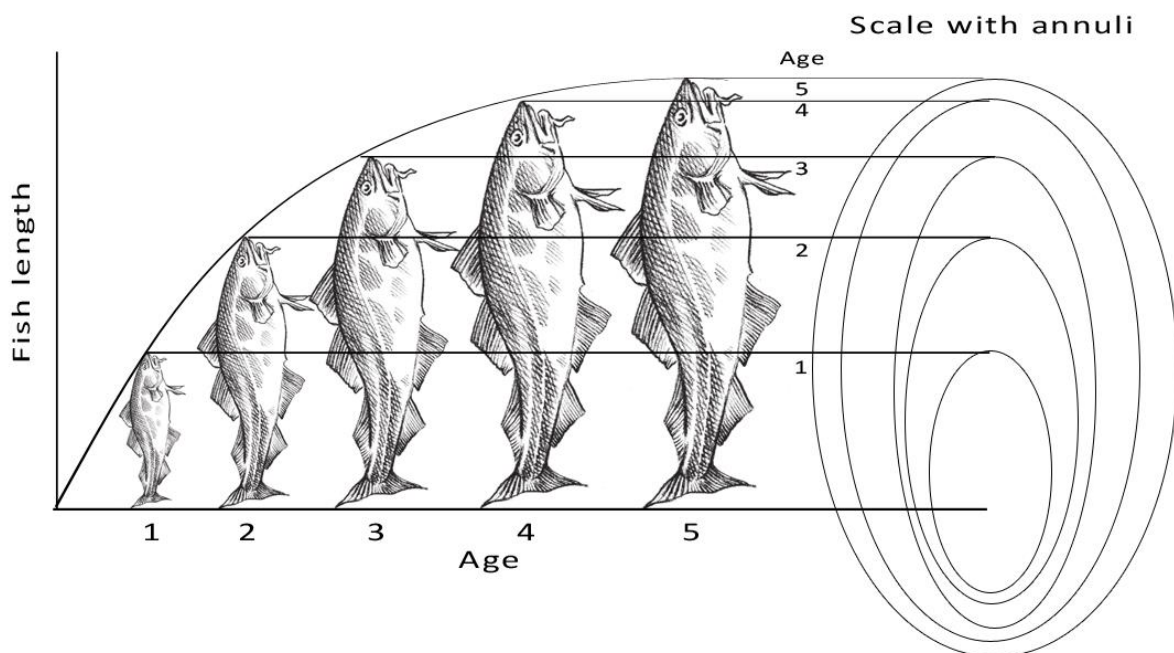
### 2.4.4 Age estimation from scales

Growth and age estimation generally involves analysis of calcified or bony structures, such as otoliths, fin rays and spines, scales, vertebrae, cleithrum bones and so forth, all depending on fish species. In this study scales was used, as it involves a non-lethal removal procedure. Scale samples were taken from the medial region of the caudal peduncle ('the wrist of the tail'), as this is where first scale formation takes place for many species (Sire & Arnulf, 1990), and so represent the oldest scales. Regenerated scales were removed, as they exhibit incomplete growth patterns and are not suitable for reading.

All prepared scales were first cleaned to remove skin-remains; this was done with Ajax window cleaner. Each individual scale was soaked in Ajax for 3 min, and then the skin was scraped off using a fingernail before being dried off with a paper towel. The scale was then compressed between two glass slides and mounted for viewing under a microscope. In order to get estimates of fish age, the scales were magnified and photographed using a Leica MZ 16 A Stereomicroscopes with the attached Leica DFC420 (Leica Microsystems (Switzerland) Ltd Business Unit SM, CH-9435 Heerbrugg) digital microscope camera, standardizing the picture taking at a 20x resolution.

Cod possess what's called cycloid scales where rings (circuli) are added as they grow. The size and spacing between the circuli depend (and so the growth of the scale and fish) on the fish's ambient temperature, available food and other abiotic and biotic factors. Growth

periods can be seen in the scales as the circuli produce distinct congregated zones (annuli) according to the amount of fish growth. In the summer season when food is abundant circuli are deposited 'thicker' and more widely spaced. In winter when food is scarce and the temperature drops, the annuli are composed of tightly deposited circuli, and together these zones represent the fish's first year growth. In this way age was estimated by counting the growth increments on each scale (Figure 2) (Cailliet, Love & Ebeling, 1996; A. Dannevig, 1933; Lea, 1910; Salvanes, Giske & Nordeide, 1994; Weatherley & Gill, 1987). The method was validated in the best possible manner within the given time frame by separate readings. IA read the scales three individual times, with a time interval of 2 months. The result was compared to the one-off individual readings of EM and EMO, and the age which the readers shared greatest consensus over (median age) was denoted as most correctly estimated age and used further in the data analyses. Reading was carried out without knowing length or weight of the individual.



**Figure 2** Illustration of the relationship between scale length (growth) and cod length (growth).

In order to find length at age 1 ( $L_1$ ) the Fraser-Lee back-calculation method was employed. This is used to estimate the fish's length at age from calculations using scale radius, fish length and radius of the first growth increment read from scale. The Fraser-Lee method was proposed by Lee (1920), where he adapted Fraser's (1916) original approach.

The Fraser-Lee equation:  $L_t = c + (L_F - c)(S_i / S_r)$

Lee (1920) described  $c$  as the correction factor (the length of the fish at the time of scale formation),  $L_t$  is length of fish at time  $t$  (length at age),  $L_F$  is current length of fish,  $S_i$  is length of scale at age  $i$  (scale increment) and  $S_r$  is current length of scale (scale radius).

## 2.5 Behavioural analyses

Acoustic tagging data (receiver logs) was at first handled within the VUE database (Vemco Division, Amirix Systems Inc., Halifax, Canada) before finally all data was processed within the R software (version 2.15.00; The R Foundation for Statistical Computing 2012). In advance of undertaking any analyses, the dataset was examined to see if there were any correlated explanatory variables (Zuur, 2009), following this both weight ( $r=1.0$  with length) and age ( $r=0.85$  with length) were excluded as explanatory variables and thus eliminated from the dataset.

Out of 80 cod tagged throughout the study area, 39 were included in the statistical modelling of behavioural traits. The fish left out were excluded on one of the following criteria; (1) dead, (2) harvested, (3) dispersed out of area or (4) tag malfunction. Individuals were classified as dead ('natural causes') when fluctuations in horizontal and/or vertical movement ceased, but signals continued to transfer from an unchanging depth and location. Individuals were classified as harvested when the high reward T-bar tag was returned to Flødevigen and the fish was no longer detected by the receivers within the study area or when fish disappeared in the middle of the study area (see Appendix 3 for depth profile examples). The study period encompassed the months June, July and August. The rationale for this was to ensure a reasonable sample size while also being able to compare behaviour among months.

### 2.5.1 Pre-analytical data processing

In order to quantify the cod's movement behaviour we used a position estimation algorithm proposed by Simpfendorfer et al. (2002). This 'position averaging' method uses raw output files from VUE (receiver logs) to estimate the average horizontal position (latitude and

longitude) of each fish during sequential time period intervals of 30 minutes. The outcome yields each fish's short-term centre of activity (30 min), rather than providing its exact position estimate at a given time (Simpfendorfer et al. 2002). Depth information was added to the averaged positions in order to create a more comprehensive spatial picture where both vertical and horizontal positions could be examined. To produce metric measurements, the coordinates were converted from geographic Lat/Lon to UTM (Universal Transverse Mercator).

This position averaging output can be utilized for numerous further analyses on the fish's movement behaviour to produce estimates of vertical and horizontal positioning (cumulative distance travelled, home range, net movement and depth utilization).

### **Home range estimation**

Burt (1943) defined an animal's home range as "... that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range", meaning the spatial distribution of the behaviours animals undertake to survive and reproduce. For the purpose of this study, home range was defined as the area where the individual is expected to be located 95% of the time; the area containing 95% of the individuals utilization distribution (Gitzen, Millspaugh & Kernohan, 2006; Worton, 1989). By using 95% (compared to 100%) one omits the occasional exploratory movements that are considered to be outside the animal's normal activity space (Burt, 1943). Core area was also identified (UD50), which is the activity space most frequently utilized (highest importance). Home ranges were estimated by applying standardized kernel density estimation with a kernel smoothing parameter of 50 (user defined bandwidth,  $h_0=50$ ) which produced a biologically sound home range output for all cod. A standardized smoothing parameter makes comparisons of home range sizes possible, while at the same time ensuring reproducibility of results.

Home range size was estimated across two different temporal scales (for comparison only) – (1) monthly for June, July and August and (2) for the whole period the fish was present within the study area - where the former estimates were utilized further in the data



processing process. Home range location and size were identified using the R package 'adehabitat' (Calenge, 2006).

### **Cumulative distance travelled**

Cumulative distance travelled is the sum of all movements undertaken by the fish at a given time interval. Extracting all coordinates from the position average output file made it possible to calculate the cumulative distance by adding up the distance measurements between detection coordinates.

### **Depth measurements**

Mean, minimum, maximum depth and vertical range was calculated from the position averaging output file.

### **2.5.2 Model selection**

Linear Mixed-Effect Models (LME) (Pinheiro, Bates, DebRoy & Sarkar, 2002; Zuur, 2009) were fitted to analyse the effects of month (M; categorical variable with three levels, 6, 7, 8), body length (L; continuous variable), K-factor (K; continuous variable), length at age 1 ( $L_1$ ; continuous variable), presence of gill parasites, fish lice and black spots (GP, FL, BS; all categorical variables with two levels, 1=present, 0=absent) on one of the six response variables; home range size (HR), cumulative distance (CUMDIST), minimum depth (MINDEPTH), maximum depth (MAXDEPTH), mean depth (MEANDEPTH) and vertical range (RANGE). All response variables were numeric and all, excluding Range and Maxdepth, were log-transformed. The seven covariates were fitted as fixed effects, not including any interactions terms seeing that it would not make biological sense to do so. Individuals (ID) were modelled as random factor; when random factor is specified the randomness inherent in the data (repeated observations of individuals) is accounted for and so one overcome pseudoreplication (Millar & Anderson 2004). The response variables were chosen on the basis that they prove relevant when evaluating fish's spatial ecology and the explanatory variables were considered appropriate to represent factors able to influence the fish's movement behaviour.

Both top-down and step-up manual model selection was performed by comparing second order Akaike Information Criterion (AICc) values of a set of a priori selected candidate

models (Burnham & Anderson 2002). AIC provides an estimate of model suitability based on a trade-off between goodness of fit and model complexity/parsimony (number of parameters included, addition of parameters penalizes model AIC) (Bozdogan, 2000). By using second order AIC (AICc) a small sample size ( $n=39$ ) is corrected for (Hurvich & Tsai 1989; Burnham & Anderson 2002). When comparing models, the simplistic measure delta AICc was employed, which allowed us to evaluate each model relative to the best model and when  $\Delta AICc$  is  $>2$  the model is said to have substantial evidence for its validation (Burnham & Anderson 2002).

Models were fitted using Maximum Likelihood (ML) estimation via the *lme* function in the R library *nlme* (Pinheiro et al., 2002). Model selection was carried out for all response variables (Appendix 5; Table 10).

# 3 Results

## 3.1 Cod body size and parasites

Cod size ranged from 30 to 80 cm (Figure 3). Tagged cod had a mean length of 47 cm ( $\pm 11.2$  SD) and the portion of the fish included in the data analyses had a mean total length of 49.3 cm ( $\pm 12.1$  SD) and a weight range from 0.28 to 4.76 kg, where mean weight measured was 1.34 kg ( $\pm 0.98$  SD). Of all the cod tagged, I observed 64 fish infected with Black spot disease (*Cryptocotyle lingua*), 14 with Gill parasites (*Lernaeocera branchialis*) and 36 with Fish lice (*Caligus elongates*). For simplicity, the abbreviations BS, GP and FL will be used to describe these parasites from here onwards.

Condition factor (K) and length at year 1 ( $L_1$ ) was calculated: K ranged from 0.78 to 1.18 and had a mean of 0.98 ( $\pm 0.9$  SD);  $L_1$  ranged from 9.2 to 26 cm and with a mean of 15.4 cm ( $\pm 4.2$  SD).

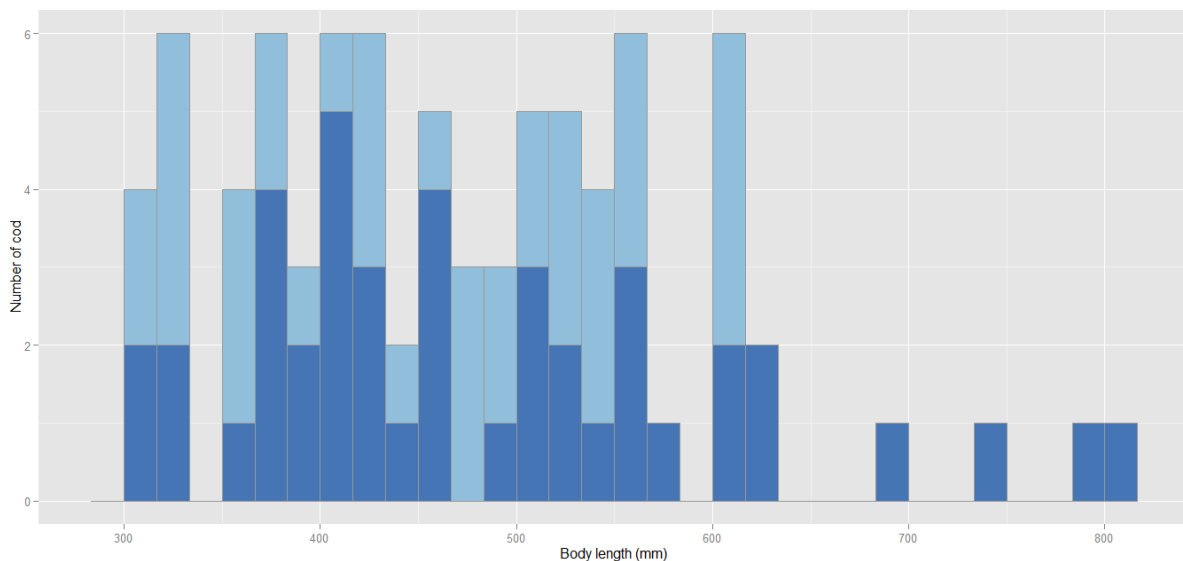


Figure 3 Size distribution of cod captured, tagged and released in Sømskilen, Skagerrak in 2012. Light blue: all tagged cod; Dark blue: portion of the tagged cod which was included in the behavioural analyses.

