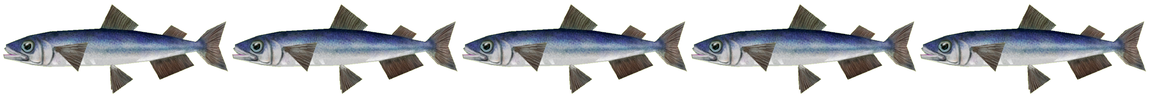
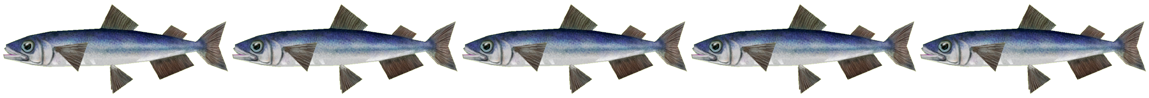


Barents Sea capelin and us;
Do they really mature and migrate at 14cm? Or have we become prisoners in our own Platonic allegory?

How shall we respond?



Henry Seal

Thesis for the Partial Fulfillment of the Degree
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Acknowledgements

This is hardly the winning of an Oscar or an Olympic gold medal so let's keep it short, sweet, and academic. Firstly I would like to thank Arild Folkvord who has kept me on my toes and provided great feedback at each stage. His experience of guiding so many before me through the masters kept me on the tracks. Secondly my thanks go to Bjarte Bogstad. He has a unique style, cut somewhat from the "mad scientist" cloth, and I think that is just absolutely excellent. In addition, contained in his head is a quite phenomenal amount of knowledge, which was always an incredibly useful resource to have access to. I must thank him for being generous with his time and always interested in what's going on. I am bursting with gratitude for my supervisor, Georg Skaret. For a better supervisor I could not have asked. He listens, encourages exploration of every avenue, revels in the possibility of challenging what we do, how we do it, and what we take from it. Without him this thesis would surely have been an unmitigated disaster, but most of all I have enjoyed the time we spent together in meetings just talking about broader subjects and anything that interested me. I shall owe any future career that I take in this field to his installation of enthusiasm. Keep up the good work.

Time for a beer I think.
Cheers.

Contents

Abstract

Capelin (*Mallotus Villosus*) are an important component of the Barents Sea ecosystem. As zooplankton consumers they play a role in channelling energy up the food web, and they have the potential to represent a biomass of several million tonnes. Their population has undergone booms and crashes, as one may expect of a high production, high mortality species, and our management of the fishery is based around preventing a >5% chance that the spawning stock biomass will fall below 200,000 tonnes. They are surveyed in the autumn, before a maturity model is applied and natural mortality is factored in during their migration to the spawning sites, leaving a total allowable catch (TAC). Our present model is a simple cut off of 14cm, and anything longer is assumed to spawn that year. This may be too simplistic however, as it possibly does not reflect the biological situation on the ground, which could lead to miscalculations of the spawning stock and the accompanying TAC. In this investigation I used the survey data and catch data in a comparison to assess the 14cm cut off, and following this made models which would better reflect the length and age distributions seen in the catch. Its seems likely that the biomass of capelin migrating has been overestimated every year, and that we need to do further work to assess the spawning stock in order to get a better handle on capelin maturity.

Introduction

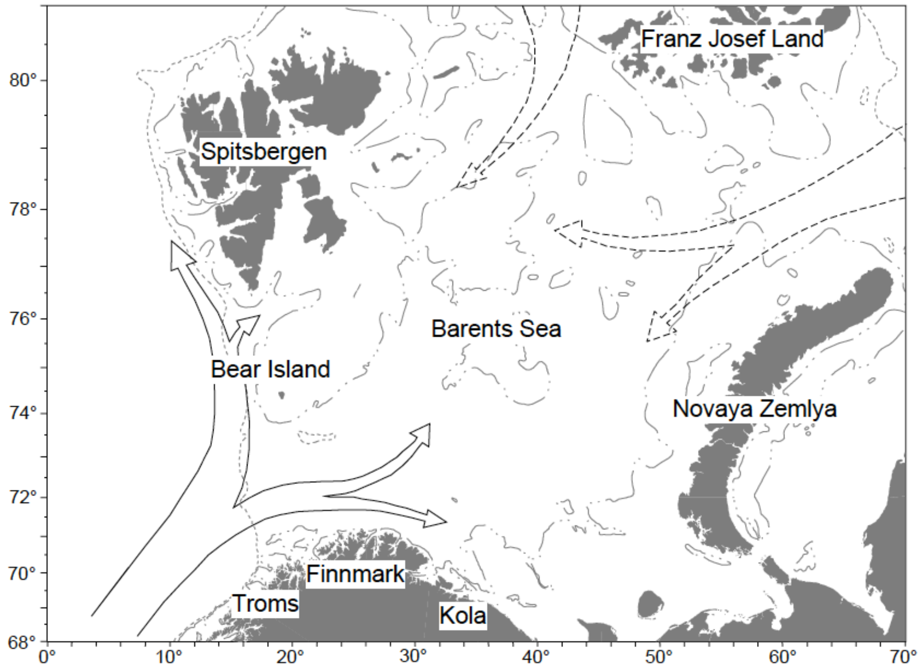

Fig. 1. (Gjøsæter, 1998). The Barents Sea including influential currents. From the south the North Atlantic and Norwegian Coastal currents bring warm water, and from the north and east Arctic currents bring cold water.

The backdrop

The Barents Sea is the area bounded by Spitsbergen and Franz Josef Land to the north, the Norwegian and Russian coastlines to the south, the island of Novaya Zemlya to the east and the edge of the continental shelf to the west. The depth ranges from less than 100m to deeper trenches of over 400m. As displayed in Fig. 1 the Barents Sea is subject to currents bringing colder Arctic water south, and warmer Atlantic/Coastal water north. The polar front is defined by where these currents meet, and this in combination with the movement of more localised water masses dictates to where the ice sheet extends during the seasonal freezing and melting. During the winter, when at its greatest extent, the ice sheet will run from the south of Novaya Zemlya to the south of Bear Island (74-75°N), and at its lowest (in mid September) from around the north of Spitzbergen to the south of Franz Josef Land (80-81°N), although the extent is declining over time (Comiso, 2012; Stroeve *et al.*, 2012).

In April the ice sheet starts to recede and is accompanied by a spring bloom of phytoplankton. Nutrient rich water transported from deeper parts of the Arctic ocean and the North Atlantic enable the rapid growth of phytoplankton and result in the Barents Sea being an exceptionally productive area (Sakshaug, 1997; Carmack and Wassmann, 2006). This production is inter-annually variable, depending on the extent of the ice sheet and the inflow of warmer and well mixed Atlantic water in a given year, and locationally variable, since topographically induced upwelling, or shallow areas with high winds, for example, will be better mixed than more stable areas (Carmack and Wassmann, 2006). Following the phytoplankton are herbivorous, omnivorous and carnivorous zooplankton, forming species rich communities whose make up is heavily influenced by the temperature and salinity of the area (although the majority of biomass will be made up of few species) (Dvoretsky and Dvoretsky, 2010).

As we continue our journey up the trophic levels there is at this point a diversity bottle neck, as the main fish consumers of zooplankton in the Barents Sea are capelin (*Mallotus villosus*), herring (*Clupea harengus*) and polar cod (*Boreogadus saida*), although these three species do not by any means hold equal importance in the conversion of planktonic biomass into fish biomass (Gjøsæter, 1998). Krill and shrimp species also feed on plankton, and upon these fish and small crustaceans feed larger fish, both pelagic and demersal stocks of which are heavily utilised by humanity including Northeast arctic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), deep-sea redfish (*Sebastes marinus*, *Sebastes mentella*), Greenland halibut (*Reinhardtius hippoglossoides*), and long rough dab (*Hippoglossoides platessoides*), along with the krill, deep water shrimp, and larger crustaceans such as red king (*Paralithodes camtschaticus*), and snow (*Chionoecetes opilio*) crab.

Thanks to the high seasonal productivity there are several marine mammals that temporarily visit the Barents Sea to exploit this summer feeding opportunity. These include minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*), humpack (*Megaptera novaeangliae*), and blue (*Balaenoptera musculus*) whales, white beaked dolphins (*Lagenorhynchus albirostris*), killer whales (*Orcinus orca*), harbour porpoises (*Phocoena phocoena*), and occasionally bowhead whales (*Balaena mysticetus*) and narwhals (*Monodon monoceros*). Meanwhile permanent mammalian residents include walruses (*Odobenus* *rosmarus*), bearded (*Erignathus barbatus*), harp (*Pagophilus groenlandicus*), harbour (*Phoca vitulina*), grey (*Halichoerus grypus*), and ringed (*Pusa hispida*) seals, and beluga whales (*Delphinapterus leucas*). Polar bears (*Ursus maritimus*) inhabit Spitbergen and Franz Josef land, and use the sea ice for hunting. There are also many sea birds (abundances fluctuating seasonally) that use the Barents Sea, such as greater black backed gulls (*Larus marinus*), auks (*Alcidae*), kittiwakes (*Rissa tridactyla*), fulmars (*Fulmaris glacialis*), guillemots (*Uria lomvia*) and Arctic skuas (*Stercorarius parasiticus*).

Getting to know our subject

So now that we have oriented ourselves and got some context (that the Barents Sea is an ecologically important area, supporting numerous charismatic species and rich fisheries) we turn our attention to the humble capelin; a pelagic, planktivorous fish, with a maximum length of ~21cm, living to a maximum age of about 5 years.

In February the mature capelin comes into the coastline of northern Norway and Russia in schools of up to hundreds of tonnes, to spawn, with routes (usually two or three used in a year) and sites likely linked to temperature and bathymetry (Gjøsæter, 1998; Olafsdottir and Rose, 2012). Spawning then takes place between around 15°E and 37°E (although not all of this coastline will be used) and typically occurs between 15m and 70m depth (Gjøsæter, Ushakov and Prozorkevich, 2011) on sandy or gravel substrate to which the eggs will adhere. The incubation period is dictated by the temperature, from around 20 days at 7°C to 80 days at 2°C(Gjøsæter and Gjøsæter, 1986). Individual growth is then highly variable both between years and within the same year class in the same year (Gjøsæter and Gjøsæter, 1986; Gjøsæter and Loeng, 1987), probably due to temperature differences (Gjøsæter and Loeng, 1987) and food availability (Gjosater, Dalpadado and Hassel, 2002). Metamorphosis occurs at a length of around 75mm, about 12 months after hatching (Vesin, Leggett and Able, 1981; Gjøsæter, 1998). Until the capelin are capable of sustained self-propulsion they will live in the central Barents Sea, but when it comes to their second spring (by now 1.5 years old) they will be ready to engage in the extensive summer/autumn feeding migration. The first movement is to the south in April to catch the earliest phytoplankton bloom which occurs closer to the coast than their overwintering areas. They then travel north to accompany the retreating ice edge which carries with it a 30-50km wide zone of high productivity due to the stabilising of the upper water levels thanks to the freshwater runoff from the melting ice

(Sakshaug, 1997). The locations of the feeding areas will change based on the hydrographical conditions, before the bloom subsides in late October to November and the capelin move back south and west to overwinter once again in the central Barents Sea (Gjøsæter, 1998).

Capelin engage in diurnal vertical migration, however this is more pronounced in the mature part of the stock, and changes through the seasons. In March and April the capelin will descend to the lower water layers during the daytime, and ascend to the upper layers at night. Once the 24 hour light of the polar summer takes effect the vertical migration reduces in distinction but is still visible with some rhythm. During September it once again grows in strength in the mature capelin, whilst the immature capelin seem to remain in the upper layers at all times. The polar night returns from October at which point the mature capelin remain close to the sea bed and disperse for their migration, before coming back together and schooling in the intermediate and upper layers again pre spawning in January (Gjøsæter, 1998). The pattern of vertical distribution may be liable to change in unusual circumstances however, such as a lack of preferred prey in the upper water layers forcing the capelin to switch prey and search in deeper layers (Mowbray, 2002).

The diet of capelin is mostly made up of amphipods, copepods and euphausiids (krill) (Gjøsæter, 1998). However they have changing feeding habits as they grow, favouring copepod prey when small, before reducing the proportion of the diet made up of copepods and starting to prey more selectively on euphausiids once the fish is of a sufficient size to tackle them (Vesin, Leggett and Able, 1981; Dalpadado and Mowbray, 2013). The growth of young capelin is correlated with abundance of small zooplankton, and the growth of older capelin with abundance of larger zooplankton (Gjosater, Dalpadado and Hassel, 2002), indicative that capelin are subject to at least some bottom up control. The presence of krill is an important factor determining the growth of adult capelin, since krill are rich in fat (E. L. Orlova *et al.*, 2002), and switching to an alternative feeding strategy will not replicate this nutritional value, although capelin do show preference for feeding on the larger stages of their zooplankton prey and larger prey items with higher fat content in general (Gjøsæter, 1998). It is important for capelin to obtain as high a fat level as possible during the feeding season since it is assumed that there will be little or no feeding through the winter, or indeed to provide the adults with the necessary energy to invest in sex cells pre spawning (Orlova *et al.*, 2010). When considering the feeding ecology of the capelin we must bear in mind that the Barents Sea should not be thought of as a stable and homogenous environment. There can be large (>2°C) differences in surface water temperature in the same year between northern and southern areas, or western and eastern, or the same area from year to year (Emma L. Orlova *et al.*, 2002) (due to the bottom topography and varying strengths of the currents) which will influence the species composition and spatial distribution of zooplankton communities (Dvoretsky and Dvoretsky, 2010).

Barents Sea capelin are osmerid fish, and are considered for management purposes to be semelparous (post sex death). There is evidence to suggest that physiologically speaking females are capable of being iteroparous (spawning more than once) (Forberg, 1982), and as an evolutionary strategy this could potentially be beneficial (Huse, 1998) (optimal reproductive strategies frequently differ between sexes), however we do not see the skewed sex ratio that would be expected were females to survive spawning and return again the following year (Gjøsæter, 1995). Despite the iteroparity of females in other populations, the oceanic Barents Sea capelin is semelparous, with the males using the last of their energy and sustaining high rates of injury during the side to side spawning process (during which they dig into the substrate)(Huse, 1998) and even apparently unharmed females dying a short time after spawning, resulting in near total mortality (Christiansen *et al.*, 2008).

As alluded to above there are other capelin populations; Icelandic, Newfoundland, and Norwegian fjord. There has been discussion over the connectedness of the Barents Sea and fjord populations, and the conclusion is that whilst the two populations are not genetically isolated, they seem to be physically separate and do not interbreed (Gjøsæter, 1998), although further work in this field may be yielding genetic difference controlling phenotypic traits (Georg Skaret, pers. comm.). This investigation is dealing exclusively with the Barents Sea stock.

Adult capelin. Photo: https://godfisk.no/sjomatskolen/fakta-om-fisk-og-skalldyr/lodde/

Pillars of the ecosystem

Capelin play a key role in the Barents Sea ecosystem (Carscadden and Vilhjálmsson, 2002). Previously I mentioned that the three main converters of planktivorous mass to fish mass were herring, capelin and polar cod, but not equally importantly. Although blue whiting and 0-group fish (of which 0-group capelin fluctuates in proportion) should be added as two more significant stocks in this regard (Eriksen, Bogstad and Nakken, 2011). The capelin is often the most key to this process, and forms a part of the diet of 21 fish species, 18 seabirds, 3 seals, and 8 cetaceans (Dolgov, 2002). The estimated of biomass of Barents Sea polar cod since 1999 has been between <1 and 2 million tonnes (Hop and Gjøsæter, 2013), whilst capelin reached almost 9 million in 1975, and was stable typically between around 4 to 6 million from 1972 to 1984, before undergoing major fluctuations since. As may be expected polar cod does better when capelin is not present, but possibly surprisingly capelin equally also does better without the presence of polar cod (Orlova *et al.*, 2009). It is clear that capelin is typically the more abundant, despite recent collapses, and this translates into high zooplankton consumption. There is an inverse relationship between zooplankton abundance and capelin abundance (Gjøsæter, Bogstad and Tjelmeland, 2002), and capelin schools graze down and exhaust the local supply of zooplankton in a matter of a few days (Hassel *et al.*, 1991). There is also a negative relationship between the biomass of krill and the size of the capelin population (Eriksen *et al.*, 2017). It is only juvenile herring that inhabit the Barents Sea, which drift in when the Norwegian spring spawning herring produces a particularly strong year class accompanied by a strong inflow of Atlantic water to the Barents Sea (Gjøsæter, 1995). They will spend the first few years of life here before returning to the Norwegian sea. This means that the number of herring present is rather variable.

The effect capelin has on the zooplankton community impacts the Barents Sea ecosystem, but our main focus lies in the opposite direction; the role capelin plays in the ecology of higher trophic organisms. They are the most important food item for cod (Bogstad and Gjøsæter, 2001), who from 1984 to 2000 consumed between 0.2 to 3.5 million tonnes annually (average 1.2 million) (Dolgov, 2002). The majority of this consumption was by cod in the 25-90cm range and between 3 and 6 years old. Despite that cod actually appear to consume less capelin than would be expected based on a random foraging model (Johannesen and Lindstrøm, 2009), it has previously been shown that their growth rate may stunted without the presence of adequate capelin volumes (Gjøsæter, Bogstad and Tjelmeland, 2009). With a highly financially lucrative 2016 Northeast arctic cod catch of 850,000 tonnes from an estimated stock of over 3.5 million tonnes (ICES, 2017) (around double the average from 1984-2000) it is fair to say that the capelin takes on more significance than one may have anticipated upon first viewing of this unglamorous character. When capelin is abundant it is estimated that as much as a further million tonnes will be consumed by seabirds, seals and whales (Gjøsæter, 1998). These high consumption values and the high ecological importance of capelin are symptomatic of species with high production, high mortality, employing a grow fast, reproduce and die young style of strategy. Having said this, despite the key role capelin has played in the ecosystem there does seem to be a weakening of trophic links as the climate warms, resulting in more bottom up control of the ecosystem and less dependence on individual species (Johannesen *et al.*, 2012).

Them and us, our relationship with capelin

The so far unmentioned consumer of capelin is of course the fishing industry. The stock is utilised as part of a joint Norwegian-Russian management structure, with both nations contributing to stock assessment and the catch quota then divided 60/40 in favour of Norway. The apparent stability of a standing stock of over 4 million tonnes was shattered in 1985 when the stock collapsed to less than 1 million tonnes, and remained depressed until 1990 when it rebounded back to close to 6 million tonnes from a 1989 stock of under 900,000 tonnes, of which the spawning stock biomass was less than 200,000 tonnes (demonstrating the phenomenal production that the capelin stock is capable of). Similar collapses occurred from 1993-1997, 2003-2006, and 2015-2016, due to successive recruitment failures. The driving mechanism behind these failures would seem to be predation. “Hamre’s hypothesis” postulates that larval mortality at the hands of particularly strong juvenile herring classes is to blame for the failure of capelin to recruit, and this does seem to be true, but does not seem to explain entirely the situation. Juvenile herring have certainly been the main contributors to capelin collapses (Gjøsæter and Bogstad, 1998), but the stock depression has been exacerbated by the incessant predation from juvenile cod and other predators (Gjøsæter *et al.*, 2016). It seems likely that the stable stock seen for 15 years prior to the first observed collapse was an exception, rather than the rule, and that the fluctuations seen since are the norm (Gjøsæter, 1998; Yndestad and Stene, 2002).

Human activity likely did not cause the stock collapses seen in capelin, but may have amplified their effects and delayed recovery (Gjøsæter, 1995). Capelin had always been utilised via beach seining from both the Norwegian and Russian coasts, but in the late 1950s when the Norwegian spring spawning herring stock collapsed commercial purse seiners began to focus their effort on the capelin, at this point still on the coastal spawning stock. From 1968 a summer fishery began in the open sea on the whole stock, and until the late 1970s there were no restrictions on the fishery. The 1977 catch of 3 million tonnes was the peak of the capelin fishery. From 1981-1984 the first total allowable catches (TAC's) were allocated based on the joint Norwegian-Russian acoustic surveys, often above scientific advice, and being taken in both the autumn (affecting both maturing and immature individuals) and the spring (affecting only the mature stock component). At this point the management criteria was to maintain a spawning stock of 500,000 tonnes whilst leaving 2 million tonnes available to predators (based on a stock-recruitment relationship determined from the few years of relatively poor data available which indicated that recruitment failure would be more likely if the spawning stock was to fall below this level). In 1978 the first length based restrictions were introduced; those fish under 11cm in length must make up 15% or less of the weight of the catch. This was modified in 1981 such that fish under 11cm should make up no more than 10% of the number of individuals. In the same year a minimum mesh size of 16mm was introduced into both the trawl and purse seine fisheries.

