Mastergradsoppgave

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Relationship between modelled drift of eggs and larvae and the geographical variation in recruitment of cod (*Gadus morhua*) and pollack (*Pollachius pollachius*) in Tvedestrandsfjorden

Høgskolen i Telemark
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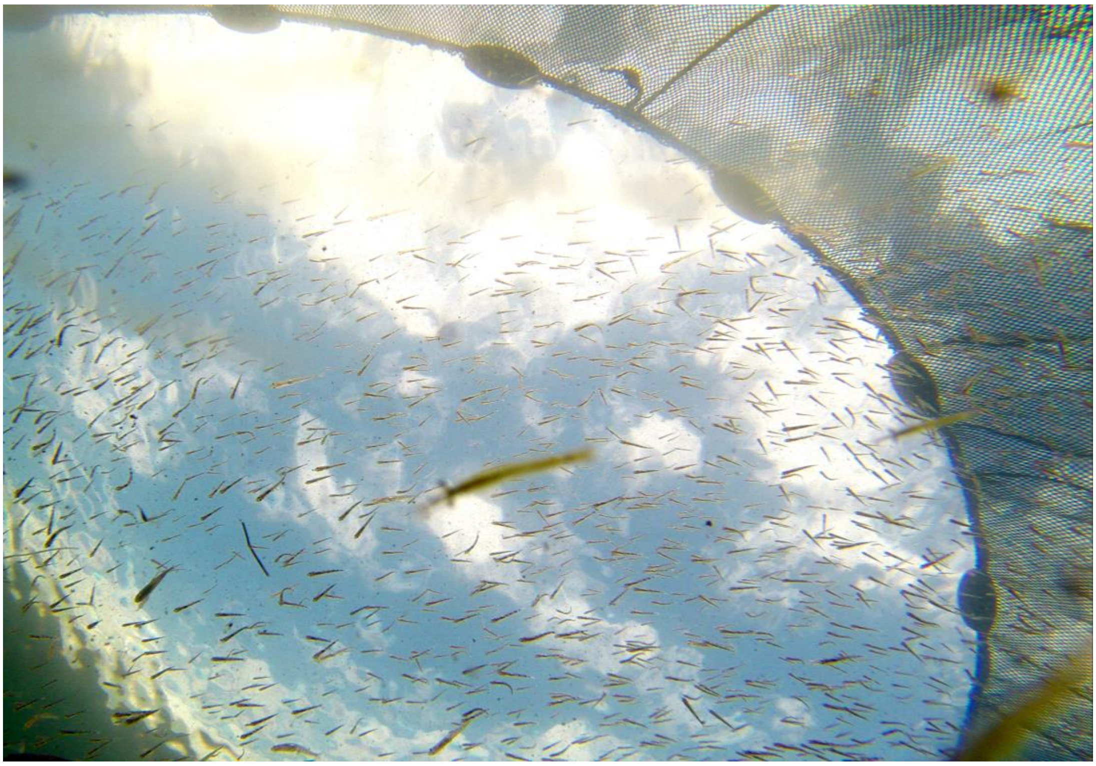

Photo: Espen Bierud (IMR)

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Sammendrag

Oseanografiske strømmodeller er mye brukt til og modellere partikkel drift i marine økosystemer. I vår studie er egg og larver fra torsk (*Gadus morhua*) og lyr (*Pollachius pollachius*) brukt som partikler i modellen for å evaluere om drift eller andre faktorer er avgjørende for den geografiske variasjonen i rekruttering i Tvedestrandsfjorden, en beskyttet fjord i Sør-Norge. Studien sammenligner den modellerte geografiske fordelingen av partikler etter drift med den målte geografiske fordelingen av nylig bunnslåtte 0-gruppe rekrutter (yngel). Egg ble samlet i gyteperioden (mars – april 2014) og den høyeste egg-tettheten var i den indre delen av fjorden, hvor modellen forutsa høy retensjon av partikler. Egg ble «sluppet» i drift modellen, basert på feltdata. Fordelingen av egg etter 30 dagers drift antydet høyest tetthet i det innerste området av Tvedestrandsfjorden og det innerste området av en tilknyttet fjordarm, Eikelandsfjorden. I løpet av en strandnot undersøkelse i Juni 2014, ble 3 0-gruppe torsk og 39 0-gruppe lyr fanget. Tettheten av lyr yngel var høyest i det indre området, det samme området som modellen antydet høyest tetthet av egg-partikler etter drift. Den modellerte egg-tettheten og andre faktorer som areal dekket av strandnot, flora type og dekningsgrad av flora hadde ikke en signifikant påvirkning på mengden lyr når de ble vurdert sammen i en generalisert lineær modell. Resultatene kan ikke konkludere om den oseanografiske modellen kan forklare den geografiske variasjonen i rekruttering eller ikke. Potensielle årsaker til den dårlige rekrutteringen av torsk i Tvedestrandsfjorden i 2014 er diskutert i oppgaven.

Abstract

Oceanographic current models are frequently used to predict particle drift in marine ecosystems. In our study, eggs and larvae of cod (*Gadus morhua*) and pollack (*Pollachius pollachius*) are used as particles in the model in order to evaluate if drift or other factors are decisive for spatial variation in recruitment in Tvedestrandsfjorden, a sheltered fjord in southern Norway. The study compares the modelled geographical drift distribution of particles with the measured geographical distribution of newly settled 0-group recruits. Eggs were collected in the spawning period (March – April 2014) and the highest egg-densities were found in the inner half of the fjord where the model predicted high retention of particles. Eggs were “released” in the drift model, based on our field data. The distribution after 30 days of drift suggested highest density in the innermost area of Tvedestrandsfjorden and the innermost area of a connected fjord arm, Eikelandsfjorden. During a beach seine survey in June 2014, 3 0-group cod and 39 0-group pollack individuals were caught. The density of juvenile pollack was highest in the innermost areas, the same area as the model predicted highest egg-particle densities after drift. Neither the modelled egg-density nor the factors area covered by the beach seine, flora type and coverage of flora were significantly affecting the amount of pollack when considered together in a generalized linear model. The results cannot conclude if the oceanographic model can explain the spatial variation in recruitment or not. Potential causes for the low recruitment of cod in Tvedestrandsfjorden in 2014 are discussed in the thesis.

Contents

Preface

This thesis completes my Master education at the Department of Environmental and Health Studies (INHM) at Telemark University College (TUC) in Bø. The thesis is within the field of Marine Biology and is a collaboration between TUC and the Institute of Marine Research (IMR) in Flødevigen (Arendal). Most of the work was conducted in Flødevigen. The fieldwork started in March 2014 and the thesis was finished in April 2015.

I would like to thank the staff at IMR, Flødevigen for their scientific and logistic support, and I am very grateful for getting the chance to cooperate with this institution. A special thank goes to my supervisor Sigurd Heiberg Espeland (IMR) for making this possible, giving me great feedback and sharing his knowledge. I will also thank Espen Lydersen and the counselors at INHM for all support.

Kristiansand, 08.05.15

Kristine Langenes

1 Introduction

1.1 Population management

Because of the mobility and distribution of many fish populations managing fish stocks on an international scale is important to maintain healthy populations and biodiversity. As the fishing industry is of great importance along the coast of Norway, this industry is very dependent on high natural production sustainability, and biodiversity, also at long term scale. This requires careful management and conservation of whole ecosystems (Dahl et al., 2007). Commercially important fish species like the gadoids cod (*Gadus morhua*) and herring (*Clupea harengus*) have been focused on and monitored for many years, and harvesting regulations have existed for many years to avoid overfishing (ICES, 2014c). Species without commercial value have been given little attention even though all species have functional roles in the ecosystem and might be a commercial resource in the future. An example of species that suddenly caught attention is the wrasse (Labridae), as several species within this family are used as cleaner fish to remove salmon lice (*Lepeophtheirus salmonis*) from farmed Atlantic salmon (*Salmo salar)* (Bjordal, 1991; Darwall et al., 1992; Skiftesvik et al., 2014). Managing this new fishery in a sustainable way without any ecological knowledge on these species is difficult, and overfishing quickly becomes a threat (Espeland et al., 2010).

Knowledge about essential recruitment factors in fish stocks is important when trying to understand population dynamics as fluctuating population sizes. Successful recruitment, or good recruitment, often means that numbers of individuals produced are high enough to tolerate a sustainable anthropogenic harvesting. It is well documented that cohorts and thereby recruitment may show large year-to-year variations, due to factor as spawning success, survival rate from egg to larvae to young fish, food availability, predation and environmental factors are often key parameters (Jakobsen T, 2009). Forecasting the recruitment success is an important scientific issue when trying to estimate the future stock biomass and assess potential needs for conservation measures. It is extremely hard to predict recruitment estimates, and bad years are difficult to forecast. The landings, fish stock conditions (age and size), environmental factors (climate change and pollution pressures) must also be considered when preparing management advices (ICES, 2014c). The cod stock in Skagerrak (ICES subdivision IIIa) is managed as a separate unit of North Sea cod, and includes both cod from Denmark and fjord habitats along the Swedish and Norwegian coast (ICES, 2014a). The spawning stock biomass (SSB) and the recruitment have been close to its lowest the latest years (fig 1). Overfishing, availability of food, predation and cannibalism has been pointed to as the most important factors(ICES, 2014b). Thus, advice is given about stronger harvesting regulations with an aim of increasing the stock biomass in a long-term rebuilding plan. As mentioned above, the cod in the fjords (fjord cod) are not managed separately, but together with the offshore (pelagic) population, even though the fjord cod are biologically not part of the offshore Skagerrak/North Sea population. The local fjord populations still suffers the same faith and follows a rebuilding plan and are in great need of conservation. Measures like minimum legal size and gear restrictions have been taken for years (Forskrift om utøvelse av fisket i sjøen, 2005), but the Skagerrak fjord cod populations is still close to its lowest level. Recreational fishing counts for a great amount of the catch on fjord cod, especially close to the cities, and managing the recreational fishing is very challenging (ICES, 2014b).

