

**A 100 year perspective on the life  
history of coastal cod (*Gadus morhua*)  
from the Søndeledfjord in Skagerrak**

**Marthe Bråthen Lund**

**Master of Science thesis  
2008**



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

## **Preface**

This master thesis could off course not have been done without help:

First I have to thank my supervisors Nils Chr. Stenseth, Esben Moland Olsen and Sigurd Heiberg Espeland. Nils Chr. for giving me this exiting thesis, and Sigurd for all the help at the lab and all the technical data imputes. Esben for the help at the field, lab, computing, writing and for putting up with all my questions.

Thanks to my local fisherman Helga Larsen for letting us accompanying him in his boat.

Flødevigen Marine Station for letting me be apart of the research, giving me a place to sleep, lending me labs and for given me the opportunity to meet all the kind and helpful people.

Everyone in my room 3320, Gry, Elin, Mali, Elianne, for giving me a dinner partner, Silje, for making me quite, Therese, for all the help and laughter and a special thanks to Adine, for giving be a social life in Arendal, and for all the “Skagerrak cod imputes”.

I also have to thank Oda, Annette, Kim Magnus, Truls, Vegard, Arild and Andre for these five years at “bio” and specially Evelyn for encourage in me in the late hours.

Most important my family; my mom and dad for always having faith in me, by brother Henrik for the very nice picture, my brother Aksel for all the “hence” and “due to” and by dog Buster for being my best friend.

And last my Mads, for everything!

## Abstract

Many fish stocks today are declining due to the heavy harvesting and the increasingly demand for more food caused by the growing human population. Life-history trait as age and size at maturity are affected, the fish are getting smaller and younger at maturity. The selection is caused by genotypic selection and or phenotypic plasticity. A problem with this investigation is that few scientific surveys cover no more then a few decades. It is not known when the selection started and there is a danger of adopting a “shifting baseline”.

In this study a small selection of the Skagerrak cod (*Gadus morhua*), situated in the Søndeledfjord were studied. The data was sampled in November 2006 by repeating a study done in 1905 by Dahl and Dannevig. The cod data from 2006 was compared with the data from 1905, to see if there were any change in the size and age at maturity. By comparing today's` data with data sampled 100 a years ago, the baseline might be more correct. The data were sampled by accompanying a local fisherman using eel-pot as traps.

I predicted that the cod would mature earlier today because of the high exploitation rate the cod has experienced. The results showed the opposite, hence they are maturing later today. They are bigger and older at maturity and they grow faster. Catch-per-unit-effort data also indicate that there might be less fishing today than in 1905. The results might indicate that the decrease in fishing activity resulted in stronger natural selection and increased growth. Phenotypic plasticity may also contribute to the increased growth, due to the less intraspecific competition after the heavy fishing. The trade-off between growth and reproduction, leads to later maturation. The changes could have been difficult to spot if the comparative data were relatively fresh. Hence it was advantageous and helpful to the study's integrity that the data from the original study was a 100 years old. These results indicate that the cod in the Søndeledfjord may be living in better conditions and that the selection by the fishing can be reversed.

# Contents

<b>Preface</b> .....	<b>1</b>
<b>Abstract</b> .....	<b>2</b>
<b>Contents</b> .....	<b>3</b>
<b>1 Introduction</b> .....	<b>4</b>
<b>2 Materials and methods</b> .....	<b>7</b>
2.1 Study area .....	7
2.2 Study species .....	8
2.3 The historical Dahl and Dannevig survey .....	8
2.4 Field work .....	9
2.5 Lab work .....	11
2.5.1 <i>Measuring</i> .....	11
2.5.2 <i>Otolith reading</i> .....	12
2.6 Statistical analysis .....	13
2.6.1. <i>The data</i> .....	13
2.6.2 <i>Age and length distribution</i> .....	14
2.6.3 <i>The growth, maturity and harvest</i> .....	14
<b>3 Results</b> .....	<b>16</b>
3.1 Length and age distributions .....	16
3.1.1 <i>The length distribution</i> .....	16
3.1.2 <i>The age distribution</i> .....	18
3.1.3 <i>The age at maturity</i> .....	19
3.2 Modeling growth and maturity pattern, harvest .....	20
3.2.1 <i>Growth</i> .....	20
3.2.2 <i>Maturity</i> .....	22
2.3 <i>Fishing</i> .....	24
<b>4 Discussion</b> .....	<b>25</b>
<b>5 Conclusion</b> .....	<b>29</b>
<b>6 References</b> .....	<b>30</b>

# 1 Introduction

Many commercially exploited fish stocks have declined drastically over the last decades. Probably as much as three quarters of the world fish stock are either fully exploited, overexploited, depleted or recovering from depletion (FAO 2006). Moreover, fishing is nearly always non random and may lead to both ecological and evolutionary changes in the exploited population (Law 2000). For instance age and size at maturity are important life-history traits, linked to survival, growth, reproductive effort and lifetime fecundity. They are all factors that may change in response to exploitation (Stearns 2004). The selection imposed from fisheries often favor individuals that mature earlier. Many such examples exist e.g. the Northeast Arctic cod (Heino et al. 2002a), Gulf of Maine and Georges Bank cod (Barot et al. 2004), the Norwegian spring-spawning herring (Engelhard & Heino 2004) the North sea plaice (Grift et al. 2003) and Northern cod (Olsen et al. 2004a). Selection for earlier maturation has also been found in modelling population (de Roos et al. 2006).

The selective from the fishing is caused due to that the different fishing gears settle the size of the fish in the catch (Julliard et al. 2001). Many are designed to catch the larger and indirectly the older ones. Also the spatial distribution of the fishing is selective because fish stocks are not distributed randomly and the fishing fleets do not fish at random (Law & Grey 1989, Law 2000). Law and Gray (1989) were one of the first to propose that harvesting from fisheries could lead to evolution, and suggesting that this evolution would lead to a much smaller total yield.

When human-induced life history changes really began is not very well documented. Most research covers only the last few decades, while there is much less research dating further back in time (Pauly 1995). Pauly introduced in 1995 a new expression the; “shifting baseline”, meaning that the researchers accept the stock size and species composition that existed at the beginning of their career as the baseline, and use this to investigate the changes. The next generation uses a new baseline, hence the change will at time gradually be underestimated (Pauly 1995). Since its introduction, the focus on this problem has increased (Lotze & Milewski 2004, Bunce et al. 2008). It exists different data sources that can help in revealing the historic population status. Among them the so-called “grey” literature (Pinnegar & Engelhard 2008) is also present.

It exist two hypotheses for maturity changes often observed in exploited populations e.g. there are two ways that fishing can lead to phenotypic change. The first one is the

*compensatory response*; it is a purely phenotypic response, and involves no change in the genotype composition within the stock. The second hypothesis involves *genetic selection*, where fishing drives an evolutionary response in the population, e.g. a change in the maturation genotype composition (Trippel 1995, Law 2000).

The compensatory hypothesis is a response to a reduction in the stock size induced by harvesting leading to reduced intraspecific competition (Trippel 1995, Law 2000). This leads to less competition for food, and therefore higher growth rates. Hence the fish will reach the size required for maturation sooner. Hence they become younger at maturation (Engelhard & Heino 2004). The body size at maturation could then be either smaller or larger, depending on the underlying relationship between age and size at maturation e.g. the shape of the maturation reaction norm (see below). Evidence for this compensatory hypothesis has been shown among others, in the Norwegian spring-spawning herring (Engelhard & Heino 2004).

A genetic response to selection may occur in heavily harvested populations where only a few late maturing fish will survive to reproduce. This will over time lead to a selection for early maturing individuals. Simply because they will have a better chance to reproduce before they get caught, provided that age and size at maturation is a heritable trait (Trippel 1995, Law 2000). Importantly, size selective fishing alone is not enough to cause evolution. It also requires that age and size at maturation are heritable traits, e.g. that there are genetic differences between those fish that get caught and those that do not (Law 2000). To date, support for a genetic selection response has been reported for several commercially harvested fish stocks, e.g. the George Bank and the Gulf of Maine cod (Barot et al. 2004) and in the Northern cod (Olsen et al. 2004a).

Some populations have been exploited so severely, that a collapse has been the result. This has happened in the southern Labrador and eastern Newfoundland (Olsen et al. 2004a). The population has not recovered although the fishing has been low or non-existent. This indicates that a genetic change may have occurred in growth in response to size-selective fishing (Swain et al. 2007). Furthermore, these examples show that evolution can be rapid e.g. taking place within a contemporary time frame. Most convincingly, a famous field-experiment with the Trinidadian guppy *Poecilia reticulata* documents a significant evolutionary change in life-history within only 7-11 generations (Reznick & Ghalambor 2005). This is in great contrast to the more traditional perspective that evolution is a slow process, not visible on an ecological time scale.