The science of management

Unusually, acoustic estimates (in conjunction with sampling trawls) are used to produce the absolute numbers of individuals in length and age classes, and thus a total stock biomass. Due to the semelparity of Barents Sea capelin it isn't possible to use traditional virtual population analysis/sequential population analysis methods, which even if usable, would likely be inaccurate due to the high natural mortality of capelin (Gjøsæter, 1998). Thus the entire stock must be covered in the autumn in order to give an accurate picture of its size and composition. In 1982 Hamre and Tjemeland calculated that the majority of the TAC should be taken in the winter (as opposed to harvesting all stock components in the autumn), since this would leave a much larger amount of capelin available to predators, with little loss of yield. It also would reduce uncertainty around the forecast of what the stock would be doing ahead of time, since there would only be 3-4 months between the survey and the catch, rather than the (potentially) over a year that elapses between survey and catch the following autumn. However it wasn't until 1998, after 2 collapses totalling 9 years with a zero TAC, that the summer fishery was stopped. To this day the fishery is restricted geographically to south of 74°N, and temporally to between January and April.

What was required for the management of the fishery was a model that could split the stock into the mature and immature components, and then forecast the mature stock up until spawning (coming winter fishery accompanied by 100% natural mortality post spawning), and the immature component right through the entire year until the next survey was to take place (for next year's summer/autumn fishery) including splitting this 'year+1' stock into new maturing and immature components. The model created for the task was called 'Capelin' (Tjelmeland, 1985), and it required input of the maturing process, the natural mortality and hypothetical fishing mortalities in order to give stock as a function of future fishing mortality. However the natural mortality applied to the maturing component of the stock was too simplistic (Gjøsæter, Bogstad and Tjelmeland, 2002), and since in 1984 a cod stomach sampling programme had commenced the next step was to introduce the predation by cod over winter to the model (Bogstad and Gjøsæter, 1994). Again this was implemented in something of an ad hoc way, and was in fact only used for the 1991-93 fishing seasons before the next stock collapse and a return to zero TAC.

Work continued via the study of stomachs on quantifying the predation by cod on the capelin during the winter (Bogstad and Gjøsæter, 2001), and since it was apparent that juvenile herring had played a key role in the recruitment failures leading to the collapses it was decided that the potential effects of herring should also be quantified in the model (Gjøsæter and Bogstad, 1998). Since 1998 two models have been used in conjunction; 'Bifrost' and 'Captool'. Bifrost calculates the trajectories of both the mature and immature capelin, working out how many will mature and applying natural mortality to forecast numbers of survivors in each component, before Captool runs different catch quota scenarios. Since the output is probabilistic (for example the probability of the stock falling below a certain size or probability of the stock growth taking a particular trajectory), the old management target of maintaining 500,000 tonnes of spawners was no longer applicable. In 1998 the new strategy of never allowing a greater than 5% chance of the spawning stock falling below 200,000 tonnes (B_{lim}) (recall the successful recruitment in 1989 with a spawning stock biomass of only around 100,000 tonnes, this is the lowest level which has produced a strong year class). Despite the B_{lim} being 300,000 tonnes less than the previous management target (because the model is precautionary and works based on probabilities) the actual TAC's advised are probably lower under this management regime than they would be with the previous, as B_{lim} of 200,000 tonnes (95% probability of being above this level) corresponds to a median spawning stock biomass of 400,000-500,000 tonnes and the mortality during winter is generally higher than under the previous management regime(Gjøsæter *et al.*, 2015).

Growth and maturity

Every year more stomachs are sampled, more work is done on the diets of Barents Sea predators, more climate research is used to predict the pattern of water movements and the effect on the ecosystem, we gather more and more knowledge about mortality, but the facet of the model that we are concerned with from here on is the maturation function. How does one separate the maturing stock component from the immature, predicting how many capelin will migrate from the central Barents Sea to the south to spawn, and thus be exposed to the fishery. Currently if a capelin is >14cm in length when surveyed in the autumn then it is classed as maturing and will spawn that year, as the sigmoid curve used in the maturity model has a steepness so extreme as so virtually act as a cut off (Tjelmeland and Bogstad, 1993).
It is possible to make a good assessment of whether a female capelin will spawn imminently by looking at the oocytes and determining which phase they are in, and this scale created by Forberg is still in use at IMR today, whilst a scale developed by Monstad in 1971 is used for males. The growth of the oocytes is split into a first growth phase (found in all females >10cm) and a second, with the second lasting less than a year it is assumed that if there are oocytes in second growth phase the fish must be spawning this year (Forberg, 1982, 1983).

Sexual maturity is a function of length in capelin, with multiple year classes being represented on the spawning grounds in any given year. And since spawning goes on over the course of several months we can also categorise 'early' or 'late' spawners (that is to say that not all capelin which will spawn must be in the same stage of maturity at the same time, increasing the difficulty of predicting ahead of time who will spawn and who won't). To add further complication to this picture there is not necessarily a set length at which capelin will mature and spawn; younger fish must reach a higher length before maturing than older fish. This is likely to be due to competing energy requirements, since a younger fish of length x must have invested a lot more energy/unit time in growing than an older fish of the same length, which is able to invest more into the growth of sex cells (Forberg and Tjelmeland, 1985). Furthermore the length at maturity can also vary significantly from year to year and from region to region within the Barents Sea (Forberg and Tjelmeland, 1985). There is also sexual dimorphism at play, with the males maturing at (and achieving) a larger size than females (Gjøsæter, 1998; Baulier, Heino and Gjøsæter, 2012).

Faith or science?

Tjelmeland and Forberg's maturity model gave an L50 (length at which 50% of the population are mature) of 13.8cm for females, and 14.6cm for males. However because of the length dependent sigmoid curve that the model uses and the steepness of the curve (generated by Bifrost) a small error at this point could lead to a large miscalculation in the maturing stock, since the length classes around this maturation cut off point tend to be some of the most abundantly filled (Gjøsæter *et al.*, 2015). The consequence of setting the length at maturity too high would be an underestimation of the spawning stock, and therefore the TAC would be lower than necessary, thus the fishing industry suffers. The consequence of setting the length at maturity too low would be an overestimation of the spawning stock, a TAC that is too high, and the capelin and other species that prey on capelin suffer.

Can we improve?

The literature regarding maturity is for the most part rather old, and the use of a 14cm cut off to predict the spawning stock may leave some room for improvement. It has also never been validated by studies of the spawning stock which it is tasked with predicting. As just mentioned, the stock is very condensed into a few 0.5cm length categories, especially those found close to the 14cm cut off. Figure 2 shows that on average 9.3% of the surveyed population of 2+ capelin fall into the 13.5-14cm category, 9.2% from 14-14.5cm and 8.3% from 14.5-15cm. Each of these 0.5cm categories in most years represents many tens (at times even into the hundreds) of thousands of tonnes of capelin, so the consequences of moving the cut off even 0.5cm in either direction could have a significant impact on our prediction of how many capelin are migrating, and consequently an impact on the spawning stock estimation.

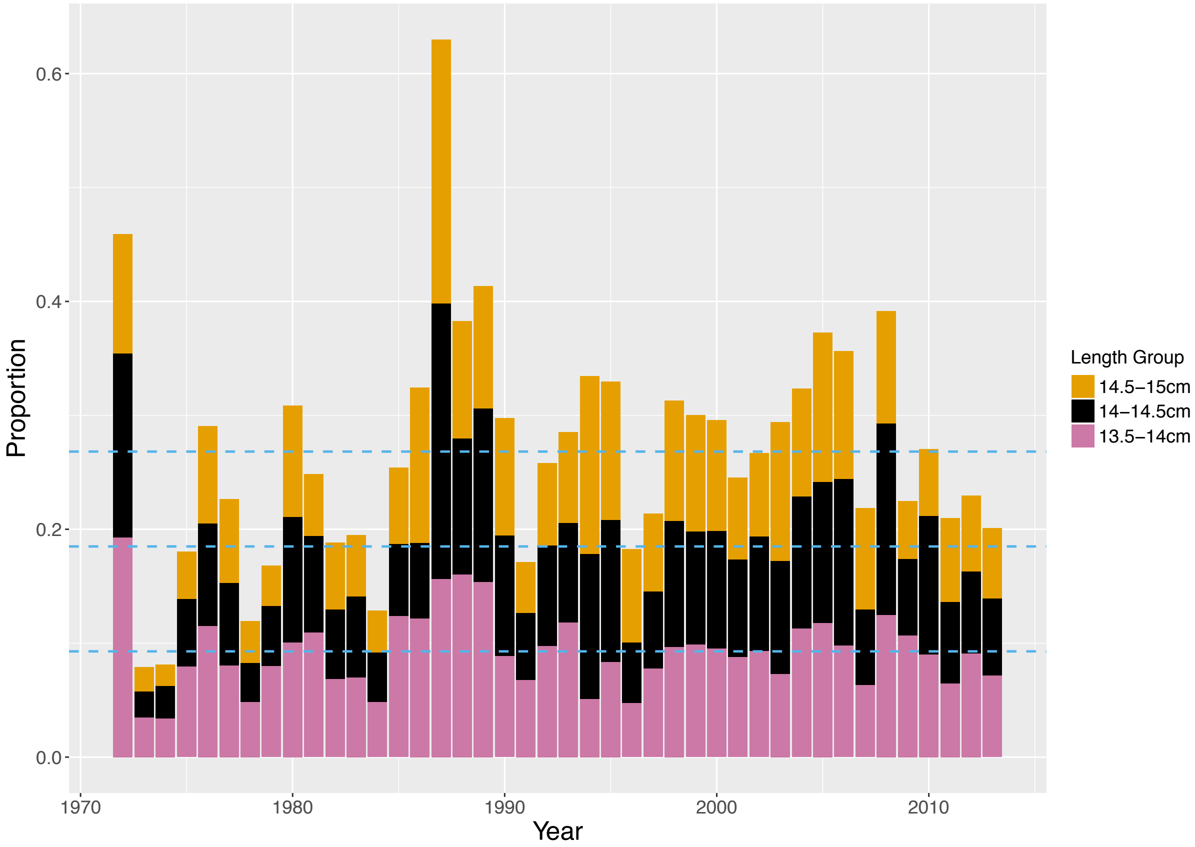

Figure 2: The proportion of capelin aged 2+ at the time of survey, in the 0.5cm length categories closest to the 14cm cut off. The blue dotted lines are the mean value for each length category.

In this study I intend to use the catch data taken during the January-April fishing season by the Norwegian fleet (who are required to provide samples for scientific purposes), to make a comparison between the surveyed population and the spawning stock. The aim is to carry out an assessment of whether a 14cm cut off, above which we assume fish will mature and spawn, is a reasonable way to predict who will migrate and who will not. To do this I shall compare the length and age distributions of fish in the catch, with the predicted length and age distributions generated by various models including the 14cm cut off. Further to this I shall investigate whether condition may play a role in the migration decision, and whether there is any growth in the period between the survey and catch. To phrase these aims as hypotheses:

- Using a 14cm cut off as a proxy for maturation does not produce an accurate forecast of the spawning stock.
- It is possible to improve our forecasting ability by introducing other factors to our models (e.g. age).
- There is no growth between survey and catch.

- Condition significantly influences the maturation and migration propensity of capelin.

Materials and Methods

Survey evolution

This investigation does not require the collection of new data, but instead uses historic data. Therefore we shall first look at the surveys, before addressing the collection of commercial data. Much of the following description is described by (Gjøsæter, 2011). Survey data is collected annually in autumn, and I shall be using a continuous time series from 1972 to 2013. 1972 is regarded as the true beginning of this time series, despite the fact that surveys had taken place before this, since the previous surveys had been largely based on trial and error and cannot be seen as having standard methodology. The collection was carried out by scientists from the Institute of Marine Research (IMR), Bergen, alone, from 1972-1974. From 1975-1977 scientists and vessels from the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Murmansk, were involved in the surveys and all data was shared, however it was then worked on separately by each institute. From 1978 the stock became shared and joint survey reports are produced with joint meetings of scientists from both sides to plan beforehand, and analyse and discuss afterwards. From 1978-1983 scientists from each institute would spend time aboard vessels of the other, enabling better standardisation of methods and insight into how each operated. This apparently stopped from 1984-1991 but from 1992 onwards there has always been a Russian scientist on board the lead Norwegian vessel (with the exception of 1998 where roles were reversed).

From 1972-1985 the survey was carried out primarily to assess capelin and hydrographical features, with assessments of herring incorporated from 1985 and polar cod from 1986. At this point the stated aim becomes “to cover all the economically important stocks in the area”, in addition to plankton and environmental features. From 1995-2002 the survey aims narrowed again somewhat and focussed on the pelagic species, plankton and hydrography. In 2003 there was a radical change, with the advent of the Barents Sea Ecosystem Survey; a true beast involving up to 217 vessel days (2004), assessing hydrography, pollution, plankton, 0-group fish, pelagic fish, demersal fish, benthos, diet studies, biodiversity, marine mammals, sea birds, and any other special investigations that may be required.

Year	Dates	Vessels used (acoustic, biological)	Capelin coverage	Samples	No. length measured	No. Aged	Echosounders used
1972	05/08-11/09	2 (2, 2)					EK-38
1973	16/09-08/10	2 (2, 2)					
1974	15/09-12/10	2 (2, 2)					
1975	12/09-15/10	3 (3, 3)					
1976	11/09-01/10	3 (3, 3)					
1977	16/09-07/10	3 (3, 3)					
1978	14/09-11/01	3 (3, 3)					
1979	30/08-28/09	3 (2, 3)	"not likely large numbers of adults outside area of estimate"				
1980	10/09-05/10	3 (3, 3)	"coverage complete"				
1981	07/09-04/10	3 (3, 3)	"distribution area covered"				
1982	07/09-10/10	4 (4, 4)	"distribution area covered"				EK-400, EK-38
1983	06/09-30/09	4 (4, 4)	"distribution area covered"				
1984	04/09-24/09	4 (3, 4)	"distribution area covered"				
1985	06/09-06/10	4 (4, 4)	"better coverage than in previous years"				EK-400
1986	03/09-13/10	5 (5, 5)	"all substantial occurrences included"				
1987	06/09-12/10	7 (3, 6)	"all substantial occurrences included"				
1988	08/09-21/10	6 (3, 6)	"all substantial occurrences included"				
1989	12/09-03/10	6 (6, 6)	"north eastern and central coverage not satisfactory… probably does not affect estimates"				EK-500, EK-400
1990	07/09-06/10	6 (6, 6)	"coverage of some boundary areas not satisfactory… probably does not affect estimates"				
1991	12/09-06/10	6 (6, 3)	"more or less satisfactory"				
1992	10/09-06/10	5 (5, 5)	"as good as in previous years"				
1993	09/09-03/10	5 (5, 5)	"satisfactory"				
1994	08/09-03/10	5 (5, 5)	"satisfactory"				
1995	12/09-01/10	4 (4, 4)	"satisfactory"				EK-500
1996	12/09-02/10	4 (4, 4)	"satisfactory"				
1997	12/09-02/10	3 (3, 3)	"non-satisfactory"				
1998	10/09-06/10	4 (4, 4)	"satisfactory"				
1999	06/09-04/10	4 (4, 4)	"satisfactory but not synoptic"				
2000	04/09-03/10	4 (4, 4)	"probably the most complete coverage obtained (thus far)"				

2001	03/09-04/10	4 (4, 4)	"probably the most complete coverage obtained (thus far)"	244	26778	7848	
2002	06/09-06/10	5 (5, 5)	"relatively good"	180	17428	5637	
2003	22/07-02/10	5 (5, 5)	"difficult to compare… total coverage achieved"	326	14436	2956	EK-60, EK-500
2004	01/08-04/10	4 (4, 4)	"difficult to compare… good coverage obtained"	642	25104	3933	
2005	01/08-05/10	5 (5, 5)	"almost total coverage by dense grid"	558	22625	3677	EK-60
2006	08/08-05/10	5 (5, 5)	"almost total coverage by dense grid"	650	26382	3551	
2007	01/08-30/09	5 (5, 5)	"total coverage"	553	33162	4878	
2008	01/08-04/10	5 (5, 5)	"total coverage"	524	27780	4106	
2009	07/08-03/10	4 (4, 4)	"successful coverage… with some ice limitation"	766	30821	4688	
2010	09/08-26/09	5 (5, 5)	"total coverage"	461	34391	4865	
2011	10/08-05/10	4 (4, 4)	"nearly total coverage"	521	35142	4413	
2012	08/08-30/09	4 (4, 4)	"some coverage missing in north east"	540	34223	4264	
2013	09/08-31/10	4 (4, 4)	"area larger than previous year"	592	32394	4520	

Table 1: Key information for all surveys used. The numbers in brackets indicate how many vessels contributed to the acoustic measurements and how many to the biological measurements. The assessment of coverage is in the form of a direct quote taken from the survey report itself in order to give a flavour of the wording used in self assessment of coverage. Statistics for the number of samples, and how many fish were length and age measured only appear from 2001 onwards. The echosounders used are specified only when a change occurs.

Survey design

From the beginning of our time series there was already a good understanding of the distribution of capelin in the Barents Sea. During the autumn capelin are often schooling and feeding, typically dominating the pelagic zone (with some exceptions where problems were encountered with mixing with polar cod (Gjøsæter, 1998)). They typically occupy midwater out of the acoustic dead zone close to the bottom or the surface, which makes them ideal acoustic targets(Gjøsæter, 1998).

Surveys have used a regular grid pattern with what should be considered a random starting point (Dommasnes and Røttingen, 1984; Tjelmeland, 2002) aimed at covering as much of the capelin population as possible. The coverage must be done as synoptically as possible to minimise the effects of migration (Gjøsæter, Dommasnes and Røttingen, 1998). From 1988 onwards, main areas of distribution are surveyed with transects 10-20nm apart, with the remaining areas using transects 20-40nm apart. Prior to this the main areas were surveyed with a north south grid with 1° longitude apart, with adjustments depending on capelin distribution. When the area coverage was analysed according to guidelines set out by (Aglen, 1983) it was found that increasing survey effort will in this case not significantly improve precision. In the early days of the survey the majority of transects were in a north-south orientation, before changing to an east-west orientation by the late 1980s. Figures 3 and 4 illustrate the change that has occurred in the survey pattern and coverage between the beginning and end of our time series. As recommended by (Nakken and Midttun, 1972) the survey grid is flexible, with scientists using prior knowledge and current observations to make day to day adjustments (in communication with all vessels involved) to grid structure.

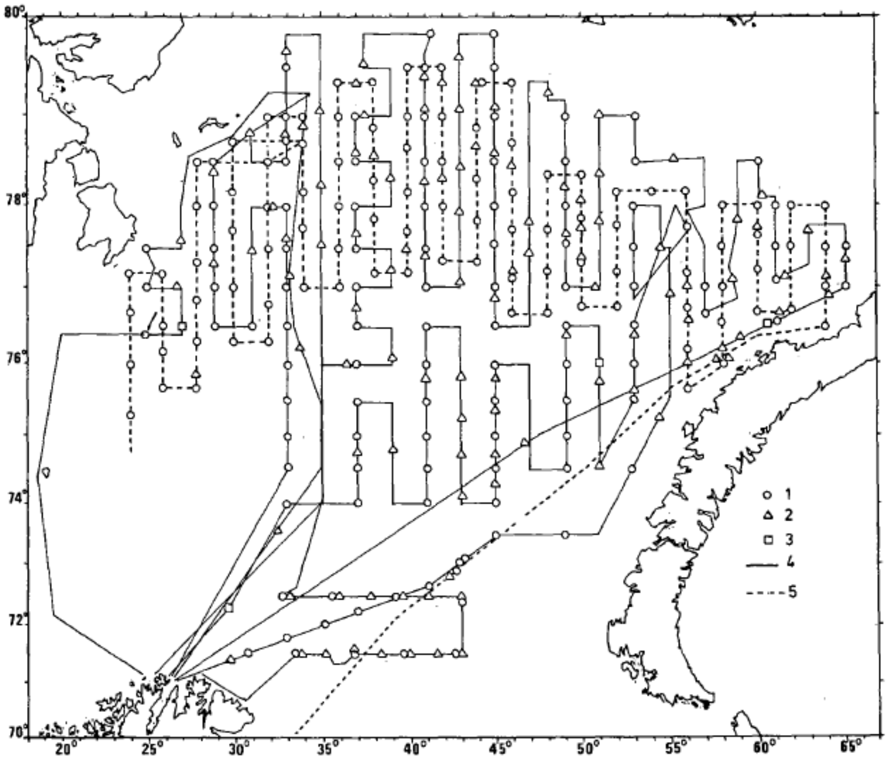

Figure 3: The 1975 survey tracks by: 4) R.V. G.O. Sars and R.V. Johan Hjort. 5) R.V. Poisk. 1) represents hydrographic stations. 2) Pelagic trawl. 3) Bottom trawl.