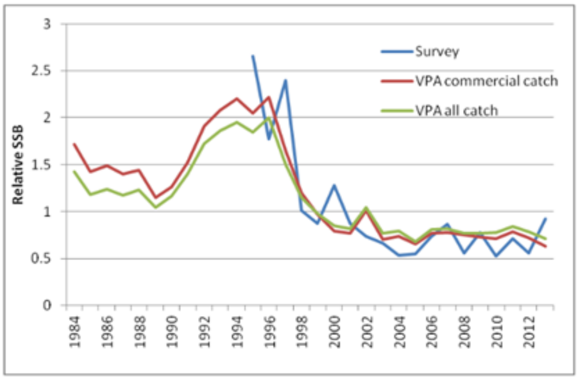

Figure 1 *The trends in coastal cod spawning stock biomass (SSB). Each series are shown relative to its 1995-2013 average. The survey SSB is calculated with the same maturity ogive as in the VPA.*

The cod have been thoroughly monitored over many years, but the first ICES advice on the pollack (*Pollachius pollachius*) stock was in 2011. The biomass of the stock cannot be estimated or monitored by the regular trawl surveys nowadays because of very low abundance, which means that the advice on pollack are based on very limited data. The advice given suggest that there should be no fishery or bycatch in the Skagerrak region the next years (ICES, 2014d). The advice is based on a reconstructed a hundred year long time series on the stock with data from trawl surveys (Cardinale et al., 2012). This time series showed a clear decline in the adult biomass and length of pollack after the peak of landings in 1960s, which suggest that overfishing is the likely cause. The landings of pollack in Skagerrak have been very low ever since, and pollack is not a target for fisheries nowadays. There is still about 2000 tons of pollack caught each years, mainly as bycatch, in the coastal areas of Skagerrak. The amount caught by recreational fishing is unknown (ICES, 2012).

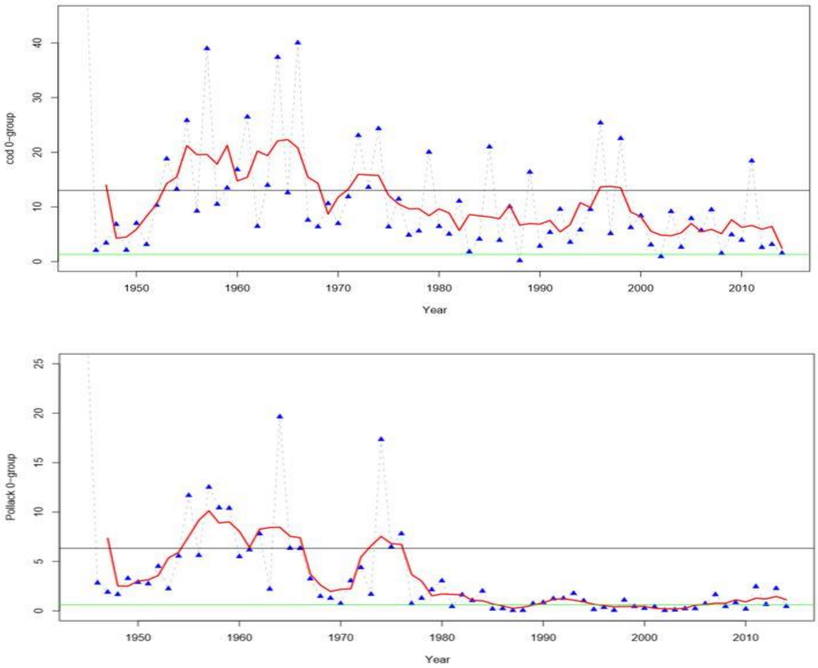

Figure 2 *The amount of 0- group cod (upper graph) and pollack (lowest graph) from a long beach seine series conducted along the Skagerrak coast by the Institute of Marine Research (IMR). The blue points are the average number of individuals based on all hauls in Skagerrak a given year. The red line is a floating 5-year average, the horizontal black line is the long-term average (based on the blue points). The green line illustrates 10% of the long-term average.*

Data from almost a century long beach seine series conducted along the Skagerrak coast show the same trends as the trawl surveys used by ICES. This time series monitors the young stages of several gadoid species present at shallow depths along the shore, and is a good tool for showing time trends. Several local populations of gadoids have collapsed during the last century and have not been able to recover. Shifts in available prey items may be a cause of the collapses, and the shifts in prey abundance may be linked to increase in eutrophication and pollution (Johannessen, 2014). This demonstrates the complexity of an ecosystem. The abundance of 0- group cod and pollack along the Skagerrak coast line is now at extremely low levels compared to earlier days (fig 2) (Espeland and Knutsen, 2014). This enhances the need of effective conservation measures so the populations can recover before it is too late.

1.2 Biology

The Skagerrak coastal cod populations seems to be separated into smaller subpopulations with unique genetic compositions (Jorde et al., 2007). The populations are limited to small geographic areas (often one fjord), and migrate very little despite their ability to migrate over large distances (Espeland et al., 2008). Retention of young stages in addition to limited movement or homing behavior of adults are the likely reason why this genetic diversity among populations appears (Knutsen et al., 2007; Knutsen et al., 2011). In the case of fjord cod, the oceanographic conditions favor retention, and creates a barrier that makes advection of eggs and larvae into the fjord an unlikely event. This means that repopulating the fjords if a population is extinct can only happen if enough adult cod migrate in to the fjord to spawn (Myksvoll et al., 2013). Cod along the Skagerrak coast seems to have local variation in life history traits like age at maturity in addition to the genetic diversity (Olsen et al., 2004). Extinction of a fjord population will cause a loss of unique genes that probably have traits better adapted to that specific fjord environment, compared to other populations of cod. In addition to fishing restrictions, a step on the way to conserving the fjord cod is by mapping the areas they use during their most vulnerable life stages. The Norwegian Environmental Agency has a mapping program that includes mapping the cods spawning sites and important nursery habitats like eelgrass (*Zostera marina)* beds. This information can be used to avoid anthropogenic destruction of the areas or restrict the activity during the most vulnerable periods of the year (Direktoratet for Naturforvaltning, 2007).

Knowledge on the pollack population and biology is very limited. Heino et al. (2012) suggested that pollack may have closed populations in the fjords of Norway, like the fjord cod. A study of the genetic structure of pollack on a large scale do not fully support the “closed” population hypothesis. Charrier et al. (2006) found very limited genetic differentiation across the European coastal waters. It is commonly stated in the literature that the pollack favor more exposed areas than fjord cod (Fromentin et al., 1997) and seems to migrate from the coastal areas to offshore and deeper areas when they turn three year old (Cohen et al., 1990). To which extent these statements are empirically tested is uncertain.

Cod and pollack spawn pelagic during spring and the interactions between physical and biological factors determine the geographical distribution and abundance of the young ones. The properties of their eggs are of great importance when determining where the eggs drift with the currents. The eggs vertical distribution in the water column affects whether the eggs are target of local retention or disperse over large areas. Cod eggs can according to Russel (1976), adjust their buoyancy to gravity and mechanical forces (waves, currents etc.). The buoyancy are affected by salinity and the specific gravity of the egg increase with development (Russel, 1976). Ciannelli et al. (2010) found that the coastal cod eggs were neutrally buoyant at shallow depths in Tvedestrandsfjorden in southern Norway. This trait place the eggs in the water layer moving up the fjord to a sheltered area with less current and water exchange. Their results suggest that the properties of the egg in addition to the local ocean currents are of great importance for the population structure. Retention of eggs is high in fjords with shallow sills, like many of the fjords along the Skagerrak coast (Knutsen et. al, 2007). Experiments performed by Stenevik et al. (2008) confirmed that eggs in many areas along the Norwegian coast are placed in subsurface water layers where local retention is higher than at the surface. The wind patterns along the coast also affects the currents in the fjords, and Asplin et al. (1999) suggested that the coastal cods timing of spawning, depth and buoyancy of eggs have evolved to reduce dispersal and give young favorable nursery habitats. During the spring spawning the wind cause downwelling, which transport the cod eggs and larvae up the fjords. Study from the Gulf of Maine showed the same, larval retention and survival was most favorable when the wind caused downwelling, and the larval vertical migration at late stages enhanced the effect (Churchill et al., 2011). At southern latitudes, where timing of spawning is less dependent on temperature and season, they found that reef fish concentrate their main reproduction activity to periods when the wind and currents are weak enough to avoid dispersal of the egg and larvae (Abesamis and Russ, 2010).

The timing and geographical location of the spawning is of great importance for offspring survival, because it determines to some degree the habitat and availability of resources at later stages (Chambers and Trippel, 1997). The spawning period of cod in the North Sea ranges from February – April, and varies with water temperature (Russel, 1976). The pollack spawn from February - June across its distribution range and is observed to spawn from about 10°C in the wild, although no temperature range is documented (Bjornsson et al., 2010). Newer studies (from captivity) suggested a spawning period from February – march with successful spawning of pollack kept at 7.5 - 8°C (Wilson et al., 2014). Suquet et al. (2005) reported the spawning period in captivity to be March- May and found 12 °C to be close to the upper temperature limit, while spawning with water temperature of 8°C gave the most successful outcome. Another beneficial trait for successful recruitment is a common peak of reproductive activity for both sexes and that the males spawn longer than females. Alonso-fernandez et al. (2013) found this trait for pollack and Hutchings and Meyers (1993) reported the same for cod, in addition they concluded that older individuals of both sexes had a longer spawning period than young individuals. Older and bigger females produce more and bigger eggs, which enhance the chance of offspring survival (Hixon et al., 2014) and this maternal effect needs to be taken into consideration when managing vulnerable populations (Calduch-Verdiell et al., 2014). In addition to the favorable oceanographic conditions during spring, the timing is important when considering predation risk and availability of food resources. The match-mismatch hypothesis considers the food issue, and states that recruitment will be high when the peak abundance of prey occurs at the same time as the predator (Durant et al., 2007). The prey also need to be of the right size at the right time. A mismatch between predator and prey are likely to enhance negative effects of selective fishing (like the commercial cod-fishing) (Beaugrand et al., 2003). At high latitudes, the timing of the match- mismatch between the larval stage and its prey is of even greater importance. Kristiansen et al. (2011) stated that the duration of the overlap between larvae and prey is a key factor for survival and that warm years have the longest overlap period.