## 3.2 Age estimation from scales

Age was estimated for all but five fish, where regenerated scales proved unreadable (Figure 4 and Figure 5). Cod age ranged from 2 to 6 years, where mean age of the fish in my study was 3.4 years (Table 1).

**Table 1** Estimated age of cod based on three separate readers.

<b>ID</b>	<b>Age</b>	<b>ID</b>	<b>Age</b>
7288	2	7338	4
7293	3	7339	5
7298	3	7341	3
7300	2	7342	3
7303	2	7343	5
7305	4	7344	5
7306	3	7346	4
7307	2	7347	4
7308	3	7349	2
7309	3	7351	4
7311	2	7353	3
7312	3	7356	3
7313	3	7357	6
7314	5	7358	4
7318	3	7359	4
7321	3	7360	4
7325	2	7362	3
7327	4	7363	6
7328	5	7364	3
7333	4	7365	2
7334	4	7366	3
7336	3		

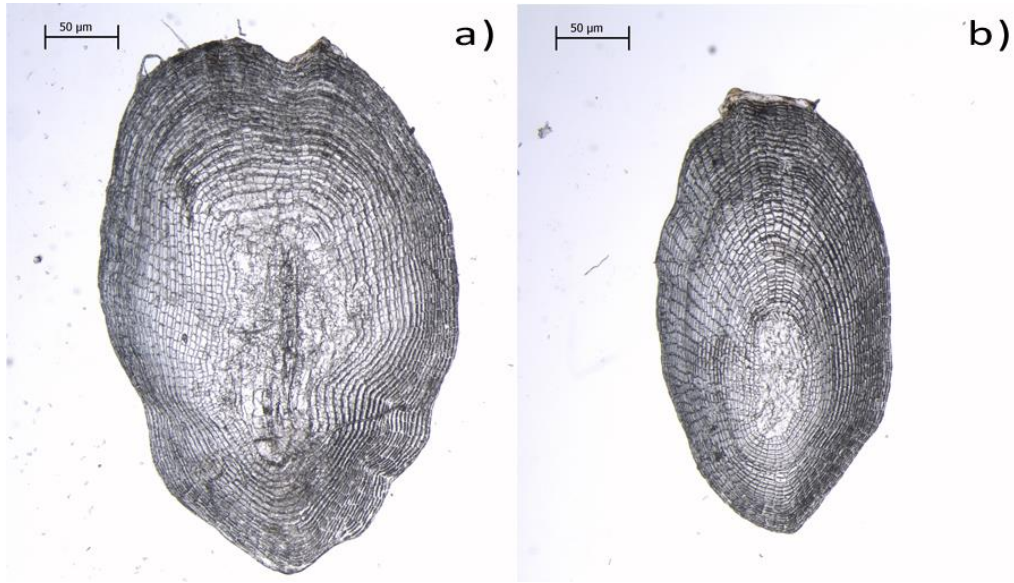


Figure 4 Two examples of regenerated cod scales; a: scale from cod measuring 60cm; b: scale from cod measuring 39cm.

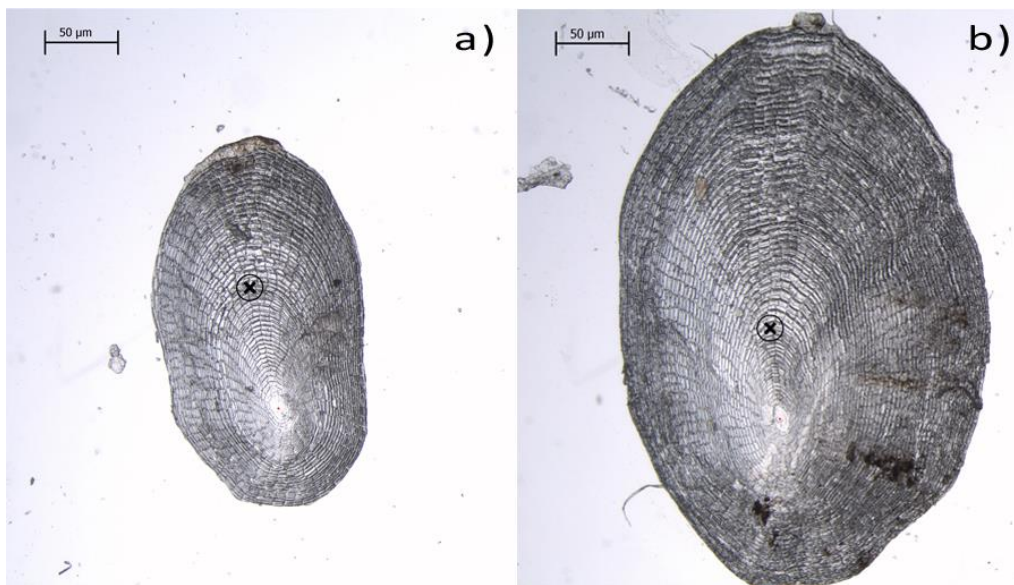


Figure 5 Two examples of typical cod scales where the first estimated growth increment have ( $L_1$ ) have been marked off; a: scale from cod measuring 37 cm; b: scale from cod measuring 69 cm.

### 3.3 Home range sizes

The home range sizes (95% kernel UD) varied substantially among individuals, ranging from 0.094 km<sup>2</sup> to 4.87 km<sup>2</sup> for the whole study period (June-July-August), with mean monthly HR being 0.97 km<sup>2</sup> ( $\pm 1.07$  SD). Monthly variations in average HR were also apparent with June yielding an average HR size 0.92 km<sup>2</sup> ( $\pm 0.87$  SD), while July yielded 0.43 km<sup>2</sup> ( $\pm 0.23$  SD) and August 1.56 km<sup>2</sup> ( $\pm 1.43$  SD). Examples of individual home ranges are provided in Figure 6- Figure 10.

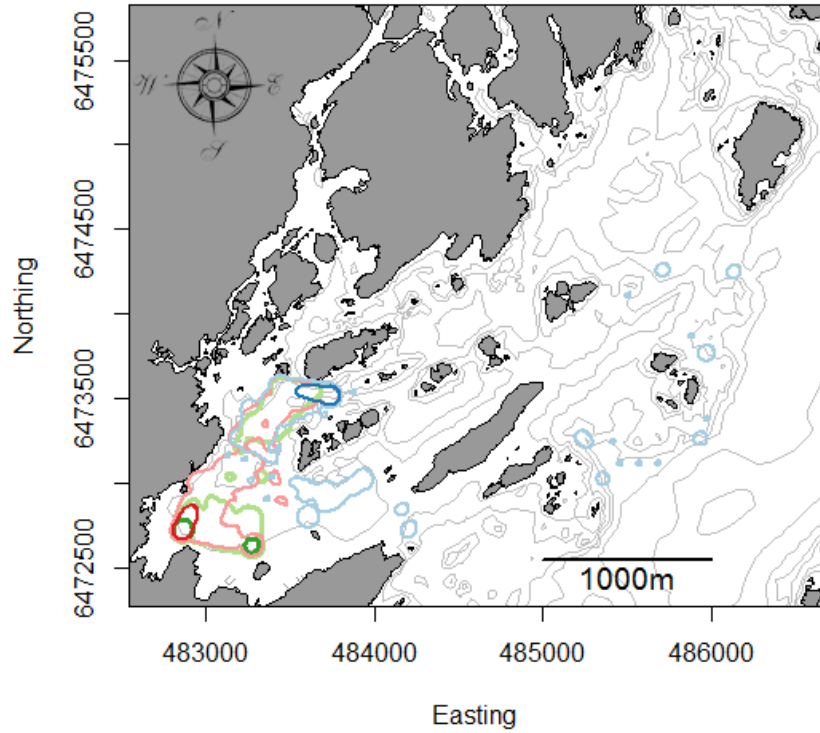


Figure 6 Home range estimate for fish 7298 (33 cm); green lines represents home range estimated from June; red lines represents home range estimated from July and blue lines represents home range estimated from August. Lighter coloured lines indicate the 95% kernel UD and darker coloured lines indicates the core HR area (50% kernel UD).

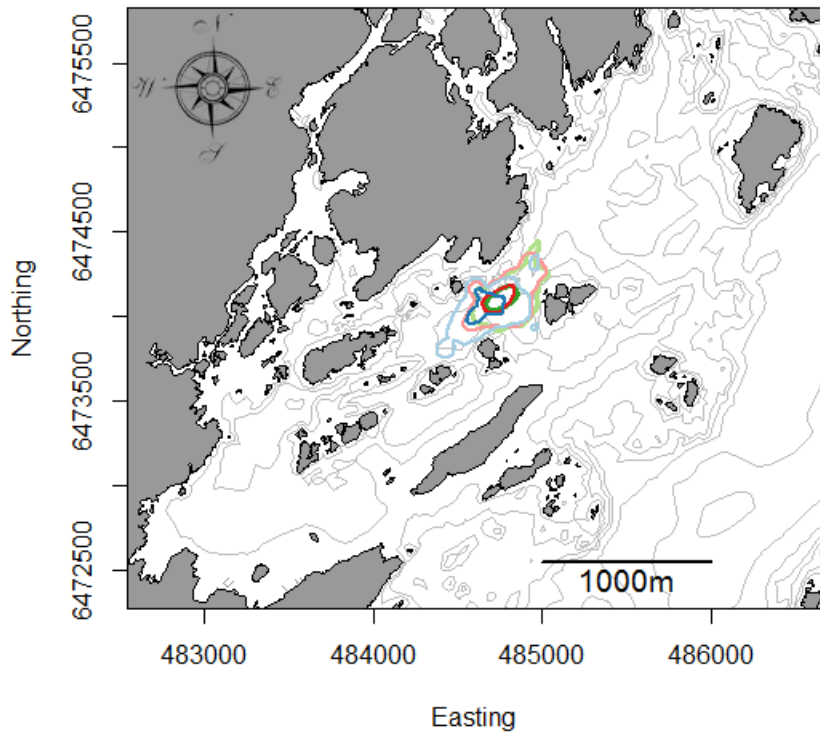


Figure 7 Home range estimate for fish 7303 (40 cm); green lines represents home range estimated from June; red lines represents home range estimated from July and blue lines represents home range estimated from August. Lighter coloured lines indicate the 95% kernel UD and darker coloured lines indicates the core HR area (50% kernel UD).

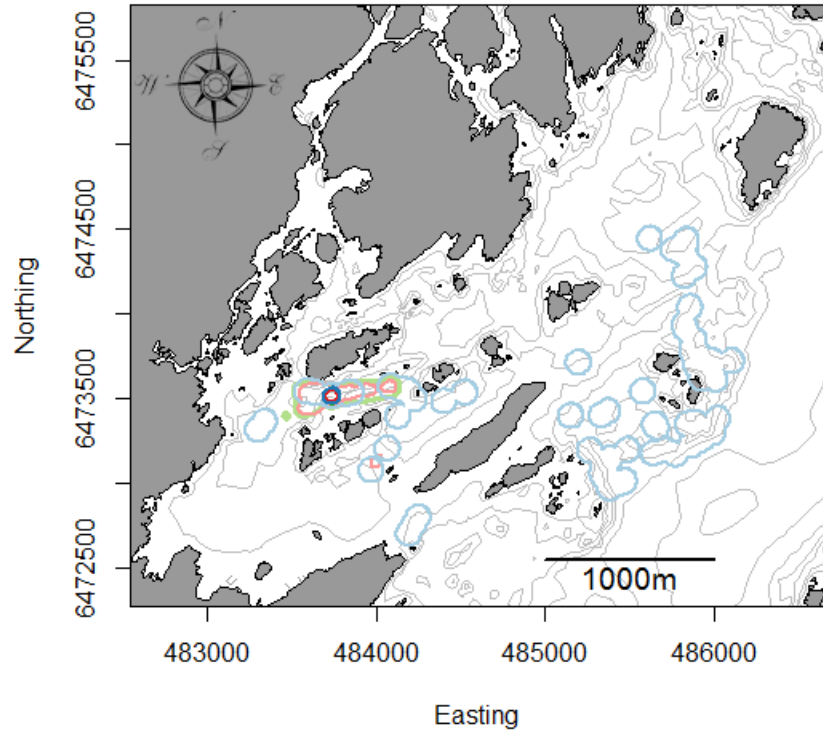


Figure 8 Home range estimate for fish 7328 (69 cm); green lines represents home range estimated from June; red lines represents home range estimated from July and blue lines represents home range estimated from August. Lighter coloured lines indicate the 95% kernel UD and darker coloured lines indicates the core HR area (50% kernel UD).

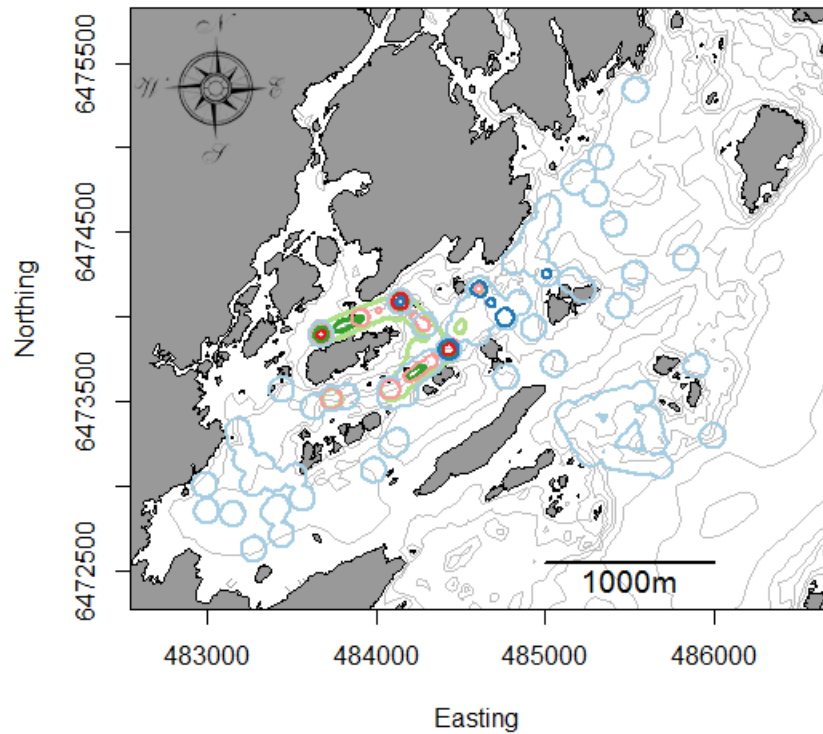


Figure 9 Home range estimate for fish 7344 (56 cm); green lines represents home range estimated from June; red lines represents home range estimated from July and blue lines represents home range estimated from August. Lighter coloured lines indicate the 95% kernel UD and darker coloured lines indicates the core HR area (50% kernel UD).