In summary, both genetic selection and phenotypic plasticity might result from size selective fishing (Law 2000). It is very important to make a distinction between them because

they have different management implications. The genetic selection will be hard to reverse. While the phenotypic plasticity could readily be reversed by just reducing the level of exploitation (Law 2000, de Roos et al. 2006). However, disentangling plastic and genetic changes caused by fishing is not an easy task. The most applied method today is the maturation reaction norm method (Heino et al. 2002b, a, Grift et al. 2003, Barot et al. 2004). A reaction norm is defined as a set of phenotypes produced by genotypes over a range of environmental conditions (Stearns 2004). The core idea is that phenotypic plasticity should shift the phenotype along the reaction norm, while a genetic selection should change the reaction norm itself (Ernande et al. 2004). The reaction norm gives the probability of becoming mature as a function of age and length, and describes the maturation process independently from the growth and survival process (Barot et al. 2004).

In contrast to the maturation reaction norm method, the more traditional approach for describing maturity is to estimate maturity ogives. These do not give the probability of *maturing*, but instead the probability of *being mature* as a function of age or size (Jorgensen 1990, Bromley 2000, Olsen & Vollestad 2005, Jorgensen & Fiksen 2006). A maturity ogive will be determined not only by the underlying maturity pattern (e.g. the reaction norm), but also on prevailing conditions for growth and survival (Heino et al. 2002a).

In addition to age and length, the condition of the fish may also influence the probability of maturing (Jorgensen & Fiksen 2006, Marshall & McAdam 2007). In years when the cod stock is in better condition, larger portions of the population may mature, implying that the maturity will depend on the amount of stored energy reserves (Marshall & McAdam 2007). In this respect liver weight especially, is an important parameter (Jorgensen & Fiksen 2006).

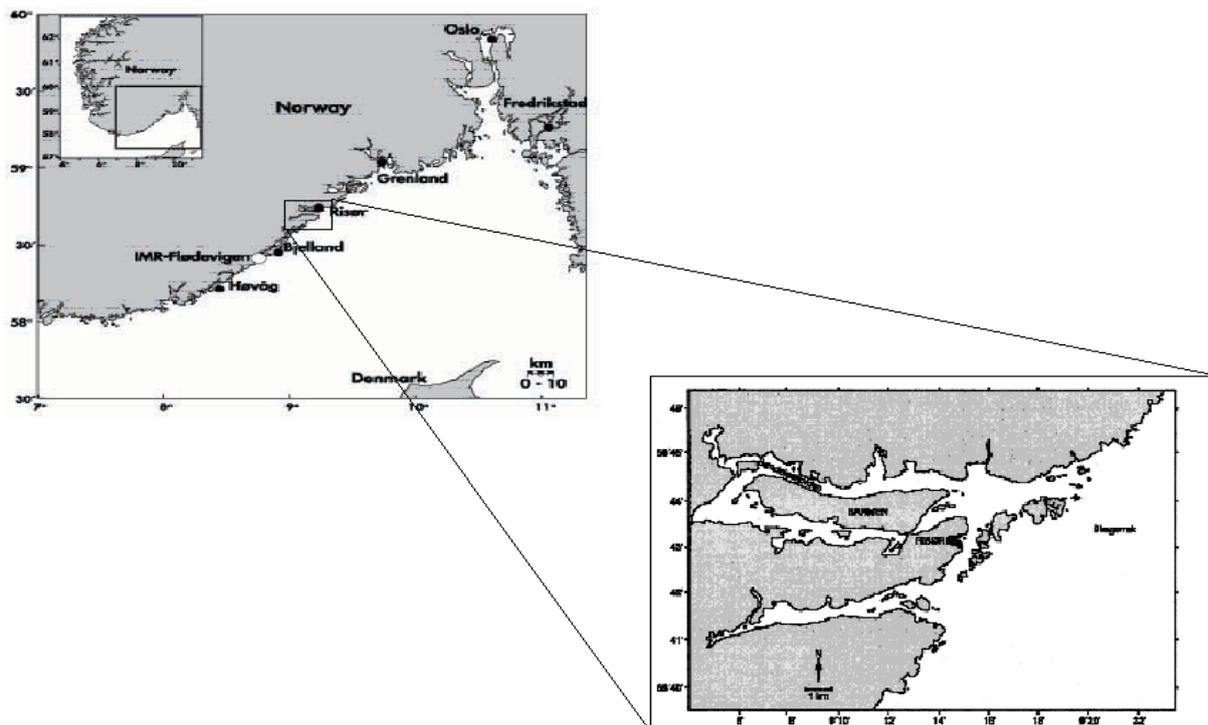
In this master thesis I have highlighted the problems concerning “shifting baseline”, by using particularly old cod data from a study conducted more than a century ago (Dahl & Dannevig 1906). Comparing the old life-history data with present day data sampled as part of my thesis (2006). Both data sets were sampled from the Søndeledfjord, Skagerrak in the south of Norway. This gives a 100 year perspective on the life-history of the Skagerrak coastal cod (*Gadus morhua*), across a very long time-span compared to earlier studies.

In particular I wanted to see if there were any differences between the age- and length-specific maturity today and from 100 years ago. I predicted due to the increasingly high exploitation of the Skagerrak cod populations they would mature earlier today than in 1905. Regarding growth rates, a compensatory response caused by reduced fish density is expected to have occurred, because of less intraspecific competition.

## 2 Materials and methods

### 2.1 Study area

The study was conducted in the Søndeledfjord in Skagerrak, southern part of Norway (Figure 1). The fjord is divided in a northern and southern part, the “Nordfjorden” and the “Sørfjorden”, divided by the island, Barmen. The two fjords have almost the same size, and they are connected at the inner part. The Nordfjorden is the broadest of the two fjords, with a more open connection to the sea. It is also the deepest, 180 m in the outmost part, but is getting much more shallower at the middle of the fjord, down to 40-50 m close to the island Frøyne (Dahl & Dannevig 1906). Here, the fjord turns south to meet the Sørfjorden. The Sørfjorden is getting deeper, down to 75 m at the innermost part past the rendezvous point with Frøyne. Eastwards, out of Sørfjorden the depth is 60 m with grooves on 30-40 m. The fjord ends with a narrow straight only a couple of meters deep (Dahl & Dannevig 1906).



**Figure 1.** Map of the study area; south of Norway and a detailed map of the Søndeledfjord (taken from <http://www.aquarius.geomar.de/omc> and edited).

## 2.2 Study species

The Norwegian Skagerrak cod stock is a mix of several local coastal cod populations (Knutsen et al. 2003). Currently any of these coastal cod stocks, mature already at an age of two years with a length of about 30 cm (Olsen et al. 2004b, Olsen et al. 2008) They usually spawn in fjords during February and March (Knutsen et al. 2007)

The juvenile cod stock stays in habitat with kelp and eelgrass coverage to hide from their biggest threats, which is predation from larger cod and other large piscivores. Reaching one year of age, the cod adopts a mature pattern of movement and use the entire fjord for feeding. But they are still relatively stationary (Lekve et al. 2006, Esbeland et al. 2007). As they grow they change to increasingly larger prey (piscivorous). Small cod eat smaller crustaceans, while larger cod prey on fish and large decapods (Hop et al. 1993). Coastal cod grow faster, and mature earlier than North Atlantic cod populations (Fromentin et al. 1997).

The Norwegian Skagerrak cod has been proved to be very stationary; they do not interbreed freely, but group in to local populations and stay partly isolated from each other. This indicates that genetic different population may arise, without any physical barriers (Knutsen et al. 2003, Jorde et al. 2007). The population unit is limited to 30 km or less in geographic extent (Jorde et al. 2007). The cod along the Skagerrak coast also differ in length and age at maturity, which is linked to the sub-structure (Olsen et al. 2004b, Olsen et al. 2008).

Fishing along the Skagerrak coast, causes most of the mortality of the fish, especially fish over 1 year (Julliard et al. 2001). It has also been studied and concluded that there are considerable differences between the Skagerrak cod stocks. In the Swedish part of Skagerrak there has been a drastic decline in abundance, probably due to overfishing (Svedang & Bardon 2003, Olsen et al. 2008). While the cod stock in the southwestern part of Skagerrak has been shown to be in better condition according to catch-per-unit-effort data (Olsen et al. 2008).

## 2.3 The historical Dahl and Dannevig survey

The data from the 1905 were a part of a bigger investigation for studying the effect of releasing reared cod eggs and larvae into the fjords to enhance the cod stock (Dahl &

Dannevig 1906). To see the effect they had to investigate how large the spawning stock was originally. Dannevig, the head of the Flødevigen rearing station only wanted to investigate the fjords where the cod eggs and larvae was going to be released. In addition, the zoologist Dahl wanted to investigate other fjords. So they investigated together, the Sønedeledfjord and the Hellefjord. Dahl investigated the rest of the fjords alone. They both wrote a rapport of these studies. It is the data from the Sønedeledfjord which is being used in this study.