Duration of egg stage, larval stages, growth of larvae and juveniles is highly affected by water temperature (Pepin et al., 1997). The size of cod eggs is known to decline over the spawning season and amount of eggs spawned per batch is dome shaped (Bachan et al., 2012). A reason for this can be the decline in maternal reserves for use in egg production (Kjesbu et al., 1991). Duration of cod egg stage from fertilization to hatching varies from about 20 days in 4°C to 10 days in 10°C, 12°C is thought to be around their upper limit and the optimal temperature is about 6°C (varying a bit with salinity) (Russel, 1976). Pollack in captivity had an egg stage lasting from 6 to 7 days around their optimal temperature of 10°C. Newly hatched pollack larvae in the study of Suquet et al. (1996) was around 3 mm which is around one millimeter smaller than newly hatched cod. Russel (1976) suggested that the cod larvae is able to migrate vertically after only a few days, being positively phototactic in moderate light. A more recent study from on the Georges Bank show that cod larvae is found in the subsurface water layer and start migrating at a size of 6-7 mm, going deeper at daytime. The range of the diel vertical migration increase with larval size, they become pelagic juveniles (>20 mm) and start associating with the bottom at about 40 mm. The juvenile cod use about 1-2 months on the change from pelagic to demersal lifestyle (Lough and Potter, 1993). Information about settlement and behavior of pollack larvae and juveniles are limited.

1.3 Goal of the study

The recruitment success of pelagic spawning fish and the geographical distribution of the species are greatly affected by oceanographic conditions, which vary some from year to year. The local currents and stratification of the water column are influenced by freshwater input, wind and the large ocean currents. In fjords the general circulation pattern is an outflowing surface layer, which vary in thickness and an inflowing subsurface layer with higher salinity than the layer above (Dahl et al., 2007).

Oceanographic current models are widely used for simulating particle drift along the coast and in the fjords. The models are limited in space and time, and use a wide range of information to simulate oceanography as close to reality as possible. These models are often used to simulate drift of fish eggs and larvae. The models match quite well with field observations of currents and hydrography, but the results from modelling drift of fish eggs and larvae are rarely tested against field studies (Espeland et al., 2013). Furthermore, there are many other factors influencing settlement and survival of recruits each year, meaning that the current pattern is not the only essential factor determining the faith of the fish. Testing the actual route of drift is very challenging, because it is hard to mark and track the egg and larvae. The number of eggs and natural mortality is extremely high in gadoids.

The goal of the study is to test the relationship between the predicted geographical distribution of eggs and larvae after drift, with the geographical distribution of newly settled offspring. This will mainly test whether the drift of eggs and larvae or spatial variation mortality factors are the strongest predictor of small scaled geographical (one fjord) variation in recruitment. The study will compare amount of eggs found in spawning areas with estimations of drift based on an oceanographic model and amount of newly settled recruits from a beach seine survey. The results can be useful for local and national management and conservation, by identifying important areas and traits in the life history of the cod and pollack.

2 Materials and methods

2.1 Study area, Tvedestrandsfjorden

Tvedestrandsfjorden is located in the municipality Tvedestrand on the southern coast of Norway (fig 3), with connection to the Skagerrak Sea and the city of Tvedestrand is located in the bottom of the fjord. Tvedestrandsfjorden is a 8 km long fjord, with several sills and basins. The inner basin is the deepest with depths down to 85 m and it is separated from the outer basin (Oksefjorden) with a sill of 15 m depth and the island Furøya. The outer basin reach down to 65 m. Specially the inner part of the fjord has low oxygen levels and quite high loads of organic contaminants, in particular PCB and TBT (Kroglund et al., 2003). The winds along the coast outside the fjord affect the current pattern. Winds blowing from the northeast cause the surface water to flow in the fjord, causing out-fjord flow in the lower water layers, while the reverse flow pattern occurs with winds from southwest. This affects the retention of cod eggs and larvae (Ciannelli et al. 2010). A large part of the investigated area is a marine protected area (MPA), meaning that the fishery activity is restricted by law. All fishing is prohibited in one part of the fjord, the no-catch zone, while other zones allow some fishing activity (Forskrift om bevaringssoner i Tvedestrand, 2012).

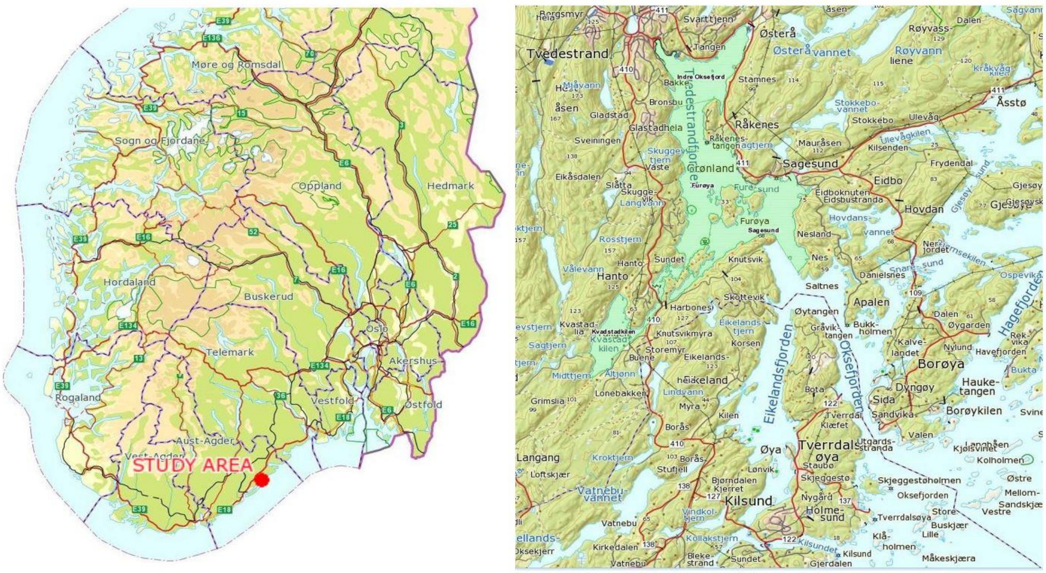

__Figure 3__ The study area, Tvedestrand, is located along the southern coast of Norway, shown here with a red point (left panel). A more detailed map of Tvedestrandsfjorden is

shown at the right panel, the green shaded area is the marine protective area (MPA) with regulations regarding harvest and fishing (map from: http://kart.fiskeridir.no/)

2.2 Species description

The coastal cod (*Gadus morhua*) and Pollack (*Pollachius pollachius*) is target species in this study because of their biology and need of conservation. Information about their populations and reproductive biology is mainly in the introduction.

Cod and pollack share many features, including being in the family "gadidae" which is a part of the order codfishes. They often share the same habitat and are common in Norwegian waters. Pollack and cod also compete for the same resources and can prey on each other and themselves (Jonsson, 2000). The life stages of interest in this study were mainly the eggs and newly settled 0- group juveniles. Cod eggs in the North sea have an expected size range between 1.16 - 1.60 mm while the eggs of pollack are in the narrow range of 1.10 – 1.22 mm in diameter (Russel, 1976). The early egg stages have no unique visual characteristics and can only be identified by size measurement. The overlapping diameter range makes species identification difficult, and makes genetic identification the only certain way of discriminating eggs with overlapping size. The juveniles and adults are easily recognized visually, they both have strong under-bite, pollack are silver colored with a distinctly crocked lateral line (fig 4) and cod have a brownish pattern and "beard" under its chin (Moen and Svendsen, 2004).

Figure 4 *Spawning pollack female in June 2014 in Tvedestrandsfjorden. Photo: Even Moland (IMR)*

2.3 Data collection

2.3.1 Plankton net hauls

Plankton net hauls to estimate the density and distribution of pelagic fish eggs were performed at 11 selected stations representatively covering the assumed spawning areas from the bottom of the fjord to the outer area (fig 5). Sampling was conducted on 15.03.14, 31.03.14 and 11.04.14. The spatial densities of eggs give information about the geographical extent of the spawningareas in the fjord. A motorized boat was used for transportation and as a working platform. The boat had a handheld Garmin 76 Cx GPS, used to mark and located the stations. One plankton net haul was taken at each station from 30 m of rope, which means that the depth sampled from was slightly varying because of the currents taking the net slightly sideways at some locations. At the innermost station, all samples were taken from only 25 m of rope because the depth was only 28 m. The plankton net was a modified standard WP2 net with diameter of 56 cm opening, 500 µm mesh size, a cup in the bottom for collecting eggs and weights for it to sink effectively. The plankton net was pulled up with approximately 0.5 m/sec with help from an electric winch, to filter the water efficiently (Barnes, 1949). The samples were transferred from the cup at the bottom of the net and into a properly marked bottle through a funnel and the cup was rinsed with a squeeze bottle containing sea water. The samples were stored in a cooling bag onboard the boat and in a refrigerator in the laboratory. The samples were sorted in the laboratory straight after fieldwork (1-2 hours later) using a microscope, the eggs were transferred into a small container marked with station number. All the eggs were photographed through a microscope, before being put on ethanol (eggs shrink in ethanol). Afterwards the pictures were used for species determination by measuring the diameter of the eggs with a program called "Motic Images plus 2.0^{ML}". Eggs with diameter of 1.185 – 1.50 mm are determined to be cod while eggs of pollack are determined to be in the size rage of 1.10 – 1.185 mm. The reason why a clean cut between the size ranges were chosen in this study, was that an overlap of sizes (like in reality) would put around half the eggs in both categories. Distinguishing between the two species is not of great importance in this study, since all the egg-particles are given the same properties in the current model.