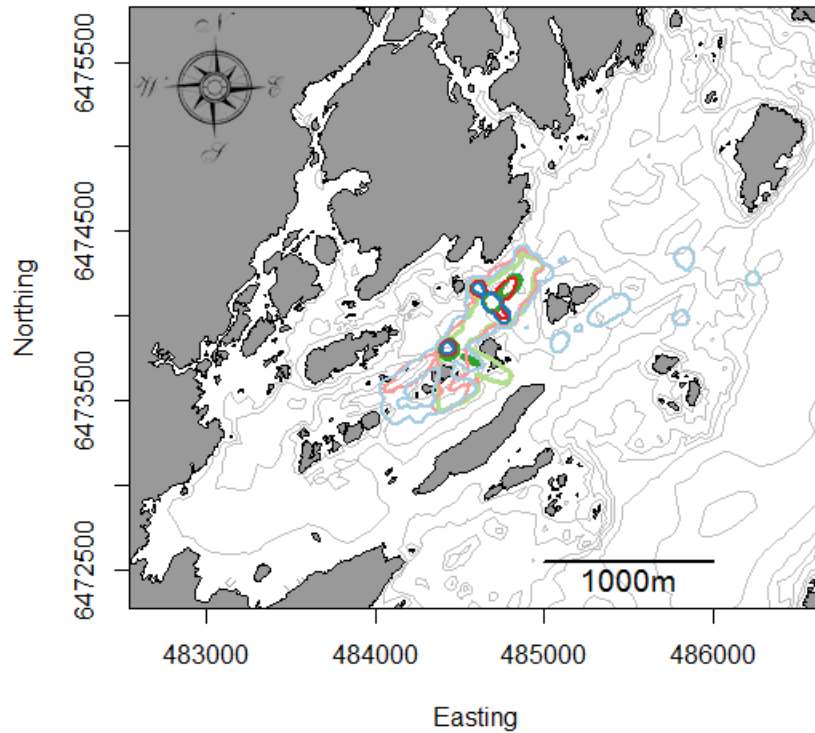


Figure 10 Home range estimate for fish 7363 (79 cm); green lines represents home range estimated from June; red lines represents home range estimated from July and blue lines represents home range estimated from August. Lighter coloured lines indicate the 95% kernel UD and darker coloured lines indicates the core HR area (50% kernel UD).

The statistical modelling supported these observations on home range variation. The most parsimonious model explaining home range variation included Month, Length<sub>1</sub> and BS as an explanatory variable. The second best alternative model ( $\Delta$  AIC 1.78) included additionally K-factor and GP as explanatory variables. Because of the similarity of AIC values between these two models ( $< 2$  units), model selection is not straightforward. As a conservative approach, inference was based on the simpler model (Table 2).

Table 2 Results of linear mixed-effect models of home range (km<sup>2</sup>) from 39 tagged cod in Sømshølen in the Skagerrak, Norway, in 2012. Random effect is cod ID. Parameter estimates are log transformed. Bold CI values indicate important model variables.

Variable	$\Delta$ AICc	Estimate	SE	p	95% confidence interval	
					Lower	Upper
<b>Model 1</b>	<b>0.00</b>					
Intercept		13.150	0.439	0.000	12.295	14.005
July		-0.336	0.159	0.038	<b>-0.645</b>	<b>-0.027</b>
August		0.441	0.159	0.007	<b>0.132</b>	<b>0.750</b>
Length <sub>1</sub>		-0.003	0.002	0.265	-0.007	0.002
BS_1		0.592	0.218	0.011	<b>0.159</b>	<b>1.025</b>



### 3.4 Cumulative distance

Cumulative distance travelled by individual cod ranged from 9.96 km to 185.93 km for the whole study period (June-July-August), with mean cumulative distance being 115.93 km ( $\pm 39.23$  SD). The between-month variations in average cumulative distance were as following; June having an average of 125.65 km ( $\pm 32.78$  SD), while July had 114.49 km ( $\pm 39.08$  SD) and August had 107.43 km ( $\pm 43.88$  SD).

The most parsimonious model explaining variation in cumulative distance moved included Month, Length, Length<sub>1</sub> and BS as explanatory variables. The second best alternative model included only Length, Length<sub>1</sub> and BS as explanatory variables ( $\Delta$  AIC 1.86). Although included in both the best models, the estimated effects of Length and Length<sub>1</sub> were small and with confidence intervals overlapping zero (Table 3). The model chosen for inference (Table 3) indicated that BS infection had a positive effect on cumulative distance moved.

**Table 3 Results of linear mixed-effect models of cumulative distance travelled (km) from 39 tagged cod in Sømskilen in the Skagerrak, Norway, in 2012. Random effect is cod ID. Parameter estimates are log transformed. Bold CI values indicate important model variables.**

Variable	$\Delta$ AICc	Estimate	SE	p	95% confidence interval	
					Lower	Upper
<b>Model 1</b>	0.00					
Intercept		11.898	0.249	0.000	11.416	12.380
July		-0.126	0.057	0.032	<b>-0.236</b>	<b>-0.015</b>
August		-0.126	0.057	0.031	<b>-0.237</b>	<b>-0.015</b>
Length		-0.001	0.001	0.010	-0.002	0.000
Length <sub>1</sub>		0.002	0.002	0.302	-0.001	0.005
BS_1		0.341	0.125	0.010	<b>0.095</b>	<b>0.588</b>

### 3.5 Vertical selection

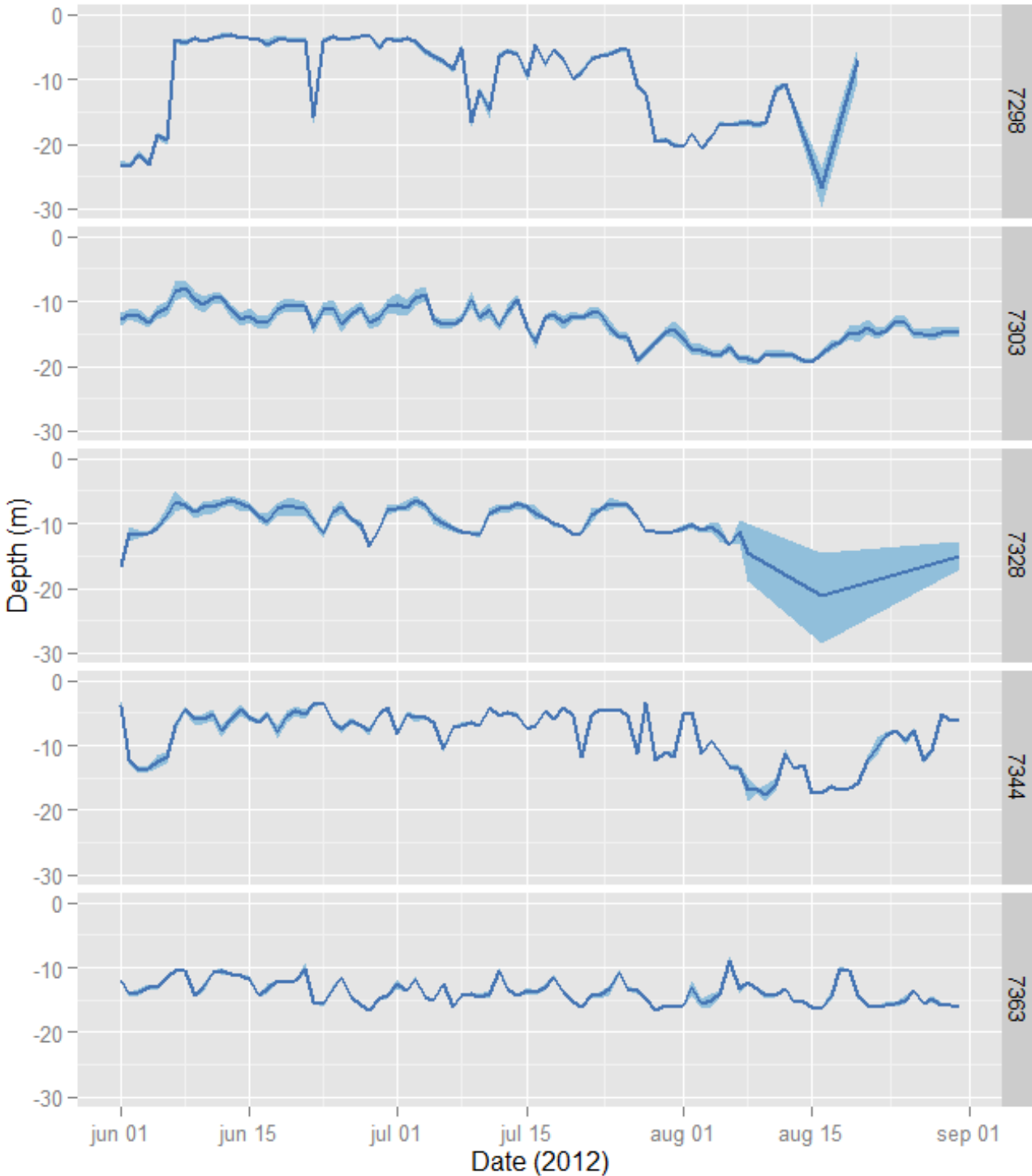


Figure 11 Vertical range for fish 7298 (33 cm), 7303 (40 cm), 7328 (69 cm), 7344 (56 cm) and 7363 (79 cm). Blue line: mean depth; light blue shading: min and max depth.

### 3.5.1 Mean depth

The overall mean depth throughout the study period for all cod was 13 m ( $\pm 4.7$  SD). The between-month variations in mean depth were as following; June having a mean of 11.56 m ( $\pm 4.13$  SD), while July had 12.49 m ( $\pm 4.02$  SD) and August had 15.22 m ( $\pm 5.19$  SD). Individual examples of depth use are provided in Figure 11.

Statistical modelling supported the effect of Month on mean depth. The most parsimonious model included Month, Length<sub>1</sub> and BS as explanatory variables. Two alternative models also received some support (within 2 AIC units of the selected model). One of these included Month, Length<sub>1</sub>, FL and BS ( $\Delta$  AIC 1.22), while the other candidate model included Month, Length<sub>1</sub>, K-factor and BS ( $\Delta$  AIC 1.47). The most parsimonious model suggested that fish infected with BS occupied somewhat deeper waters than non-infected fish (Table 4). The effect of Length<sub>1</sub> was not clear (Table 4).

**Table 4 Results of linear mixed-effect models of mean depth (meter) from 39 tagged cod in Sømskilen in the Skagerrak, Norway, in 2012. Random effect is cod ID. Bold CI values indicate important model variables.**

Variable	$\Delta$ AICc	Estimate	SE	p	95% confidence interval	
					Lower	Upper
<b>Model 1</b>	0.00					
Intercept		1.998	0.232	0.000	1.547	2.449
July		0.086	0.055	0.126	-0.022	0.194
August		0.261	0.055	0.000	<b>0.153</b>	<b>0.369</b>
Length <sub>1</sub>		0.001	0.001	0.354	-0.001	0.004
BS_1		0.250	0.116	0.040	<b>0.019</b>	<b>0.481</b>

### 3.5.2 Min depth

Minimum depth recorded ranged from 0 to 10 m, with the average min depth recorded across individuals were 2.12 m ( $\pm 1.93$  SD). The between-month variations in min depth were as following; June having a mean of 1.91 m ( $\pm 1.72$  SD), while July had 1.87 m ( $\pm 1.63$  SD) and August had 2.57 m ( $\pm 2.33$  SD).

Model selection indicated that none of the explanatory variables had clear effects on minimum depth used. The most parsimonious model included an effect of Length<sub>1</sub>, but this

effect was unclear with confidence interval overlapping zero (Table 5). An alternative model also including an effect of FL had a fairly similar AIC score ( $\Delta$  AIC 0.86).

**Table 5** Result of linear mixed-effect model of minimum depth (meter) from 39 tagged cod in Sømskilen in the Skagerrak, Norway, in 2012. Random effect is cod ID. Parameter estimates are log transformed.

Variable	$\Delta$ AICc	Estimate	SE	p	95% confidence interval	
					Lower	Upper
<b>Model 1</b>	0.00					
Intercept		-2.775	1.556	0.079	-5.850	0.300
Length <sub>1</sub>		0.016	0.010	0.120	-0.004	0.035

### 3.5.3 Max depth

Maximum depth recorded ranged from 17 to 70 m, with average max depth being 27.95 m ( $\pm$ 9.32 SD). The between-month variations were as following; June having a mean of 26.76 m ( $\pm$ 7.39 SD), while July had 24.75 m ( $\pm$ 5.19 SD) and August had 32.35 m ( $\pm$ 12.33 SD).

Model selection on max depth resulted in three candidate models having fairly similar AIC scores ( $\Delta$  AIC < 2). The effect of Month on max depth was supported by all these three models. The most parsimonious model also included an effect of Length<sub>1</sub> and BS infection, but these effects were not very clear (Table 6). The two alternative models had Length<sub>1</sub> and K-factor ( $\Delta$  AIC 0.10) or Length<sub>1</sub>, K-factor and BS ( $\Delta$  AIC 1.70) as explanatory variables in addition to Month.