Two different tables from the 1905 survey were used. The first one (page 24 Chapter II “Torskens gyting”) gave the length of a 787 size sample of cod, fished autumn 1905 in the Sønedeledfjord (Dahl & Dannevig 1906). The other one gave the length, age and maturity of a sample of 138 cod (table E4 in Bilag II). The 138 cod sample was not apart of the 787 cod sample. They were taken at different occasions in November 1905 (Dahl & Dannevig 1906).

In the report there were two tables that provides information on the amount of cod harvested in November in 1905, one from local fishermen (Tab C 1 in Bilag II), and one from Karl A. Jensen (Tab C2 in Bilag II) (Dahl & Dannevig 1906), a wholesaler who at that time bought considerable amounts of the cod caught in the Risør area. The data from the tables is divided between cod from the Sønedeledfjord and from outside Risør, and only data from the Sønedeledfjord were used in my thesis.

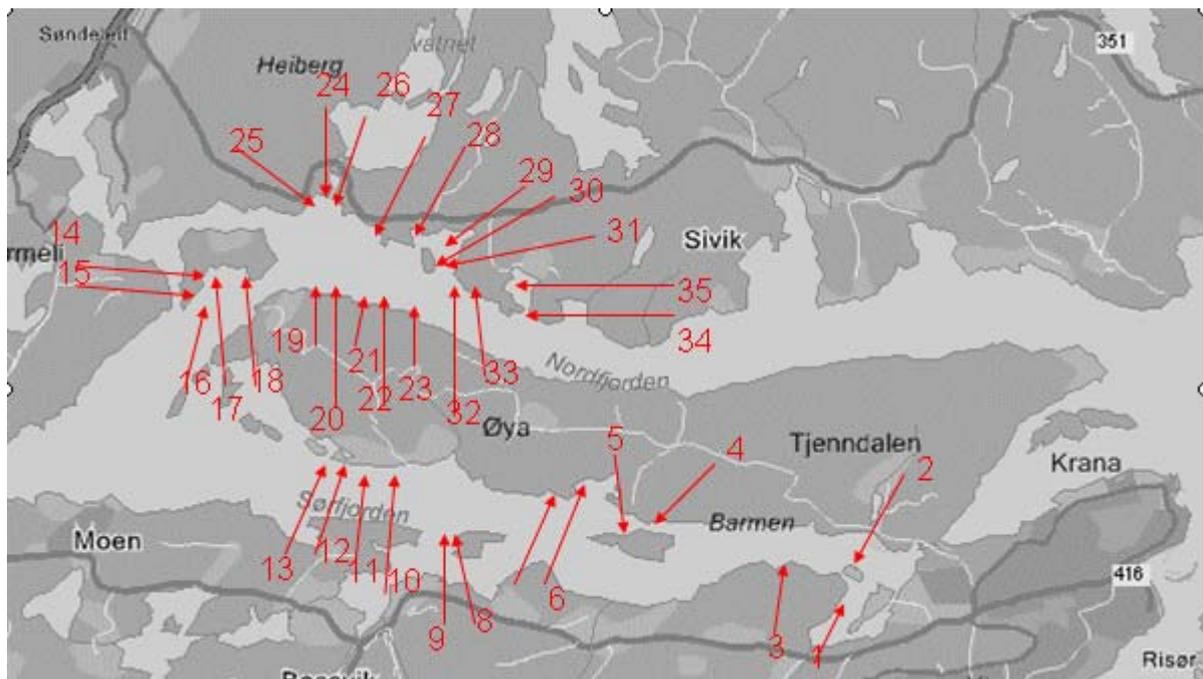
## 2.4 Field work

The field work was done on three occasions in November 2006 (Nov. 7, 13 and 22, see Figure 2). This was in the same month as Dahl and Dannevig (1905) conducted their sampling. The sampling was done by Esben Moland Olsen (IMR Flødevigen, supervisor), Helge Larsen and me. Helge Larsen is a local eel-fisher, and he uses eel pots, and fishes in both Nord- and Sørfjorden almost all year around, except when ice covers the fjord. He also catches other fish in his eel pot, among them, cod. The openings on the eel pots were approximately 1 meter. He has his eel pots in shallow water, from 1 to 5 meters. Dahl and Dannevig (1905) also used pots as their fishing method, but whether or not it was eel pots or cod pots is not known.

Each fish were handled on exactly the same way; killed by knocking the head, and then placed in plastic bags. The fish from the same pot were put in the same bag, and tagged. The sampling location of the fish was noted on a map during the field work (Figure 2). The number of the pot; the fjord; the locality; the number of pots in that locality; the duration of the fishing and the number of fish was filled in a form. The dead decomposed fish were not

used, because it would be difficult to get real sample measurement later in the lab. A few tagged fish (from an ongoing tagging study organized by IMR Flødevigen) was noted and released immediately, these were not used in the further analysis.

The eel pots were then placed out in the water again, in a different place close by. If the catching was unsuccessful, the eel pots were moved to a different place, changing location. The amount of time each pot had been fished also varied. The first collection date (7<sup>th</sup> of November) had seen the pots being out day and night for 3 or 10 days. The 2<sup>nd</sup> collection date (13<sup>th</sup> of November) had seen the pots out for 6 days. At the last collection (22<sup>nd</sup> of November) they had been out 9 days. No information on the fishing time of each pot was provided by dataset from 1905. The total number of cod caught, were 504 samples (168, 143 and 191 respectively). The bags were taken back to the Flødevigen Research Station, for further processing of the fish.



**Figure 2.** Map of the Søndeledfjord with the localizations of the eel pot from the 2006 field work marked with red ( [www.gulesider.no/kart](http://www.gulesider.no/kart), edited in power point)

## 2.5 Lab work

### 2.5.1 Measuring

The lab work was done at the fishing lab at Flødevigen immediately following field sampling, maximum 1-2 days after collection. Depending upon the number of fish captured. All this work was done by my supervisor, technicians from the research station and myself.

Each fish was handled on exactly the same way. The length was measured as the fork length, the length from the anterior part (the mouth) to the tip of the median caudal fin rays (Anderson & Neumsann 1996). They were measured on a plate with tape measure in mm. The fish was opened by cutting carefully, using a scalpel, for not to spoil any of the inner organs, from the gills backward to the gut opening. The sex was determined and the maturity revealed according to a scale from 1-5 (see table 1), by looking at the gonads. The head was dissected to get the otoliths; by cutting longitudinally from the eyes and through the brain (Devries & Frie 1996). The two otoliths were then removed by a tweezer, cleaned and put in envelopes, for later reading.

In addition the total body weight, liver weight, and gutted weight (the fish without the organs) was measured in grams, and a DNA sample was taken on some of the cod. These additional data were collected by routine, while not used further in this thesis because no comparative data existed in the historical sample from Dahl and Dannevig (1905).

Table 1. Maturing scale used within the Institute of Marine Research

Stage	Description
1	Juvenile/immature: Gonads are small, eggs or milt not visible to naked eye
2	Maturing: Gonads are developing (maturing) visible eggs and milt
3	Running: Ovaries and testes are in running condition
4	Spent/ resting: Shortly after spawning. Gonads are usually loose and reddish. Eggs or milt not visible
5	Uncertain: uncertain between 1 and 4

### 2.5.2 Otolith reading

Otoliths are known as earstones, consisting of calcium carbonate and proteins, they are located in the inner ear (Wootton 1998). They help the fish in hearing and balance. There are three of them; sagitta, asteriscus, lapillus, the largest one sagitta is the one used in aging (Devries & Frie 1996, Wootton 1998).

The otoliths have different zones or rings that alternate and are used in our research to determine the age of the fish. The opaque zone represents a period of fast growth, occurring in the summer season. The translucent zone (hyaline) represents a period of slow growth occurring in winter when the fish uses its energy on reproduction (Bagenal & Tesch 1978, Wootton 1998). The winter zone (hyaline zone) is used to find the age of the fish, one translucent and one opaque zone correspond to one year, one annuli (Devries & Frie 1996, Wootton 1998).

The otoliths were read at the lab at Flødevigen by me, after a learning period with Esben Moland Olsen (supervisor) and a highly experienced technician (Kate Enersen, IMR Flødevigen). The first 200 otoliths were read twice.

All the otoliths were prepared identically before the reading. They were cracked in two at the center (length-wise). It is very important to crack them as closely to the middle as possible, to avoid missing early rings (Devries & Frie 1996). The otoliths were then placed flat on the fingertip and split in two. To make the annuli more easily readable, the otoliths were sandpapered gently to make it smoother, and burned by a lighter, with the cracked surface faced to the flame with a 1 cm distance (Bagenal & Tesch 1978, Devries & Frie 1996). The opaque zones kept their original colour as the translucent zones turned brown. The otoliths were then removed from the flame and cooled.