Figure 5 *The 11 different station where the plankton net hauls were performed in March and April 2014 was evenly distributed in the fjord (map from (2015): http://kart.fiskeridir.no/).*

2.3.2 Beach seine survey

Beach seine hauls were selected for the sampling due to the extensive use for catching young of the year recruits along the Skagerrak coast (Tveite, 1971, Lekve et al., 2002). This means that there is a large reference material for possible comparison and high level of experience on using the beach seine properly. The beach seine hauls were performed 19.06.14, 23.06.14 and 27.06.14 at in total 14 stations from the innermost basin to the outer skerries (Fig 6). Sampling stations were roughly selected as to represent both areas with predicted low and high densities of egg-particles after drift and represent the transect from the inner fjord basin to the outer skerries. The stations had a variety of bottom habitats and were chosen out in field based on the bottom habitat, depth and possibility to stand on land. The habitat was put in 3 categories after flora type (numbers from the field-data sheet); 1: eelgrass (*Zostera marina*), 2: Seaweed/kelp (macroalgae; members of red-, green- and brown alga) and 4: Eelgrass/seaweed/kelp. The degree of flora coverage at the bottom was also put in 3 different categories; 2: few plants, 4: many plants and 5: full coverage (table 1). Beach seine hauls cannot be conducted on all types of sea floor as the seine may get stuck on rough bottom. The reason why the time period was chosen was to avoid the mortality that occurs during summer, and hopefully hit the peak of settlement, the time when the young stages of cod and pollack are most abundant (Johannessen, 2014).

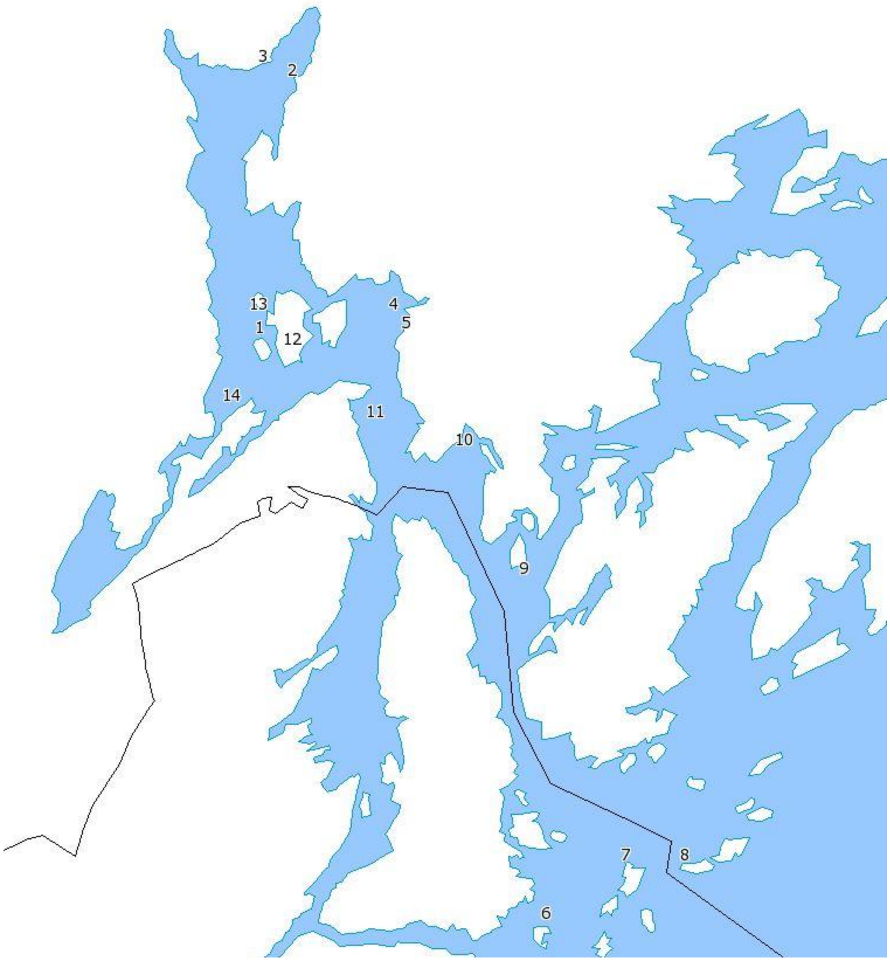

Figure 6 *The numbers equals the 14 beach seine stations sampled in field in June 2014 in Tvedestrandsfjorden (map from (2015): http://kart.fiskeridir.no/).*

The beach seine was 40 m long and 1.7 m high. In each end of the seine, there are two 30 m long ropes and the stretched mesh size is 10 mm. The area covered by 1 haul varied from 164 m^2 to 845 m^2 with an average of 540 m^2 (SD of 183 m^2) (fig 12 and 13). The depth varied between stations, ranged from 2 to 15 m, but most hauls were in the shallow end of the interval. A motorized boat was used for transportation and to deploy the seine in a semicircle from shore to shore. Two persons were pulling the beach seine with the ropes along the bottom and together as a bag with the catch in along the shoreline. One person was observing the beach seine from the boat and assisting if the beach seine was stuck. The whole catch was sorted and the species, number of individuals and size of up to approximately 20 randomly chosen individuals were noted before being released at the same location (video from fieldwork at: https://youtu.be/Amr1xMA1HBo, Havforskning, 2015). A handheld Garmin 76Cx GPS was used to mark the track of the seine, so the area covered could be estimated afterwards. The interval of the GPS position updates was set to 1 sec, the most frequent possible, to get a high precision for the track log. The start and end positions recorded were later compared to known map positions so to assure that the precision was more accurate than the +/- 10m regularly reported as minimum precision for the given GPS.

Table 1 *Overview of the different habitat and flora coverage at the 14 beach seine stations sampled in June 2014 in Tvedestrandsfjorden. Numbers in parenthesis equals the codes in the field data sheet and is used in other figures.*

Station	Habitat (flora)	Flora coverage
1	Eelgrass (1)	Full coverage (5)
2	Eelgrass/seaweed/kelp (4)	Few plants (2)
3	Eelgrass (1)	Full coverage (5)
4	Eelgrass (1)	Full coverage (5)
5	Seaweed/kelp (2)	Many plants (4)
6	Seaweed/kelp (2)	Full coverage (5)
7	Eelgrass/seaweed/kelp (4)	Many plants (4)
8	Eelgrass/seaweed/kelp (4)	Many plants (4)
9	Eelgrass (1)	Full coverage (5)
10	Eelgrass/seaweed/kelp (4)	Many plants (4)
11	Seaweed/kelp (2)	Full coverage (5)
12	Eelgrass/seaweed/kelp (4)	Few plants (2)
13	Eelgrass/seaweed/kelp (4)	Full coverage (5)
14	Eelgrass (1)	Full coverage (5)

2.4 Data analyses

2.4.1 Oceanographic models

Construction of oceanographic models and simulation drift of particles has evolved greatly with increased computer performance and now constitute an entire field of knowledge. Details of this process were deemed too complicated to perform within the scope of a master thesis and was conducted by oceanographer Jon Albretsen at IMR Flødevigen. The following paragraph gives a brief overview of the model concept.

The models were used to estimate the probable drift of eggs and larvae from their observed spawning sites. The hydrodynamic model applied was the Regional Ocean Modeling System (ROMS, 2014; Shchepetkin and McWIlliams, 2005). This model gives a time-variant estimate of the ocean's hydrography (salinity and temperature) and currents based on e.g. high-resolution bottom topography, atmospheric forcing, tides, offshore currents and hydrography and local river runoff (see more details from the comparable model system described in (Albretsen et al., 2011). An additional, Lagrangian model called "Ladim" was used to estimate the drift of the particles based on ocean current information from ROMS on a very fine scale (see (Espeland et al., 2013) for more details). The drift simulations were based on hourly currents calculated at a grid with 50 m horizontal resolution. The model was run with climatic conditions from 2013 and 2014, the 2014 current regime is used in most figures, while the 2013 current regime is used for comparison. Eggs and larvae in the model will hereby be called egg-particles or particles, while real egg will be referred to as eggs. Particles were released in a uniform geographical distribution throughout the entire fjord. To analyze specific situations, particles were selected in numbers in accordance with the relative number of eggs found at the different field stations, but they were scaled up by a factor of 40. The particles were released in the model on dates corresponding to the sampling dates in March and April. Additionally, some particles were released at locations without observed spawning activity to look at the drift from these areas in addition to the drift from the spawning sites. In reality eggs may drift vertically as well as horizontally, and the vertical movement is dependent on the density of the egg in relation to the water density. However very small errors in both egg-particle density and water density may lead to large vertical movement in the model, mostly resulting in the particles moving to the surface in the model. Several studies do find the eggs in waters well below the surface (Ciannelli et al., 2010) indicating that the current vertical precision of the models are too low. In this study egg-particles were fixed in the water layer they were released, not allowing for vertical movement. The particles were tracked in the model for 30 days and the position of each egg-particle was recorded at the end of every day. The particles released 11.04 were only allowed to drift for 20 days, because the model was limited to March and April. In the drift probability estimates it is assumed that those egg-particles is at the same position at day 30 as they were at day 20. The figures presented in the results only show the drift estimates from the cod and pollack egg data gathered 15.03, because of low abundance of eggs the other sampling dates. Particles could not be simulated to drift out of the model domain and eggs ending up at the model border at any time during drift were considered ‘lost to the open sea’ and removed from further particle movement simulation. The south eastern border of the model was the border where particles ended, and was located approximately 3 km off the coast. The number of particles leaving the model dependent on release location and depth was counted and taken as an indication of advection. The remaining particles that spend the entire 30 days period without hitting the model border was taken as an indication of retention.