**Table 6** Results of linear mixed-effect models of maximum depth (meter) from 39 tagged cod in Sømskilen in the Skagerrak, Norway, in 2012. Random effect is cod ID. Bold CI values indicate important model variables.

Variable	$\Delta$ AICc	Estimate	SE	p	95% confidence interval	
					Lower	Upper
<b>Model 1</b>	0.00					
Intercept		38.27	8.89	0.00	20.97	55.58
July		-0.25	1.23	0.84	-2.65	2.14
August		3.90	1.23	0.00	<b>1.51</b>	<b>6.30</b>
Length <sub>1</sub>		-0.03	0.02	0.11	-0.07	0.01
BS_1		-8.90	8.03	0.28	-24.87	7.08

### 3.5.4 Vertical range

The cod's utilization of the water column (vertical range) varied during the study period, with minimum range comprised of 11.83 m and maximum range covered 62.49 m. Average vertical range recorded for all months was 25.82 m ( $\pm 9.16$  SD). The between-month variations in vertical range were as following; June having a mean of 24.84 m ( $\pm 7.67$  SD), while in July average vertical range was 22.88 m ( $\pm 5.45$  SD) and in August average vertical range utilized covered 29.79 m ( $\pm 11.91$  SD) of the water column.

Model selection supported effects of Month and Length<sub>1</sub> on vertical range, while an alternative candidate model including Month, Length<sub>1</sub> and K-factor as explanatory variables also scored well ( $\Delta$  AIC 1.67). The most parsimonious model indicated a negative effect of Length<sub>1</sub> on vertical range (Table 7).

**Table 7 Results of linear mixed-effect models of vertical range (meter) from 39 tagged cod in Sømskilen in the Skagerrak, Norway, in 2012. Random effect is cod ID. Parameter estimates are log transformed. Bold CI values indicate important model variables.**

Variable	$\Delta$ AICc	Estimate	SE	p	95% confidence interval	
					Lower	Upper
<b>Model 1</b>	0.00					
Intercept		29.309	2.946	0.000	23.543	35.075
July		-0.135	1.261	0.915	-2.602	2.333
August		3.277	1.261	0.012	<b>0.809</b>	<b>5.744</b>
Length <sub>1</sub>		-0.038	0.018	0.042	<b>-0.074</b>	<b>-0.002</b>

## 4 Discussion

With the aim of obtaining information on how behavioural traits and life history traits can influence cod's space use, I analysed patterns of movement and behaviour at different temporal scales and related this to the individual's 'life history traits'. Previous studies on animal activity patterns have found allometric relationships between home range size and body mass (e.g. Kramer & Chapman 1999; McNab 1963; Kelt & Van Vuren 2001), where Tupper & Boutilier (1995) found a parallel relationship between cod size and home range size. In my study I did not detect a correlation between size of individual fish and their home range size (as postulated), I did however observe that all movement behaviours (with the exception of minimum depth) varied on a temporal scale, and curiously, the presence of black spot disease was found to partly explain the variation observed in three of the investigated movement behaviours (cumulative distance, mean depth and home range size). This study provides new insights into how stationary coastal cod in my study area 'Sømskilen' behave and move. I discuss my findings in light of the stock status of Norwegian coastal cod on the Skagerrak coast, suggesting conservation initiatives and the need for direct management of these populations.

### 4.1 Horizontal activity patterns

Two horizontal movement behaviour parameters were examined; home range size and cumulative distance travelled.

Average home range size of cod was  $0.97 \text{ km}^2$ . A temporal variation in home range size was observed, with an 33.6% decrease in mean home range size from June to July;  $0.92 \text{ km}^2$  to  $0.43 \text{ km}^2$  and an 44.1% increase in August compared to June, when recorded mean home range size was  $1.56 \text{ km}^2$ . Home range size was also found to be correlated with prevalence of BS (59.2% increase; Table 2).

Temporal changes in cod's horizontal movement patterns are most probably related to the seasonal changes in water temperature and the concurrent effect temperature will have on the cod itself and the distribution of its prey species. Interestingly, the optimum temperature for fish depends on amount of food ingested, and a decrease in food ration results in a decrease in optimum temperature for growth (Brett, Shelbourn & Shoop, 1969).

Hop, Gjosaeter & Danielssen (1992) studied the feeding patterns of Norwegian coastal cod in Skagerrak over 3 consecutive years and found that diet composition vary seasonally, where cod rely more on pelagic food sources (increased frequency of fish and shrimp taken) during autumn and winter, compared to spring and summer. This may relate to the temporal variation observed in the horizontal distribution of cod where home range size decreased in July and increased in August. As feeding habits change temporally, so will the cod's spatial extent when the fish have to relocate in order to find the appropriate prey. In concordance to this, Lawson & Rose (2000) come to the conclusion that the local movements of coastal cod in Placentia Bay, Newfoundland, are related to depth and feeding behaviour (and not temperature based). Another study from the southern Gulf of St. Lawrence observed seasonal differences in what habitat variables that were associated with cod distribution; depth was postulated to be a predictor of prey distribution and thus controlling habitat choice during the summer feeding season; while temperature seemed to be the main controlling variable in winter when feeding rate was low; regardless of controlling variable, the cod were seen to occupy shallow waters during summer and deeper waters during winter (Swain, Chouinard, Morin & Drinkwater, 1998). However, the results above may not be transferrable to my study, due to the substantial size of both study areas and the associated great depth range and habitat.

Earlier studies have found a linear relationship between home range size and body size (e.g. Jetz et al. 2004; Kramer & Chapman 1999; McNab 1963), where larger animals inhabit a larger area. Fish size, nor length or length<sub>1</sub>, was not found to influence the home range size as predicted *a priori*. This prediction was based on extensive literature supporting the notion that larger animals require larger areas to compensate for their higher mass-specific energetic needs.

As mentioned above, home range size was found to be correlated with prevalence of BS. Black spot disease (*Cryptocotyle lingua*) is caused by an infection by a parasitic digenean worm (Class Trematoda), which uses fish as an intermediate host in their heteroxenous life cycle (Bricknell, Bron & Bowden, 2006). The black spots displayed on the host's body surface is a pigment reaction in the connective tissue sheath where the parasite (in a larval metacercaria stage) is encysted in the host tissue (Bricknell et al., 2006).

Parasites have the ability to manipulate nearly all aspects of their host's ecology by inducing physiological and/or mechanical changes (Neilson, Perry, Scott & Valerio, 1987), which can cause alternations in the community- and ecosystem structure that the infected animal belongs to (Thomas et al. 1999; Preston & Johnson 2012). Both physiological effects stemming from drained energy stores and mechanical effects can impede normal locomotion and bodily functions subsequently leading to substantial changes in the behavioural patterns exhibited by the affected individual.

In my study, home range size of cod was found to be influenced by the presence of black spot disease (*C. lingua*), where infected animals showed an increase in home range size. I could not find any causative explanation to this in the reviewed literature, relating to a correlation between black spot disease and changes in host activity pattern, *per se*. The reason for a lack of resources on this area could be that it is a neglected topic, seeing that the common belief is that the parasite only occupy fish as a dormant stage in its life cycle (Davies & Knowles, 2001), unable to affect the host. Fish acts as *C. lingua*'s second intermediate host and the parasite's final and definitive hosts are piscivorous birds and mammals in which they metamorphose into adult forms (Bricknell et al., 2006).

Barber & Wright (2005) point out that since *C. lingua* also can encyst in the cornea, it is expected to cause vision impairment and consequently bring about behavioural changes, but it is hard to relate this to my study seeing I did not take notes on presence of eye-cysts and it currently remains as an untested theory in the literature (Barber & Wright, 2005).

A plausible explanation for an increase in home range size with presence of parasitism could be that *C. lingua* is in fact able to manipulate the cod's behaviour, perhaps in ways that makes the fish more susceptible to predation, benefiting the parasite's transmission to their definitive hosts (Lafferty 1999; Thomas et al. 2005; Poulin 2010; Hammond-Tooke et al. 2012). By increasing a fish's boldness and exploratory level and concurrently its activity level, the cod may become more vulnerable to predation and the parasite will complete its life cycle (Wootton, 1998). Earlier studies on parasite-host interactions confirm this. An example from the model species three-spined stickleback (*Gasterosteus aculeatus*) infected with multiple cestode parasites (*Schistocephalus solidus*) display impeded swimming ability and were found to swim nearer the surface where they were more at risk from avian predation (Barber & Huntingford, 1995; Giles, 1983, 1987;



Ness & Foster, 1999). I can only speculate whether this change in behaviour applies for *C. lingua* as well, however, more research is needed to confirm or refute this theory.

Other ectoparasitic infections, such as gill parasites (*Lernaeocera branchialis*) and fish lice (*Caligus elongates*), are found to cause mortalities and a several other health issues in their hosts. *L. branchialis* infections have the potential to induce anaemia, lower haemoglobin levels, weight loss (emaciation), lower reproductive capacity, reduce liver lipid content, reduce circulation (poorer oxygen absorption), delay gonadal maturation, lower fecundity and reduce growth rate, all which may contribute to a display of abnormal behaviour (Khan & Lacey, 1986; Khan, 1988) subsequently increasing the infected fish's susceptibility to stress and predation (Hemmingsen & MacKenzie, 2001; Khan & Lacey, 1986).

One can speculate whether the right distinction have been made between cause and effect; it seems more probable that fish exhibiting a more explorative behaviour are more likely to be more exposed to habitats with higher infection rates, namely shallow littoral areas where the parasite's first intermediate host resides; the periwinkle species *Littorina littorea* (Davies & Knowles, 2001). Supporting evidence for this theory is provided by the results from cumulative distance analysis, where presence of *C. lingua* is correlated with an increase in cumulative distance travelled (34.1% increase; Table 3).

Cumulative distance travelled also appears to vary temporally, where a 12.6% decrease was observed in both July and August. This suggests that as summer progresses the cod become less active in their movements. A likely explanation for this can be that during summer the cod's feeding regime changes, from a more pelagic based prey selection to predominantly relying on benthic prey items (Hop et al., 1992). Benthic feeding may provide a less abundant, yet more constant source of food, making a switch from active to more passive feeding behaviour (Salvanes, Skjæraasen & Nilsen, 2004) and subsequently lowering the cumulative distance travelled by the individuals. This observed temporal shift in activity pattern show that the fish display a plastic response in accordance with changes in their surrounding environment, thus not conforming to the concept of intra-individual behavioural stability proposed by Réale et al. (2007).

## 4.2 Vertical activity patterns

Four vertical movement behaviour parameters were examined; minimum, maximum, mean depth and vertical range.

Average minimum depth utilized was 2.12 m ( $\pm 1.93$  SD) for the whole study period, and little temporal variation was found; no variable was seen to affect minimum depth (Table 5).

Average maximum depth recorded was 27.95 m. A temporal variation was observed; in June the majority of the fish were found in waters holding a maximum depth of 26.76 m ( $\pm 7.39$  SD), in July the fish made local movements into shallower grounds holding a maximum depth of 24.75 m ( $\pm 5.19$  SD) before moving into deeper waters in August, at 32.35 m ( $\pm 12.33$  SD). Together with mean depth (which increased in July) and vertical range (which decreased in July), all three parameters were found to significantly increase in August. Several factors may influence a cod's vertical position; biotic interactions (prey assemblage, predation risk), the physio-chemical properties of its environment (light, current speed, temperature, salinity, oxygen, hydrostatic pressure), the cod's internal environment (satiation level, physiological condition, body size and swimbladder volume) (Løkkeborg, 1998; Strand & Huse, 2007; Wootton, 1998) and these factors' concurrent influence on feeding. My study took place outside of the spawning season so spawning is excluded as an explanatory factor here, likewise is predation as cod in this size range experience negligible predation pressure (human predation omitted) (Pálsson, 1994).

The vertical distribution of cod in Sømiskilen could well be determined by its ambient environment, such as the thermocline and pycnocline. Previous studies indicate that the coastal cod exhibit vertical migrations in relation to temperature (Danielssen & Gjørseter, 1994; Danielssen, 1969; G. Dannevig, 1966; Fromentin et al., 2000), where the fish respond to seasonal temperature fluctuations in the water column, residing in shallow water during autumn and spring and moving deeper during summer and winter months. No physio-chemical measurements were obtained during my study, but by extrapolating temperature data from Flødevigen's continuous measuring database, an inverse trend in mean cod depth and temperature was found (Appendix 4, Figure 14). The fact that the fish went deeper down when temperature in the water column rose during the summer months agrees with

the literature, but seeing that the Flødevigen's dataset only represents thermal data from one location, the results from this remain speculative.

Cod is an opportunistic, omnivorous benthic feeder, and during 1987-1989, Hop et al. (1992) studied the seasonal feeding patterns of two populations belonging to the Skagerrak coastal cod stock: in Risørfjord and in the Flødevigen area. They found that the diet composition varied seasonally for all size-classes, but since the medium-sized fish (15-45 cm) is the size-class comparable to my study population (median fish size = 46 cm), the main focus here will be on their diet composition. Their spring (April-May) diet consisted mainly of bivalves, polychaetes, decapods, amphipods and fish (compared to the diet of larger cod (> 60 cm) which included polychaetes, fish, anomuran- and brachyuran crabs). During summer (June-July) cod consumed a reduced amount of fish, but the frequency of decapods increased (especially anomuran crabs); prey items also included gastropods, polychaetes and amphipods (larger cod ate almost exclusively brachyuran crabs and fish). In autumn (August-November) occurrence of fish in the diet increased, as did frequency of brachyuran crabs (while the larger fish continued to predominantly prey on brachyuran crabs and fish).

In summary, the findings of Hop et al. (1992) suggest that cod feed deeper down in the water column as summer and autumn progresses, preying more on benthic, rather than pelagic, organisms. This feeding pattern corresponds with my results, where the individuals were observed to occupy greater depths in August.