After the preparation, the otoliths were placed on a clay of plasticine, and gently sprayed with water. They were then read in a magnifier in enlargement 1,25X or 1,6X (depended on the size of the otolith), with light from the side (Bagenal & Tesch 1978). I found that all the cod had already started the winter zone along the outer margin, as they were caught in October/November. According to standard procedures at Flødevigen (Kate Enersen, pers. com.) this zone is usually not accounted for as a year, before January. However, I wanted the age of the cod the next spring, when they were spawning. So I added the outer zone as a year. Hence I used the age, the fish would have during upcoming spawning season in the statistical analyses of growth and maturity. Some of the zones were indistinctive, also after the preparations. This made some of the otoliths hard to read, and one

sample was impossible to read, which was noted. The difficult samples were checked by my supervisor. It became easier to recognize the zones after some time. This is why the first 200 otoliths were read twice.

## 2.6 Statistical analysis

### 2.6.1. The data

The two tables from Dahl and Dannevig survey and the data from the my lab work was error checked. Some of the maturity numbers from the lab work were a little uncertain and listed between 1 and 2, and 2 and 3. They were all rounded down since Dahl and Dannevig had been restrictive with their maturity data (Dahl & Dannevig 1906).

The maturity data from 2006 was initially given as an index number from 0-5, differing from the two point scale, 0 (immature) and 1 (mature) given by the 1905 data (Dahl & Dannevig 1906). For the comparison, the 2006 dataset was adapted to the two-point scale by giving the immature (0 and 1) as 0 and the mature (2 and 3) as 1.

According to Dannevig (1933), the method used for reading otoliths in 1905 was most likely biased by one year. He concludes that at the time, that the first zone in the otoliths was recognized as a winter zone, so a fish that was noted as one year was instead only 6 months old (Dannevig 1933). So the age data from 1905 had to be subtracted by 1. This was also checked with a graph by plotting 1905 data with and without subtracting 1 year, together with our 2006 data. Note that this will introduce some uncertainty, regarding the historical comparisons on growth and maturity at age. The comparison on the size distribution and maturity at length should be more secure.

The different data (length, the different weights and also weight against length regression) from 2006 were plotted to look for outliers. Two fish, did stand out as deviations, and were subsequently cut out from the rest of the analysis. The division of the two sexes was also checked, with 51 % female and 49% male in my sample.

### 2.6.2 Age and length distribution

Histograms were plotted in the statistical program “R” (R Development Core Team 2006) edition 2.4.1; with the length and age distribution and maturity of the different ages of the different dataset of 1905 and 2006. The mean, standard deviation, maximum and minimum, were measured for length and age distribution. The data was also checked to see if the different distributions were significantly different from each other. The length distribution of 1905 and 2006 together looked normally distributed, so a linear model was used. But the age distribution of 1905 and 2006 together were not normally distributed, but rather skewed left-wise. Hence a non parametric test, the Wilcoxon rank sum test was used. This is a test which compares the median instead of the mean of the two distributions (Crawley 2005). The maturity at the different ages with number and proportion of immature vs. mature in 1905 and 2006 were sat in a table.

### 2.6.3 The growth, maturity and harvest

The different growth rates in 1905 and 2006 were analyzed by making a model with length and age, both as continuous variables and with years as factors (1905 vs. 2006). I first made a model with an interaction effect between *year* and *age*, but this was not found significant. So a model without the interaction was then developed

$$(1) \text{lm}(\log(\text{length}) \sim \log(\text{age}) + \text{factor}(\text{year}))$$

The model was checked for normality, and plotted with the data from 1905 and 2006 in the same graph with two separate growth curves. The age data is denoted only in whole numbers. Hence you will not get a smooth curve. In order to get a continuous curve of this data, the prediction function was used. This function estimates values of age versus length of the collected data (Crawley 2005).

To analyze the age and length at maturity, a logistic regression of the data was performed as a glm (generalized linear model) with family binomial, this is due to the response variable being mature or immature as a binary response variable and the explanatory variables were both categorical- or factor-variable (*year*) and continuous or numeric variable (*length* and *age*) (Crawley 2005).

I computed two regressions, one with *length\*year* against maturity and one with *age\*year* against maturity

$$(2) \text{ maturity} \sim \log(\text{length}) * \text{year}$$

$$(3) \text{ maturity} \sim \text{age} * \text{year}$$

This division was made because the age data was more uncertain than the length data (see above). Note that the regression with maturity as the response variable (maturity ogives), does not separate between first time spawners and repeat spawners. The models only express the probability to be mature. The length parameter data was given in log (length), to compress the length data.

The data in the two models was divided into the year 1905 and 2006. It was then plotted as two curves in two different graphs (one graph with the ages, and one with lengths). As the response variable is binomial, you will not get a smooth curve. Hence, the predict command were used to produce a smooth curve

A glm (generalized linear model) regression on the two age data samples were computed to find the age (A50), at which point it is 50% probable for the sample population to be mature. The same exercise was conducted the length probability (L50). Computing data collected in 1905 and 2006. To get the 50% probability, the formula

$$(4) \text{ logit}(p/1-p) = \beta_0 + \beta_1$$

was used.  $\beta_0$  is the intercept estimate in the summary table and  $\beta_1$  is the length or the age estimate.

The harvest for the Søndeledfjord from 1905 and 2006 respectively was also compared; to see if there were any differences. First, I used catch data supplied by the Norwegian Directorate of Fisheries; it was data from the fishing delivery office in Risør from 1977-2005. Only the cod data were used. Second, both the data from 1905, from the local fishermen and from Karl A. Jensen were used. Because no professional cod fishers today use pots as their fishing equipment, we had to use data from our own fishing, to compare the data from the two tables from 1905. Note that from the data collected in 2006, duration of catching samples (fish) is known, while the 1906 data did not disclose how long the catch time lasted.

## 3 Results

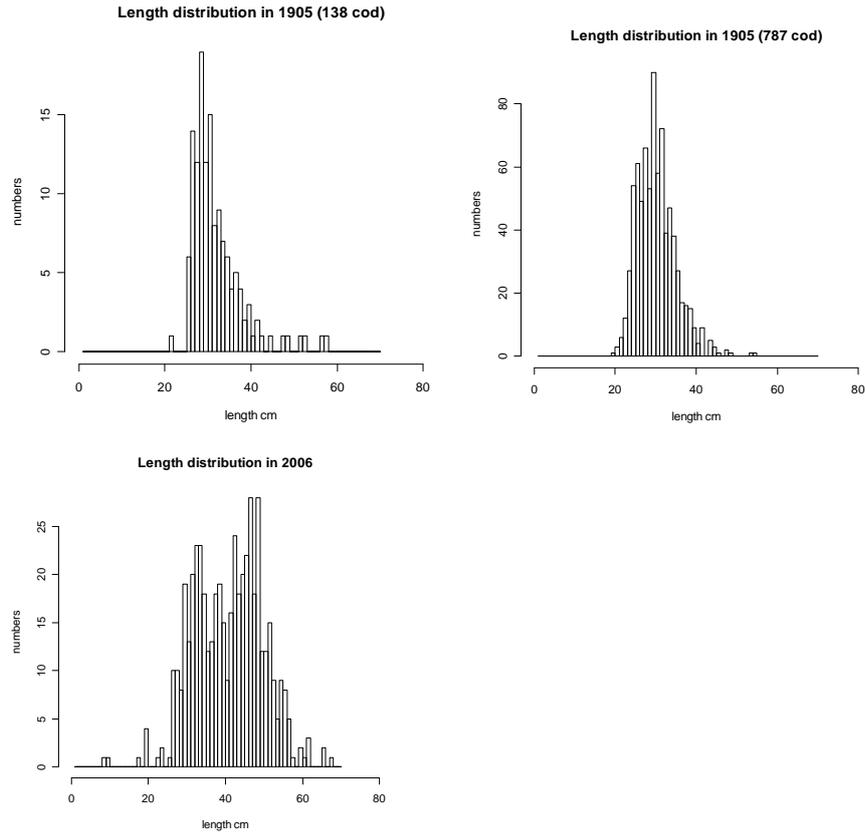
### 3.1 Length and age distributions

#### 3.1.1 The length distribution

The cod samples from 2006 have a wider length-distribution compared to the two samples batches from the 1905 data. 2006 data batch displayed cod from 8.5cm to 68.0cm while the cod in the two graphs from 1905 displayed fish from 20/22cm to 55/58cm (Figure 3). Comparing the two samples from 1905, the length distribution from the 138 cod batch looks similar to the 787 cod batch. Hence they represent a good selection of the total 787 batch population. This is supported by the fact that the mean value is 32.4cm with standard deviation being 6.1 for the 138 cod sample. And the mean value of 30.7cm with 4.8 as standard deviation displayed for the 787 cod sample (Table 2).

Comparatively the 2006 batch contains proportionally much longer samples than the 1905 batch; with the mean value of 41.0 and standard deviation of 9.0 (Table 2). The appearance of the graph indicates that the distribution has shifted to longer cod in 2006.

To see if the mean length in 1905 and 2006 was significantly different, a students' "t-test" was performed. The mean value turned out to be significant different ( $p < 2e-16$ ) (Table 3).