2.4.2 Statistics

The program Microsoft Excel (2013 Ink) was used for plotting the raw field data and for making some of the figures in this study. The GPS data was downloaded using the Garmin specific software Mapsource (version 6.16.3, available from: http://www8.garmin.com/support/download_details.jsp?id=209) and exported as csv format. All data was imported as text (csv) files to R software (version 3.1.0) (R Development Core Team, 2014)) for statistical analysis and plotting most of the figures. Transformation of coordinates and spatial analysis was mainly performed using the libraries rgdal, spdep and splancs in R (Bivand and Piras, 2015). Coastal contours from “the Norwegian Mapping Authority” (Statens kartverk, 2014) was imported as easting and northing (UTM32). All other imported map information of the area was converted from WGS84 to UTM32. Most of the data presented are untreated, and show direct numbers.

To compensate natural variability in the circulation pattern that was not resolved by the current model, a random contribution was added to the particles velocity when simulating particle movement in “LADIM”. The random-walk corresponds to a small modification of the particles velocity each time step, a random velocity between -2 and +2 cm/s is added to the current model velocity. This means that a particle location at any time is a realization of a potential track, but not a deterministic endpoint at that time. To generalize from the particle positions the locations were transformed to a geographic probability distribution (Kernel distribution). This was done by substituting every particle location with a small density distribution and then summing all distributions for all particles. To do this the kernel smoothing function kernel2d of the splancs library in R was used, however the smoothing factor, or the width of the kernel, was chosen as the reference smoother (Worton, 1989) from the adhabitat package. The resulting probability distribution gives an estimate of the geographical distribution of the area most likely available as nursery for cod and pollack. The kernel distribution (hereby called density distribution) is chosen as an additional way of presenting the geographical distribution of particles after drift because it illustrates the density of particles in a good way and compensates for the uncertainty in the ending positions of each particle.

A generalized linear model function in R was used to look at the significance of habitat (flora), density of egg-particles after drift, cover of flora and area hauled (m^2) on the amount of juvenile pollack. This function counts cover and habitat as a categorical factor variable, and looks at the effect of these, area hauled and density of particles on the amount of pollack as in a linear regression model. The relationship was tested using the following formula:

$$P_i = \beta_0 + \beta_1 A_i + \beta_2 D_i + \beta_{Fi} + \beta_{ci} + \varepsilon_i \qquad \textbf{\textit{(Formula 1)}}$$

P_i is the number of pollack recruits in the i_{th} beach seine haul given as a function of area (A), density of particles after drift (D) from the density distribution (kernel), flora type (F) and flora cover (C) at the i_{th} beach seine haul location. β_0 is the study specific intercept. The effect of the area (A) of the i_{th} haul was mapped onto the response by the linear slope β_1. The effect of D (density of particles after drift) was mapped by the linear slope $\beta_{2.}$ The β_{Fi} and β_{ci} are respectively flora and cover specific offsets of the effect on the i_{th} haul. ε_i is a normally distributed independent error term for the i_{th} beach seine haul.

3 Results

3.1 Plankton net hauls

The size distribution of the eggs, collected with the plankton net, shows that the majority of the eggs were in the size range of 0.8 and 1.0 mm in diameter. Very few eggs above 1.1 mm in diameter were present after the 15.03 2014 (see fig 7). The total amount of eggs at the different dates were not varying much, highest number of eggs on 11.04 (918) and lowest number on 15.03 (807). The number of eggs in total increased with time, but the number of eggs between 1.1 and 1.5 mm in diameter (cod and pollack eggs) decreased (accounted for 19.7% of the eggs 15.03, 1.92% 31.03 and 0.65% 11.04). Since 15.03 was the only day with a fear fraction of the eggs belonging to cod (82 eggs in total) and pollack (77 eggs), this data was used in the particle drift modelling.

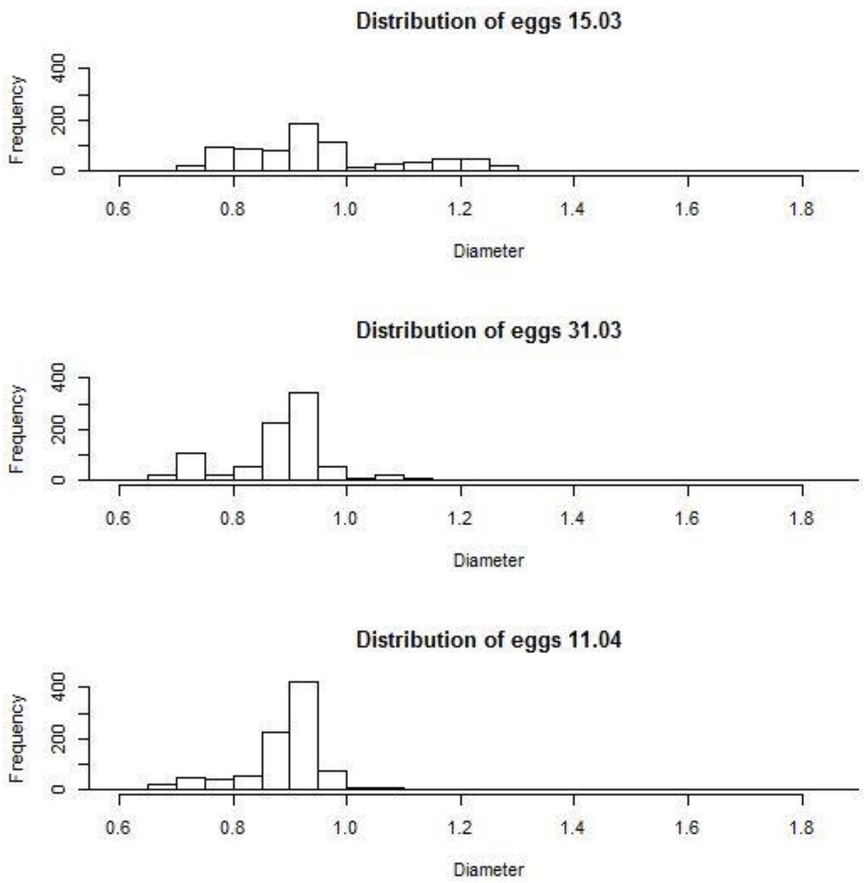

Figure 7 *Size distribution (diameter in mm) of the eggs caught in the plankton net hauls 15.03, 31.03 and 11.04 2014 in Tvedestrandsfjorden. The height of the bars indicate number of eggs in each diameter interval.*

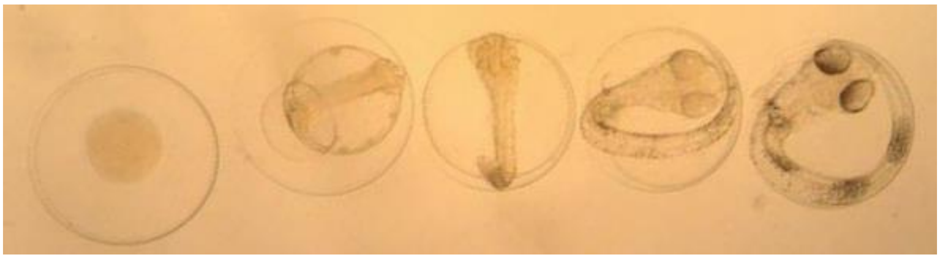

Figure 8 *Development stages of the cod egg from left being stage 1 to the right with the last stage before hatching, stage 5. Photo Hanne Sannæs, IMR.*

The eggs from 15.03.14 were mostly early stages (stage 1-3, see fig 8), the egg-data from this day is therefore useful when estimating the geographical extent of the spawning areas, as for a release location for the eggs in the oceanographic model. More developed stages were common later in the season, on 31.03 and 11.04. Very few eggs were at the latest stages, where it is possible to determine the species visually. Figure 8 was a template when evaluating the egg stages. Station 8 (the 11.04) was one of the few places where a late stage cod egg was collected, and some newly hatched larvae were found at station 11 at the 15.03 (see fig 9).

Figure 9 *The left picture show a late stage cod egg from station 8, 11.04 2014. The egg was measured to be 1.16 mm in diameter. The picture to the right show 2 cod larvae from station 11 the 15.03 2014*

The geographical distribution of the cod-, pollack eggs and the total number of eggs (all species, all 3 days) found in March and April 2014 is quite limited. It is clear that the majority of the eggs were at the stations in the inner part of the fjord, the area inside and around the island Furøya (fig 10). Station 4 had the highest number of eggs for both species (13 cod and 15 pollack), but station 1 had the highest number of pollack eggs (16) while cod eggs were most abundant at station

6 (14). The number of cod eggs 31.03 were 3 in total, while no cod eggs were present 11.04 (therefor no panel for this day in fig 10). The number of pollack eggs 31.03 was 14 in total and 6 the 11.04.