Numerous studies have discussed organism's diel vertical migration (DVM) patterns, where the typical DVM behaviour exhibits a recurrent shift between residing nocturnally in shallow water and diurnally in deep water. It is hypothesized that this behaviour acts as a trade-off between foraging success and predator avoidance (e.g. Clark & Levy, 1988) or that DVM is related to the physiological state of the animal and its thermoregulatory strategy (as mentioned previously). No temperature measurements were obtained during my study, likewise, I did not examine the cod's diel vertical behaviour, but I believe the incentives behind DVM are transferrable for a larger temporal scale and can account as plausible explanatory variables for the monthly variations observed in the vertical migrations in my study. My fish occupied deeper ranges during the course of summer, subsequently as the water column heated up, which is the same pattern observed for cod diurnally. Espeland et al. (2010) proposed that the fish in their study (body length = 26-45 cm) indeed utilize DVM

as a response to ambient temperature and food availability; therefore it can be reasonable to assume that the fish in this study were seeking deeper down in cooler waters to achieve thermoregulation necessary for optimal digestion.

### 4.3 Unknown and un-included variables

My study was undertaken with the *a priori* assumption that fish size and condition (K-factor) would account for the majority of the variation seen in an individual's behavioural pattern. But contradictory to my beliefs, this was not seen. This means that there are other factors, of either biological and/or ecological origin, not included in my analysis which may account for the observed variation in the activity- and behavioural patterns.

Other variables which would have been interesting to incorporate include; temperature (temperature preferendum), sex (sex-biased patterns of activity), growth rate, habitat characteristics, spawning site, stomach contents (prey selection), salinity and bathymetry (position in relation to seabed).

Further, diurnal vertical activity patterns (DVM) and sources for variation in condition of the fish would have been interesting to examine. Additionally, extending the study to incorporate a whole year and investigating the occurrence of seasonal changes in cod behaviour would have been very interesting to look at. Extending the study period sounds good in theory, but may prove difficult in practice seeing that cod mortality in Sømiskilen have been found to be as high as 75 % (Olsen & Moland, 2011).

### 4.4 Evaluating study design uncertainties and potential sources of error

Statistical uncertainties arise when numerous analyses (other than LME) can create similar results; movement patterns and abundance of coastal cod have been studied earlier by utilizing GAMs (Generalized additive models) (Cardinale & Svedäng, 2004; Espeland et al., 2010; Espeland et al., 2008); likewise, GLMs have been utilized in analyses investigating the relationship between home range and its predictors (e.g. in turtles: Seminoff, Resendiz, & Nichols (2002); in roe deer: Börger et al. (2006); or for Mary River cod, *Maccullochella peelii*

*mariensis*: Simpson & Mapleston (2002); Cardinale & Svedäng (2004) also used GLM in their cod abundance analyses).

Since only 39 individuals were included in the analyses, there is a potential risk that the fish are not a representative sample of the population; these fish are the ones that entered the fyke nets, meaning that my sample could be comprised of fish that exhibit a more active and/or bold behaviour and may so be biased. This is speculative of course; a large variation in activity pattern was indeed found (mean HR size  $2.52 \text{ km}^2 (\pm 1.6)$ ), so the sample may very well be a true subset of the Sømskilen cod population.

When estimating home range size, a fixed smoothing parameter was used across all individuals ( $h_0=50$ ). Choosing the optimal smoothing parameter is important as smoothing is a bias-variance trade-off aimed to increase precision while lowering bias (Simonoff, 1996). Increasing the smoothing parameter results in a loss of detail, while a lowering causes details to be highlighted leading to increased fragmentation of the mapped area (Powell, 2000). Knowing the theory behind optimal smoothing parameters and observing the change in practice by testing a wide range of kernel sizes (10 – 90), in addition to trying out the mean square error (MSE) method, a fixed kernel size of  $h_0=50$  was found to yield the most reasonable output and allowed for comparisons among individuals.

Even though age was excluded from all analyses (as it showed a strong correlation with length), it is worth mentioning that age estimation should be carried out with caution. Distinguishing the growth increments on cod scales can be very difficult as the fish does not experience significant periods of slow growth and its these zones ('winter zones'), which forms as more tightly deposited circuli, that are counted. There are also issues regarding false zones, which may appear due to unusual events (e.g. atypical temperature), spawning, disease and so forth. In addition, cod growth is not linear (Dannevig, 1933; Summerfelt & Hall, 1987; Wootton, 1998), as younger fish are seen to have a higher growth rate than older conspecifics. This can have resulted in ages being underestimated for older individuals.

Further, when the proportionality between fish length and scale circuli is weak (non-linear), back-calculation methods for estimating length at year 1 ( $L_1$ ) prove unreliable (Ibáñez, Britton & Cowx, 2008).

Age estimation validation could have been better. When scale samples were taken,

replication was not considered and a random number of scales were collected. In order to account for intra-individual variation in scale formation and growth, a minimum number of scales should be collected; Graham (1915) proposes to examine at least 10 scales per individual, Ericksen (1999) recommends no less than 20 scales and Kennedy (1970) collected about 50 scales from each individual and estimated ages based on at least 3 scales. To test the reproducibility of the ageing, scales should be read by more than one reader over several reading intervals (e.g. Ericksen (1999) propose at least 3 separate readings). Kennedy (1970) validated his estimations by reading 4 scale samples at two separate occasions at intervals of more than 1 month, this yielded identical readings 85% of the time (while 98.5% of the readings differed by no more than 1 year). The age estimation carried out by the readers here showed poor agreement: 46.3%, 24.4% and 65.8% agreement between the 3 independent readers. This demonstrates that a different approach to validate the age estimation should have been used and that the validity of the  $L_1$  variable is dubious and hence pose as a poor factor for explaining the variation in depth range (as found in my analysis).

## 5 Conclusion and conservation incentives

This study illustrates that behavioural traits vary on a temporal scale; and that predictions based on populations of conspecifics are scale dependent.

Both horizontal and vertical activity patterns changed over the course of summer, where cod were observed to become less active (lower cumulative distance) while inhabiting a wider range (larger home range) at greater depths at the end of the study period. My findings are somewhat inconclusive as no causality could be attributed to the shift in behaviour, but ultimately, I believe that the horizontal shifts reflects- or are a consequence of the vertical shifts that the fish make in order to seek optimal temperatures, something that superimposes a shift in diet composition – or vice versa.

The localized sub-populations of coastal cod in Skagerrak, with their distinctive demographic properties and inherent residency, are especially vulnerable to the effects of destructive external forces (e.g., localized overfishing, climate change, pollution (Ames, 2004; R. Myers, Barrowman & Hutchings, 1997)).

The Rio Declaration presented in 1992 at the Earth Summit presents 27 extensive principles concerning the environment and sustainable development, emphasizing for instance the necessity for all citizens to address environmental issues and Principle 15 explicitly states that *“In order to protect the environment, the precautionary approach shall be widely applied by States according to their capabilities. Where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation”* (Strong, 1992; UN, 1993). In accord with this, at the World Summit on Sustainable Development in 2002 a commitment was made to rebuild the world’s fish stocks to their maximum sustainable yield levels by 2015.

The conservation of intraspecific diversity is, as mentioned, crucial for the persistence of small stationary populations (e.g. Ryman, Utter & Laikre, 1995); these populations should, in theory, be protected by the Rio Convention on Biodiversity. In light of the positive response even a partial protection had on the Atlantic cod population in a Marine Protected Area on the Skagerrak coast (Moland et al., 2013), we see what ‘little’ initiative it takes to

make a big difference. In only four years the cod within the MPA were on average 5 cm longer than the cod within the control areas. In addition to increasing population density and fish size of the target species, MPAs provide protective measures on many levels, e.g., conserve the intraspecific genetic diversity, have the ability to restore the population's natural age structure, increase the productivity of the ecosystem and the MPA will benefit the ecosystem(s) on a multispecies level (Roberts, Hawkins & Gell, 2005 and references therein). It is postulated that MPAs can prove highly efficient when protecting populations relying on a confined spatial scale such as stationary coastal cod populations, but in order to implement ecologically meaningful marine reserves, robust knowledge and understanding of habitat use, movement and behavioural patterns need to be obtained.

I suggest complementing population based fishery management with MPAs to protect and conserve the biodiversity of both highly mobile and strictly resident species for persistence into the future.



## 6 References

- Ames, E. (2004). Atlantic cod structure in the Gulf of Maine. *Fisheries*, 29(1), 10–28.
- Barber, I., & Huntingford, F. (1995). The Effect of *Schistocephalus solidus* (Cestoda : Pseudophyllidea) on the Foraging and Shoaling Behaviour of Three-Spined Sticklebacks, *Gasterosteus aculeatus*. *Behaviour*, 132(15/16), 1223–1240.
- Barber, I., & Wright, H. (2005). Effects of parasites on fish behaviour: interactions with host physiology. *Behaviour and Physiology of Fish*, 24, 109–149. doi:10.1016/S1546-5098(05)24004-9
- Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *The Journal of Animal Ecology*, 78(4), 699–714. doi:10.1111/j.1365-2656.2009.01531.x
- Bell, A. (2005). Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, 18, 464–473. doi:10.1111/j.1420-9101.2004.00817.x
- Bell, A., & Stamps, J. (2004). Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, 68, 1339–1348. doi:10.1016/j.anbehav.2004.05.007
- Bozdogan, H. (2000). Akaike's Information Criterion and Recent Developments in Information Complexity. *Journal of mathematical psychology*, 44(1), 62–91.
- Brett, J., Shelbourn, J., & Shoop, C. (1969). Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Board of Canada*, 26(9), 2363–2394.
- Bricknell, I., Bron, J., & Bowden, T. (2006). Diseases of gadoid fish in cultivation: a review. *ICES Journal of Marine Science*, 63(2), 253–266. doi:10.1016/j.icesjms.2005.10.009
- Burnham, K., & Anderson, D. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer.
- Burt, W. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24, 346–352.
- Börger, L., Franconi, N., Ferretti, F., Meschi, F., De Michele, G., Gantz, A., & Coulson, T. (2006). An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *The American naturalist*, 168(4), 471–85. doi:10.1086/507883

- Cailliet, G., Love, M., & Ebeling, A. (1996). *Fishes : a field and laboratory manual on their structure, identification, and natural history* (p. 202). Waveland Print Inc.
- Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3), 516–519.
- Cardinale, M., & Svedäng, H. (2004). Modelling recruitment and abundance of Atlantic cod, *Gadus morhua*, in the eastern Skagerrak–Kattegat (North Sea): evidence of severe depletion due to a prolonged period of high fishing pressure. *Fisheries Research*, *69*, 263–282. doi:10.1016/j.fishres.2004.04.001
- Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J.-C., & Kornilovs, G. (2008). Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 1793–1801. doi:10.1098/rspb.2007.1752
- Chaieb, K., Hajlaoui, H., Zmantar, T., Kahla-Nakbi, A. Ben, Rouabhia, M., Mahdouani, K., & Bakhrouf, A. (2007). The Chemical Composition and Biological Activity of Clove Essential Oil , *Eugenia caryophyllata* ( *Syzigium aromaticum* L . Myrtaceae ): A Short Review. *Phytotherapy Research*, *21*, 501–506. doi:10.1002/ptr
- Clark, C., & Levy, D. (1988). Diel vertical migrations by juvenile sockeye salmon and the antipredator window. *American Naturalist*, *131*, 271–290.
- Coleman, K., & Wilson, D. (1998). Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, *56*, 927–936. doi:10.1006/anbe.1998.0852
- Committee on the Status of Endangered Wildlife in Canada. (2003). *COSEWIC assessment and update status report on the Atlantic cod *Gadus morhua* in Canada* (p. 76). Ottawa.
- Cryer, M., Hartill, B., & Shea, S. O. (2002). Modification of Marine Benthos by Trawling : Toward a Generalization for the Deep Ocean ? *Ecological Applications*, *12*(6), 1824–1839.
- Danielssen, D. (1969). On the migrations of the cod in the Skagerrak shown by tagging experiments in the period 1954–1965. *Fiskeridirektoratets skrifter Serie Havundersøkelser*, *15*, 331–338.
- Danielssen, D., & Gjørseter, J. (1994). Release of 0-group cod, *Gadus morhua* L., on the southern coast of Norway in the years 1986-1989. *Aquaculture and Fisheries Management*, *25*, 129–142.
- Dannevig, A. (1933). On the Age and Growth of the Cod ( *Gadus callarias* L .) from the Norwegian Skagerrack Coast. *Fiskeridirektoratets Skrifter Serie Havundersøkelser*, *4*(1), 1–145.
- Dannevig, G. (1966). *Kysttorsk. Jakt Fiske Friluftsliv*, *95*, 438–442.

- Davies, M., & Knowles, A. (2001). Effects of trematode parasitism on the behaviour and ecology of a common marine snail (*Littorina littorea* (L.)). *Journal of experimental marine biology and ecology*, 260(2), 155–167.
- Elton, C. (1958). *The ecology of invasions by animals and plants*. London: Methuen.
- Erickson, R. (1999). Scale aging manual for coastal cutthroat trout from Southeast Alaska. *Alaska Department of Fish and Game, Special Publication No. 99-4* (Vol. 99–4). Anchorage.
- Espeland, S. H., Thoresen, A. G., Olsen, E. M., Stige, L. C., Knutsen, H., Gjøsæter, J., & Stenseth, N. C. (2010). Diel vertical migration patterns in juvenile cod from the Skagerrak coast. *Marine Ecology Progress Series*, 405, 29–37. doi:10.3354/meps08524
- Espeland, S., Olsen, E., Knutsen, H., Gjøsæter, J., Danielssen, D., & Stenseth, N. (2008). New perspectives on fish movement: kernel and GAM smoothers applied to a century of tagging data on coastal Atlantic cod. *Marine Ecology Progress Series*, 372, 231–241. doi:10.3354/meps07721
- Food and Agriculture Organization of the United Nations. (2010). *THE STATE OF WORLD FISHERIES AND AQUACULTURE*.
- Frank, K. T., Petrie, B., Choi, J. S., & Leggett, W. C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308(5728), 1621 – 1623. doi:10.1126/science.1113075
- Fraser, C. (1916). Growth of the spring salmon. *Transactions of the Pacific Fisheries Society* 1915, 29–39.
- Fromentin, J., Gjøsæter, J., Bjørnstad, O., & Stenseth, N. (2000). Biological processes and environmental factors regulating the dynamics of the Norwegian Skagerrak cod populations since 1919. *ICES Journal of Marine Science*, 57, 330–338. doi:10.1006/jmsc.1999.0638
- Fu, C., Mohn, R., & Fanning, L. (2001). Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1613–1623. doi:10.1139/cjfas-58-8-1613
- Garcia, S. M., & Grainger, R. J. R. (2005). Gloom and doom? The future of marine capture fisheries. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 360, 21–46. doi:10.1098/rstb.2004.1580
- Giles, N. (1983). Behavioural effects of the parasite *Schistocephalus solidus* (Cestoda) on an intermediate host, the three-spined stickleback, *Gasterosteus aculeatus* L. *Animal Behaviour*, 31(4), 1192–1194.
- Giles, N. (1987). A comparison of the behavioural responses of parasitized and aculeatus L., to progressive hypoxia. *Journal of Fish Biology*, 30, 631–638.