**Figure 3.** The graph shows the length distribution from 1905 and 2006 respectively. Notice the different y axes.

**Table 2.** Gives the different values from the tree length distributions.

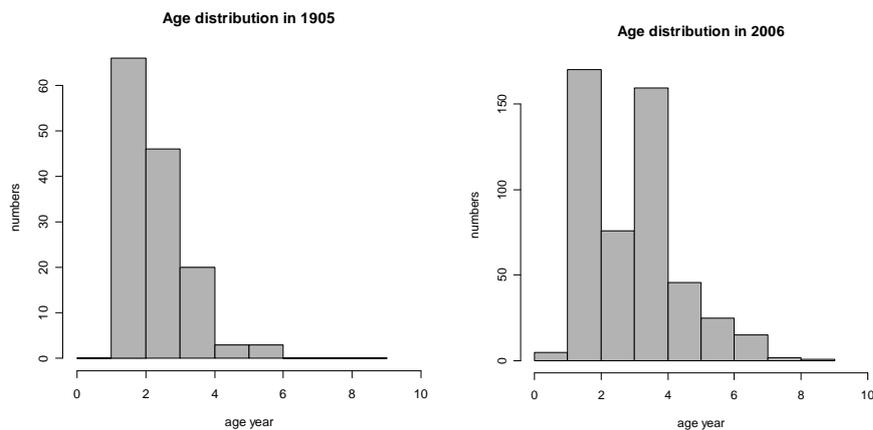
Length	1905 (787 cod)	1905 (138 cod)	2006
Max	55	58	68
Min	20	22	8.5
Mean	30.68742	32.44928	40.9918
SD	4.817682	6.063018	8.964988

**Table 3.** Display the result from the student's t test, to see if the distributions were significantly different from each other.

	Estimate	Std. Error	Pr(> t )
Intercept	5.714741	0.006842	<2e-16
Factor(År)2006	0.274532	0.010984	<2e-16

### 3.1.2 The age distribution

The age distribution only displayed data from the 138 cod sample from 1905, and the number of cod in each age group overall, was fewer compared with 2006. The mean value in 1905 was 2.8 years and standard deviation was 0.9 (Table 4). The cod ranged from 2 to 6 years, with not many samples older than 4 (Figure 4). The cod from 2006 had a wider range in age, (from 1 to 9 years) with the population being predominantly young samples. The graph in figure 4 displays more old cod from the 2006 sample. The mean value was also larger than in 1905, being 3.4 year (Table 4). To check if the difference was significant, a Wilcoxon rank sum test was performed. This test was used due to the fact that the data was not normally distributed. The result displayed that the difference in age was significant with p-value =  $3.195e-07$ .



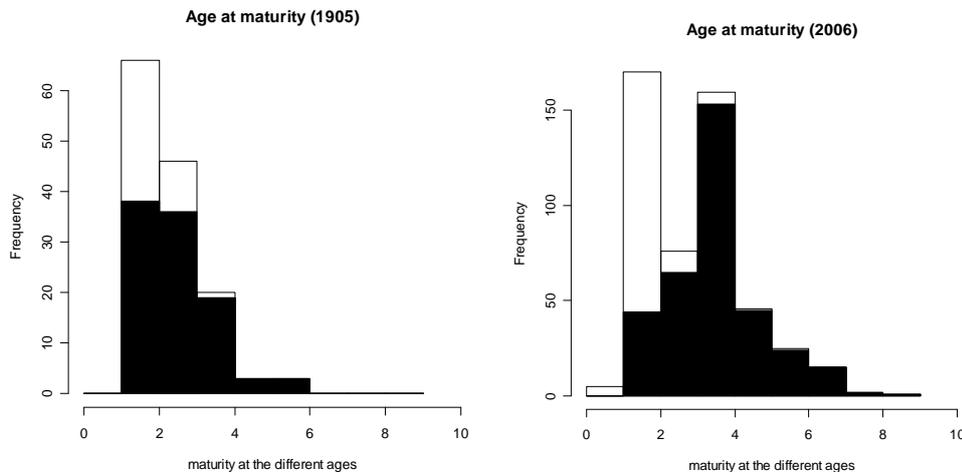
**Figure 4.** The age distribution of Skagerrak coastal cod in 1905 and 2006.

**Table 4.** The age distribution of Skagerrak coastal cod in 1905 and 2006.

Age	1905	2006
Max	6	9
Min	2	1
Mean	2.775362	3.44489
SD	0.9282124	1.40655

### 3.1.3 The age at maturity

The maturity at the different ages in 1905 and 2006 is displayed in figure 5. It is evident that a larger part of the two years old were mature in 1905 (0.57) than in 2006 (0.26), albeit that the number of two year old (immature and mature) is much bigger in 2006 (Figure 5). This is evident from and supported by the proportion of immature samples in 2006 (0,74) and 1905 (0,42) for the two years old samples (Figure 5). A greater number of four years olds were mature in 2006 than in 1905 (see figure 5 and table 5).



**Figure 5.** The age distribution of Skagerrak coastal cod in 1905 and 2006, the black parts indicate the number in each age class that is mature.

**Table 5.** The number and proportion of immature and mature Skagerrak coastal cod in 1905 and 2006.

Age	Immature (1905)	Portion Immature (1905)	Immature (2006)	Portion Immature (2006)	Mature (1905)	Portion mature (1905)	Mature (2006)	Portion mature (2006)
1			5	1			0	0
2	28	0.42	126	0.74	38	0.57	44	0.26
3	10	0.21	11	0.14	36	0.78	65	0.86
4	1	0.05	6	0.04	19	0.95	153	0.96
5	0	0	1	0.02	3	1	45	0.98
6	0	0	1	0.04	3	1	24	0.96
7			0	0			15	1
8			0	0			2	1
9			0	0			1	1

## 3.2 Modeling growth and maturity pattern, harvest

### 3.2.1 Growth

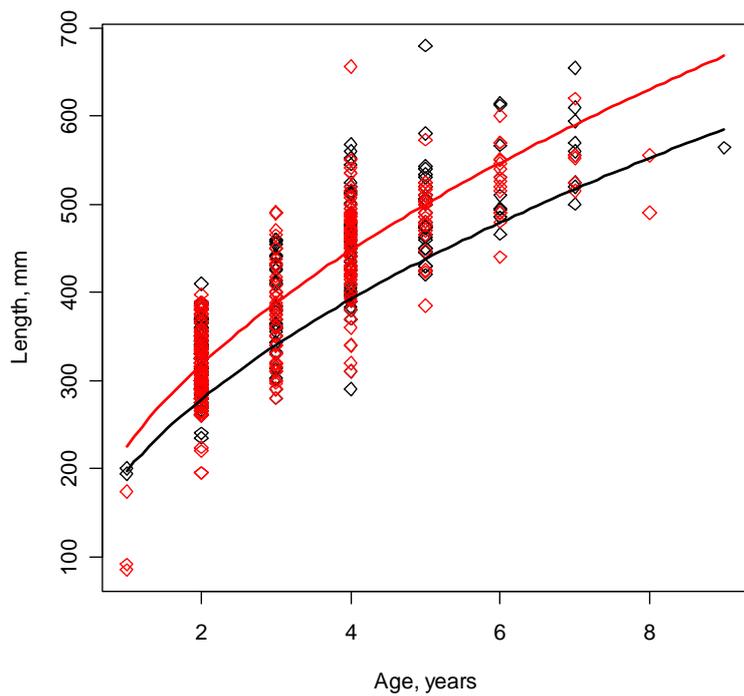
To see if the cod grew at different relative rates in 2006 compared to 1905, model (1) with the length, age and year was used. All estimates turned out to be significant when the interaction was discarded (Table 6). Evaluation of the model was then performed to look for non normality, and the residual plot showed no unexplained trends.

The model was then plotted (Figure 6). The present study (2006) and the historical data (1905) overlapped pretty well with each other, especially within 2-7 year samples. But the data from the oldest and youngest cod samples are somewhat spread out. These data deviate substantially from the rest (Figure 6).

The growth curves run through the majority of the points and it is clear that the cod in 2006 grew faster than the cod in 1905. They are longer in all age classes. The difference between the two curves becomes larger with the age (Figure 6).

**Table 6.** The growth model (1) of Skagerrak coastal cod  
 $\text{lm}(\log(\text{length}) \sim \log(\text{age}) + \text{factor}(\text{year}))$  with all the estimates significant.

(1) $\text{lm}(\log(\text{Length}) \sim \log(\text{Age}) + \text{factor}(\text{Year}))$	Estimate	Std. Error	Pr(> t )
(Intercept)	5,28727	0,01608	<2e-16
$\log(\text{Age})$	0,49379	0,01255	<2e-16
$\text{factor}(\text{Year})2006$	0,13216	0,01205	<2e-16



**Figure 6.** The two growth curves of Skagerrak coastal cod, with the actual data behind as points, from 1905 (black) and 2006 (red).