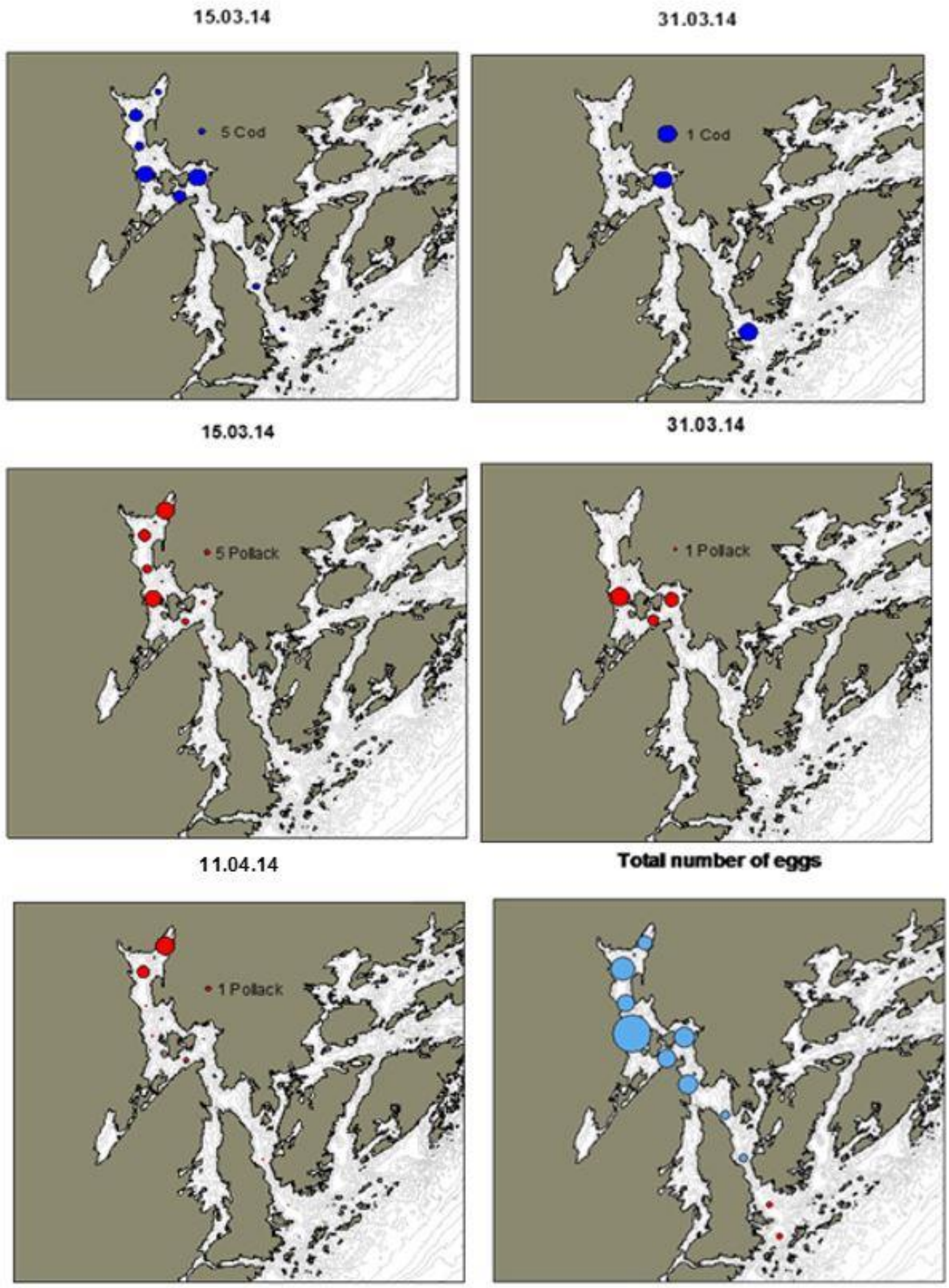

Figure 10 *The circles illustrates the geographical distribution of the eggs and are scaled according to the amount (with a reference circle) of eggs caught in Tvedestrandsfjorden 15.03, 31.03 (both cod and pollack) and 11.04 2014 (just pollack). The two upper panels illustrates the cod eggs (blue circle), the three next panels illustrates the pollack eggs (red circles). The bottom right panel show the geographical distribution of all the eggs caught all three days of fieldwork (all sizes, including cod and pollack).*

3.2 Beach seine survey

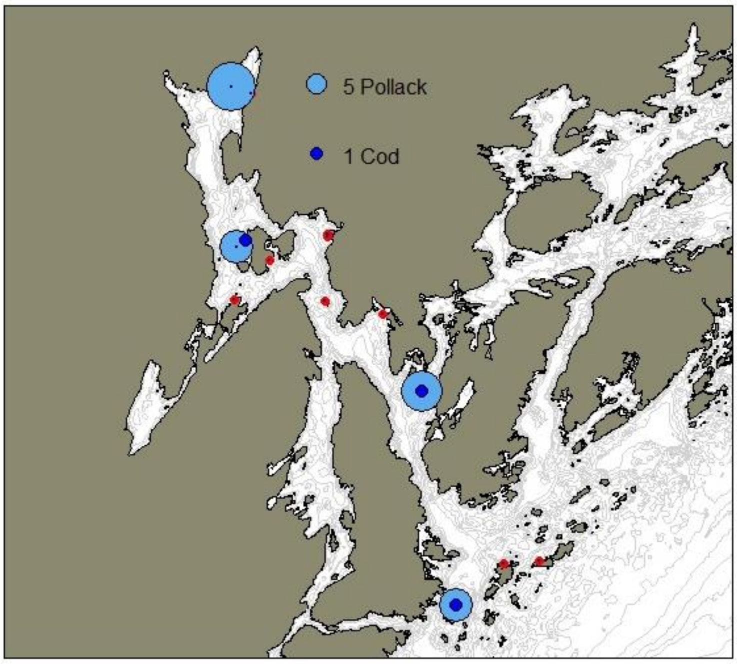

Figure 11 *Abundance and geographical distribution of 0-group cod (dark blue circles) and pollack (light blue circles) caught in the beach seine in June 2014. Red dots are the stations investigated. The circles are scales after number of recruits.*

There were few cod caught during the beach seine survey in June 2014, only 3 in total (0.2 in average pr haul) and no geographical distribution pattern is seen (fig 11). Pollack were more abundant in the survey and were caught in greater numbers, 39 in total, at four different locations (2.6 pr haul in average). The inner area of the fjord was the area with most pollack, 12 caught here during one haul. The amount of cod and pollack caught in the beach seine survey consisted of a very small part of the whole catch.

The area covered by the beach seine at each station varied to some extent (fig 12). The haul at station 4 covered the smallest area, while hauls at station 3 and 13 covered the largest area. The number of pollack in relation to the size of the beach seine hauls is investigated (fig 13). The largest haul had no catch of pollack, while the second largest haul had most pollack. The smallest haul (< 200 m^2) had one pollack.

Most of the beach seine hauls were without any pollack. It is visually hard to determine the significance of the relationship between size of the area hauled and the amount of pollack, although it seems like a size of more than 500 m^2 is beneficial.

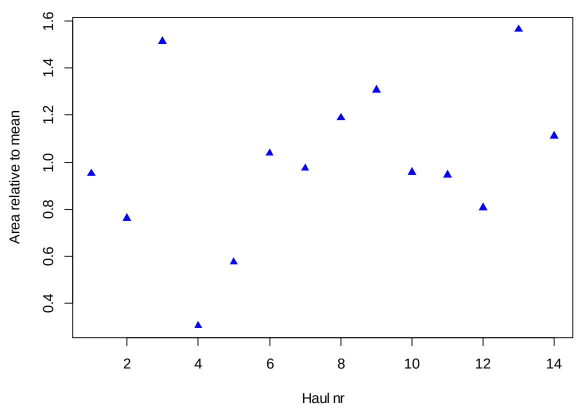

Figure 12 *Area cover by the beach seine relative to the mean in June 2014. The haul number equals to the stations sampled.*

The relevance of flora and cover at the beach seine stations on amount of pollack are investigated. It seems most likely to find pollack where the habitat is fully covered with eelgrass (fig14), this is where the median number of pollack is highest. The box-plots of these factors (flora 1 and cover 5) are tall with the upper and lower whiskers ranging from 0 to 12 pollack. A mix of eelgrass, seaweed and kelp with a low degree of coverage looks like a bad combination for pollack (0 pollack caught). When interpreting these figures one must take into account the low number of stations with each combination of flora and coverage (see table 1 in methods).

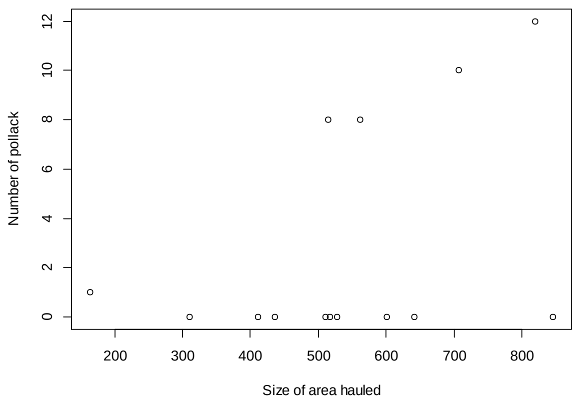

Figure 13 *Number of pollack caught in the beach seine and the size of the haul they were caught in. The size (area) of the haul is in m^2.*

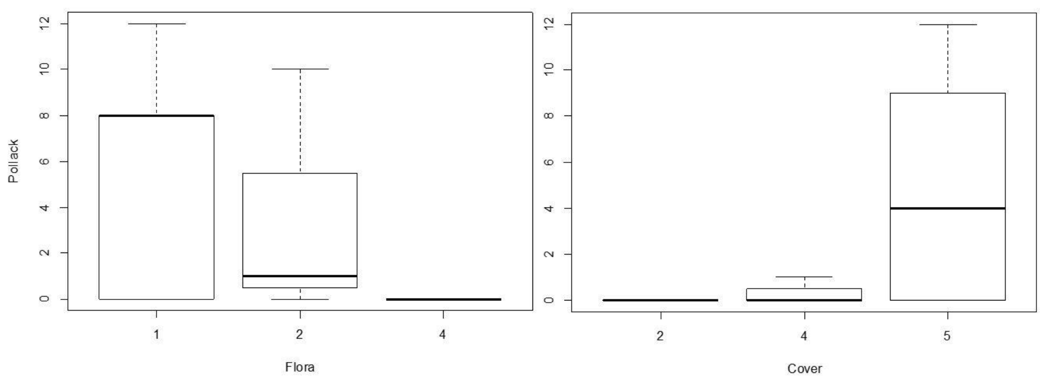

Figure 14 *The two box-plots shows the number of pollack at each flora category to the left (1= Eelgrass, 2= Seaweed/kelp, 4= Eelgrass/seaweed/kelp) and cover category to the right (2=Few plants, 4=Many plants, 5=Full coverage).*