- Gitzen, R. A., Millspaugh, J. J., & Kernohan, B. J. (2006). Bandwidth Selection for Fixed-Kernel Analysis of Animal Utilization Distributions. *The Journal of Wildlife Management*, 70(5), 1334–1344.
- Gjørseter, H., Dommasnes, A., Falkenhaus, T., Hauge, M., Johannesen, E., Olsen, E., & Skagseth, Ø. (2009). Havets ressurser og miljø 2009. *Fisken og havet, særnr.1*, 126–127.
- Gjørseter, J., Enersen, K., & Enersen, S. (1996). Ressurser av torsk og andre fisk i fjorder på den Norske Skagerrak kysten. *Fisken og havet*.
- Gjørseter, J., Knutsen, J., Knutsen, H., Olsen, E., Enersen, K., & Enersen, S. (2007). *Torsk på Skagerrakkysten; mengde, dødelighet og kondisjon* (p. 22).
- Gosling, S. (2001). From mice to men: what can we learn about personality from animal research. *Psychological Bulletin*, 127(1), 45–86.
- Graham, M. (1915). A precise method for determining the first “winter” zone in cod scales.
- Hammond-Tooke, C., Nakagawa, S., & Poulin, R. (2012). Parasitism and behavioural syndromes in the fish *Gobiomorphus cotidianus*. *Behaviour*, 149(6), 601–622. doi:10.1163/156853912X648903
- Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, 23(4), 202–210. doi:10.1016/j.tree.2008.01.003
- Hemmingsen, W., & MacKenzie, K. (2001). The Parasite Fauna of the Atlantic Cod , *Gadus morhua* L. *Advances in Marine Biology*, 40, 1–80.
- Heupel, M., Semmens, J., & Hobday, A. (2006). Automated acoustic tracking of aquatic animals : scales , design and deployment of listening station arrays. *Marine and Freshwater Research*, 57, 1–13.
- Heupel, M., & Simpfendorfer, C. (2002). Estimation of mortality of juvenile blacktip sharks , *Carcharhinus limbatus* , within a nursery area using telemetry data. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 624–632. doi:10.1139/F02-036
- Hop, H., Gjosæter, J., & Danielssen, D. S. (1992). Seasonal feeding ecology of cod (*Gadus morhua* L.) on the Norwegian Skagerrak coast. *ICES Journal of Marine Science*, 49(4), 453–461. doi:10.1093/icesjms/49.4.453
- Huntingford, F. (1976). A comparison of the reaction of sticklebacks in different reproductive conditions towards conspecifics and predators. *Animal Behaviour*, 24(3), 694–697.
- Huntingford, F., Metcalfe, N., Thorpe, J., Graham, W., & Adams, C. (1990). Social dominance and body size in Atlantic salmon parr, *Salmo solar* L. *Journal of Fish Biology*, 36(6), 877–881.

- Hurvich, C., & Tsai, C. (1989). Regression and time series model selection in small samples. *Biometrika*, 76(2), 297–307.
- Hutchings, J. (1996). Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 943–962. doi:10.1139/f96-097
- Hutchings, J. (2005). Life history consequences of overexploitation to population recovery in Northwest Atlantic cod ( *Gadus morhua* ). *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 824–832. doi:10.1139/F05-081
- Hutchings, J. A. (2000). Collapse and recovery of marine fishes. *Nature*, 406, 882–885.
- Hutchings, J., Cote, I., Dodson, J., Fleming, I., Jennings, S., Mantua, N., Peterman, R., et al. (2012). Climate change, fisheries, and aquaculture: trends and consequences for Canadian marine biodiversity. *Environmental Reviews*, 20(4), 220–311. doi:10.1139/a2012-013
- Hutchings, J., & Myers, R. (1994). What Can Be Learned from the Collapse of a Renewable Resource? Atlantic Cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 2126–2146.
- Ibáñez, A., Britton, J., & Cowx, I. (2008). Relationship between scale growth checks, circuli formation rate and somatic growth in *Rutilus rutilus* (L.) a fish farm-reared cyprinid. *Journal of Fish Biology*, 72(4), 1023–1034.
- ICES. (2012). *Report of the ICES Advisory Committee 2012, Book 6* (p. 447).
- IUCN. (2012). *The IUCN Red List of Threatened Species* (p. Version 2012.2.).
- Jackson, J. B. C., Alexander, K., & Sala, E. (2011). *Shifting Baselines : The Past and the Future of Ocean Fisheries*. Island Press.
- Jakobsen, T. (1987). Coastal cod in northern Norway. *Fisheries Research*, 5(2), 223–234.
- Jetz, W., Carbone, C., Fulford, J., & Brown, J. (2004). The Scaling of Animal Space Use. *Science*, 306(5694), 266–268.
- Jones, K., & Godin, J. (2010). Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. *Proceedings of the Royal Society B: Biological Sciences*, 277, 625–632. doi:10.1098/rspb.2009.1607
- Jorde, P., Knutsen, H., Espeland, S., & Stenseth, N. (2007). Spatial scale of genetic structuring in coastal cod *Gadus morhua* and geographic extent of local populations. *Marine Ecology Progress Series*, 343, 229–237. doi:10.3354/meps06922

- Julliard, R., Stenseth, N., Gjøsæter, J., Lekve, K., Fromentin, J., & Danielssen, D. (2001). Natural mortality and fishing mortality in a coastal cod population: a release-recapture experiment. *Ecological Applications*, *11*(2), 540–558.
- Kelt, D. a, & Van Vuren, D. H. (2001). The ecology and macroecology of mammalian home range area. *The American naturalist*, *157*(6), 637–45. doi:10.1086/320621
- Kennedy, W. (1970). Reading scales to age Pacific cod (*Gadus macrocephalus*) from Hecate Strait. *Journal of the Fisheries Research Board of Canada*, *27*, 915–922.
- Kesteven, G. L. (1996). A fisheries science approach to problems of world fisheries or: three phases of an industrial revolution. *Fisheries Research*, *25*(1), 5–17. doi:10.1016/0165-7836(95)00437-8
- Khan, R. (1988). Experimental transmission, development, and effects of a parasitic copepod, *Lernaeocera branchialis*, on Atlantic cod, *Gadus morhua*. *The Journal of Parasitology*, *74*(4), 586–599.
- Khan, R., & Lacey, D. (1986). Effect of concurrent infections of *Lernaeocera Branchialis* (Copepoda) and *Trypanosoma murmanensis* (Protozoa) on Atlantic cod, *Gadus morhua*. *Journal of wildlife diseases*, *22*(2), 201–8.
- Knutsen, H., Jorde, P. E., André, C., & Stenseth, N. (2003). Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. *Molecular Ecology*, *12*, 385–394.
- Knutsen, H., Olsen, E., Jorde, P., Espeland, S., André, C., & Stenseth, N. (2011). Are low but statistically significant levels of genetic differentiation in marine fishes “biologically meaningful”? A case study of coastal Atlantic cod. *Molecular Ecology*, *20*(4), 768–783. doi:10.1111/j.1365-294X.2010.04979.x
- Kramer, D., & Chapman, M. (1999). Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes*, *55*, 65–79.
- Kurlansky, M. (1997). *Cod; A Biography of the Fish That Changed the World* (p. 294). Penguin Books.
- Lafferty, K. (1999). The evolution of trophic transmission. *Parasitology Today*, *15*(3), 111–115.
- Lawson, G. L., & Rose, G. a. (2000). Seasonal distribution and movements of coastal cod (*Gadus morhua* L.) in Placentia Bay, Newfoundland. *Fisheries Research*, *49*(1), 61–75. doi:10.1016/S0165-7836(00)00187-9
- Lea, E. (1910). CONTRIBUTIONS TO THE METHODICS IN HERRING-INVESTIGATIONS. *Journal du Conseil*, *1*(53), 7–33.

- Lee, R. (1920). *A review of the methods of age and growth determination in fishes by means of scales.*
- Lindholm, J., Auster, P., Ruth, M., & Kaufman, L. (2001). Modeling the Effects of Fishing and Implications for the Design of Marine Protected Areas: Juvenile Fish Responses to Variations in Seafloor Habitat. *Conservation Biology*, 15(2), 424–437.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J., Hector, A., Hooper, D., et al. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808. doi:10.1126/science.1064088
- Løkkeborg, S. (1998). Feeding behaviour of cod, *Gadus morhua*: activity rhythm and chemically mediated food search. *Animal behaviour*, 56(2), 371–378. doi:10.1006/anbe.1998.0772
- McNab, B. (1963). Bioenergetics and the Determination of Home Range Size. *The American Naturalist*, 97(894), 133–140.
- McNeely, J., Miller, K., Reid, W., Mittermeier, R., & Werner, T. (1990). *Conserving the world's biological diversity.* Gland: International Union for conservation of nature and natural resources.
- Mertz, G., & Myers, R. (1998). A simplified formulation for fish production. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 478–484. doi:10.1139/f97-216
- Millar, R., & Anderson, M. (2004). Remedies for pseudoreplication. *Fisheries Research*, 70(2), 397–407.
- Moland, E., Olsen, E., Knutsen, H., Garrigou, P., Espeland, S., Kleiven, A., André, C., et al. (2013). Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before–after control-impact study. *Proceedings of the Royal Society B: Biological Sciences*, 280, 1–9.
- Munday, P., & Wilson, S. (1997). Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. *Journal of Fish Biology*, 51, 931–938.
- Myers, R. A., Hutchings, J. A., & Barrowman, N. J. (1997). Why do Fish Stocks Collapse ? The Example of Cod in Atlantic Canada Reviewed work ( s ): WHY DO FISH STOCKS COLLAPSE ? THE EXAMPLE OF COD IN ATLANTIC CANADA. *Ecological Applications*, 7(1), 91–106.
- Myers, R., Barrowman, N., & Hutchings, J. (1997). Inshore exploitation of Newfoundland Atlantic cod (*Gadus morhua*) since 1948 as estimated from mark-recapture data. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(1), 224–235.

- Møller, D. (1969). *The Relationship Between Arctic and Coastal Cod in Their Immature Stages Illustrated by Frequencies of Genetic Characters*.
- Nations, U. (1993). *Report of the United Nations Conference on Environment and Development, Rio de Janeiro, 3-14 June 1991* (p. vol. 1 (Resolutions adopted by the Conference)). New York.
- Neilson, J., Perry, R., Scott, J., & Valerio, P. (1987). Interactions of caligid ectoparasites and juvenile gadids on Georges Bank. *Marine Ecology Progress Series*, 39, 221–232. doi:10.3354/meps039221
- Ness, J., & Foster, S. (1999). Parasite-Associated Phenotype Modifications in Threespine Stickleback. *Oikos*, 85(1), 127–134.
- Olsen, E. M., Knutsen, H., Gjøsæter, J., Jorde, P. E., Knutsen, J. A., & Stenseth, N. C. (2008). Small-scale biocomplexity in coastal Atlantic cod supporting a Darwinian perspective on fisheries management. *Evolutionary Applications*, 1(3), 524–533. doi:10.1111/j.1752-4571.2008.00024.x
- Olsen, E. M., & Moland, E. (2011). Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. *Evolutionary Ecology*, 25, 695–710. doi:10.1007/s10682-010-9427-9
- Olsen, EM, Heino, M., Lilly, G., Morgan, M., Brattey, J., Ernande, B., & Dieckmann, U. (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428, 932–935. doi:10.1038/nature02453.1.
- Olsen, EM, Knutsen, H., Gjøsæter, J., Jorde, P., Knutsen, J., & Stenseth, N. (2008). Small-scale biocomplexity in coastal Atlantic cod supporting a Darwinian perspective on fisheries management. *Evolutionary Applications*, 1(3), 524–533. doi:10.1111/j.1752-4571.2008.00024.x
- Olsen, EM, Lilly, G., Heino, M., Morgan, M., Brattey, J., & Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod ( *Gadus morhua* ). *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 811–823. doi:10.1139/F05-065
- Olsen, Erik, Aanes, S., Mehl, S., Holst, J. C., Aglen, A., & Gjøsæter, H. (2010). Cod , haddock , saithe , herring , and capelin in the Barents Sea and adjacent waters : a review of the biological value of the area. *ICES Journal of Marine Science: Journal du Conseil*, 67(1), 87–101.
- Ottersen, G., Olsen, E., Van der Meeren, G., Dommasnes, A., & Loeng, H. (2011). The Norwegian plan for integrated ecosystem-based management of the marine environment in the Norwegian Sea. *Marine Policy*, 35, 389–398. doi:10.1016/j.marpol.2010.10.017



- Pálsson, O. (1994). A review of the trophic interactions of cod stocks in the North Atlantic. *ICES Marine Science Symposia*, 198(553-575).
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2002). The R Core Development Team. 2009. nlme: Linear and Nonlinear Mixed Effects Models: R package version 3.1-93.
- Poulin, R. (2010). Parasite Manipulation of Host Behavior : An Update and Frequently Asked Questions. *Advances in the Study of Behavior*, vol.41 (1st ed., Vol. 41, pp. 151–186). Elsevier Inc. doi:10.1016/S0065-3454(10)41005-0
- Powell, R. (2000). Animal home ranges and territories and home range estimators. In L. Boitani & T. Fuller (Eds.), *Research techniques in animal ecology: controversies and consequences*.
- Preston, D., & Johnson, P. (2012). Ecological Consequences of Parasitism. *Nature Education Knowledge*, 3(10), 47.
- Réale, D., Reader, S., Sol, D., McDougall, P., & Dingemanse, N. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318. doi:10.1111/j.1469-185X.2007.00010.x
- Reed, D., & Frankham, R. (2003). Correlation between Fitness and Genetic Diversity. *Conservation Biology*, 17(1), 230–237. doi:10.1046/j.1523-1739.2003.01236.x
- Roberts, C. M., Hawkins, J. P., & Gell, F. R. (2005). The role of marine reserves in achieving sustainable fisheries. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 360, 123–32. doi:10.1098/rstb.2004.1578
- Rose, G. (2007). *Cod: The Ecological History of the North Atlantic Fisheries* (p. 591). Breakwater Books.
- Rowell, C. (1993). *The effects of fishing on the timing of maturity in North Sea cod (Gadus morhua L.) in "The Exploitation of Evolving Resources"* (pp. 44–61). Berlin: Springer.
- Russell, E. (1943). TRAWLING AND THE STOCKS OF FISH. *Journal of the Royal Society of Arts*, 91(4635), 198–206.
- Ryman, N., Utter, F., & Laikre, L. (1995). Protection of intraspecific biodiversity of exploited fishes. *Reviews in Fish Biology and Fisheries*, 5, 417–446.
- Salvanes, A., Giske, J., & Nordeide, J. (1994). Life-history approach to habitat shifts for coastal cod , *Gadus morhua L. Aquaculture and Fisheries Management*, 25, 215–228.
- Salvanes, A., Skjæraasen, J., & Nilsen, T. (2004). Sub-populations of coastal cod with different behaviour and life-history strategies. *Marine Ecology Progress Series*, 267, 241–251.