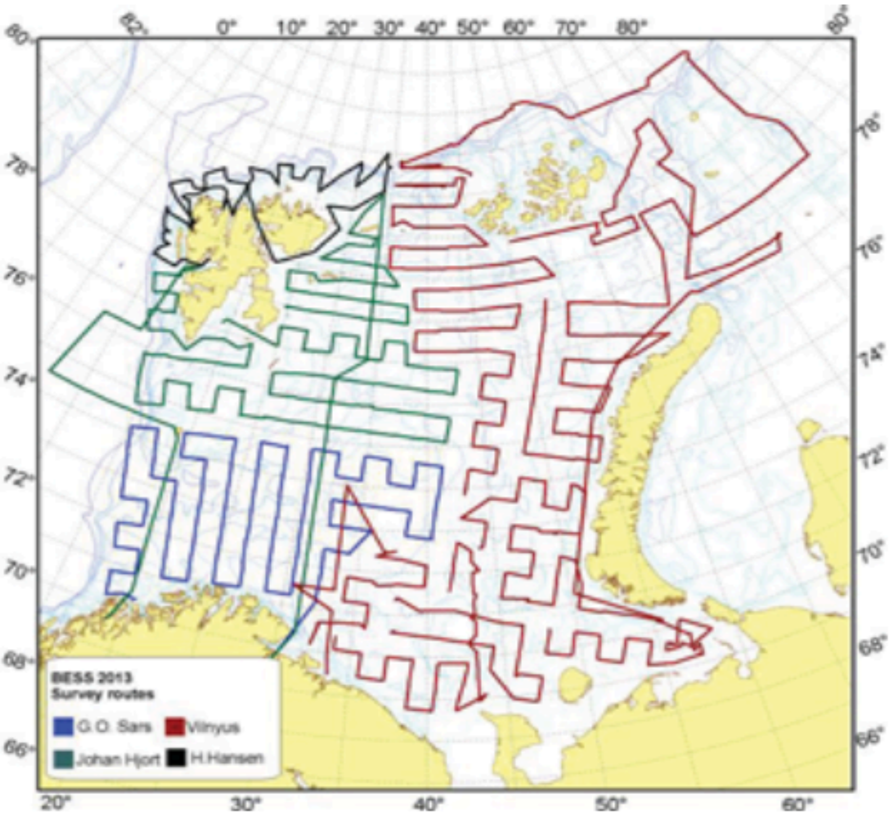

Figure 4: The survey tracks taken during the Barents Sea ecosystem survey in 2013.

Problems that have been encountered during the course of the survey have been: ice limitation, denial of entry to Russian EEZ for Norwegian vessels, military activity closing areas, bad weather, equipment/vessel malfunction, trawl loss, personnel sickness/injury, time lag, and intercalibration problems. All of these are mentioned in survey reports and the impacts are assessed. None of these represent systematic problems, rather incidental occurrences.

Knowledge through sound

Throughout our time series the population of Barents Sea capelin has been determined by the use of acoustic surveys alone. The most important objectives of these surveys are to; a) determine a total biomass of capelin. b) determine the biomass of capelin in 0.5cm length intervals. c) determine the biomass of capelin by age. Objectives b) and c) have different purposes, with the biomass by length being used to forecast the spawning stock (using the 14cm cut off), and age being more relevant in the case of the younger capelin in order to determine recruitment (since it would appear that the year class strength is more or less established by August in the first year of life (Gundersen and Gjøsæter, 1998)). To build this picture trawl hauls are taken during the survey to collect the necessary biological data, which shall be addressed later.

The acoustic method can be found explained in detail that is too extensive for these pages, eg. (Dalen and Nakken, 1983; Maclennan and Simmonds, 1992), so rather let us review the basic principles that allow an understanding of the technique, using symbols as defined by (Maclennan, Fernandes and Maclennan, 2002). The energy of the echoes returning to the echo sounder (transducer) are detected and the information is sent to and recorded by the echo integrator, the output of which is the area backscattering coefficient, s_a (allocated to species by the cruise leader and instrument chief on Norwegian vessels, and acousticians on Russian). The mean ability of the fish to reflect sound, $\bar{\sigma}$, the number of fish per unit of area, ρ_A, and the s_A (nautical area scattering coefficient, s_a extrapolated to a square nautical mile) relate thus:

$$s_A = \bar{\sigma} \cdot \rho_A$$

The total number of fish, N, in the survey area, A, can therefore be given as:

$$N = \rho_A \cdot A = \frac{s_A}{\bar{\sigma}} \cdot A$$

The biomass can then be calculated by multiplying by the average weight, however this investigation is concerned only with the numbers of individuals.

The ability of a single fish to reflect sound can be described using the terms target strength, TS, which relates to the acoustic cross section, σ. The relationship between the two is:

$$TS = 10 \cdot \log\,(\sigma\,/4\pi)$$

Target strength varies depending on the physical attributes of the target, for example a fish with a gas filled swim bladder will return a stronger echo than one without, with the aspect of the fish, and with length (L). For Barents Sea capelin, a generic relationship between TS and L is established for assessment purposes as:

$$TS = 19.1 \cdot logL - 74.0$$

And corresponds to:

$$\sigma = 5.00 \cdot 10^{-7} \cdot L^{1.91}$$

This was not fully established until 1985 (Dommasnes and Røttingen, 1984), with earlier survey estimates depending on counting traces on echograms and comparing these with returned echo strength, resulting in variation from year to year in the conversion factors used between echo return and numbers of fish (and therefore variation in target strength). Thankfully as our knowledge improved, calculations were done to re-assess all of the previous years of data using the new conversion factor, and the results of the re-estimations are used in this investigation. Other investigations seem to be in agreement with this target strength (O'Driscoll and Rose, 2001; Olsen and Jørgensen, 2002; Jørgensen, 2003), and also conclude that the tilt angle of capelin is unlikely to have as large an impact on the target strength as it does on some other fish species (Olsen and Jørgensen, 2002; Jørgensen, 2003)

Using the technology

To go from integrator output to a geographical distribution of numbers of individuals by length and age the survey area is divided into rectangles, usually of one degree latitude and two degrees longitude. These are called basic acoustic blocks. The echograms are scrutinised and contributions from the seabed, false echoes, bubbles and noise are removed. The mean s_A value is calculated for each five square nautical miles until 1987, and from 1988 onwards, per square nautical mile. This process was done manually until 1997 before the introduction of "MapInfo"; a computer programme that makes the calculations automatically and can more accurately allocate values to blocks. Each of the acoustic blocks will contain 1-4 vessel transects, and from 6-40 5 mile average s_A points, depending on the latitude and density of capelin. Multiple frequencies are used when available, with higher (e.g. 120kHz) emissions used to ascertain how much of the backscatter seen at 38kHz is due to plankton. However in many cases the Russian vessels had access to only the 38kHz frequency. 38kHz is the frequency used for biomass estimation, and the TS-L relationship seen earlier is used for the 38kHz data.

Biological samples are required to make a length distribution, so trawling is carried out whenever the echosounder recordings change appearance (to check changes in species composition or length distribution), or when there is a need for biological data (such as at prescribed trawl stations). It is assumed that our trawl samples are representative of the images that we see on the echogram, and it is down to the technical expertise and experience of the operator to decide when this no longer applies (an important judgement due to highly negative impact of using a non-representative length distribution on the accuracy of results). At times the operator must also use their judgement when calculating the mean s_A value of the block, especially at the edge of the population distribution, to ascribe a "representative" value. To add further pressure on the operator there are varying numbers of trawls per block, with some having multiple, some only one, and some none. The assignment of length distributions to blocks is therefore based on scrutinising the echogram readings and assigning known length distributions from blocks close by with similar readings. In one block there may be several types of readings, so several corresponding length distributions must be applied and weighted accordingly.

Using the length distribution, the target strength, and the s_A value we now have all we need to calculate the number of fish by length per basic acoustic block (ρ_A).

The number of fish by age is calculated by making "keys" which give the percentage age distribution in each length group and mean weight of each length group. This is not done on a block by block basis but by combining blocks which share almost identical age and weight at length characteristics, since mean length and weight at age can be quite different for different areas of the Barents Sea. Consequently, this process creates 3-5 sub areas and the weight at length, and length at age keys, are applied to each separately, with all blocks in the sub area sharing the same key.

Ensuring technical consistency

It is crucial that the output of all vessels participating in each cruise are directly comparable, and that we can compare results from different echo sounders and post processing systems. To this end there have always been calibrations done either before or whilst engaged in the survey. From 1981 there have been calibrations using standard targets, which are known to maintain as consistent a target strength as is practically possible across the whole hydrographical range required (for example a copper sphere of 60mm diameter has a target strength of -33.6 dB at 38kHz (Foote, 1983; Foote *et al.*, 1987)). Using standard spheres it is possible to check the consistency and reliability of echo sounder performance, and it is specified that this must have taken place "recently" in order for a vessel to be used (there is no technical definition of "recent" but as an example the 1998 report reveals that calibration 5 months prior to the survey qualified, despite being sub optimal and ignoring temperature effects on acoustics).

In addition, between vessel calibrations were undertaken until the year 2000, although calibration using spheres can be considered reliable from the 1980s so quite why this procedure was continued for so long is unclear. See appendix I for details.

There have been significant advancements in acoustic technology and research over the course of this time series. This should be seen as increasing our certainty of estimations over time, but not invalidating earlier estimates. Figures 5 and 6 show what an acoustic operator would have been interpreting towards the beginning of the time series, and the contrast with what is available by the end. Every survey conducted was done to the best abilities of those involved and by making best usage of the technology available.

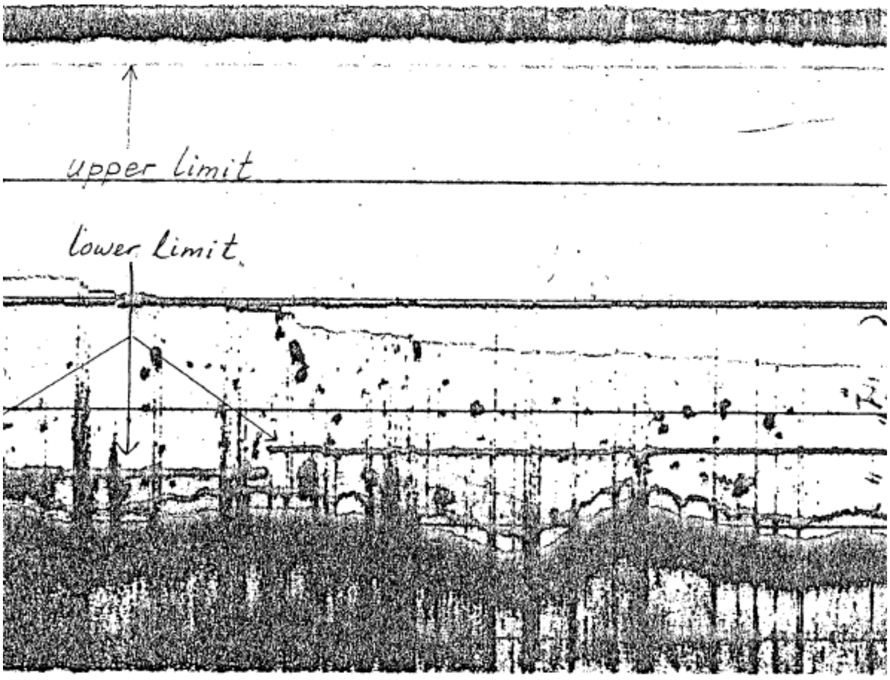

Figure 5: An example of the echo recordings from R.V. Poisk during the survey of 1979. Compared to modern echo sounding it does look rather crude.

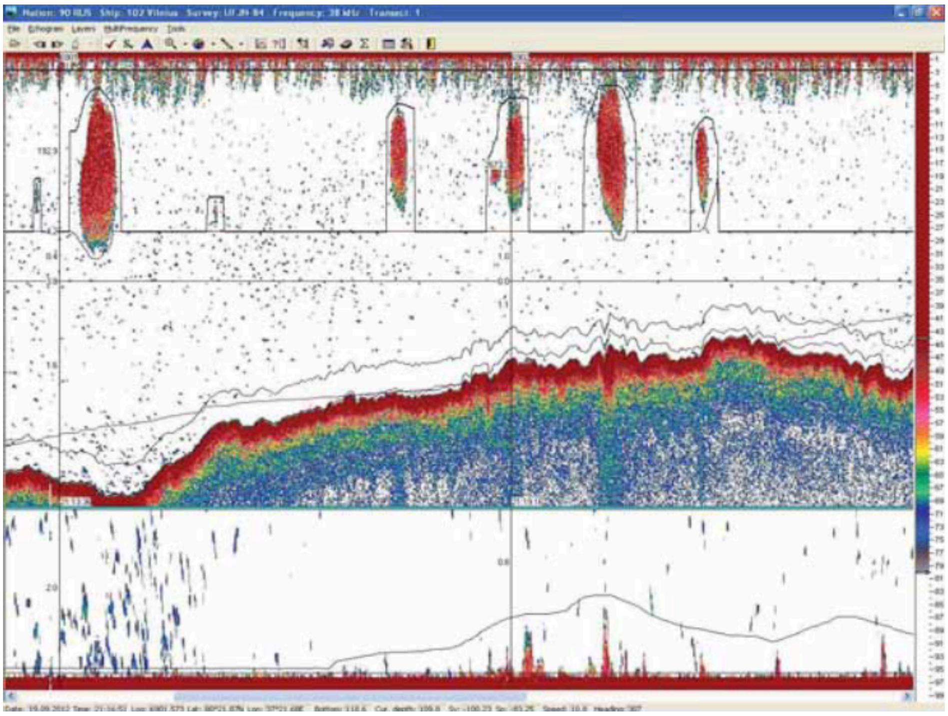

Figure 6: An example of echo recordings of capelin schools by "R/V Vilnius" during the ecosystem survey of 2012.

From screen to reality

Biological sampling is key to interpreting what we see using acoustic technology. Multiple types of trawl have been used through the course of our time series, with Norwegian vessels using a "Harstad" (approximate opening area 300m^2) or "Åkra" (approximate opening area 600m^2) trawl, and the Russian vessels typically using larger commercial trawls (approximate opening area 1900m^2). The cod end is equipped with a net of mesh size 4mm in order to prevent capelin escape, and it is preferred that a trawl is towed at a single depth (although in some years a multisampler was fitted to one vessel to take samples at multiple depths). It is preferred that trawl samples are taken from every concentration that makes a significant contribution to the s_A value of the acoustic block, and multiple trawls may be needed if the registrations change in appearance. Dense concentrations should be sampled more regularly than sparser concentrations (Dalen and Nakken, 1983). This is needed for species identification and the taking of biological characteristics.

A typical capelin sample will consist of 100 fish selected at random from the overall catch, and the required data is recorded immediately. This was previously done using specially designed forms but now it done with the use of the electronic measuring. According to

(Gjøsæter, 1985) the following information is recorded with regards to the station: position, species, vessel name, station number, sampling gear, date, depth. The fish are length measured (rounded down to nearest 0.5cm) and weighed (in grams), before ageing and any other investigation such as sexual maturity stage or stomach content analysis takes place. The trawl samples are not used to provide any quantitative data on the density or number of fish, which is determined acoustically.

It is very important to understand the selectivity of any trawl used to collect data. As already mentioned it is crucial that the length distribution of the sample is representative of the population from which it is taken for both the use of length dependent target strength and for the sample weighting procedure when moving from basic acoustic blocks to sub areas. Scientists have always been aware of this, and to illustrate this point, in 1992 there were some differences observed in mean lengths between Russian and Norwegian vessels, so in 1993 an investigation was carried out to establish whether trawl selectivity was an issue. Trawling was carried out before and during acoustic calibration using the same gear as in 1992, with all four participating vessels (2 Norwegian, 2 Russian) trawling before, and 3 (2 Norwegian, 1 Russian) during. Each trawl lasted for half an hour and capelin lengths were compared. It was concluded that there were no systematic differences in methods of length measurement or trawl selectivity, and observed variation was likely a product of differing fish distributions. In 2013 there is a note that there were differences in trawl rigging and trawling procedure between institutions, and a recommendation was made for calibration in future.

Age determination

The method of age determination for capelin is covered in detail by (Gjøsæter, 1985) and (Gjøsæter, 1998) so here shall be presented some brief information. Otoliths (specifically sagittae) are used in the age determination due to a lack of scales in the early part of life, and the presence of fairly well defined growth zones in capelin. At least 20-40 (or more) specimens from each sample should be aged, with the number required determined by whether there has been much sampling in the area already, or whether the area is providing uniform length distributions. Capelin are considered to all share one birthday, on January 1st, thus the age reading is not an exact age of the fish but rather the number of winters that it has lived through. The certainty with which the reader feels they can give an age is represented by a “readability number”. It was estimated in 1985 that there were some errors in ageing but that these errors probably did not have any practical implication (Gjøsæter, 1985).

Since 1999 there has been an otolith exchange programme and biannual workshops between PINRO and IMR scientists with the objective of ensuring there are no systematic differences in the reading of otoliths. This has resulted in improvements in agreement between both sides on otolith reading, and by 2007 the inter-institute variation in readings was no larger than the within institute variation, which is very small (Gjøsæter *et al.*, 2008).

Commercial data

There is no survey for capelin in the winter, since the winter cruise operated by IMR in the Barents Sea investigates demersal fishes primarily, with only very occasional pelagic trawling. The only data available on the reproductive part of the stock is therefore data from the fishery. Data from the Norwegian fleet from January to April shall be used. The Norwegian catch represents a large majority of the total catch, and whilst there were also catches taken outside this time period previously, it is the capelin spawning population which serves this investigation. This is the population fished between January and April. Commercial fishing primarily takes place in the Varanger - east Finmark area (3), with some to the west in the west Finmark area (4), Bjørnøyrenna (12) areas, and on occasion as far west as Troms (5), and sometimes to the east in areas 10, 11, and 2 (all as designated for use in fishery statistics by Fiskeridirektoratet) north of Murmansk and west of Novaya Zemlya. Figure 7 shows a typical distribution of where the winter capelin fishery operates.

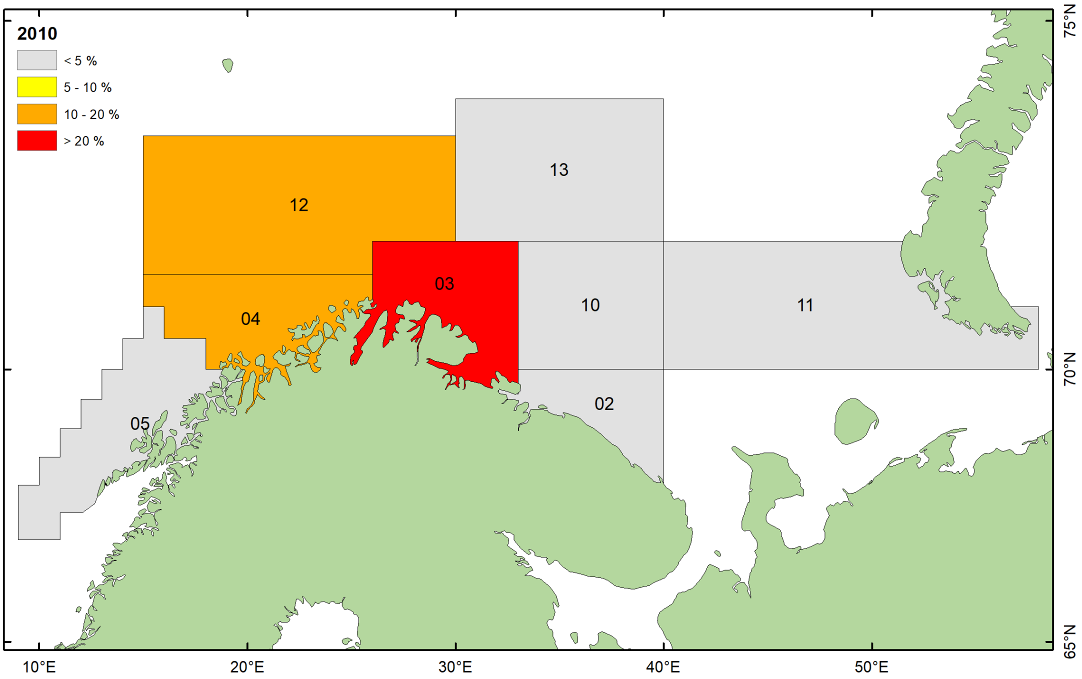

Figure 7: A map with the areas, as defined by Fiskeridirektoratet, where spawning capelin are found and fished. The shading represents the percentage of total catch. Data is from 2010, courtesy of Johanna Fall.

The commercial fishery must provide samples to IMR for analysis. All catches must also be reported and positions, weights etc. logged, and we can consider the Norwegian fishery statistics reliable. Discarding and slipping are illegal. The catch is taken primarily by purse seine. (Gjøsæter, 1985) describes the sampling programme used in the taking of commercial sampling. Of every catch landed at a meal/oil processing factory roughly 100 fish are taken for length sampling. For further biological data collection such as ageing two factories are selected, one easterly and one westerly. Samples of around 100 fish are then taken from around every fourth catch, frozen, and sent to IMR in Bergen. Not every sample will be processed by IMR but instead the focus is on achieving good spatial coverage. These procedures prevent the circumvention of the need to provide industry data by simply collecting one huge sample from one vessel, taken on one day of the season, for example, and go as far as possible to ensuring the samples taken will be as representative as possible of the population. The catch sample data does have attached meta data including location however I did not use this as it is not in an easily accessible format and it would have been a huge task to extract and compile it all.

All survey and catch data is taken from IMR databases.