3.3 Oceanographic models

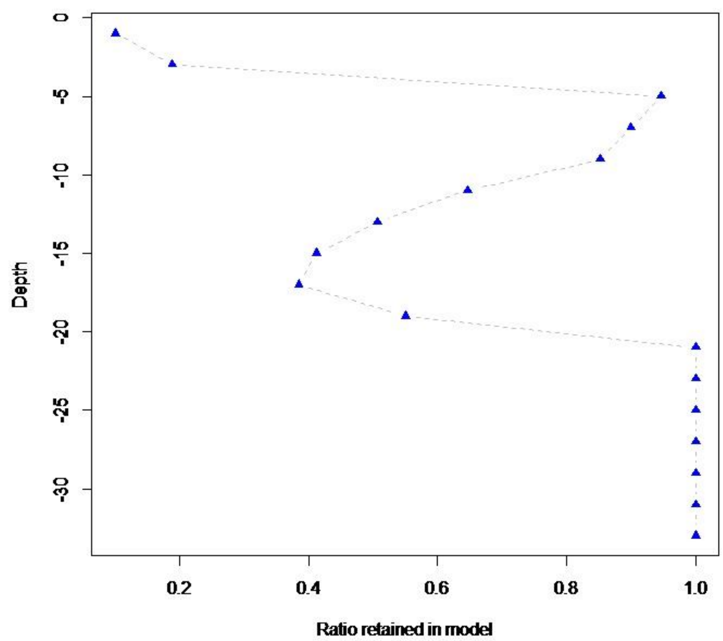

Figure 15 *The ratio of particles retained in the modelled area (fjord) after drift vary at different depths. The particles were released in a uniform geographic distribution and evenly distributed at all depths. The model is based on environmental conditions in March and April 2014 in Tvedestrandsfjorden.*

Drift simulations of egg-particles in Tvedestrandsfjorden indicated that the fjord retained a large amount of the particles released from 20 m and deeper (fig 15). A very high fraction of particles is retained between 5 and 10 m depth (80-90 %). The particles located in the 10-20 m deep water layer has a smaller ration retained in the fjord (40-50 %). The particles in the surface layer have a high chance of being advected out of the modelled area. The geographical position of the particles released in the model are also of great importance when considering retention (see fig 16). The particles released in the inner part of the fjord are more or less retained in the modelled area. The outer area and some local spots along the shore seems to have conditions that favor advection of the particles. The varying environmental conditions each year affects the amount of particles being advected out of the fjord. The 2013 current regime seems to take a greater fraction of the eggs out of the fjord compared with the 2014 current regime (fig 16).

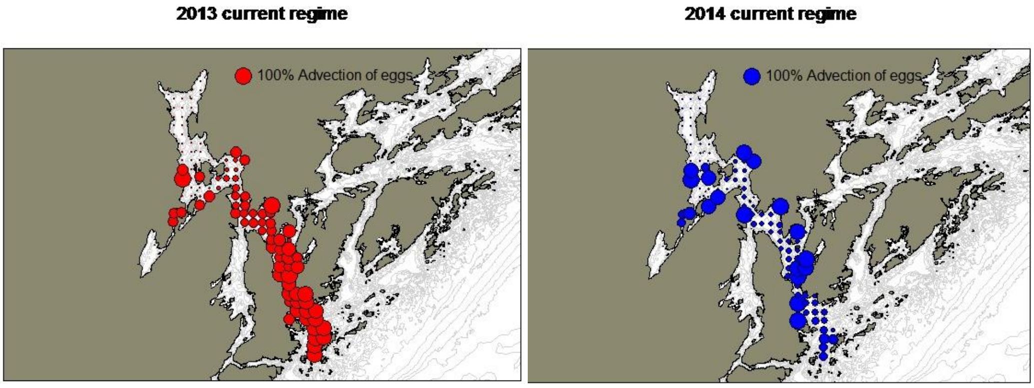

__Figure 16__ The amount of particles advected out of the modelled area after drift vary with different current regimes (here 2013 to the left in red and 2014 to the right in blue). The particles were released in a uniform horizontal and vertical distribution in the whole fjord.

The modelled drift scenario of egg-particles (based on field data) released on 15.03 2014 is illustrated with 10 days interval (fig 17). There is no clear visually difference in the geographical distribution of cod and pollack egg-particles. There is a continuous change in the distribution of the particles, and the highest density change from being located around the island Furøya (most eggs found here) to being in the inner area of the fjord and the Eikelandsfjorden area. The predicted amount of egg-particles advected out of the fjord are quite low (17% for pollack and 19% for cod), and suggests that most of the particles are kept in the fjord.

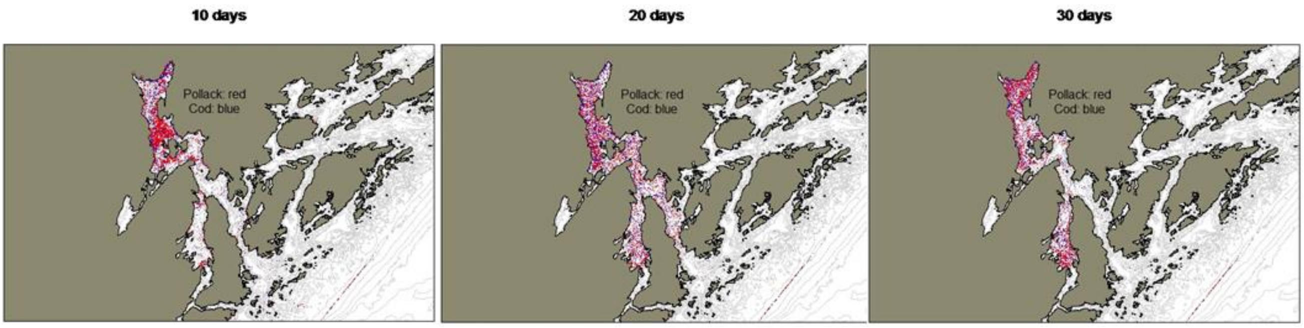

__Figure 17__ The modelled drift of egg-particles based on the eggs found during fieldwork 15.03 2014 is shown here with 10 days interval. The red dots represent the pollack egg-particles, while the blue represent cod. After 30 days of drift 19% cod and 17% of the pollack egg-particles were advected out of the modelled area (seen as a line of dots in the right corner). The drift was based on current regime and environmental conditions from the actual dates in 2014 (15.03 – 14.04).

The inner part of the inner fjord-basin and the inner part of Eikelandsfjorden is where there are highest densities and probability of finding the egg-particles of both species (fig 18). The density distribution makes it easier to see where the actual highest density appears (compared with fig 17). There are only very small visual differences between the distribution of cod and pollack egg-particles after drift. The 100% distribution covers the whole fjord and some of the outer skerries, making this area available for some of the egg-particles to reach using the currents.

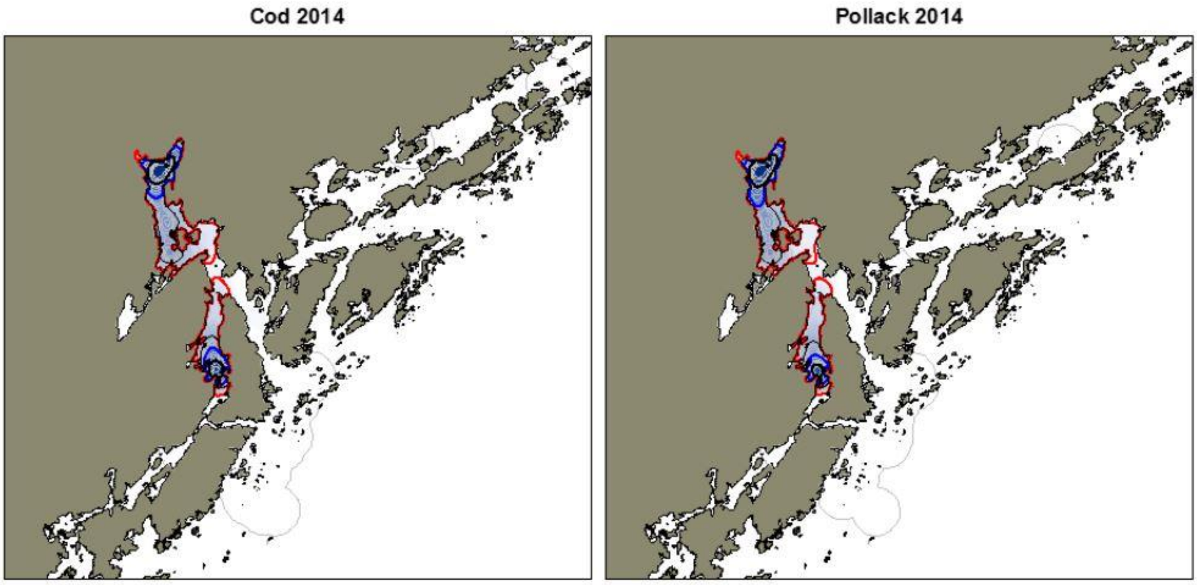

Figure 18 *The density distribution of the particles (assumed cod egg-particles to the left and pollack to the right) after 30 days of drift in Tvedestrandsfjorden in 2014. The grey line shows 100% of the density distribution, the red line 95%, the thin black line 75%, the thick blue 50% and the thick black 25%. The amount of egg- particles were chosen according to the eggs found in field, and given the same properties. The drift was based on current regime and environmental conditions from the actual dates in 2014 (15.03 – 14.04).*