- Seminoff, J., Resendiz, A., & Nichols, W. (2002). Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. *Marine Ecology Progress Series*, 242, 253–265.
- Sih, A., Bell, A., & Johnson, J. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378. doi:10.1016/j.tree.2004.04.009
- Sih, A., Kats, L., & Maurer, E. (2003). Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Animal Behaviour*, 65, 29–44. doi:10.1006/anbe.2002.2025
- Simonoff, J. (1996). *Smoothing methods in statistics*. Springer.
- Simpfendorfer, C. A., Heupel, M. R., & Hueter, R. E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 23–32. doi:10.1139/F01-191
- Simpson, R., & Mapleston, A. (2002). Movements and habitat use by the endangered Australian freshwater Mary River cod, *Maccullochella peelii mariensis*. *Environmental Biology of Fishes*, 65, 401–410.
- Sire, J., & Arnulf, I. (1990). The development of squamation in four teleostean fishes with a survey of the literature. *Japanese Journal of Ichthyology*, 37(2), 133–143.
- Smedbol, R., Shelton, P., Swain, D., Frechet, A., & Chouinard, G. (2002). *Review of population structure, distribution and abundance of cod (Gadus morhua) in Atlantic Canada in a species-at-risk context* (p. 134).
- Strand, E., & Huse, G. (2007). Vertical migration in adult Atlantic cod ( *Gadus morhua* ). *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 1747–1760. doi:10.1139/F07-135
- Strong, M. (1992). The promises and challenges of UNCED'92. *Ocean & Coastal Management*, 18(1), 5–14.
- Summerfelt, R., & Hall, G. (1987). *Age and Growth of Fish* (p. 544). Iowa State University Press.
- Svedäng, H. (2003). The inshore demersal fish community on the Swedish Skagerrak coast: regulation by recruitment from offshore sources. *ICES Journal of Marine Science*, 60, 23–31. doi:10.1006/jmsc.2002.1329
- Svedäng, H., & Bardon, G. (2003). Spatial and temporal aspects of the decline in cod (*Gadus morhua* L.) abundance in the Kattegat and eastern Skagerrak. *ICES Journal of Marine Science*, 60, 32–37. doi:10.1006/jmsc.2002.1330

- Swain, D. P., Chouinard, G. A., Morin, R., & Drinkwater, K. F. (1998). Seasonal variation in the habitat associations of Atlantic cod ( *Gadus morhua* ) and American plaice ( *Hippoglossoides platessoides* ) from the southern Gulf of St . Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 2548–2561.
- Thomas, F, Poulin, R., Meeüs, T., Guégan, J., & Renaud, F. (1999). Parasites and ecosystem engineering: what roles could they play? *Oikos*, *84*(1), 167–171.
- Thomas, Frédéric, Adamo, S., & Moore, J. (2005). Parasitic manipulation: where are we and where should we go? *Behavioural processes*, *68*(3), 185–99.  
doi:10.1016/j.beproc.2004.06.010
- Thurstan, R. H., Brockington, S., & Roberts, C. M. (2010). The effects of 118 years of industrial fishing on UK bottom trawl fisheries. *Nature communications*, *1*(15), 1–6.  
doi:10.1038/ncomms1013
- Tilman, D. (1996). Biodiversity: Population Versus Ecosystem Stability. *Ecology*, *77*(2), 350–363.
- Tort, L., Puigcerver, M., Crespo, S., & Padros, F. (2002). Cortisol and haematological response in sea bream and trout subjected to the anaesthetics clove oil and 2-phenoxyethanol. *Aquaculture Research*, *33*, 907–910.
- Tupper, M., & Boutilier, R. (1995). Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. *Marine Ecology Progress Series*, *118*, 295–300.
- Van Leeuwen, A., De Roos, A., & Persson, L. (2008). How cod shapes its world. *Journal of Sea Research*, *60*, 89–104. doi:10.1016/j.seares.2008.02.008
- Walters, C., & Maguire, J. (1996). Lessons for stock assessment from the northern cod collapse. *Reviews in Fish Biology and Fisheries*, *6*, 125–137.
- Ward, A., Thomas, P., Hart, P., & Krause, J. (2004). Correlates of boldness in three-spined sticklebacks ( *Gasterosteus aculeatus* ). *Behavioral Ecology and Sociobiology*, *55*, 561–568. doi:10.1007/s00265-003-0751-8
- Watling, L., & Norse, E. a. (1998). Disturbance of the Seabed by Mobile Fishing Gear: A Comparison to Forest Clearcutting. *Conservation Biology*, *12*(6), 1180–1197.  
doi:10.1046/j.1523-1739.1998.0120061180.x
- Weatherley, A., & Gill, H. (1987). *The biology of fish growth* (p. 443). London: Academic Press.
- Wilson, D., Clark, A., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, *9*(11), 442–446.

- Wilson, D., Coleman, K., Clark, K., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, *107*(3), 205.
- Wolf, M., & Weissing, F. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, *27*(8), 452–461.  
doi:10.1016/j.tree.2012.05.001
- Wootton, R. (1998). *Ecology of Teleost Fishes* (Second edi., p. 386). Kluwer Academic Publishers.
- Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., et al. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, *314*, 787–790. doi:10.1126/science.1132294
- Worton, B. (1989). Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology*, *70*(1), 164–168.
- Wroblewski, J., Neis, B., & Gosse, K. (2005). Inshore Stocks of Atlantic Cod Are Important for Rebuilding the East Coast Fishery. *Coastal Management*, *33*(4), 411–432.  
doi:10.1080/08920750500217930
- Zuur, A. (2009). *Mixed effects models and extensions in ecology with R*. Springer.

# Appendix 1

**Table 8 Information gathered of the 80 tagged cod. ID: identification number of each individual; DAL: days at large; L: total length (mm); W: weight (g); K: Fulton's condition factor; COL: colour; TH: tail height (mm); TW: tail width (mm); BS: black spots; GP: gill parasites; FL: fish lice.**

ID	DAL	L	W	K	COL	TH	TW	BS	GP	FL
7287	84.90	440	855	1.00	Brown	21	18	Yes	No	No
7288	119.36	420	695	0.94	Brown	20	13	Yes	No	Yes
7289	1.66	430	725	0.91	Brown	20	12	Yes	No	Yes
7290	95.90	410	660	0.96	Brown	21	11	Yes	Yes	Yes
7291	107.26	420	835	1.13	Brown	21	13	Yes	No	No
7292	110.96	520	1330	0.95	Brown	22	16	Yes	No	No
7293	189.81	390	615	1.04	Brown	18	12	Yes	No	No
7294	136.97	560	1770	1.01	Brown	24	18	Yes	No	No
7295	75.81	360	560	1.20	Red	17	11	No	Yes	Yes
7296	216.98	600	2150	1.00	Brown	28	18	Yes	No	Yes
7297	92.15	520	1085	0.77	Brown	29	12	Yes	Yes	Yes
7298	121.79	330	400	1.11	Brown	16	8	Yes	No	No
7299	55.11	380	530	0.97	Brown	17	10	Yes	No	No
7300	217.98	350	505	1.18	Brown	17	10	Yes	No	No
7301	216.02	300	340	1.26	Red	16	9	No	No	No
7302	213.50	300	255	0.94	Brown	14	8	Yes	No	No
7303	217.85	400	625	0.98	Brown	20	12	No	No	Yes
7304	215.85	490	1050	0.89	Red	23	12	No	Yes	No
7305	217.81	560	1825	1.04	Brown	28	16	Yes	Yes	Yes
7306	140.08	420	715	0.97	Brown	20	13	Yes	No	Yes
7307	199.54	450	815	0.89	Brown	21	13	Yes	No	No
7308	169.37	460	820	0.84	Brown	21	12	Yes	No	Yes
7309	217.86	400	670	1.05	Brown	20	13	No	Yes	No
7310	94.95	330	325	0.90	Brown	15	8	Yes	No	No
7311	217.86	300	280	1.04	Brown	13	8	Yes	No	Yes
7312	208.10	430	720	0.91	Brown	21	13	Yes	No	Yes
7313	215.15	410	630	0.91	Brown	19	12	Yes	No	Yes
7314	145.99	740	4210	1.04	Brown	34	20	Yes	No	No
7315	88.39	500	1270	1.02	Brown	23	15	Yes	No	Yes
7316	93.00	420	690	0.93	Brown	19	12	Yes	No	No
7317	105.38	330	365	1.02	Brown	16	9	Yes	No	No
7318	213.85	440	730	0.86	Brown	20	13	Yes	No	No
7319	164.74	560	1630	0.93	Brown	27	18	Yes	No	Yes
7320	213.77	600	1910	0.88	Red	26	18	Yes	No	No
7321	214.38	460	1080	1.11	Red	21	14	No	No	No
7322	211.30	470	1100	1.06	Brown	24	16	Yes	No	No
7323	215.02	460	945	0.97	Brown	21	14	Yes	No	No
7324	89.72	490	1170	0.99	Grey	24	15	Yes	No	Yes
7325	213.61	370	495	0.98	Red	18	12	No	No	Yes

7326	213.93	540	1540	0.98	Grey-Brown	26	16	Yes	No	Yes
7327	181.72	460	920	0.95	Brown	22	14	Yes	No	No
7328	173.96	690	2880	0.88	Brown	30	20	Yes	No	No
7329	97.09	600	1940	0.90	Brown	29	16	Yes	No	Yes
7330	210.85	560	1780	1.01	Brown	26	15	Yes	No	Yes
7331	98.66	540	1325	0.84	Brown	24	16	Yes	No	No
7332	89.63	510	1350	1.02	Red	23	16	Yes	No	No
7333	209.98	500	1320	1.06	Brown	24	13	Yes	No	No
7334	202.96	610	2000	0.88	Red	28	18	Yes	No	No
7335	5.37	380	510	0.93	Grey	17	10	Yes	No	No
7336	150.82	380	545	0.99	Brown	19	10	Yes	Yes	No
7337	209.69	520	1195	0.85	Brown	23	14	Yes	No	Yes
7338	211.68	520	1465	1.04	Grey	25	15	Yes	No	Yes
7339	170.18	630	1945	0.78	Brown	28	17	Yes	No	Yes
7340	90.35	540	1695	1.08	Brown	28	19	Yes	No	No
7341	209.84	370	500	0.99	Brown	18	11	Yes	No	Yes
7342	158.78	330	345	0.96	Brown	15	9	No	No	No
7343	209.00	500	1330	1.06	Red	23	14	Yes	No	No
7344	206.96	560	1580	0.90	Brown	25	15	Yes	No	No
7345	111.85	480	1145	1.04	Brown	23	15	Yes	Yes	Yes
7346	209.00	510	1190	0.90	Brown	24	15	Yes	No	No
7347	203.56	490	1135	0.96	Brown	22	13	Yes	No	Yes
7348	206.92	390	670	1.13	Brown	19	11	Yes	Yes	Yes
7349	207.00	400	700	1.09	Brown	19	10	No	No	Yes
7350	83.55	610	2450	1.08	Brown	31	21	Yes	Yes	No
7351	206.86	580	2105	1.08	Brown	26	17	Yes	No	No
7352	206.90	330	370	1.03	Brown	14	8	Yes	No	Yes
7353	204.99	370	470	0.93	Brown	17	10	No	Yes	Yes
7354	25.95	360	455	0.98	Brown	16	9	No	No	Yes
7355	151.88	350	450	1.05	Red	16	9	No	Yes	No
7356	204.91	560	1850	1.05	Red	28	17	Yes	No	Yes
7357	121.89	800	4765	0.93	Red	37	21	No	No	No
7358	204.60	630	2405	0.96	Brown	27	18	Yes	No	No
7359	202.85	600	2130	0.99	Brown	27	16	Yes	Yes	Yes
7360	200.71	530	1330	0.89	Grey-Brown	24	14	Yes	No	Yes
7361	203.89	320	360	1.10	Brown	15	9	Yes	No	No
7362	201.78	390	665	1.12	Red	20	13	No	Yes	Yes
7363	122.48	790	4050	0.82	Brown	30	22	Yes	No	Yes
7364	202.86	410	645	0.94	Brown	19	12	No	No	No
7365	105.96	310	325	1.09	Red	18	9	No	No	No
7366	187.06	540	1630	1.04	Brown	25	16	Yes	No	No

## Appendix 2

Table 9 Estimated age of cod based on three separate readers. The age the readers shared greatest consensus over was chosen as most correct age and used for further analysis.