My analysis

My investigation of the data shall move in a logical way from broad to more focussed enquiry. We wish to compare the population surveyed (August to October), with the population in the catch (January to April), post migration. It is therefore required to compare catch data in year *x* with survey data in year *x* - 1. Whenever catch and survey data appear in the same figure, **the year quoted is the year of the catch**, not the survey. Capelin are considered to share the same birthday (January 1st), thus age comparisons are made between 'age' in survey, and 'age + 1' in catch. **All data used is numbers of individuals**, not biomass. For both age and length based analysis the original numbers of individuals are converted into proportions of the total. Only age 2+ fish at the time of survey are included, as there are virtually no fish in the catch age 2 (i.e. age 1 at time of survey). All figures are constructed to conform with http://www.cookbook-r.com/Graphs/Colors_(ggplot2)/#a-colorblind-friendly-palette. Catch data is collected in 1cm length categories from 1973-1999, and 0.5cm length categories from 2000 onwards, whilst survey data is always collected in 0.5cm length categories.

General exploration of the data

Firstly the length distributions of survey and the corresponding year's catch were plotted in order to get a feel for the structures, the differences between the two, and to reveal any obvious trends that have taken place over time. The proportions of each age class were next plotted separately for survey and catch, again for general examination.

In order to rule out any potential lowering of the 14cm cut off the proportions of the catch by 1cm length categories were plotted in order to check how many fish are being caught that are <14cm in length.

Length distributions forecast by a 14cm cut off and a 15cm cut off were then plotted against length distributions seen in the catch to check for conformity. Due to the extremely high proportion of capelin found within a 4cm range it is beneficial for the more intricate analysis of length based data to use only 0.5cm length categories (year 2000 onwards). Better resolution data will provide more precise results. This is also after the cessation of the autumn fishery, removing that potential source of uncertainty with regards its' effects on the data.

Since age is likely to play a role in maturation length (Forberg and Tjelmeland, 1985; Gjøsæter, 1998), the age distribution forecast by the 14 and 15cm cut offs was then compared to the age distribution in both the catch and the survey population. This enables a visualisation of how well the cut offs are predicting which capelin will form the spawning stock. As this is just age distributions under different circumstances there is no need to be restricted to the 0.5cm length categories, and all years are plotted.

Modelling

In order to test different types of maturation curve, models were made representing different cut offs and differently shaped sigmoid curves. They were assessed by checking how well they predicted the proportion of 3 year old fish in the catch, since the catch from 2000 onwards (1991 onwards, but 2000+ is being used for the reasons given above) has been largely dominated by 3 and 4 year olds. The code for each model can be found in appendix II. The 'winning model' (model 11):
(x14*0.05) + (x14.5*0.15) + (x15*0.35) + (x15.5*0.6) + (x16*0.7) + (x16.5*0.8) + (x17*0.85) + (x17.5*0.9) + (x18*0.95) + (x18.5*0.99)
These are the proportions of each length category that are allocated to the mature stock, applied irrespective of age. The number is the bottom limit of the length category, hence x14 represents 14-14.5cm etc. Nothing <14cm will migrate. Everything >18.5cm is summed and will migrate. The 14cm model simply sums all fish >14cm.

The progression from here was to take this model a step further and use different maturity curves for different age classes, as seen in figure 8, to determine whether this is able to do a better job of forecasting both age and length distributions resulting in different propensities to migrate between different age groups. This is the model 'Tiresias':
2 years old: (x14*0.125) + (x14.5*0.25) + (x15*0.375) + (x15.5*0.55) + (x16*0.85) + (x16.5*0.99)
3 years old: (x13*0.15) + (x13.5*0.3) + (x14*0.7) + (x14.5*0.8) + (x15*0.9) + (x15.5*0.99)

All 4+ fish, all 2 year olds >16.5cm and all 3 year olds >15.5cm, are assumed to migrate. The output of the model is the number of individuals by age class and by length class that are assigned to the maturing stock. We can call this the ‘expected’ migrating population.

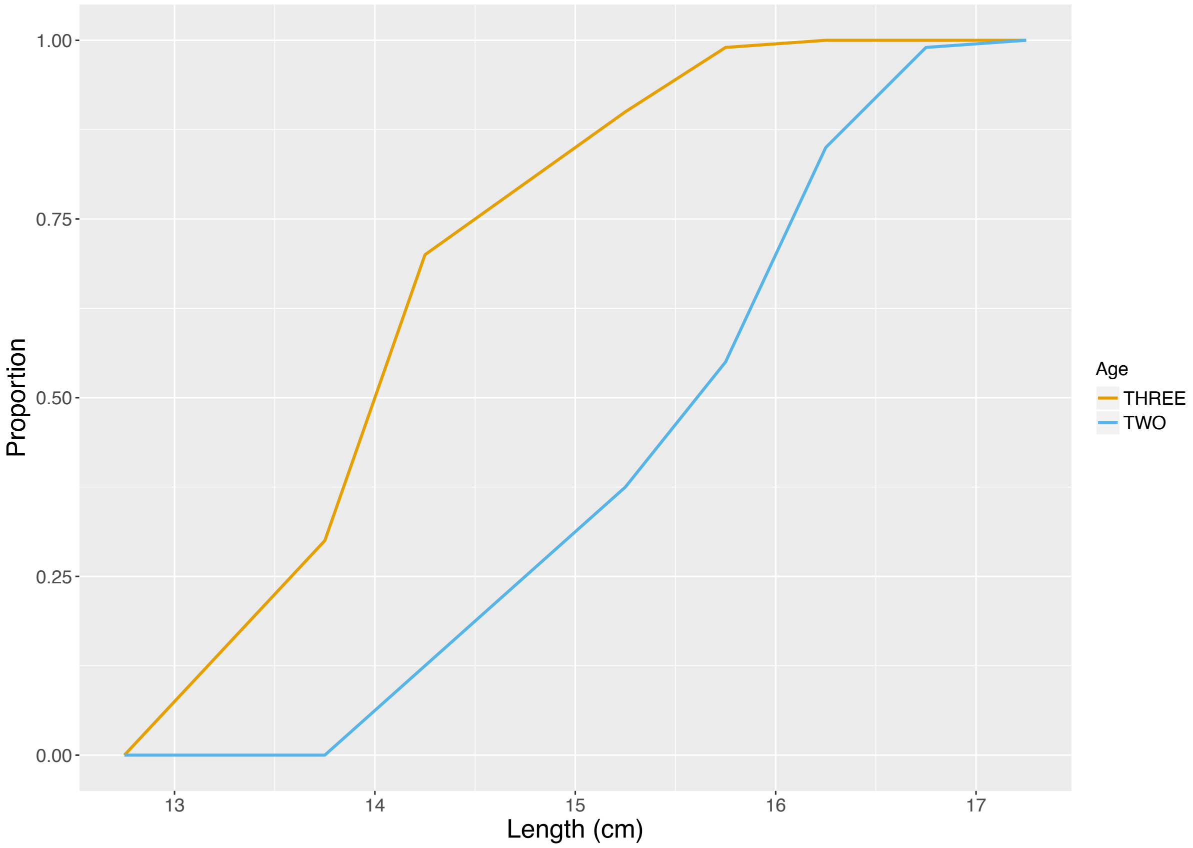

Figure 8: The proportion of the population that will mature according to ‘Tiresias’, over the length range from 0% maturating to 100% maturating. Age is at time of survey. The majority of three year old fish will mature over a shorter length range and from a lower starting length. The two year old fish will not start to mature until a higher length, and the proportion will rise at a slower rate initially before becoming more rapid as it climbs towards 100% maturing.

Plots were then made of the proportion of 3 year olds and 4 year olds forecast by ‘Tiresias’, a 14cm cut off, and a 15cm cut off, each vs the proportion observed in the catch. A linear model, (geom_smooth(method="lm")), was used to insert a line of best fit on the expected values, and this is easily compared to an ideal line (x=y). The line of best fit cannot tell the whole story as a model could produce the correct line but with an unacceptably high variance, making it functionally useless as a predictive tool. For this reason the margins of errors (difference between observed and expected) were analysed, gathering the mean, median, variance, and standard deviation. The mean error was calculated after converting negative values to positive, and along with the median, gives an indication of the accuracy.

The standard deviation and variance tell us how much variation there is in the margin of error. Were the errors consistent, or were there some years with large errors and some with small errors. It is the standard deviation of the difference between observed and expected, not the standard deviation of the model output itself. This tells us the precision. A standard deviation of 0 would not alone mean that the model is a good predictor, only that it is consistent in its error. When used with the mean and median we can make judgement on the accuracy and precision and therefore we have some idea of how well the model is functioning.

Having already plotted length distributions generated by 14 and 15cm cut off models the same was done for 'Tiresias'. It is important that the model should generate a representative age and length distribution, rather than just one or the other. These two categories together will allow for a much more accurate identification of which individual fish are migrating, rather than simply replicating one or the other in isolation which has less power of identification, and can lead to incorrect estimations of numbers.

For further verification of the validity of what 'Tiresias' is doing, the biomass of the estimated maturing stock was plotted, as forecast by 'Tiresias', 14 and 15cm models. This allows us to make an opinion on whether 'Tiresias' is coming to the age and length distributions that it does, simply by excluding the majority of fish and choosing a very small subset which fits catch data for most years, but in fact would generate a biomass that is unfeasibly small to be realistic. If we decide that the biomass is potentially realistic then it shows us to what extent we may be overestimating the maturing stock and extrapolate potential consequences of that.

Growth between survey and catch

To investigate whether growth is occurring between survey and catch the length distributions of 3 year old fish surveyed and 4 year old fish caught (the same age class) were plotted. Applying the same method to 2 year olds surveyed/3 year olds caught would not work, since many of the surveyed population will not mature in that year, and it would give the appearance of growth having taken place, rather than the longest subset of the population migrating. We expect that almost all 3 year olds surveyed will mature, thus the catch should be a good representation of the surveyed population, and show us whether growth has occurred in the intervening time.

Condition

Average weight by length and age is contained in the survey data. The objective was to determine whether condition of 2 year old fish in the survey would have a significant correlation with the proportion of 3 year olds in the catch. If this were to be significant then it could potentially be another variable to add to the modelling process and improve our forecasting abilities further. Condition was described by (mean weight/(mean length*3)*100. A generalised linear model (binomial) was used to determine significance of both condition and length (separately) on the proportion migrating.

Results

To migrate or not to migrate - Does size matter?

There is a clear difference in the length distribution seen in the survey and the catch. The survey data can take the form of a normal distribution (e.g. 1999), lognormal (e.g. 1985) or show signs of separate cohorts (e.g. 2010). On 22 out of 28 occasions the modal length in the survey is lower than 14cm. The length distribution seen in the catch is more stable in shape, with a constant normal distribution, and a modal length usually found between 16 and 17cm (Figures 9 and 10).

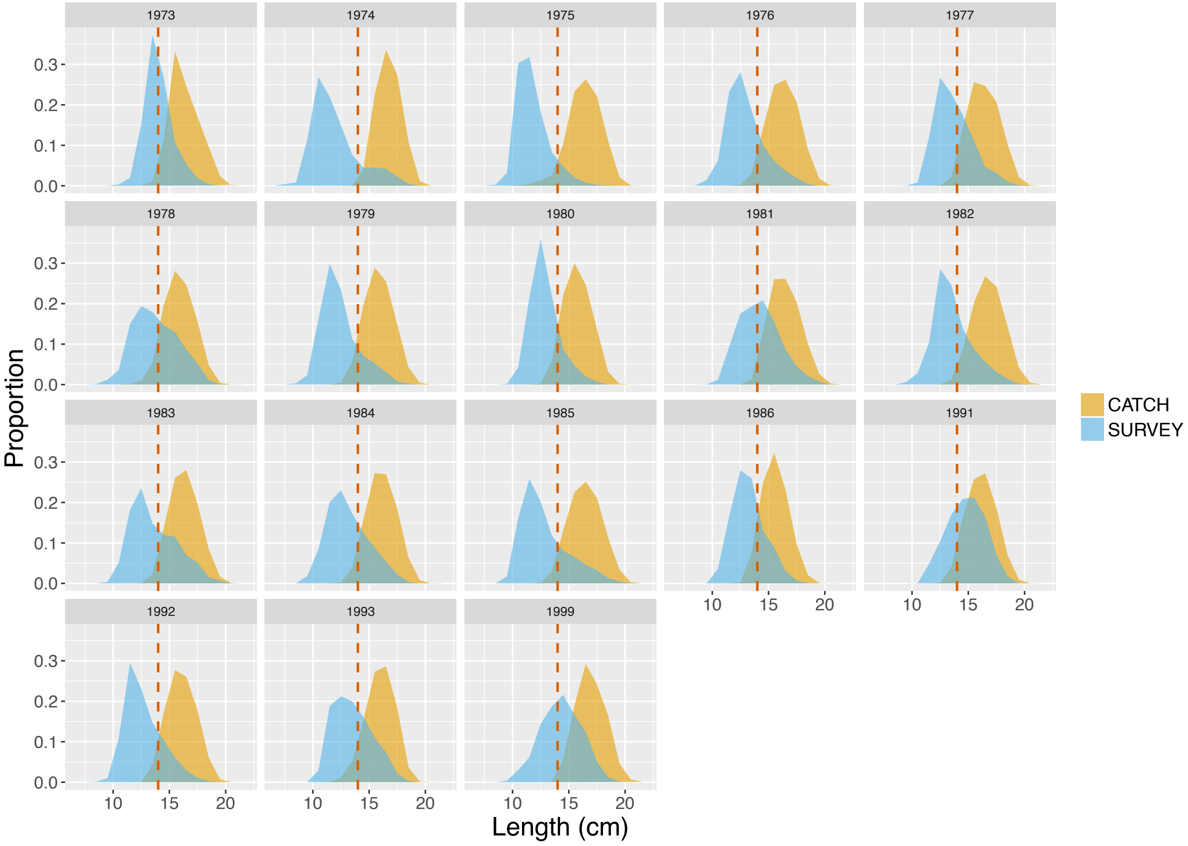

Figure 9: A direct comparison of length distributions (proportion by length) of capelin aged 2+ years in surveys and 3+ catches. Those years with 0 catch are not included. The colour indicates the source of the data, the dotted line marks the 14cm cut off point. Catch data collected over 1cm length intervals.

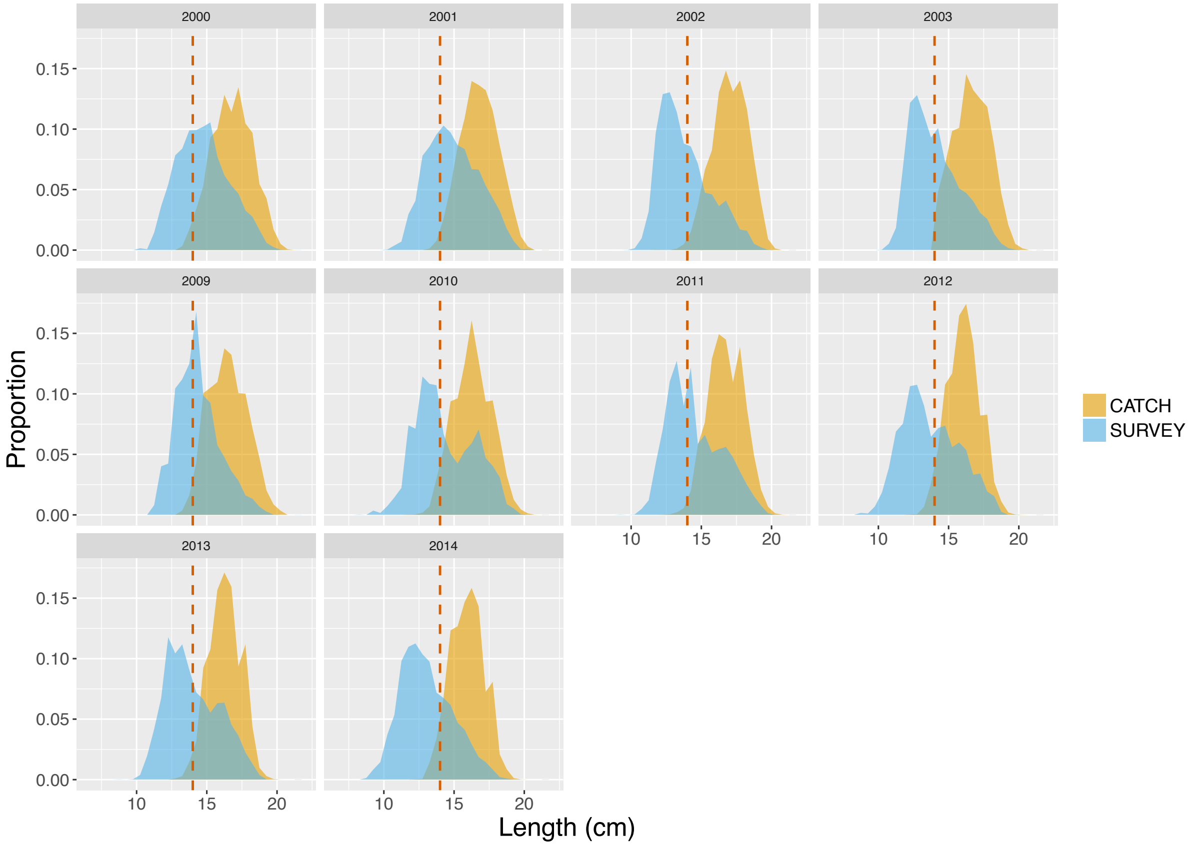

Figure 10: A direct comparison of length distributions (proportion by length) of capelin aged 2+ years in surveys and 3+ catches. Those years with 0 catch are not included. The colour indicates the source of the data. The dotted line marks the 14cm cut off point. Catch data collected over 0.5cm length intervals.

These results alone do not necessarily serve to back up an entirely length dependent maturation, since it could be the incidental effect of age dependent maturation (during which time growth happens but is not of primary importance).

Can we make predictions of who will spawn based on age?

The proportion of fish aged 2 in the survey is far greater than the proportion of fish aged 3 in the catch (the same year class) (figures 11 and 12). Despite around a 75% average representation in the survey they typically represent under 25% of the catch before the first stock collapse and cessation of the fishery in 1987. The shape of the fluctuations of age 3+ fish in the survey and that of the 4+ fish in the catch can be seen to be taking similar trends, the implication being that by this age the catch is a representative sample of the surveyed population.

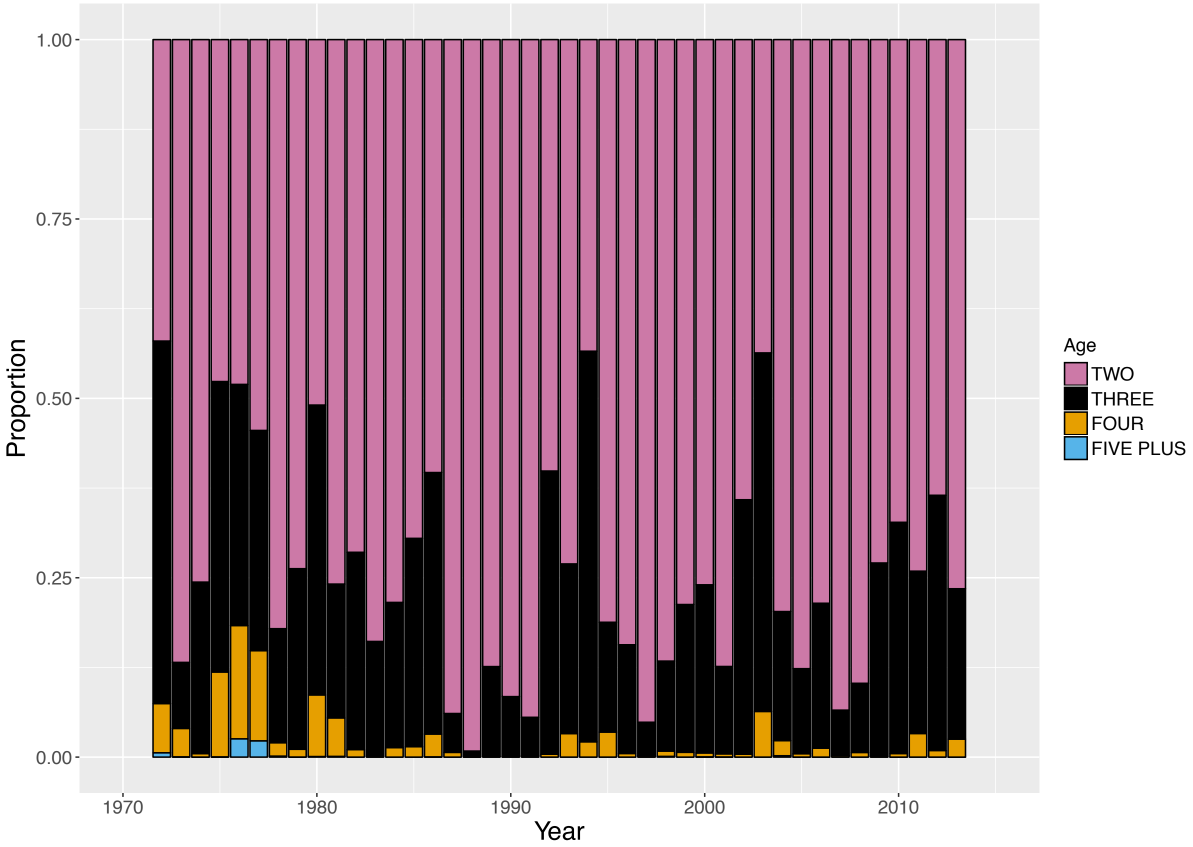

Figure 11: The proportion of fish of each age by year, in the survey. Colours are chosen so that each year class is identifiable by colour when compared with figure 4.