### 3.2.2 Maturity

Binomial maturity regression analyses were performed on the global model for both the length and age successfully. Hence all the parameters were significant (Table 7). The maturity analysis with the length variable is shown in Figure 7. It displays the probability of being mature at a specific length in 1905 and 2006 respectively. The probability of being mature at shorter length was higher in 1905 than in 2006 (Figure 7). At approximately 450 mm it was 100 % probability of being mature both in 1905 and 2006 (Figure 7).

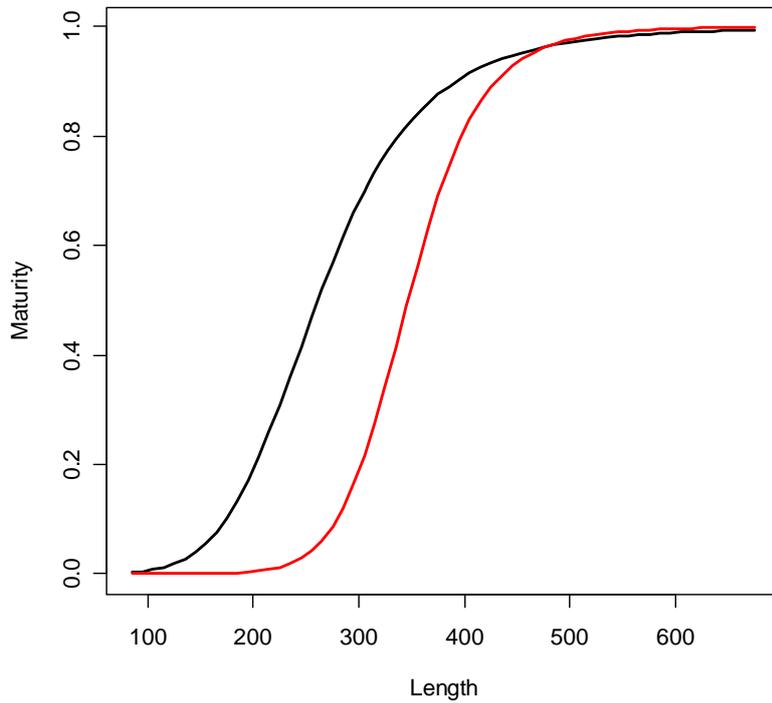
In 1905 the length of the cod was 261.1 mm at 50 % probability of being mature (L50), while in 2006 the L50 was 346.5 mm (Table 8).

The probability of being mature at a specific age is displayed in figure 8. Fish overall matured earlier in 1905. At about 6 years it was 100% probability of being mature in both 1905 and 2006 (Figure 8).

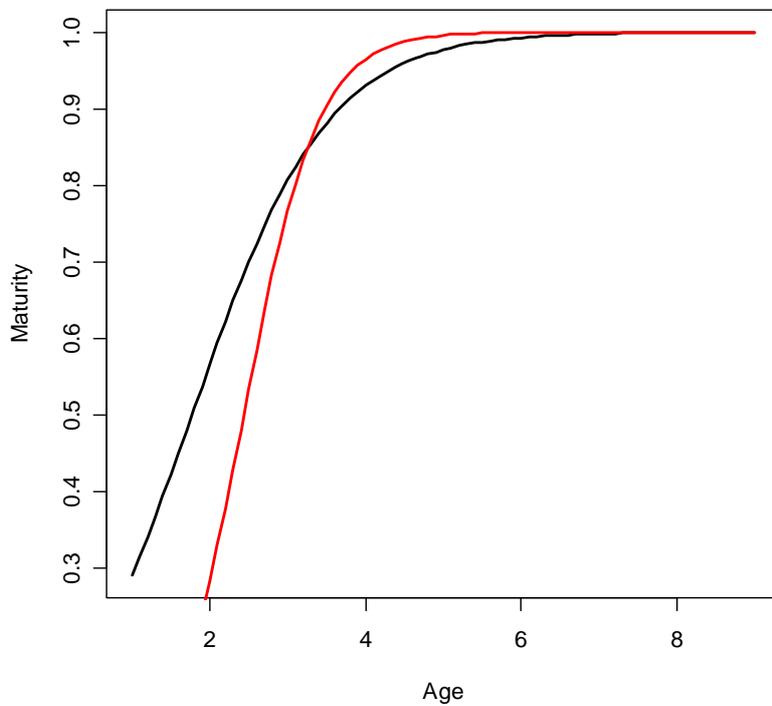
The age at 50 % probability of being mature (A50) in 1905 was 1.77 years, while the A50 in 2006 was 2.44 years (Figure 8, Table 8).

**Table 7.** The two binomial maturity regression analyses of Skagerrak coastal cod, with all the estimates significant.

<b>(2) maturity ~ length * year</b>	<b>Estimat</b>	<b>Std. Error</b>	<b>Pr(&gt; z )</b>
Intercept	-30,168	9,773	0,00202
log(Length)	5,421	1,71	0,00153
Year2006	-29,498	11,16	0,00821
log(Length):(Year)2006	4,782	1,939	0,01366
<b>(3) maturity ~ age * year</b>	<b>Estimat</b>	<b>Std. Error</b>	<b>Pr(&gt; z )</b>
Intercept	-2,0504	0,8163	0,012009
Age	1,1592	0,3288	0,000422
factor(Year)2006	-3,0886	0,9569	0,001248
Age:factor(Year)2006	0,9499	0,3823	0,012977



**Figure 7.** The probability of being mature for Skagerrak coastal cod, at different lengths (in mm). Red curve shows cod in 2006, and the black curves shows cod in 1905.



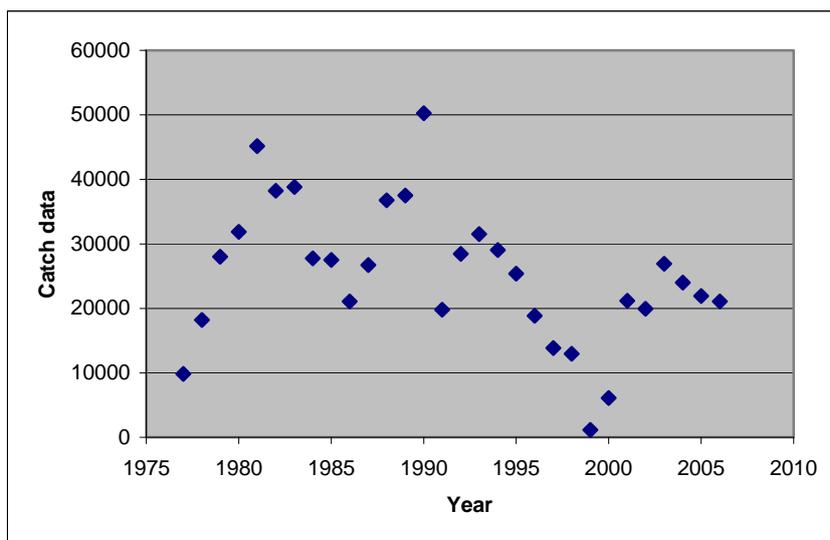
**Figure 8.** The probability of being mature for Skagerrak coastal cod, at different ages. Red curve shows cod in 2006, and the black curves shows cod in 1905.

**Table 8.** Values for the length and age at 50 % maturing analyses.

1905:Maturity ~ log(Length)	Estimat	Pr(>lzl)
Intercept	-30,168	0,00202
Length	5,421	0,00153
2006:Maturity ~ log(Length)	Estimat	Pr(>lzl)
Intercept	-59,6654	<2e-16
Length	10,2031	<2e-16
1905:Maturity~ Age	Estimat	Pr(>lzl)
Intercept	-2,0504	0,012009
Age	1,1592	0,000422
2006:Maturity ~ Age	Estimat	Pr(>lzl)
Intercept	-5,139	<2e-16
Age	2,1091	<2e-16

### 2.3 Fishing

The illustration of the catch-data in Risør from 1977 to 2005 is shown in Figure 9. It displays that the catch fluctuates, tending a downward trend, reaching a low point in 1999 (Figure 9).



**Figure 9.** An illustration of the cod landings in Risør from 1977–2005. Data is from the fishing delivery office in Risør.

When comparing the pot catches in Risør in 1905 and 2006, both batches of data from 1905 revealed higher catch-per-unit-effort in 1905 than 2006. The data from the local fishermen was 7644.12 gram pr. pot and data from Karl A. Jensen who at that time bought most of the fish was 8407.41 gram pr pot. The catch-weight ratio from our fishing in 2006 gave 5017.92 gram pr pot.

## 4 Discussion

This comparison of life-history traits between the coastal cod in 1905 and 2006 in the Søndeledfjord showed that the cod in 2006 tended to be longer and older compared to cod in 1905. The growth analysis showed that the cod tended to grow faster in 2006 than in 1905. Furthermore, I found that maturity ogives were displaced towards older age and bigger size in 2006 compared to 1905. Fish tended to be mature at a younger age with a smaller size in 1905 vs. 2006. My own catch data gave an indication of less catch-per-unit-effort in 2006 vs. 1905.