ID	Aalvik	Moland	Olsen	Age	ID	Aalvik	Moland	Olsen	Age
7288	4	2	2	2	7338	4	4	3	4
7293	3	3	2	3	7339	5	6	4	5
7298	3	3	2	3	7341	3	3	2	3
7300	3	2	2	2	7342	4	3	2	3
7303	2	3	2	2	7343	6	5	3	4
7305	4	4	4	4	7344	6	5	4	5
7306	3	3	2	3	7346	4	5	3	4
7307	4	2	2	2	7347	5	4	3	4
7308	4	3	3	3	7349	3	2	2	2
7309	4	3	2	3	7351	5	4	4	4
7311	2	2	1	2	7353	3	3	2	3
7312	3	3	2	3	7356	3	3	3	3
7313	4	3	2	3	7357	6	5	7	6
7314	7	4	5	5	7358	5	4	4	4
7318	3	3	2	3	7359	5	4	4	4
7321	3	2	3	3	7360	5	4	4	4
7325	3	2	2	2	7362	4	3	3	3
7327	4	4	3	4	7363	6	4	7	5
7328	5	3	5	5	7364	4	3	2	3
7333	4	4	4	4	7365	2	3	2	2
7334	5	4	4	4	7366	4	3	3	3
7336	3	3	2	3					

## Appendix 3

Two vertical profiles showing examples of fish that were omitted from the study; one fish that died during study period and one that dispersed out of the study area during study period.

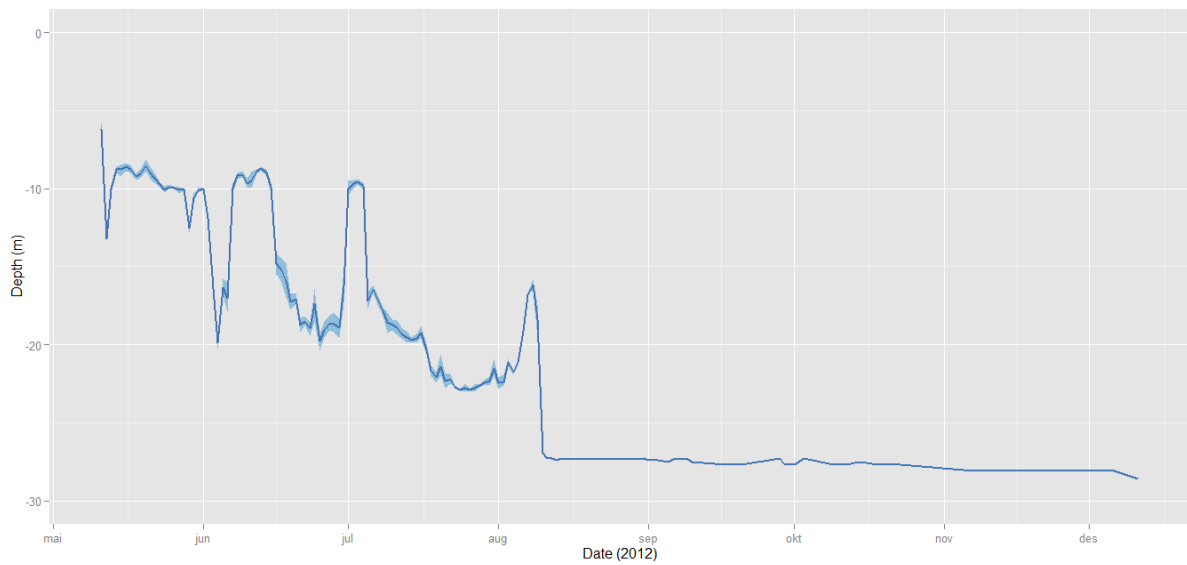


Figure 12 7325 dead

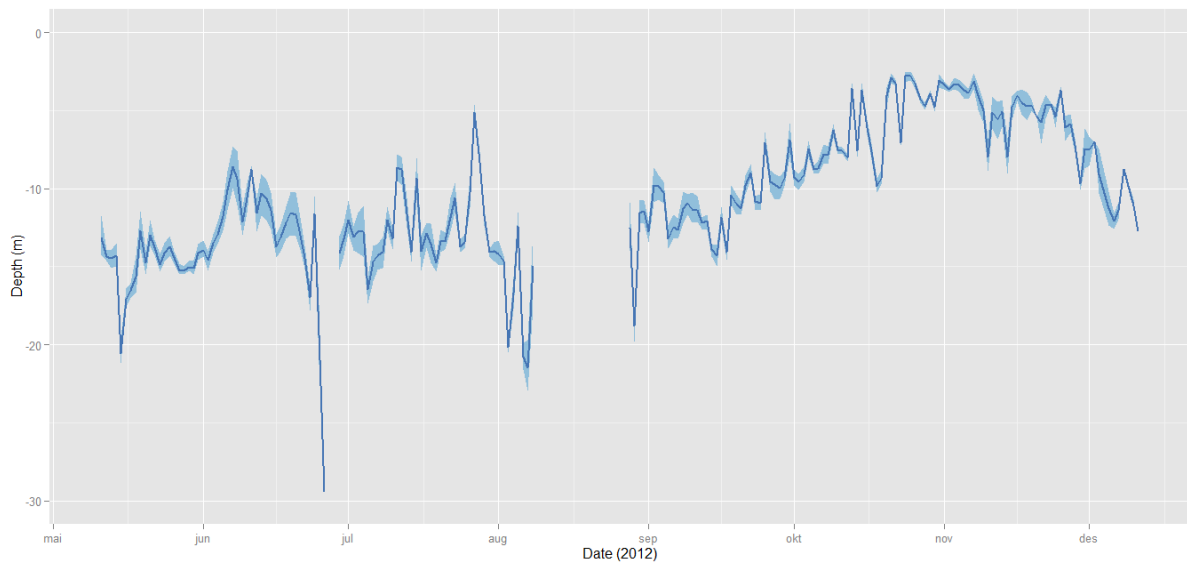


Figure 13 7318 dispersed and returned to study area



# Appendix 4

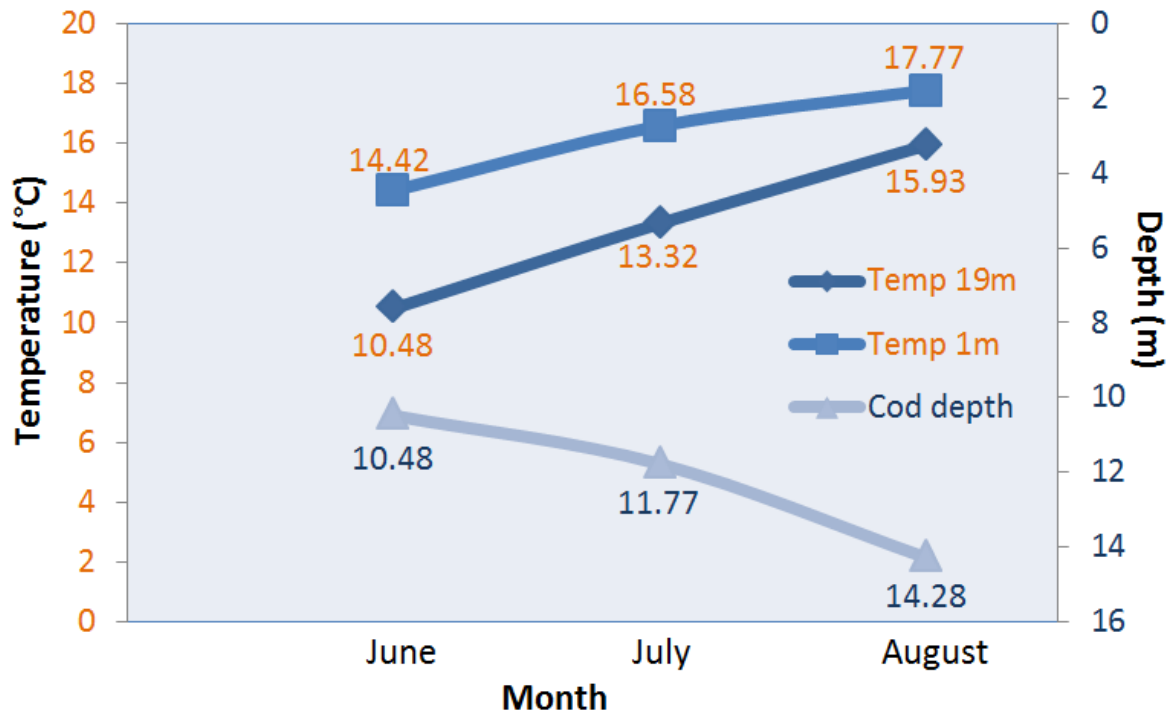


Figure 14 Graphical illustrating an inverse correlation in fish depth and temperature

# Appendix 5

Table 10 Model selection for cod movement behaviour in a semi-sheltered coastal basin on the Skagerrak coast. Where x denotes inclusion of variable in model. AICc = second order Akaike Information Criterion;  $\Delta$ AICc = difference in given model AICc and the lowest AICc for the model set. Values in bold represent the best models ( $\Delta$ AICc <2) for each given response variable.

Month	Length	Length1	K-factor	GP	FL	BS	AICc (Depth range)	$\Delta$ AICc (Depth range)	AICc (Min depth)	$\Delta$ AICc (Min depth)	AICc (Max depth)	$\Delta$ AICc (Max depth)	AICc (Mean depth)	$\Delta$ AICc (Mean depth)	AICc (Home range)	$\Delta$ AICc (Home range)	AICc (Cum dist)	$\Delta$ AICc (Cum dist)
x	x	x	x	x	x	x	646.59	9.71	455.92	13.83	642.30	8.94	57.11	7.56	238.69	8.88	62.77	6.96
	x	x	x	x	x	x	650.63	13.75	451.63	9.54	650.90	17.55	72.91	23.37	255.08	25.27	64.45	8.65
x		x	x	x	x	x	644.74	7.86	454.02	11.93	639.89	6.54	54.61	<b>5.06</b>	236.17	6.36	65.41	9.60
x	x		x	x	x	x	758.64	121.76	513.55	71.46	753.91	120.56	66.04	16.49	281.78	51.97	124.93	69.13
x	x	x		x	x	x	644.81	7.93	453.60	11.51	640.50	7.15	55.09	<b>5.55</b>	236.91	7.10	60.24	<b>4.43</b>
x	x	x	x		x	x	644.18	7.30	453.44	11.35	639.76	6.41	54.88	<b>5.33</b>	236.45	6.64	60.47	<b>4.66</b>
x	x	x	x	x		x	644.07	7.20	454.92	12.83	639.79	6.43	55.69	<b>6.14</b>	236.23	6.42	60.38	<b>4.57</b>
x	x	x	x	x	x		645.42	8.54	453.39	11.30	640.62	7.26	57.45	7.90	241.84	12.03	67.30	11.50
x							753.56	116.68	507.04	64.95	746.05	112.70	58.33	8.78	279.65	49.84	121.16	65.36
	x						758.73	121.85	503.49	61.40	758.21	124.86	83.62	34.07	304.70	74.89	118.20	62.40
		x					641.51	<b>4.64</b>	442.09	<b>0.00</b>	641.55	8.20	67.92	18.38	251.49	21.68	63.46	7.66
			x				761.78	124.91	505.52	63.43	759.19	125.83	81.62	32.08	303.64	73.83	122.59	66.79
				x			761.78	124.90	505.23	63.14	759.29	125.94	83.37	33.82	304.13	74.32	122.67	66.87
					x		761.10	124.22	503.63	61.54	758.94	125.59	83.74	34.19	304.71	74.91	122.48	66.68
						x	761.57	124.70	505.59	63.50	759.23	125.88	82.01	32.46	296.45	66.65	122.06	66.26
x	x	x			x	x											58.01	2.21
x	x	x		x		x											57.90	2.10
x	x	x	x			x											58.22	2.42
x	x	x				x											55.80	<b>0.00</b>
		x	x			x											57.66	<b>1.86</b>
x		x				x											60.63	4.83
x	x					x											119.19	63.38
x	x	x															60.60	4.79
x	x	x				x							51.90	2.36	232.13	2.33		
x		x				x							49.55	<b>0.00</b>	229.81	<b>0.00</b>		
x		x	x			x							51.02	<b>1.47</b>	231.59	<b>1.78</b>		
x		x		x		x							51.66	2.11	232.09	2.28		
x		x			x	x							50.76	<b>1.22</b>	232.17	2.37		
x		x					636.9	<b>0.00</b>	445.9	3.78								
		x	x				643.7	6.84	444.1	2.00								
			x	x			643.1	6.21	444.3	2.22								
			x		x		643.7	6.85	444.2	2.10								
		x			x		643.68	6.81	442.95	<b>0.86</b>								
			x			x	644.07	7.20	454.92	12.83								
x	x	x	x	x							638.20	4.85						
x	x	x	x		x						638.15	4.80						
x	x	x	x			x					637.31	3.96						

x	x	x		x	x		639.06	5.71
x	x	x		x		x	638.13	4.78
x	x	x			x	x	638.05	4.70
x		x	x	x	x		638.17	4.81
x		x	x	x		x	637.46	4.11
x		x	x		x	x	637.42	4.07
x		x		x	x	x	638.02	4.67
x	x	x	x				635.78	2.43
x	x	x		x			636.86	3.51
x	x	x			x		636.77	3.42
x	x	x				x	635.72	2.37
x		x	x	x			635.82	2.47
x		x	x		x		635.75	2.40
x		x	x			x	635.05	<b>1.70</b>
x		x		x	x		636.75	3.40
x		x		x		x	635.71	2.36
x		x			x	x	635.63	2.28
		x	x			x	644.00	10.65
x			x			x	750.24	116.89
x		x				x	633.35	<b>0.00</b>
x		x	x				633.45	<b>0.10</b>
x	x	x					639.18	2.30
x		x	x				638.55	<b>1.67</b>
x		x		x			639.19	2.32
x		x			x		639.14	2.27
x		x				x	644.07	7.20