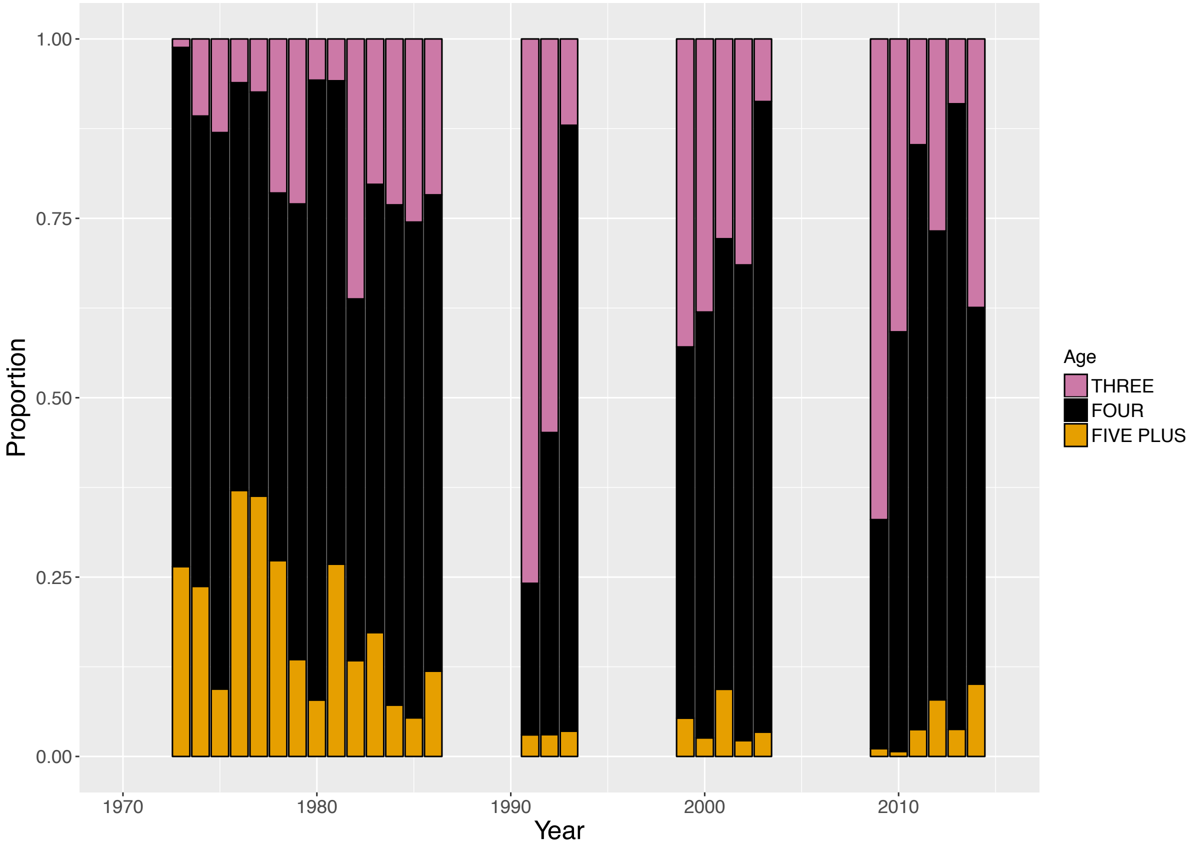

Figure 12: The proportion of fish of each age by year, in the catch. Colours are chosen so that each year class is identifiable by colour when compared with figure 3.

Assessing the validity of applying a cut off

If we consider age to be consequential for a capelin of 2 years old when making the ‘decision’ whether to migrate, but inconsequential by the following year, there may be a cut off length after which a capelin will migrate (that has been passed by surveyed 3 year olds). Typically, 10-15% of caught capelin are over 18cm, and only around 5% are below 14cm (figure 5), illustrating that almost the vast majority of the migrating population is within a 4cm length range.

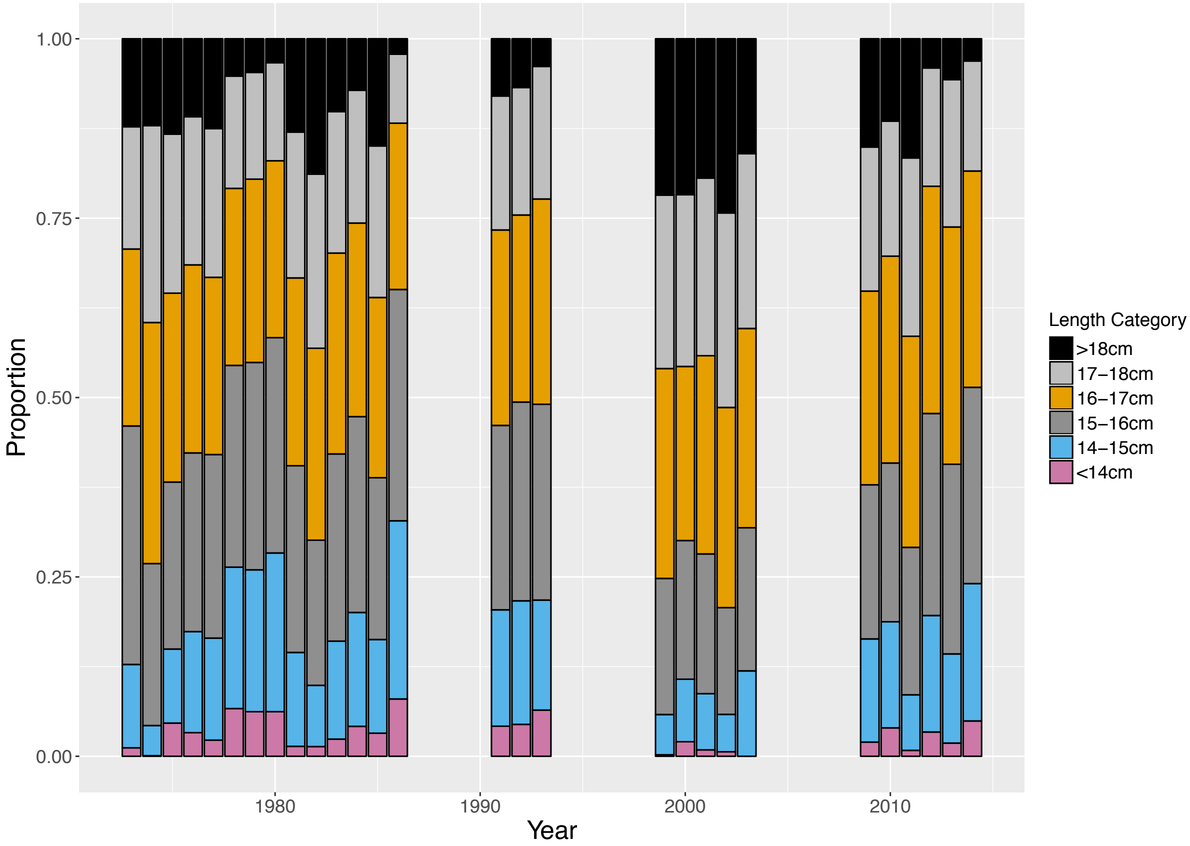

Figure 13: Proportion of the catch in 1cm length categories by year. All fish >18cm are summed. All fish <14cm are summed.

With so few fish of lower than 14cm caught (figure 13) it is reasonable to halt investigations into whether a cut off below 14cm would be a more accurate predictive tool.

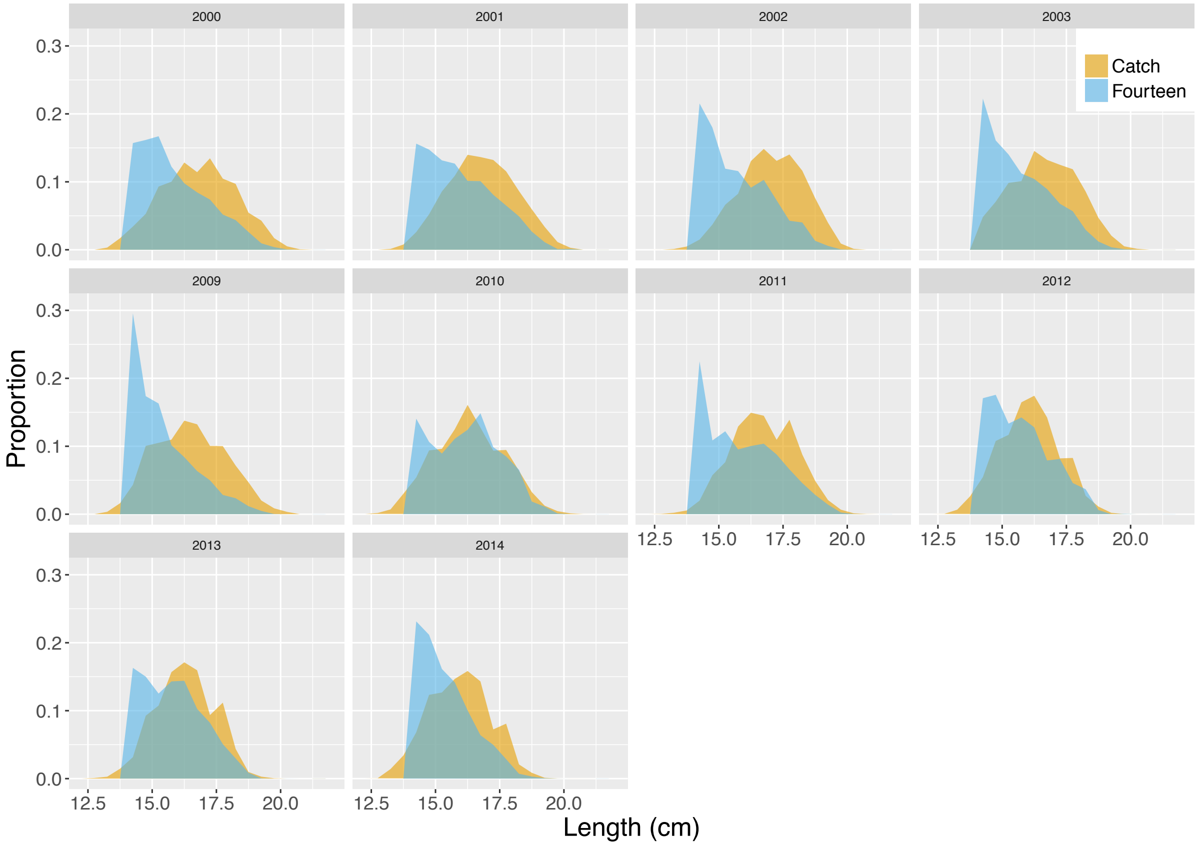

Figure 14: Forecasted length distribution according to a 14cm cut off (blue) compared to the length distribution seen in the catch (orange).

There is an obvious mismatch between the shape of the length distribution predicted to migrate by a 14cm cut off, and that of the catch (figure 14). The 14cm cut off always overestimates the proportion of fish between 14 and 15cm that migrate. The model is accounting for all fish over 14cm that migrate, since every fish over 14cm is given a 100% chance of migrating. Therefore, we can deduce that it is overestimating the total numbers, by virtue of the fact that the proportion of the distribution of the catch which is >16cm is much larger than the proportion of the distribution of the model which is >16cm, and vice versa with the proportion <16cm.

The fit generated by a 15cm cut off is improved, with the cut off replicating the curve taken by the catch after it peaks quite well (figure 15). The problems associated with the 14cm cut off are not gone however, with still too high a proportion of fish in the distribution falling in the 15-16cm category, which is not seen in the catch. As the cut off increases in length it is more likely that the larger part of the length distribution will improve in fit, but it is now suffering from the problem that it is assuming nothing under 15cm will migrate and thus missing the smaller end of the catch. No cut off length can avoid both of these problems simultaneously.

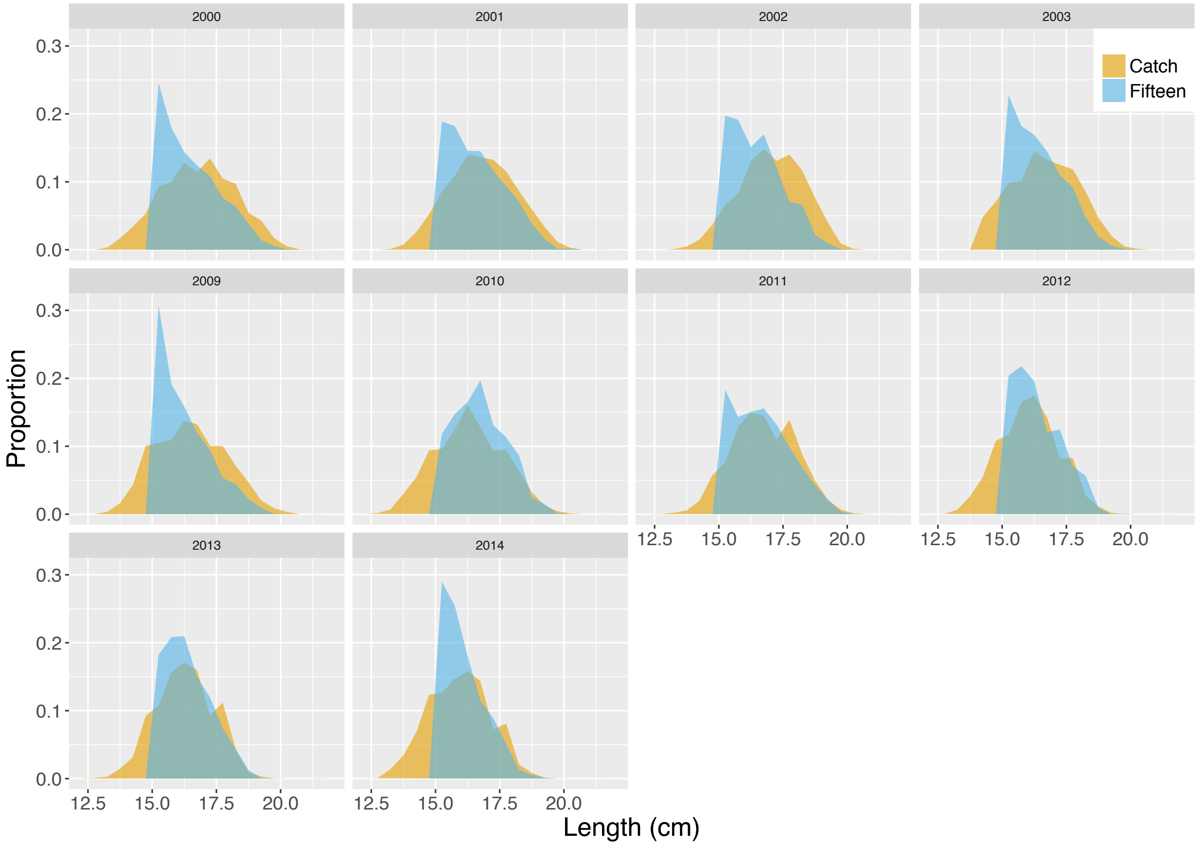

Figure 15: Forecasted length distribution according to a 15cm cut off (blue) compared to the length distribution seen in the catch (orange).

A more complex picture seems to be emerging

With the concept of the cut off appearing too simplistic (figures 14 and 15), and indications that age should be considered too (figures 11 and 12), the next avenue of investigation is to compare the age distribution in the catch with age distributions predicted by different models. When the age structure of the catch matches that predicted by a cut off we can assume that after this length, age is no longer a factor in the decision whether to migrate or not.

There are occasions where a 14cm model accurately predicts the age distribution seen in the catch (e.g. 2010), others where a 15cm model accurately predicts the age distribution (e.g. 2009), and occasions where both are inaccurate (figure 16). These are the years in which the age distribution contains a higher proportion of 4+ fish than even a 15cm model predicts. Increasing the cut off would move the predicted age distribution closer to that observed in these cases. In no years does a 14cm cut off underestimate the proportion of 3 year old fish, indicating that the threshold for migration is not below 14cm. Using this combination of length cut offs with age distributions allows us to see when a length is 'too high' as a cut off, since increasing the length cut off beyond that at which fish actually migrate will be reflected in a predicted age distribution that is biased in favour of older year classes. It is noticeable that in the years from 1973-1983 there were more 5+ fish appearing in the surveys and catches. From 1991 onwards catches have consisted almost entirely of 3 and 4 year olds.

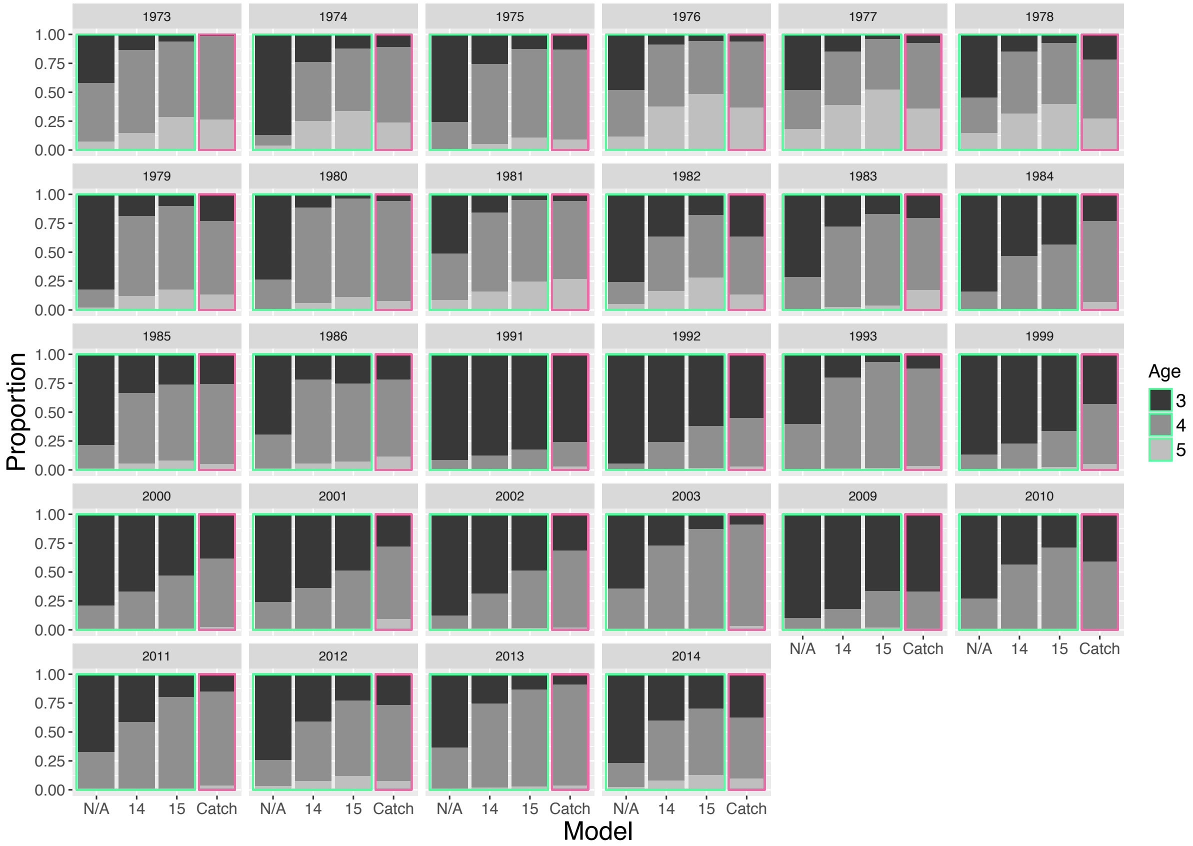

Figure 16: The age distributions seen in the survey ('N/A') and the catch, with predicted age distributions based on 14cm and 15cm cut offs.

To extend this forecasting, a comparison between the ability of multiple different models to replicate the proportion of 3 year old fish seen in the catch, based on numbers and lengths of 2 year olds at the time of survey is seen in figure 17. This includes cut offs of 13, 14, 14.5 and 15cm, an unmodified proportion of the entire 2+ population, and 5 models which adjust the steepness of the aforementioned sigmoid curve. The model with the shallowest curve performed the best overall (model 11, red line), predicting the proportion of 3 year olds with greater accuracy than the 14cm cut off in 9 of 11 years, with a mean error of 9% in comparison to 20%.