Perhaps the biggest challenge with this study was the comparative exercise of present versus 100 year old data. The methods had to be as similar as possible to support the validity and integrity of the study. Luckily a great deal of the details had been written down by Dahl and Dannevig (1906), and all the raw data were fully available in tables. Hence, it was possible to cope with the “shifting baseline” problem (Pauly 1995). The methods were as similar as possible, using the same fishing gear (pots). Although the exact design of the pots have probably changed. The time of the fishing, in November, was approximately the same. The deviation in method of reading the otoliths was adjusted (ref chap. 2.5.2). The fact that I had to use my own catch-per-unit-effort data, to compare with the landings data from 1905 presents some uncertainty.

All the descriptive analyses (length, age and maturity at age) were performed to show how the data were distributed. Highlighting that the age data compromised the most uncertain parts of the data samples. Hence reading the otoliths is a very subjective method, and to some extent it can be very difficult. It requires an experienced reader (Jorgensen 1990) to defend the integrity of such data. Reproduce ability in denoting results is important for any data collection, and the emphasis on accurate data sampling forced me to take responsibility of sampling data by myself under the supervision of highly experienced personnel. Therefore I have to declare that some inaccuracies have most likely occurred in analyzing the samples.

All the descriptive data gave evidence towards the reversed hypothesis that the length and age distribution should show significantly longer and older cod in 2006 than 1905. The mean length had increased by approximately 100 mm and the mean age had increased by around 0.6 year. This shift was significant. The length distribution from 1905 was somewhat skewed to the right with many small and a few large. This suggests that competition might influence the system in question (Lekve et al. 2002). The competition has been demonstrated

to be strongest inside the fjords like the Søndeledfjord, along the Skagerrak coast (Lekve et al. 2002). In 2006 the length distribution had changed, and it was more normally distributed.

The maturity at age displayed more elderly mature cod in 2006 than in 1905. One aspect that makes these results less clear is underlined by the results showing data of cod-size being larger in 2006 (502 cod sample) than in 1905 (138 cod sample).

The growth analysis clearly show that the cod in 2006 grew faster than in 1905 as the 2006 curve lies over the 1905 curve through all the age groups. Due to the limitations of the data samples with respect to the spread in batch numbers of “young” and “old” samples, the regional trend deviations will be significant in displaying the growth curve.

The maturity ogive method was used because the reaction norm method is a lot more complicated and need a very large sample size than the capacity of this study (Barot et al. 2004). Maturity ogive has its' limitation, albeit it only gives the probability of being mature, not becoming mature. Evidently it can not separate between first-time spawners and repeat spawners (Heino et al. 2002a). Since no cod under 2 years, were mature I tried to find the probability of becoming mature by only using the 2 year olds. This dataset however, was too small for such an exercise. However, the ogives still gives the maturity status of a stock (Barot et al. 2004).

The maturity ogives with length and age showed that a larger proportion of the fish tended to be mature at a younger age and smaller sizes in 1905 vs. 2006. This confirms the results that were pinpointed out in the length and age distribution. Including the growth curve, showing that they grew faster, were older and longer in 2006. The length at 50 % probability (L50) of being mature has increased with 8,54 cm, and the age at 50 % probability (A50) of being mature has increased with 0,67 years from 1905 to 2006.

These results conclude that the stock in the Søndeledfjord is in a better state in 2006. Comparing the efficiency (gram cod pr. pot) from 1905 to 2006 shows that it was caught over 3 kg more cod per pot in 1905 than 2006. This data is ambiguous, because it is not known whether it was connected several pots together or for how long the pots were fished in 1905. The data might show that the fishing was more efficient before, or that there were more cod. By looking at the catch data from 1977-2006, there is a downward trend of how much cod being delivered. Julliard et al. (2001) looked at the fishing of cod stock in the Risør area from 1986-1989. They found that the tourism in Aust-Agder County has increased continuously in the last 50 years, and expected that the recreational fishing might have increased. This was directed toward the younger cod stock. And had a severe impact on the stock (Julliard et al. 2001). According to this study the fishing has increased, but because they only had data from

a short time period, the problem with shifting baseline might interfere (Pauly 1995). The fishing can have increased in the last decades. But compared to 1905 it may have decreased.

My predictions to the master thesis turned out to be wrong. The maturity ogive of Skagerrak coastal cod has evidently shifted towards older age and bigger size, as compared to 100 years ago. My prediction was founded on the pre-assumption that fishing is more intense today, compared to the past. Probably there is less fishing in the fjord inside of Risør. This result is in strong contrast to the trend for the exploited cod populations today, as almost all of the studies on cod show the opposite e.g. (Heino et al. 2002a, Barot et al. 2004, Olsen et al. 2004a). None of the two hypotheses presented in the introduction seem to fit the Skagerrak coastal cod. However, this change must have had its' origin in phenotypic plasticity or the genotypic selection.

To be able to make a distinction if the changes have a genetic or phenotypic plastic origin is difficult with this data. Due to the fact that we have not used the reaction norm procedure (Heino et al. 2002a). We do not know all the other environmental elements that may change the conditions that the cod stocks have been exposed to. We only have data on the fishing (Reznick et al. 1990). I have data displaying the situation one hundred years ago, missing any data describing the development and evolution to this date.

The average heritability for the length in fish is usually 0.3, this can cause substantial evolution in just a few generations (Law 2000). Reznick and Ghalambor (2005) indicated that cod may use around 100 years for a 5-15 % change. Other studies have shown that this evolutionary process is a lot faster. Heavy harvesting may induce rapid evolution (Olsen et al. 2004a). One hundred years have passed with heavy harvesting, and it has been shown that the age at maturity is presumed to be a heritably trait open for selection (Law 2000). To reverse the trend caused by fishing. Hence reducing the harvesting by e.g. selecting for later maturity, is a lot harder. Hence, selection for later maturity is weaker (Law & Grey 1989). Studies have however shown an increase in the age and size at maturity displayed in the long-term study on guppy (*Poecilia reticulata*) (Reznick et al. 1990), in the Windermere pike (*Esox lucius*) (Edeline et al. 2007). And in the chum salmon outside of Japan (Fukuwaka & Morita 2008). These studies show the high possibility of deviations from the norm, and that we can not rule out the possibility that the genotype for length and age at maturity might have changed.

The answer to the change in the maturation might have something to do with natural selection and exploration. These are forces that operate in the opposite direction of each other. In periods with high fishing pressure, the natural selection is overwhelmed and the growth decreases, leading to earlier maturity (Edeline et al. 2007). While in periods of less fishing the

natural selection overwhelms the selection from the fishing. The growth increases, and thereby the fitness increases due to a larger body size. This also leads to reduction in the reproductive investment, due to the trade-off between growth and reproduction (Reznick et al. 1990). The fish invests later, in gonads, as a bigger size (Edeline et al. 2007). In the study on the Windermere pike science recognized this change between natural selection and fishing pressure through four periods of decreasing and increasing growth rates (Edeline et al. 2007). Parallel development seems likely to be the case with the cod stock in the Søndeledfjord. The natural selection is bigger than the fishing selection after the reduction in fishing. The highest mortality for the small cod is caused by the larger cod through predation and cannibalism. Hence, the natural selection would favor growth (Julliard et al. 2001).

Phenotypic plasticity might work against natural selection displayed in the study concerning chum salmon where the ocean conditions were leading to slower growth while the natural selection lead to faster growth. The average size maturity then remain stable or decreased (Fukuwaka & Morita 2008). In the Søndeledfjord the heavy fishing may have led to reduced intraspecific competition. There is more food for each fish so that they are able to grow faster. Phenotypic plasticity may influence the maturation probability, this has been confirmed in another recent study on the Skagerrak cod stock (Olsen et al. 2008). Both phenotypic plasticity and genetic selection through natural selection should contribute to this faster growth that I have found. Due to the trade-offs, the reproduction is being postponed.

The Søndeledfjord may be in a period of transition from being heavy fished, to a state of recovery. In the long run therefore, this faster growth could increase the intraspecific competition, increasing the population size, lower the food supply and slow the growth so the age at maturity increase (Trippel 1995).

In this study I presented data from two different time periods without any intermediate data. I tried to find a baseline, which is difficult, because commercial interests obviously did not start the fishing in the Skagerrak area on a major scale around 1905. However, the new data from 2006 was compared with data taken 100 years ago. Albeit, if the 2006 data had been compared with data recorded a few decades ago, major difference would not be disclosed. If local commercial interests had been fishing less for a couple of decades, differences in data collection would have been trivial. Ability to compare data from such a time-span, having data from a 100 years ago is not usual in science. Hopefully, a new trend in the study of size selective harvesting is contributed by this paper by further baseline studies (Bunce et al. 2008).