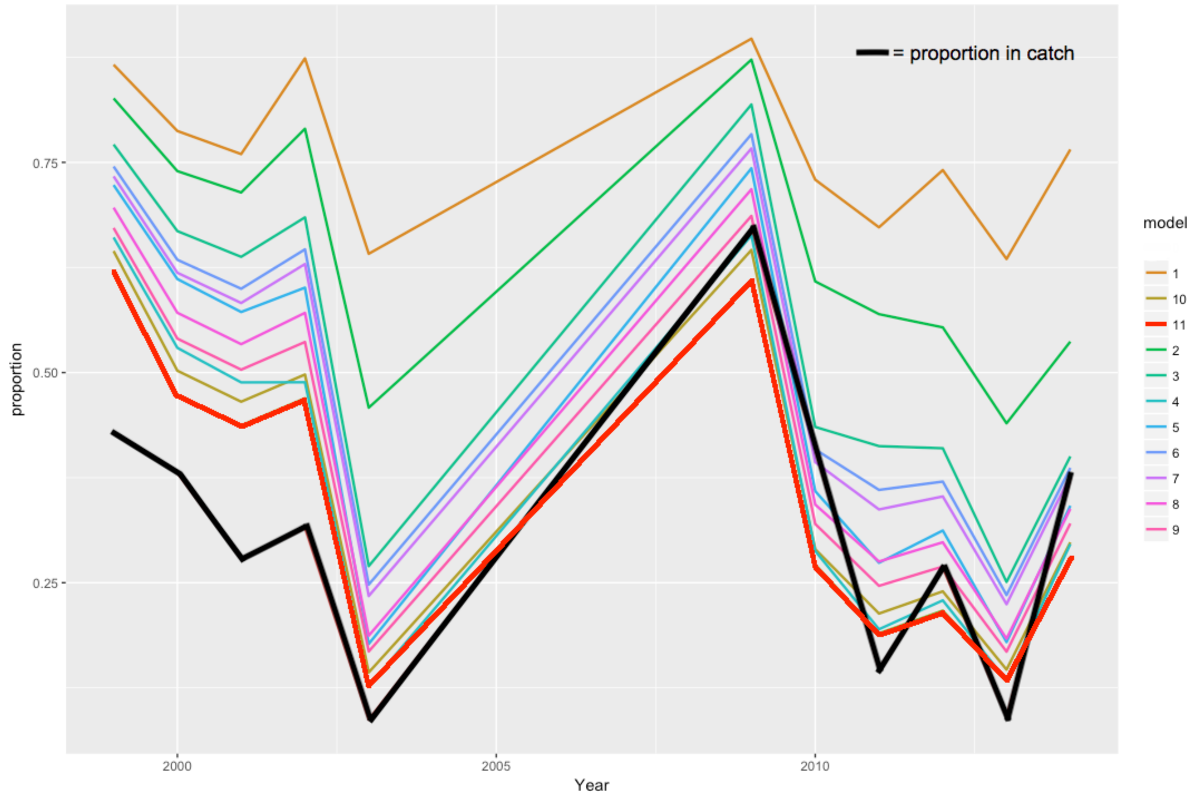

Figure 17: Proportion of the catch composed of 3 year old fish, over time, predicted by 10 models, seen next to the proportion observed in the actual catch.

All models in figure 17 applied their chosen maturity curve was to all age groups, so the chance of migration occurring was based entirely on length. It seems likely that age also plays a role; fish of the same length but different ages may have different propensities to migrate. Building on the models in figure 17 by incorporating age dependent migration, rather than just length, results in the 'Tiresias' model used in figure 18 and figure 19. This applies a shallower sigmoid curve to fish of 2 years old at survey, and a steeper curve which also starts at a lower length to those of 3 years old.

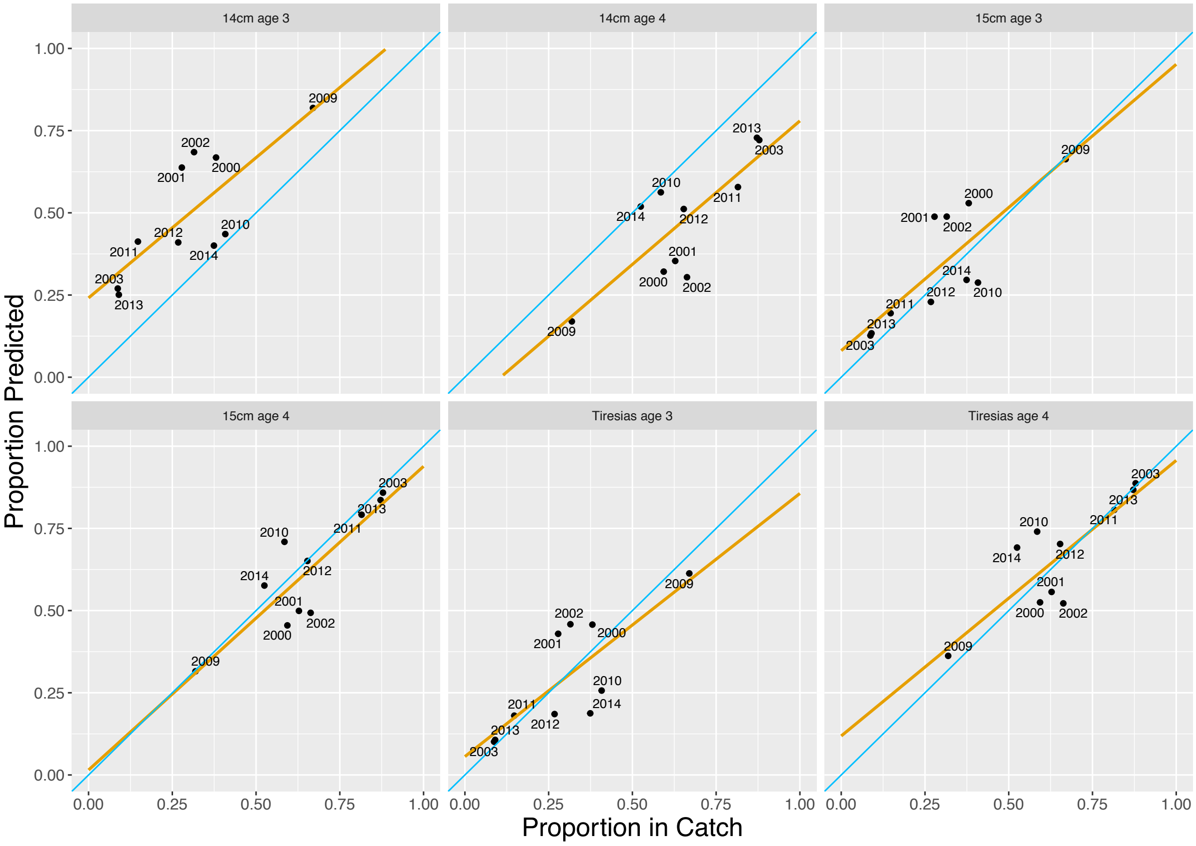

Figure 18: The proportion of the catch predicted to be made up of 3 and 4 year old fish by the age and length based model ('Tiresias'), a 14cm cut off, and a 15cm cut off. The blue line represents the perfect prediction (y=x). The orange line is a line of best fit generated by a linear model.

Model	Mean error	Median error	Variance of errors	Standard Deviation of errors
14cm age 3	0.197	0.172	0.015	0.122
14cm age 4	0.176	-0.154	0.012	0.111
15cm age 3	0.091	0.041	0.012	0.109
15cm age 4	0.07	-0.022	0.008	0.09
Tiresias age 3	0.091	0.015	0.013	0.115
Tiresias age 4	0.072	0.002	0.009	0.097

Table 2: Error table showing an analysis of the difference between observed and expected values. Mean values calculated after conversion of negative values to positive.

The 14cm model consistently overestimates the proportion of 3 year olds (mean = 19.7%), and underestimates the proportion of 4 year olds (mean = 17.6%) demonstrating low accuracy (Table 2) (Figure 18). The 15cm and Tiresias models make more accurate predictions of the age composition of the catch as demonstrated by the mean error between expected and observed (9% and 7% in both cases for 3 and 4 year olds respectively) (Table 2) (Figure 18). The standard deviation does not tell us whether the model is a good fit to our 'ideal' blue line, but how much variation there is in the margin of error across years for each model (i.e. a model that had a constant error would have a standard deviation of 0.00), thus the precision. All models have similar values of 9-12%, indicating that the errors being made are relatively stable and not fluctuating between large error in some years and minimal error in others.

Combining age and length

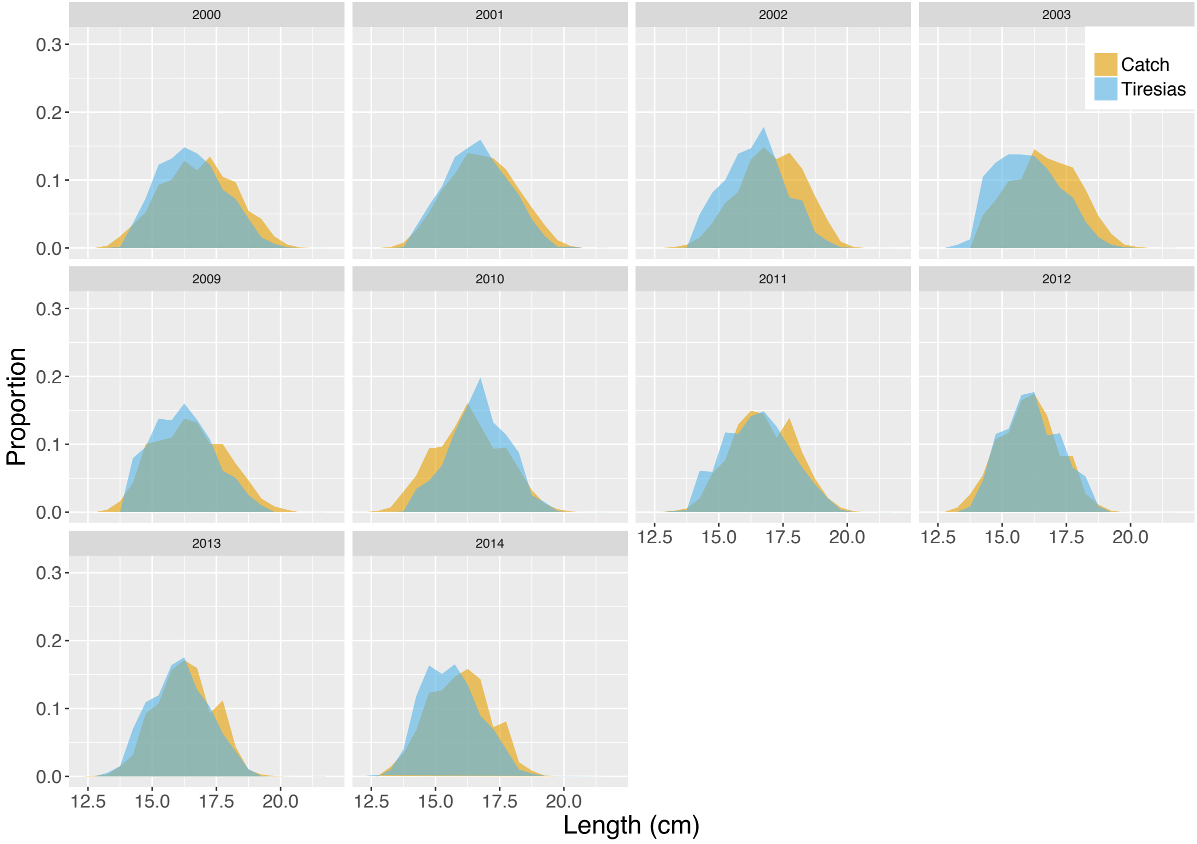

Figure 19: Forecast length distributions generated by the Tiresias model (blue), compared with length distributions seen in catches (orange).

The Tiresias model is proficient in replicating the length distributions seen in the catch (figure 19). There is no large systematic error as we see with the cut off models in figure 6 and figure 7. In most years there is still some slight overestimation of numbers below 16cm, indicated by the small portion of the catch distribution that is exposed towards the larger end of the scale. As with the cut off models these fish have been accounted for by the model, but due to a slight overestimation of smaller fish they do not represent as large a proportion of the modelled distribution.

The important consequence

The models are applied to numbers of capelin and the figures up until now have dealt in proportions. The output in numbers can be converted to biomass using the mean weights, and all models compared. In figure 20 we see the biomass allocated as ‘maturing’ by each model. The biomass predicted by a 14cm cut off ranges from 1.29 kilotonnes to 2.47 kilotonnes, ‘Tiresias’ ranges from 0.99 kilotonnes to 1.82 kilotonnes, and the 15cm cut off ranges from 0.97 kilotonnes to 1.98 kilotonnes. The mean difference between 14cm and ‘Tiresias’ is 0.55 kilotonnes.

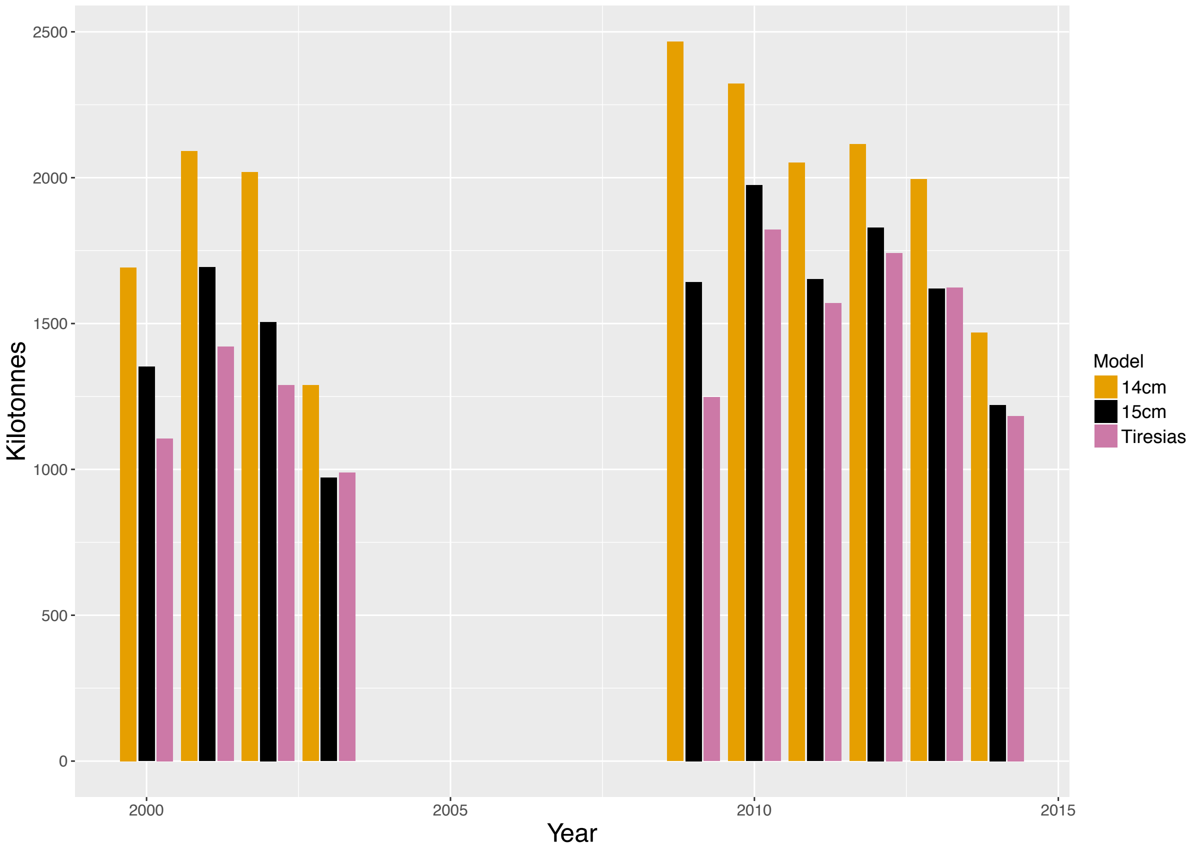

Figure 20: The biomass of capelin predicted to undergo maturation and migrate in each year with catch during our modelling period, as forecast by a 14cm cut off, 15cm cut off and by 'Tiresias'. This is not a forecast of the spawning stock, but of the maturing biomass prior to natural mortality. The year is the year that they will spawn, i.e. the year after the relevant survey.

Testing the assumption that there is no growth between survey and catch

In 2002, 2003, 2013 and 2014 the catch distribution is slightly skewed to the longer lengths than that of the survey, however not by much, and in most years there is an excellent fit between the length distribution of 3 year old fish at the time of survey, and 4 year old fish in the catch (figure 21).

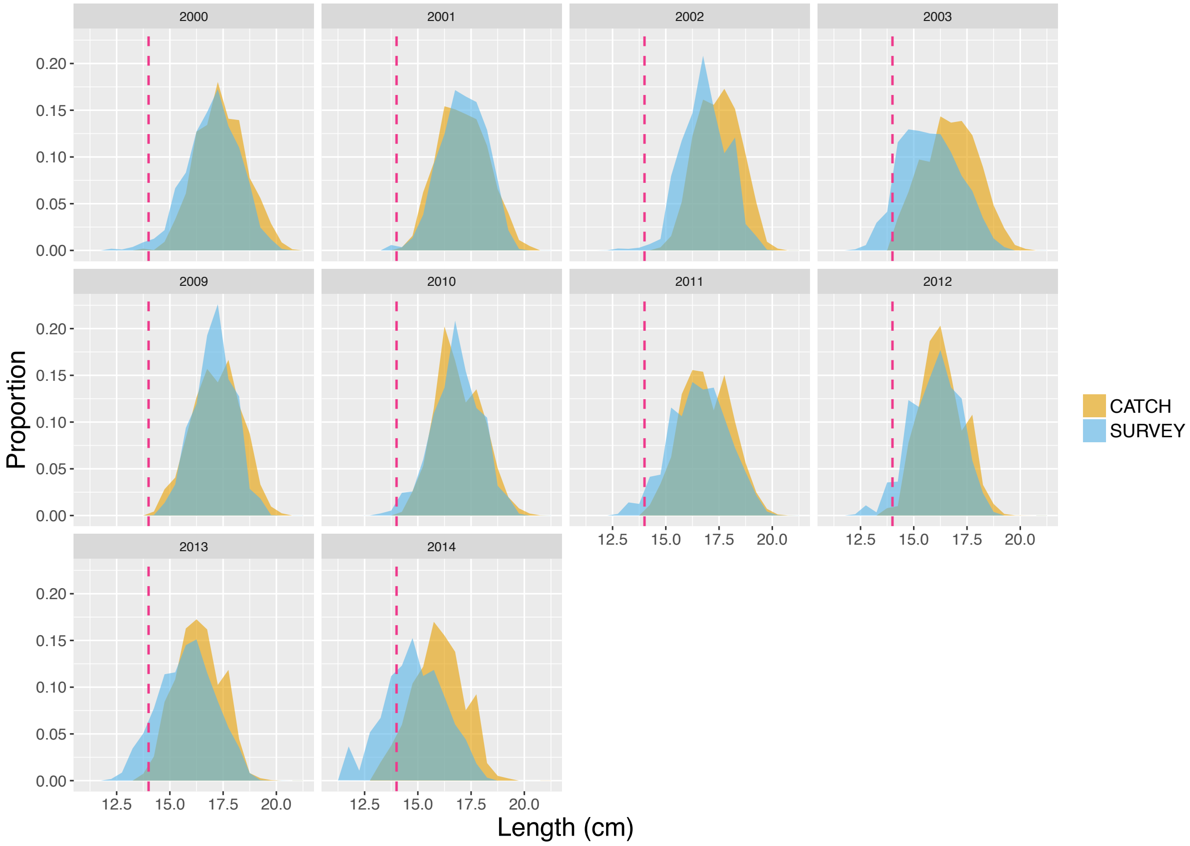

Figure 21: Length distributions of 3 year old fish in the autumn survey (blue) and 4 year old fish in the catch (orange). The dotted line indicates the 14cm point.

Condition - another relevant factor?

A glm test for a relationship between condition factor of 2 year old fish at the time of the survey, and their chances of undergoing migration, showed that there is no significant relationship (table 3). A p-value of 0.28 signifies that any apparent effect of condition could be down to random variation.

glm(formula = cbind(Migrate, Non_migrate) ~ Length + Cond, family = binomial)				
	Estimate	Standard error	z-value	p-value
Intercept	-7.6947	1.5034	-5.118	3.09E-07
Length	0.4505	0.1367	3.296	0.000982
Condition	2.751	2.5724	1.069	0.284881

Table 3: The output of a glm run to determine whether there is a significant relationship between condition and migration proportion in 2 year old fish.

This project has been undertaken with the goal of making an assessment of whether the current procedure of employing a cut off length in autumn, above which it is assumed that capelin will mature and spawn in the spring, is fair. With a better understanding of the process of maturation will come improvements in our predictions regarding how many capelin will migrate, and how best to manage the fishery in order that we can guarantee that our exploitation strategy will not significantly harm fellow predators, or the potential for successful recruitment of the next capelin year class. Simultaneously better predictions would enable the formulation of more precise management objectives (optimal harvesting), which have been lacking in this fishery.

My main findings are:

- It seems likely that age does influence the length at which a fish will migrate.
- Using a cut off length does not replicate a real world biological process.
- Further evidence to support that there is no growth in length between survey and catch.
- A persistent overestimation of the number of capelin migrating is occurring.
- There is variation from year to year in the length at which migration will occur.
- By combining age and length into a model it is possible to better predict the numbers migrating.

Discussion of results

Age as a factor

My results show that there is a difference in length distribution between the population of 2+ fish surveyed and the catch. Making conclusions about how capelin operate when it comes to who will spawn is a tricky business. Factors such as food availability (Uusi-Heikkila *et al.*, 2011), cohort strength (Gjøsæter, 1998), and general habitat characteristics (Morita, Tsuboi and Nagasawa, 2009) may play roles in determining whether certain individuals will ‘make the decision’ to spawn, all introducing variation into the picture. However in our management we look at it in a much more simplistic way and use the 14cm cut off. 14cm is certainly not too high, as almost nothing below the cut off is seen. Therefore the questions are of whether it is instead too low, and whether a cut off is close enough to the biological reality of the maturation process as to be usable.

With the situation being more complex than a simple cut off length perhaps we can start to introduce these other factors into our predictions of who will spawn. For example perhaps age has some influence, as posited by (Forberg and Tjelmeland, 1985) who found that the P_2 (length at 50% population mature) would be significantly longer for 2 year olds than 3 year olds in most years. A 2 year old fish of the same length as a 3 year old must have invested much more energy/time into somatic growth, so it would make sense that they would not have enough remaining energy to invest in reproductive growth. Thus the 3 year old spawns, whilst the 2 year old doesn't. This is the antithesis of a cut off as there are two fish of the same length who exhibit different strategies. My work shows that it's much more unlikely for 2 year old fish to mature than 3+ fish. The catch seems to be a good representation of the 3+ fish surveyed, with the ratio of 3:4+ fish in the survey matching well the ratio of 4:5+ fish in the catch. We can therefore suggest either that nearly all 3+ fish migrate, or that by this point an age threshold has been passed meaning that age is no longer a factor in determining the migration decision. The former is likely to be true since natural mortality is so high that the chance of surviving each year is not a risk worth taking, once sufficient growth has already taken place to enable spawning. 2 year olds are significantly underrepresented in the catch when compared to the survey. This is in accordance with the findings of (Tereshchenko, 2002) who concluded that with the exception of when the stock is exceptionally low, it is the survival conditions rather than the population fecundity, that will determine the strength of the next year class. Under such conditions it is favourable for capelin to spawn as soon as possible, as despite increasing fecundity with increasing length and body mass (Tereshchenko, 2002; Hedeholm, Grønkjær and Rysgaard, 2011) the effect of one year's growth will not overcome the risk of natural mortality in that year.

Purely based on the age distribution of the catch we still cannot rule out something at least close to a length cut off being in action. Perhaps the difference between ages, in terms of migration propensity at length, actually covers only a very narrow length band. Therefore whilst they are not operating exactly under a cut off length, it is close to being so. It also could be that almost all 3+ fish migrate because they are longer than the cut off by this time. It is less likely for a 2 year old to reach this cut off length but those that grow particularly fast are able to do so, leading to a small proportion of the total engaging in the migration.

Scientists are aware that the picture is more intricate than a 14cm cut off implies, however it is used for simplicity. So there is acceptance that it does not do a perfect job, and the extent to which one accepts it is dictated by the level of imperfection one is willing to accept.

Comparison of 14cm and 15cm

Length distributions forecasted by the cut off models do not match up with the length distribution of the catch, as the cut off will never produce the normal distribution required. There is a consistent overestimation of those fish closest to the cut off as they are the most abundant length groups. A 15cm cut off seems to do a better job of reducing this problem, but instead misses those fish that are under the cut off length. The impact of this would be a smaller error in the estimation of numbers, since whilst it does not include <15cm individuals it will probably be overestimating the number of fish in the 15-16cm length class. The length distribution of the catch tends to have a modal value of around 16cm, which means that at 16cm+ it is no longer possible for me to say with great confidence that not all fish migrate (the curve of the length distribution of survey and catch will take more or less the same shape after 16cm). However before the modal value of the catch, I would say with some confidence that we are travelling down a sigmoid curve of maturity that is more elongated than we use currently. Applying a less steep maturity curve will then impose the smoother building of numbers in lower length classes until the point is reached where close to 100% migrate (around which we will find the modal value), and the tailing off of numbers in the higher length classes will then occur as they are less abundant.

Combining age and cut off length

Due to the fact that there will be fish sharing a length class, but not sharing other characteristics which impact their maturation, the predictive power of using length alone is not as strong as if it were to be combined with other factors. One factor that may be able to help us is age, since it has already been discussed that it likely plays a role in length at maturation(Forberg and Tjelmeland, 1985). My results demonstrated that the age distribution of the catch is variable over time. And that we can replicate the age distribution of the catch by modifying where we put the cut off. A 15cm cut off more frequently forecasts the age distribution of the catch with greater accuracy than a 14cm cut off, but even the 15cm cut off does not go far enough on multiple occasions. These results back up my conclusions that the number of fish predicted to spawn is too high in almost all years. If the forecast is made up of a higher proportion of 2 year olds than the catch, as is the case in virtually every year at a 14cm cut off, then it will certainly be over estimating the number of individuals, since almost all 3 year olds are >14cm and will therefore be included in the estimation, thus to overestimate the proportion of 2 year olds we must be overestimating the numbers.

The years immediately post stock collapse and cessation of the fishery are interesting. The survey population when the fishery is allowed to resume is completely dominated by 2 year old fish. This is to be expected as the resumption of the fishery will be due to a strong year class coming through, a large amount of which we anticipate will migrate due to it being >14cm. In 1991 and 1992 the proportion that these fish would represent in the catch was overestimated, and the same again but to a greater extent between 1999 and 2002 after the second collapse. Overestimating the numbers meant that the spawning stock was fished harder than prescribed by our harvest control rule, which could have had negative effects on the stock recovery speed.

From knife edge to smoother curve

If we now accept that our predicted spawning stock should match the age distribution of the catch then we can compare different cut offs and other options which adjust the shape of the maturity curve to see whether this does a better job. This work demonstrates that in fact the changing of the shape of the curve enables a better age based prediction than any cut off.

As mentioned earlier, 2 year olds and 3 year olds probably follow different development of maturity at length (Forberg and Tjelmeland, 1985; Gjøsæter, 1998). To build upon the quite simple ‘model 11’, ‘Tiresias’ seeks to replicate more accurately what we believe is actually happening. The consequences are an age forecast of similar quality to the 15cm cut off, but also a much improved length distribution match between model and catch. The 15cm model does do a very good job at forecasting age distribution, however it does not do an equally good job of forecasting length. To some extent we can say that it has arrived at an almost perfect age forecast by accident, rather than because the actual individuals selected as maturing are the correct ones. Nonetheless it is more accurate than the 14cm model on both fronts.

The excellent match between both age and length seen in ‘Tiresias’ does not necessarily imply that it is making a perfect prediction. As with the age distribution alone, it would be possible to make a perfect age/length prediction by only selecting 100 fish that fit with the average catch. One reason I believe that this is not what the model is doing is that there is a subtle but noticeable tendency for the forecasted length distribution to bulge slightly outside of the catch between 15 and 16cm. The model has close to 100% of the fish >16cm in length allocated as spawners, so that slight yet frequent overestimation of fish in the 15-16cm category once again can only be due to a slight overestimation of numbers. 2010 is the only year where ‘Tiresias’ appears to underestimate the numbers, so I do not believe that there would be a major problem with ‘leaving fishable fish unfished’ due to underestimation of the maturing stock by the model.

The estimates of maturing biomass made by Tiresias are lower than with the 14cm cut off but they are not so low as to be considered hopefully unrealistic (as would be the case with the example of the selection of 100 fish to meet the criteria desired). With the exception of 2003 and 2013 it produces a lower estimate than the 15cm cut off model but tends not to display large differences. This reinforces the earlier point that the 15cm cut off gets the length distribution wrong but probably without large consequences. Hence despite the inability of the 15cm model to predict correctly ‘who’ will go, it seems to coordinate quite well with ‘Tiresias’ on the biomass estimation. On average the forecast by ‘Tiresias’ is 551.85 kilotonnes less than predicted by the 14cm model, ranging from a maximum reduction of 1.2 million tonnes (2009) to 280 thousand tonnes (2014). 2009 was a particularly bad year for the 14cm model in terms of length forecasting, and the huge discrepancy between biomasses is illustrative of the impact that the 14-15cm length class can have due to its high abundance.

Sex differences

It is known that male capelin grow longer than female capelin and that length at maturity may be dependent on sex e.g. (Gjøsæter, 1998; Huse, 1998; Eriksen *et al.*, 2008; Baulier, Heino and Gjøsæter, 2012). The data used to create ‘Tiresias’ does not include sex, and so it is possible that rather than accurately describing which capelin will spawn it instead produces an average between males and females which functions well in terms of age and length distributions. Adding sex to the model may improve the accuracy of the forecast.

Condition

Although the analysis of the relationship between condition and propensity to migrate did not yield a significant result I believe that this is only because more data is required. Growth can fluctuate widely between years due to food availability, cohort strength, competition with other species, and climate (Gjøsæter and Loeng, 1987; Gjosater, Dalpadado and Hassel, 2002; Orlova *et al.*, 2010), and there is good reason to believe that other examples where condition is shown to be a factor would be likely to apply to capelin e.g. (Ndjaula *et al.*, 2010; Jørgensen *et al.*, 2018), since we know that condition is likely to influence reproductive output. Further work could be to try to incorporate condition into the modelling process.

Discussion of methods

It is important to remember when drawing conclusions from this thesis that one should be tentative. There are unquestionably potentially large problems which could influence the results, which we shall now review.

Size selectivity - catchability

The vast majority of the commercial capelin catch is caught by purse seining vessels, capable of taking individual hauls of 500-1000+ tonnes (Georg Skaret, pers. comm.), at least for the period addressed by my modelling (2000 onwards). Although trawling probably represented a much larger portion of the catch in the early part of the time series there are no obvious trends in my results to indicate a change in the catch data over time due to a difference in catchability based on trawl/purse seine.

The fishing technique itself is probably not size selective (FAO, 1984), since the mesh size is small enough to prevent escapement of even the smaller end of the length distribution (16mm minimum from 1981). If there was significant escapement by smaller fish, the length distribution that we see in the catch would be unlikely to be a normal distribution as we see in figures 1 and 2, rather it would be more of a log normal distribution with a sharp increase and longer tail. This is assuming that the population being fished fits a normal distribution in the first place, however if the population being fished fits a log normal distribution, or one as seen in the cut off forecasts in figures 6 and 7, then escapement of smaller individuals through the netting could create a normally distributed catch.

It seems highly unlikely that large numbers of 14-15cm capelin caught in a purse seine, will force themselves through the meshes to escape and even if their behaviour was inclined to attempt this feat, the logistics of huge numbers rapidly escaping from such a large group/area seem impossible as was seen during experiments on the escapement of mackerel done by (Misund and Beltestad, 1994).

Size selectivity - human choices

The more relevant form of size selectivity would be if fishermen actively prioritise catching the largest capelin, biasing the length distribution towards the longer end of the scale.

All male capelin, and those females not yet ready to spawn, are used for fish meal and oil, whilst later in the season when females are ready to spawn they are frozen whole and used for human consumption, mostly exported to Japan ((Nofima), no date) (known as "roe capelin"). In the 1970s and 1980s 90-99% of Barents Sea capelin was used for reduction to fish meal and oil (Flaaten, 1988). The price of capelin for this purpose from 1978-1980 was 0.5284NOK/kilo, and the price of roe capelin was 1.503NOK/kilo (Flaaten, 1988). Prices accessed on 21/05/2018 (Sildesalgslag, no date) valued capelin for human consumption at 2.5NOK/kilo, meal and oil and production of fish food at 1.4134NOK/kilo, and lower quality for meal and oil at 1.2014NOK/kilo. A similar market is seen in the Canadian capelin fishery, which divides capelin into category "A" (48.502cents/kilo in 2016) or "B" (30.865cents/kilo in 2016), or uncategorised. To classify as category "A" there must be no more than 55 individuals/kilo and a minimum of 40% usable females over 13.3cm. Category "B" must have no more than 55 individuals per kilo, and minimum of 40% females of any size or condition. If the sample does not meet either category then the price is negotiated between vendor and buyer (FFAW, no date). Having said this, the price inequality existed in the 1970s and 1980s (to an even greater extent than today), yet as mentioned already, 90-99% was used for meal and oil. This implies either that it is not that easy to be specific enough with the fishing strategy to achieve a higher percentage of roe capelin, that there simply isn't that much of the total population which fits the roe capelin category, or that the demand for roe capelin isn't great enough to represent a higher percentage of catches.

Unfortunately I was not able to find more modern information about how the catch is used, however ((Nofima), no date) quotes one 'John Roald Isaksen', NOFIMA scientist, who states that 20,000 tonnes are eaten annually in Japan. If this is correct then it does not represent a significant portion of the total catch. Even with the large increase in price for roe capelin I would have doubts whether such a small sellable volume would be worth putting much additional effort into acquiring, especially with cost/day of every fishing trip being a major concern for any vessel.

In personal communication between Georg Skaret and Pål Cato Reite (captain of the purse seiner "Eros"), Mr Reite said that there has not been much of an option for size selectivity in the fishery, but that the decision of when to fish is determined by the degree of aggregation.

If there was a tendency to select the longest possible capelin then we would expect the population in the catch to be longer than the population in the survey, which is contrary to my findings. In my comparison 2014 exhibits the most marked difference, which could be explained by the catch being only 40,000 tonnes, and therefore perhaps it was profitable to target roe capelin - quality over quantity when quantity is not an option. 2003 also has a slight deviation despite a catch of nearly 180,000 tonnes. Generally there is no trend for the catch to be longer than the survey. 2003 and 2014 are the two years with the overall shortest survey length distribution. Therefore the catch is probably not selective, but most three year olds have attained the length at which they will migrate in most years. In 2003 and 2014 when there were a larger than normal number in the shorter length categories there were simply more capelin that did not migrate from that year class, and the subset that did is the longer portion of the length distribution, which then shows up in the catch.

My catch data excludes roe capelin (Gjøsæter, 1985) (assuming changes to the sampling strategy have not been made since 1985). If it is reasonable to expect the roe capelin to be at the longer end of the length spectrum then their exclusion will lower the proportion of longer capelin and increase the proportions of the rest. This is an important point because the conclusions to come later on would actually be reinforced by the length distribution shifting in this way, as it would give yet further weaken the credibility of the 14cm cut off. Of course if the quantities fished are as low as 20,000 tonnes then the effect will not be large.

Catch data - who, when, where?

(Gjøsæter, 1985) includes two paragraphs on the process of acquisition of the catch data. One sample from every fourth catch processed at a factory in the east, and one in the west, is taken, and samples are then analysed with a view to providing the maximum geographical coverage. Unfortunately I did not do any analysis of where the samples have been taken from, how many vessels contribute, how many were sampled per catch etc. because whilst this information will exist in paper or floppy disc format, it would be a quite epic undertaking to collate it and put it into a modern format in order to have a look at it. Currently the catch data is collected with recordings of the metadata, thus an active effort is made to spread the collection of data both temporally and spatially (Georg Skaret, Jaime Alvarez, pers. comm.)

We do not know how representative of the overall population the length/age/weight keys that are created from these samples are. They represent the catch from which they were taken, however there is no weighting by overall numbers in the area as would be done in the survey, as it is not known. If catches are taken early in the season vs late in the season, from one area vs another, selecting for larger individuals etc. then the keys produced would potentially be different (Harald Gjøsæter, pers. comm.). A sample of 100 individuals caught in a sub population containing 1 million individuals should of course not be given the same weight as a sample of 100 individuals in a sub population of 1 billion when assessing those two sub populations as a part of a whole. But this is potentially what is happening with the catch data.

Drawing results from acoustics

Acoustic data and physical attributes ascribed to that data, taken during the survey, both carry levels of uncertainty. When the time series used in this investigation was started it was at the inception of acoustic technology being used for biomass estimation, and during the course of those 41 years the hardware and software used in echosounding and post processing has developed, as has the method of calibration to ensure accurate results within each vessel and consistency between vessels. Accordingly there have been improvements in our ability differentiate between species more easily, obtain better resolution, improve signal/noise ratio etc. (Toresen, Gjøsæter and Barros, 1998). The allocation of physical characteristics using length/weight/age keys by weighting sample data and how widely samples can be allocated to physical areas is a potential source of error and does depend to some extent on the experience and proficiency of the acoustic technician. However (Tjelmeland, 2002) found that this is less likely to be a significant source of error than the correct identification of capelin vs other species vs noise that is not of interest.

The consequences of errors being made in the length/weight/age keys application to physical areas is that potentially large amounts of capelin could be ascribed a length/age distribution that does in fact not apply to them, which would be particularly problematic if, for example, 2 year olds were being confused with 4 year olds. This does not seem to be particularly likely to occur on a scale that would make an impact on the investigation however, since capelin do school by size (Gjøsæter and Korsbrekke, 1990), and at the very least there is a trend for the largest capelin to be found the furthest north(Carscadden, Gjøsæter and Vilhjálmsson, 2013). When dealing only with the surveyed 2+ population there is no reason to believe that there is any bias constantly affecting the length or age distributions observed to a significant degree. When potential problems have arisen they have been addressed by the scientists, for example in 1991 there was a suspicion of selectivity in the trawl on the Russian side, so in 1992 experiments were carried out side by side to verify that this was not the case.

The identification of returned signals has benefited greatly from technological improvement. The advent of multi frequency echosounders and better post processing allow the observer to better differentiate between organisms of different sizes and remove the backscatter of no interest that comes from plankton, the bottom, or surface disturbance (which is also minimised by the use of echosounders mounted on adjustable drop-keels). However the system is not perfect. If signals are interpreted incorrectly as capelin, when in fact they are, for example, polar cod, then the allocation of lengths/ages/weights of that areas capelin catches will be allocated to them, and this would create incorrect results. Since the more specific end of my project results was using data only from the 1999 survey onwards I can say that I believe that the survey data does not have large systematic errors. The data becomes less reliable as we move back in time but it was used mostly in the focussing of the investigation and to get a general picture, not to draw firm conclusions. Further to this, capelin are seen as more or less ideal acoustic targets due to their acoustically available height in the water column, their single species schooling at relatively high densities, their apparent lack of vessel avoidance, and their low intensity diurnal vertical migration (Gjøsæter, 1998).

The target strength for capelin was established in the early 1980s (Dommasnes and Røttingen, 1984), and whilst some work has been done to verify this, and further our understanding of how size and body content (gonad size etc) impacts target strength (O'Driscoll and Rose, 2001; Olsen and Jørgensen, 2002; Jørgensen, 2003; Guttormsen and Wilson, 2009) we still do not know how confident we can be in our current estimation or how the target strength could change with depth. Any adjustments to target strength would scale the biomass calculations one way or the other, however it should not make too great a difference to my results since I use only the length and age distributions which are based on the physical sampling.

Survey methodology

In later years after the inception of the Barents Sea ecosystem survey the survey time is much greater than previously, but the bulk of the capelin stock is surveyed during the latter phase. It is therefore fair to assume that coverage is still synoptic. Coverage is mentioned in the survey reports (table 1), but it is evident from the quotes that it has not always been given the full attention of the author, and the historical context of changes in coverage and what that could mean for the results is not mentioned. It is highly likely that coverage was incomplete in some years. Problems such as ice coverage, denial of access to the Russian EEZ, military activity, illness, bad weather, loss (and subsequent regain) of the trawl and logistics have all impacted upon the available survey time and course. Once again, my assessment of the situation here is that the survey design has undergone improvements over time as those organising and coordinating grew in experience and knowledge, and the data used for my modelling is considered to be reliable data by those in the field.

Demersal capelin

It has long been known that there is a portion of the population which can be found close to the sea bed. This demersal component is of course not represented in pelagic trawls, and will not be recorded as a part of the acoustic survey. It has also long been known that this component tends to be larger and older individuals. Therefore if it were to be large enough to make an impact on the overall length distributions it could change the conclusions drawn from my current comparison. It has not been well investigated just how large this component of the stock is, but for three years it was dedicated as a special subject of interest during the ecosystem survey, with calculations made based on swept area. In 2005 it was estimated that demersal capelin amounted to some 33,000 tonnes (Anon. 2006, vol. 2), with 76% (by number) of these over 14cm (compared to 54% of the overall population). In 2006 it was estimated at 44,000 tonnes (Anon. 2007, vol. 2) with 83% over 14cm (compared to 25% overall population), however were one station not to be excluded from the results (which obviously hit a substantial aggregation), that biomass estimation would leap to 147,000 tonnes. This indicates the level of uncertainty associated with this method of estimating demersal capelin. In 2007 it was estimated at 133,000 tonnes (Anon. 2008, vol. 2) with apparently no stations excluded. The biomass of mature capelin found demersally would have represented 14% of the total mature population. Since the demersal capelin tend to be larger and older individuals we can assume close to 100% migration. The impact that their inclusion would have on the assessment of whether 14cm is a valid cut off would be to further back up my assertion that it is not (assuming that they maintain a demersal lifestyle when they form part of the spawning population and are therefore inaccessible to the catch). Their inclusion in the survey would have a small effect on the length distribution, but would have a much greater effect on the catch length distribution as they would represent a larger proportion of the population.