## 5 Conclusion

This study concerning the Skagerrak cod stock in the Søndeledfjord is in contrast to nearly all other studies in the last couple of decades, conducted on cod stocks, showing a decline in age and length at maturity. The cod in the Søndeledfjord are most probably maturing later today (2006) compared to 1905. They are older and longer at maturity, and they also grow faster. The fishing data may display that they are fishing less now than a 100 years ago. The natural selection surviving and henceforth being naturally selected for bigger size, shows to be stronger than the fishing selection. The reduced intraspecific competition after the heavy fishing might also contribute to the increased growth rate. Due to the trade-off between growth and reproduction, the maturity is being postponed. These results show that the cod are probably living under better conditions. Henceforth, the fishing selection might be reversed. The changes displayed in this study based on similar methods of investigations separated by a century might not have been shown with comparative data recorded a few decades ago.

It is important to consider that age and size at maturity are not the only factors that explain maturation probability. The fish stocks' current energetic state might also be of influence to my results. An improvement in the liver weight and body weight is connected to an increase in the probability of sexual maturation in cod stocks (Marshall & McAdam 2007, Olsen et al. 2008). Results of these finding have been recorded, however they have not been analyzed yet.

The Skagerrak coastal cod population is heavily exploited cod. Hence change in age and size at maturity is a good indication of the described development. Studies on maturity change are important to be able to supervise the condition of this and other specific populations.

## 6 References

- Anderson RO, Neumsann RM (1996) Length, weight, and associated structural indices In: Murphy BR, Willis DW (eds) Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland, p 447-482
- Bagenal T, Tesch FW (1978) Age and Growth. In: Bagenal TB (ed) Methods for assessment of fish production in fresh waters IBP Handbook No 3. Blackwell Scientific Publication, Oxford, London, Edinburgh, Melbourne, p 112-114
- Barot S, Heino M, O'Brien L, Dieckmann U (2004) Long-term trend in the maturation reaction norm of two cod stocks. *Ecological Applications* 14:1257-1271
- Bromley PJ (2000) Growth, sexual maturation and spawning in central North Sea plaice (*Pleuronectes platessa L.*), and the generation of maturity ogives from commercial catch data. *Journal of Sea Research* 44:27-43
- Bunce M, Rodwell LD, Gibb R, Mee L (2008) Shifting baselines in fishers' perceptions of island reef fishery degradation. *Ocean & Coastal Management* 51:285-302
- Crawley MJ (2005) Statistics: an introduction using R, Vol. John Wiley and Sons Ltd, Chichester
- Dahl K, Dannevig GM (1906) Undersøgelser over nytten af torskeudklækning i øslandske fjorde. In: Norges F (ed) Aarsberetning vedkommende Norges Fiskerier for 1906. A/S John Griegs Bogtrykkeri, Bergen (in norwegian)
- Dannevig A (1933) On the age and growth of cod (*Gadus callaris L.*) from the Norwegian Skagerrak coast. *Director of Fisheries* 4, No. 1
- de Roos AM, Boukal DS, Persson L (2006) Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proceedings of the Royal Society B-Biological Sciences* 273:1873-1880
- Devries DR, Frie RV (1996) Determination of age and growth. In: Murphy BR, Willis DW (eds) Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland
- Edeline E, Carlson SM, Stige LC, Winfield IJ, Fletcher JM, James JB, Haugen TO, Vollestad LA, Stenseth NC (2007) Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *Proceedings of the National Academy of Sciences* 104:15799-15804
- Engelhard GH, Heino M (2004) Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Marine Ecology-Progress Series* 272:245-256
- Ernande B, Dieckmann U, Heino M (2004) Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271:415-423
- Esbeland SH, Olsen EM, Knutsen H, Gjosaeter J, Danielssen DS, Stenseth NC (2007) New perspective on fish movement: kernel and GAM smoothers applied to a century of tagging data on coastal cod. *Ices Journal of Marine Science* 64:920-928
- FAO (2006) The state of world fisheries and aquaculture 2006. Food and Agriculture Organization of the United Nation Rome
- Fromentin JM, Stenseth NC, Gjosaeter J, Bjornstad ON, Falck W, Johannessen T (1997) Spatial patterns of the temporal dynamics of three gadoid species along the Norwegian Skagerrak coast. *Marine Ecology-Progress Series* 155:209-222

- Fukuwaka M, Morita K (2008) Increase in maturation size after the closure of high seas gillnet fishery on hatchery-reared chum salmon *Oncorhynchus keta*. *Evolutionary Applications* 1:376-387
- Grift RE, Rijnsdorp AD, Barot S, Heino M, Dieckmann U (2003) Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Marine Ecology-Progress Series* 257:247-257
- Heino M, Dieckmann U, Godo OR (2002a) Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. *Ices Journal of Marine Science* 59:562-575
- Heino M, Dieckmann U, Godo OR (2002b) Measuring probabilistic reaction norms for age and size at maturation. *Evolution* 56:669-678
- Hop H, Danielssen DS, Gjosaeter J (1993) Winter feeding ecology of cod (*Gadus Morhua*) in a fjord of southern Norway. *Journal of Fish Biology* 43:1-18
- Jorde PE, Knutsen H, Espeland SH, Stenseth NC (2007) Spatial scale of genetic structuring in coastal cod *Gadus morhua* and geographic extent of local populations. *Marine Ecology-Progress Series* 343:229-237
- Jorgensen C, Fiksen O (2006) State-dependent energy allocation in cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 63:186-199
- Jorgensen T (1990) Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *Journal Du Conseil* 46:235-248
- Julliard R, Stenseth NC, Gjosaeter J, Lekve K, Fromentin JM, Danielssen DS (2001) Natural mortality and fishing mortality in a coastal cod population: A release-recapture experiment. *Ecological Applications* 11:540-558
- Knutsen H, Jorde PE, Andre C, Stenseth NC (2003) Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. *Molecular Ecology* 12:385-394
- Knutsen H, Olsen EM, Ciannelli L, Espeland SH, Knutsen JA, Simonsen JH, Skreslet S, Stenseth NC (2007) Egg distribution, bottom topography and small-scale cod population structure in a coastal marine system. *Marine Ecology-Progress Series* 333:249-255
- Law R (2000) Fishing, selection, and phenotypic evolution. *Ices Journal of Marine Science* 57:659-668
- Law R, Grey DR (1989) Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology* 3:343-359
- Lekve K, Enersen K, Enersen SE, Gjosaeter J, Stenseth NC (2006) Interannual variability in abundance and length of young coastal cod in the subtidal zone. *Journal of Fish Biology* 68:734-746
- Lekve K, Ottersen G, Stenseth NC, Gjosaeter J (2002) Length dynamics in juvenile coastal Skagerrak cod: Effects of biotic and abiotic processes. *Ecology* 83:1676-1688
- Lotze HK, Milewski I (2004) Two centuries of multiple human impacts and successive changes in a North Atlantic food web. *Ecological Applications* 14:1428-1447
- Marshall CT, McAdam BJ (2007) Integrated perspectives on genetic and environmental effects on maturation can reduce potential for errors of inference. *Marine Ecology-Progress Series* 335:301-310
- Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U (2004a) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932-935
- Olsen EM, Knutsen H, Gjosaeter J, Jorde PE, Knutsen JA, Stenseth NC (2004b) Life-history variation among local populations of Atlantic cod from the Norwegian Skagerrak coast. *Journal of Fish Biology* 64:1725-1730

- Olsen EM, Knutsen H, Gjosaeter J, Jorde PE, Knutsen JA, Stenseth NC (2008) Small-scale biocomplexity in coastal Atlantic cod supports a Darwinian perspective on fisheries management. *Evolutionary Applications*
- Olsen EM, Vollestad LA (2005) Small-scale spatial variation in age and size at maturity of stream-dwelling brown trout, *Salmo trutta*. *Ecology of Freshwater Fish* 14:202-208
- Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* 10:430
- Pinnegar JK, Engelhard GH (2008) The 'shifting baseline' phenomenon: a global perspective. *Reviews in Fish Biology and Fisheries* 18:1-16
- R Development Core Team (2006) R: A language and environment for statistical computing Vol. [2.4.1]edn R Foundation for Statistical Computing, Vienna, Austria
- Reznick DA, Bryga H, Endler JA (1990) Experimentally induced life-history evolution in a natural population. *Nature* 346:357-359
- Reznick DN, Ghalambor CK (2005) Can commercial fishing cause evolution? Answers from guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* 62:791-801
- Stearns SC (2004) *The evolution of life histories*. Oxford University Press, New York
- Svedang 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
- Swain DP, Sinclair AF, Hanson JM (2007) Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B-Biological Sciences* 274:1015-1022
- Trippel EA (1995) Age at maturity as a stress indicator in fisheries. *Bioscience* 45:759-771
- Wootton RJ (1998) *Ecology of teleost fishes*, Vol 24. Kluwer Academic Publishers. Dordrecht