Growth between survey and catch

In order for my comparison of the population at the time of survey and the population spawning, based on the catch data, it is crucial that growth (in length) does not take place between the two sampling times. If growth occurs, but it not quantified, it is no longer possible to say what length an individual in the catch was at the time of the survey. If we cannot say what length a caught individual was at the time of survey then that individual is of no use to us in terms of making statements about the length at which capelin migrate, and using that information predictively to forecast spawning stock. My comparison between three year olds in the survey and four year olds in the catch shows that there is very little difference in the length distribution. In 2003 and 2014 there is some slight displacement of the catch distribution towards the larger end of the scale but generally these results back up the long standing idea already in existence that growth does not take place between survey and catch (the current assessment model for capelin assumes no growth in this time). It is normal for capelin to still be feeding in late autumn (Gjosater, Dalpadado and Hassel, 2002), so some growth may be expected. However it is critical for capelin to accumulate enough fat to survive the winter (Orlova *et al.*, 2010), and for the maturing population they must also prioritise the production of gonads occupying a large portion of the body cavity (Gjøsæter, 1998) which is energetically demanding. Based on these factors and my analysis it seems reasonable to assume that growth in length is not occurring between survey and catch.

Variable mortality

As mentioned in the previous paragraph about growth, the validity of these results hinges on the catch being a representative sample of those capelin which 'chose' to migrate so that we can identify which surveyed fish make the migration. A potential barrier to that being the case is if the migrating population experiences variable size based mortality, since this would lead to bias in the catch results. Likewise if mortality is not selective based on size but varies throughout the migration season by time or by location, then this may also create a bias in the results since capelin do not all spawn simultaneously, and spawning will take place over a number of months and potentially a wide area(Gjøsæter, 1998). If, for example, the timing of the migration is influenced by individual size as has been studied in Norwegian spring spawning herring(Slotte, 1998), then movement and variable feeding rates of predators throughout the season would create a selective element. The main predator of capelin is cod, and we know from winter survey reports that the distribution is variable during the capelin spawning migration south (figures 22 and 23). It also seems that the distribution of cod in the summer-autumn may be moving further north east, bring it into closer overlap with the capelin population during this time(Howell and Filin, 2013) so perhaps mortality at the hands of cod will provide increasing selective pressure over time.

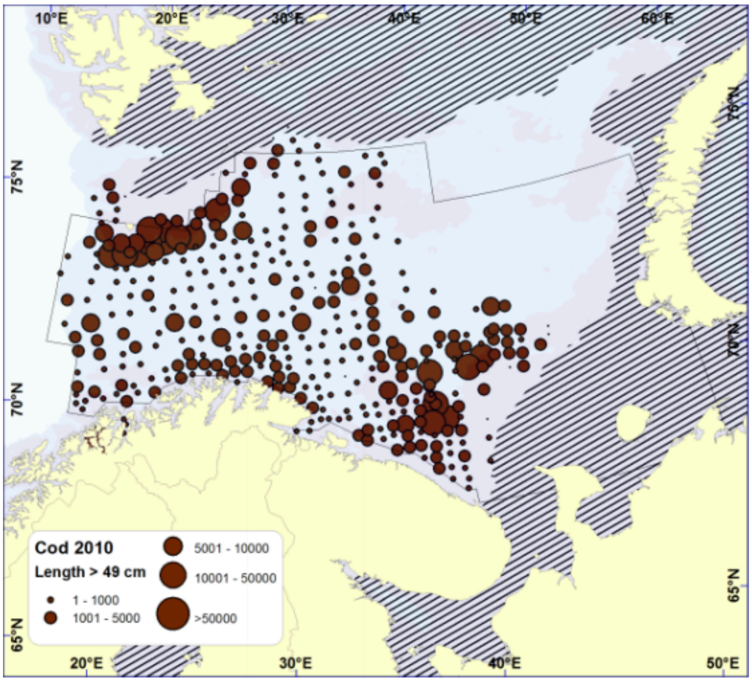

Figure 22: Cod ≥ 50 cm. Distribution in valid bottom trawl catches winter 2010 (number per nm2) from (ref). Hatched lines are ice coverage. Dots of different sizes represent the number of fish per nm^2.

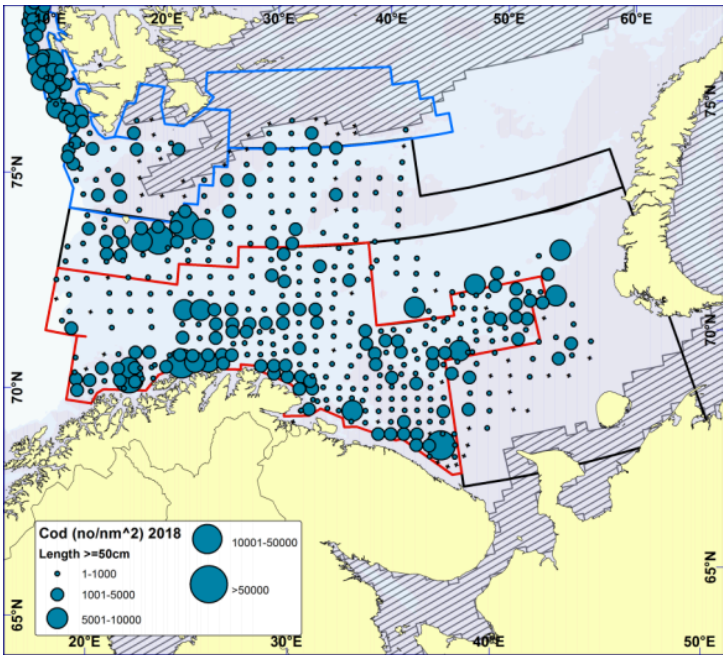

Figure 23: Cod ≥ 50 cm. Distribution in valid bottom trawl catches winter 2018 (number per nm2) from (ref). Hatched lines are ice coverage. Dots of different sizes represent the number of fish per nm^2.

We can see that the pressure faced by the migrating capelin population would differ both in strength and geographically between 2010 and 2018. In 2018 there are a larger number of 50cm+ cod along the Norwegian coastline and to the west, whilst in 2010 there are more slightly further out into the Barents Sea from the Kara coast on the east. The ice coverage is also very different. It is possible that capelin used the west coast for spawning in neither year, 1 year, or both years, and the consequences to my results of this changing predation pressure, combined with variable migration routes and spawning sites, are not quantifiable. It is safe to assume that a cod of 50cm+ can feed on any size of capelin, and therefore assume (but with less certainty) that size selectivity is not such an issue in this time (although during the autumn it would seem that cod are favouring smaller individuals (Bogstad and Gjøsæter, 2001)). Much research has been done into the predation of maturing capelin by immature cod during the migration (e.g. (Gjøsæter, 1998; Huse *et al.*, 2004; Johannesen and Lindstrøm, 2009; Gjøsæter *et al.*, 2015)), as this information forms a key part of the calculation of the spawning stock biomass and therefore the management advice, but unfortunately the level of uncertainty it implies in my results is unclear.

Autumn fishery

Up until the collapse of 1994-1998 there was an autumn fishery. Typically capelin of 13-16cm in length form the majority of the catch. The effect of fishing large numbers in this length bracket from September to November, on the length distribution seen in the catches in the spring is unknown. However, if the assumption of growth stopping from this point onwards holds then the effect may be to remove some fish from this year's spawning stock, and some from next year's. The number removed from this year will be low in comparison to the total number setting off on the migration (as the majority of the catch is taken from extremely abundant length classes), and the number removed from next year will be low as they would have undergone an entire year of natural mortality during which a large number would have died anyway. This is not a quantitative assessment of potential bias but when comparing 1999 onwards with 1993 and earlier, there is no perceptible change in length distribution that one would expect if the autumn fishery was having an appreciable effect. The fact that the autumn fishery was operating simultaneously with the survey is not ideal, but again there do not seem to be obvious changes in the survey length distributions post 1993.

Where do we go from here?

If I could prioritise one piece of future work to be done in order to further develop and build on what I have done within this project it would be to carry out a scientific assessment of the spawning stock over a number of years. It surprises me that for decades we have been working to predict it and yet have not verified our predictions evidentially, and I do not believe that helps the potentially negative image that some in the fishing industry may have of scientists.

In 2005 and 2007-2009 a series of reports were created to look into the possibility of making abundance assessments of the spawning stock in future, which could then inform quotas. The abundance estimates were affected by factors such as lack of access to the Russian EEZ and the need to carry out other investigations such as verification of target strength at the spawning grounds (Eriksen *et al.*, 2008, 2009), but overall the conclusions were positive about the possibility to make real time assessments of the migration. These investigations were carried out on board commercial vessels, which I believe is something that we should be exploring more in the future. Modern commercial vessels possess all the necessary technology to gather vast amounts of scientific data that could be potentially useful, and cooperation between scientist and fisher could create better management advice and harmony.

With modern technology we are in a better position than ever to make an assessment of the spawning stock. Maybe it is just a case of thinking a little bit outside the conventional box. For example deploying remote sonar buoys in order to at least get a feel for the scale of the overall migration over time, or to direct research vessels for much more specific surveying of the schools without wasting time and effort surveying all the empty ocean in between. Since capelin seem to approach the spawning ground demersally before forming schools as they mature (Eriksen *et al.*, 2009), and the migration is variable temporally, spatially, and in swimming speed (Eriksen *et al.*, 2008) conventional surveying becomes difficult, and the use of commercial vessels seems preferable. Perhaps with the use of sonar and more focussed and rapid surveying we would even be able to move towards an Icelandic model of harvest control (survey the stock multiple times, releasing the quota in two separate stages), which they are able to employ thanks to a compliant capelin stock (Olafsdottir and Rose, 2013), helpful bathymetry, currents, and the meeting of Atlantic and Arctic water masses (Vilhjálmsson, 2002; Olafsdottir and Rose, 2012), and is intuitively preferable to the longer term forecasts used in the Barents Sea. This was suggested by (Eriksen *et al.*, 2009) as a potential future path the Barents Sea capelin management could take.

Possibly the simplest route to get more data about the spawning migration and stock is through exploiting the IMR winter cruise which operates at this time. Currently this cruise focusses primarily on cod and haddock, so employs almost entirely demersal trawls. The number of pelagic trawls is too low to make an assessment of whether the capelin caught are being caught demersally or as the net travels through the water column (WINTER CRUISE 2015), and because pelagic capelin are not sampled we cannot use echo abundance to make length/weight/age distributions. It would be very useful to use more pelagic target trawls during the cruise to start making assessments of the population from February to March.

Our current management strategy relies on a good assessment of the stock in the autumn (more or less not a problem), an estimation of the maturity curve (definite problems, our estimation is based on very little literature, largely from the 1980s, and if we are even wrong by 1cm the difference in biomass will be tremendous), and natural mortality (always notoriously difficult to get a good firm grip on (Gjøsæter, Bogstad and Tjelmeland, 2002; Gjøsæter *et al.*, 2015)). I believe that the maturity can be better understood through further investigation.

The notion of the 14cm cut off has been around for a long time, and I think there is a danger that is has become a dogma, rather than having its efficacy tested regularly. An example of this comes from (Baulier, Heino and Gjøsæter, 2012) who looked into maturation. They found that the length over which 25% maturity becomes 75% maturity was ‘less than 2cm on average’. It is not posed explicitly as if this is a narrow length window, however it does come across that way to a reader who has not looked into capelin length distributions. In fact a 2cm distance between L_{p25} and L_{p75} would produce reductions in biomass the likes of which are seen in figure 20. Despite this finding there is no adjustment or further discussion triggered about how we should treat maturity in our spawning stock estimations.

During the survey in autumn many capelin are assessed for maturity stage on the macroscopic level (stages 1-5). It would seem logical to start using this data to make estimations. However it is not always clear how the macroscopic scale relates to the microscopic (Baulier, Heino and Gjøsæter, 2012), and even when using the microscopic scale it is not known exactly when we can be sure a capelin will spawn, be that early, late, or not at all (Forberg, 1982, 1983). So it would seem that using models based on other more easily determined factors would be beneficial, although I would not advocate attempting to incorporate every possible variable.

To conclude

(Gjøsæter *et al.*, 2015) makes the point that due to underestimation of the historic cod stock, upon reanalysis of capelin mortality with corrected cod stock (vpa analysis no longer causing changing values) our estimates of the capelin spawning stock have been consistently too high. I would put forward that once again we may need to re-evaluate what we believe, and dial our optimism back another notch, and my evidence for doing so is that ‘Tiresias’ seems to outperform our current model, and results in a reduction in biomass. This is not necessarily to say that I believe we are overfishing. Rather that we may need to revise our desire for a 200,000 tonne biomass of spawners, as it increasingly seems quite high. (ICES, 2004) recommended a B_{lim} based on the estimated median spawning stock biomass of 1989, which produced a strong year class, and was only 96,000 tonnes. This estimate would be even lower using ‘Tiresias’ to identify the maturing component, and possibly lower still depending on whether the cod stock and natural mortality was correctly estimated during that time. In light of this I would recommend that we also review our management strategy and the level of the B_{lim}.

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Appendices

Appendix I

The old style of intercalibration involves two or three vessels steaming in formation (10° angle from the midline of the lead vessel and 0.5nm behind, see fig. 24, or alternatively side by side with 0.3nm distance between) for enough time for a comparison to then be made of the echo recordings (made at 38kHz) via linear regression, and models can then be applied to standardise output. When intercalibrating in this way, the sea is stratified by depth, and these strata are called channels, for example 13-50m, 50-100m, 200-300m, and a bottom channel. During intercalibrations, each channel is scrutinised separately as there may be differences between the respective 13-50m channels, for example, whilst recording 1:1 readings in the others. Barriers to intercalibration in this manner can be bad weather, technical malfunction or fish readings that are too dense to serve as useful comparisons between vessels, however usually if an intercalibration fails it is attempted again at a later date. There are a few occasions where intercalibration has proved impossible or has registered radically different results between vessels, and in these situations the acoustic data from all vessels cannot be used.

Since the vessels are steaming at a slight distance there will invariably be some readings that are simply different due to surveying different fish/plankton concentrations. These are identified when the recordings are scrutinised side by side and removed from the analysis. The formation is designed such that the chance of hitting the same concentrations of organisms is maximised via the relatively short distance at which one vessel trails the other, but with sufficient distance and angular separation that the first vessel should not scatter the subjects, significantly biasing the output of the trailing vessel.

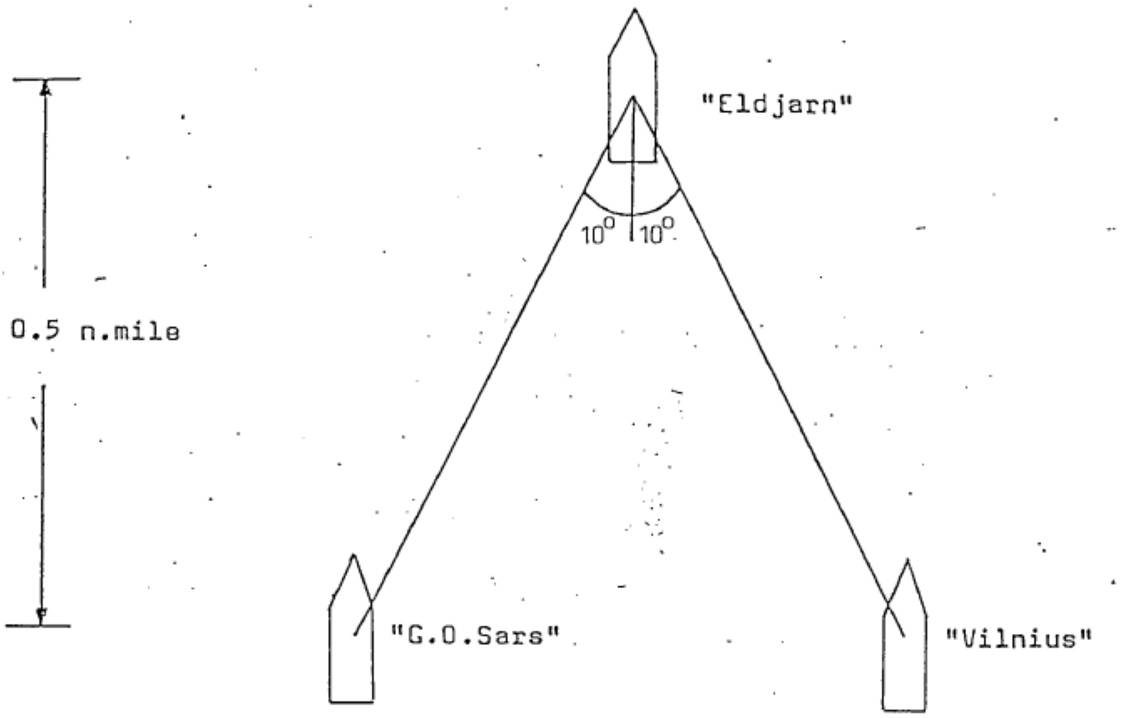

Figure 24: A diagram of the steaming formation during intercalibration between 3 vessels in 1986. More normally only 2 vessels would be involved, in which case the third would be removed from this formation. The trailing vessels are each around 920m behind and 160m horizontally offset from the lead vessel. At a typical cruising speed of 12 knots there will be around 2.5 minutes between the lead and trailing vessels.

It has been common for Russian vessels to display higher backscattering values in the uppermost channel, which seems likely to be due to only the Norwegian vessels being fitted with transducers mounted on adjustable drop keels that can be lowered in bad weather, removing the problem of excess disturbance and bubbles at the surface causing interference and erroneous readings.

Appendix II

```
sumrowall.df <- mutate(mod2Survey2, sums = x6 + x6.5 + x7 + x8 + x8.5 + x9 + x9.5 + x10
+ x10.5 + x11 + x11.5 + x12 + x12.5 + x13 + x13.5 + x14 + x14.5 + x15 + x15.5 + x16 +
x16.5 + x17 + x17.5 + x18 + x18.5 + x19 + x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 1)
sumrow13.df <- mutate(mod2Survey2, sums = x13 + x13.5 + x14 + x14.5 + x15 + x15.5 +
x16 + x16.5 + x17 + x17.5 + x18 + x18.5 + x19 + x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 2)
```

```
sumrow14.df <- mutate(mod2Survey2, sums = x14 + x14.5 + x15 + x15.5 + x16 + x16.5 +
x17 + x17.5 + x18 + x18.5 + x19 + x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 3)
sumrow15.df <- mutate(mod2Survey2, sums = x15 + x15.5 + x16 + x16.5 + x17 + x17.5 +
x18 + x18.5 + x19 + x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 4)
sumrow145.df <- mutate(mod2Survey2, sums = x14.5 + x15 + x15.5 + x16 + x16.5 + x17 +
x17.5 + x18 + x18.5 + x19 + x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 5)
sumrowgradual.df <- mutate(mod2Survey2, sums = (x13*0.05) + (x13.5*0.1) + (x14*0.5) +
(x14.5*0.8) + (x15*0.9) + (x15.5*0.95) + x16 + x16.5 + x17 + x17.5 + x18 + x18.5 + x19 +
x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 6)
sumrowgradual2.df <- mutate(mod2Survey2, sums = (x13*0.05) + (x13.5*0.1) + (x14*0.35)
+ (x14.5*0.75) + (x15*0.85) + (x15.5*0.9) + (x16*0.95) + (x16.5*0.99) + x17 + x17.5 + x18
+ x18.5 + x19 + x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 7)
sumrowgradual3.df <- mutate(mod2Survey2, sums = (x13.5*0.05) + (x14*0.2) + (x14.5*0.5)
+ (x15*0.7) + (x15.5*0.85) + (x16*0.95) + (x16.5*0.99) + x17 + x17.5 + x18 + x18.5 + x19
+ x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 8)
sumrowgradual4.df <- mutate(mod2Survey2, sums = (x13.5*0.05) + (x14*0.15) +
(x14.5*0.3) + (x15*0.6) + (x15.5*0.85) + (x16*0.95) + (x16.5*0.99) + x17 + x17.5 + x18 +
x18.5 + x19 + x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 9)
sumrowgradual5.df <- mutate(mod2Survey2, sums = (x14*0.1) + (x14.5*0.2) + (x15*0.45) +
(x15.5*0.7) + (x16*0.8) + (x16.5*0.85) + (x17*0.9) + (x17.5*0.95) + (x18*0.99) + x18.5 +
x19 + x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 10)
sumrowgradual6.df <- mutate(mod2Survey2, sums = (x14*0.05) + (x14.5*0.15) +
(x15*0.35) + (x15.5*0.6) + (x16*0.7) + (x16.5*0.8) + (x17*0.85) + (x17.5*0.9) + (x18*0.95)
+ (x18.5*0.99) + x19 + x19.5 + x20 + x20.5 + x21 + x21.5)%>%
  add_column(model = 11)
```