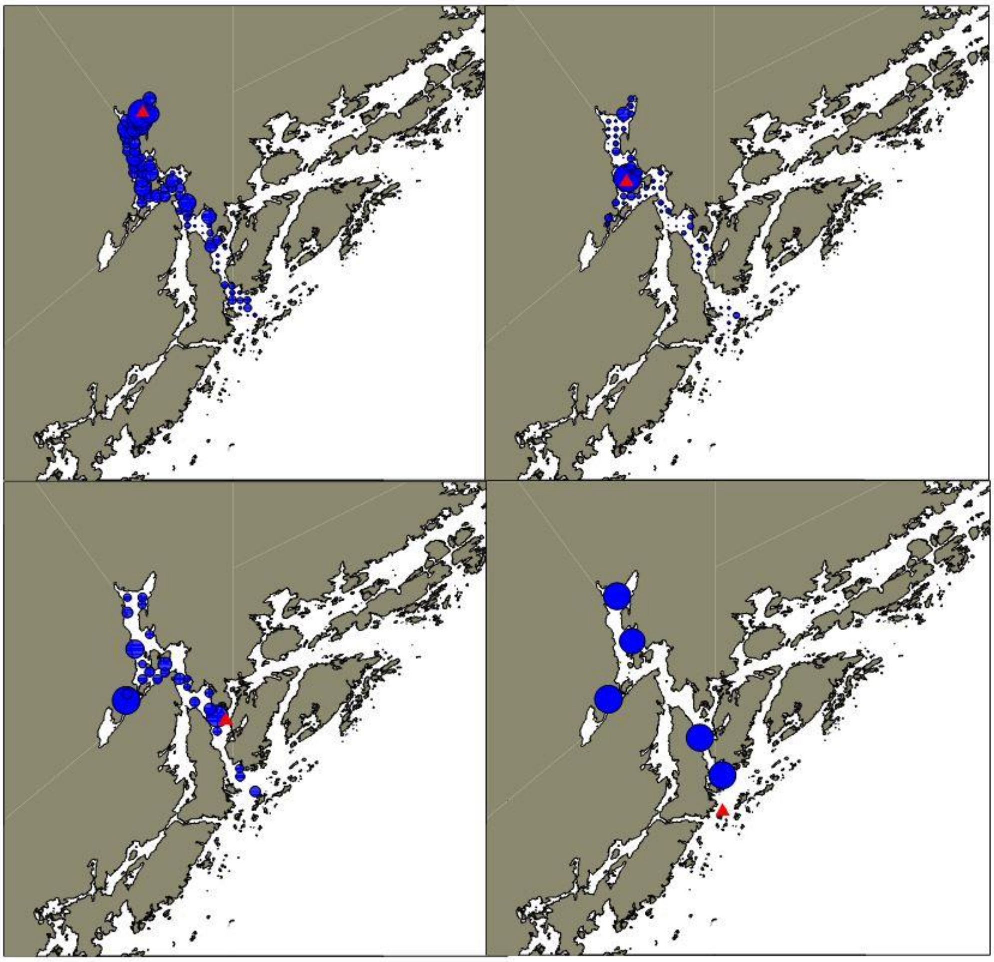

Figure 19 *Combining the data from the beach seine survey (pollack) in June 2014 with the oceanographic model data from March 2014 gives an estimation of the geographical distribution of pollack spawning areas tied to the beach seine stations. The red triangles is the location where most pollack juveniles were caught in the beach seine, and the blue circles illustrate the possible origin of the eggs. The blue circles are scaled after the probability of the egg coming from that specific area 15.03 2014 and ending up at the triangle after 30 days of drift. The model assumes that the particle (egg/larvae) settles after 30 days of drift.*

Using the oceanographic model data and "back calculating" the possible hot-spots where the eggs of the pollack juveniles caught in the beach seine may have had its origin is interesting (fig 19). In all the 4 investigated scenarios, the area around Furøya and the inner basin are the areas with the highest probability of finding the eggs which have resulted in the juveniles caught at the 4 beach seine stations. The clearest example is the potential "starting point" of the eggs reaching the inner station (upper left panel in fig 19), with most pollack in the beach seine, these seem to have come from the inner basin. This match the finding of eggs quite good (fig 10).

3.4 Pollack recruits

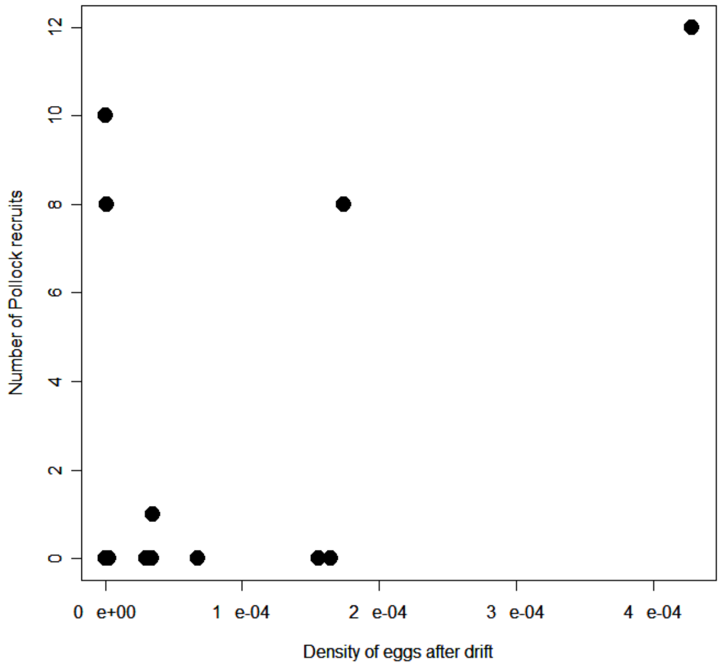

Figure 20 *The relationship between the modelled density of egg-particles after drift at each beach seine stations sampled in June 2014 and the number of pollack recruits at the same station.*

The highest density of egg-particles after drift, of all the investigated beach seine locations, was the station with most pollack recruits (fig 20). The modelled egg-particle density at this specific station was twice as high (or more), compared with the other stations investigated and close to the maximum value in the fjord (6 e-04). There is no visually clear pattern of the relationship between density of egg-particle and pollack recruits, e.g. stations with densities around 0 had 10, 8 and 0 recruits in one beach seine haul.

Previously mention factors like area covered by the beach seine haul, flora coverage, flora (habitat) and the density of eggs in the area after drift may separately affect the number of recruits. A generalized linear model was used to investigate the joint effect of all these factors. Parameters estimated and significance levels are given in table 2. None of the factors had a significant effect (all p-values <0.05) on the number of pollack recruits when considered together. The estimate for the effect of density of particles after drift on number of pollack recruits (1.097e+04) is positive and suggest that an increase in density can result in higher amount of pollack, but the result is not significant (p-value 0.39, std dev 1.206e+04). The standard deviations for all the factors results in a normal distribution range including 0 (+/- 2 std dev from estimate, 95 % confidence interval), which suggests a scenario where all the factors may have no (0) effect on the number of pollack recruits.

Table 2 *Summary statistics of the generalized linear model (formula 1) testing the significance (effect) of the factors listed in this table on the number of pollack recruits. The estimates is valid within the range of the factors investigated in this study. Flora 2 = Seaweed/ kelp, Flora 4 = Eelgrass/ seaweed/ kelp, Cover 4 = Many plants, Cover 5 = Full coverage.*

Factor	**Parameter name**	**Estimate**	**Std. Dev**	**p-value**
Intercept	β_0	1.278	6.185	0.842
Effect of area	β_1	4.534e-03	7.817e-03	0.580
Effect of density of particles	β_2	1.097e+04	1.206e+04	0.393
Flora 2 offset	β_{F2}	-0.2220	3.482	0.951
Flora 4 offset	β_{F4}	-3.405	4.055	0.429
Cover 4 offset	β_{c4}	-1.358	3.934	0.740
Cover 5 offset	β_{c4}	0.1674	4.738	0.973

4 Discussion

The purpose of this study was to investigate if the geographical variation in recruitment correlated with the predicted geographical distribution of egg-particles after drift in the oceanographic model. To evaluate the strongest predictor of the pattern of settled recruits, the results were depending on a fear amount of recruits in the fjord to come to a clear conclusion. 0-group cod were unfortunately only found in very small numbers (3 juveniles in the whole fjord), while 0-group pollack were present to some extent (39 juveniles in total, see fig 11). All the data collected still gives valuable results worth discussing, although the conclusions are based on a very low number of recruits. Field data is unpredictable, and it is always a risk that the data can be affected by anthropogenic errors. Evaluation of methods is always useful, especially if you did not get the data you were looking for. In this study, it has been important to evaluate whether the limited amount of data is method dependent or can be explained by a biological factor. Regarding the sampling methods, this study used the same method performed in multiple studies along the Skagerrak coast and other areas. The vertical plankton net haul is a commonly used method to collect eggs. The gear and procedure are identical as the one used in the Norwegian national program for mapping spawning fields for cod along the coast (Espeland et al., 2013), as also used by Knutsen et al. (2007) during a similar study in 20 fjords along the east and west coast of Norway. Knutsen et al. (2007) found that the majority of the cod eggs were located inside the sills and in the inner areas of most fjords. They also investigated Tvedestrandsfjorden and reported markedly more eggs in the inner basin, similar to our results. When Ciannelli et al. (2010) mapped the most commonly used spawning sites in Tvedestrandsfjorden over two years, they concluded that the majority of cod eggs were present in the uppermost 15 m of the water column. In addition they measured the ocean currents and found that the eggs were primarily present in the water layer flowing up the fjord to sheltered areas with less current. They did not do any attempt to track the flow path or ending point of the eggs like this study. As our samples were conducted down to approximately 30 m depth, it means that the cod eggs present should be collected by this sampling strategy. Fox et al. (2008) collected eggs with plankton collectors in the North Sea, and used the diameter of the eggs for species determination, like our study. They crossed checked with genetics, and concluded that the diameter of haddock (*Melanogrammus aeglefinus*) eggs had almost identical size range as cod, whiting (*Merlangius merlangus*), saithe (*Pollachius vires*) and pollack were a bit smaller. It is unlikely that eggs of haddock, whiting and saithe are a part of the cod like eggs caught in Tvedestrandsfjorden because they spawn in the central North Sea (Bakketeig et al., 2015, p 159,165,185). Determining the species (by egg size) in our study to be cod and pollack seems to be correct. There are little available literature on pollack egg sampling, but as their eggs are pelagic with about the same morphology as cod eggs, this collecting method should be transferable to pollack eggs. Our egg sampling method and the results should therefore be reliable and comparable with other studies.

The timing of the egg sampling and number of days sampled might have been affecting the catch and the results this study might have been clearer with more samples. In addition, weather conditions (wind strength and direction) during the spawning period of the investigated gadoids (January - May), are critical factors for the sampling result. During our sampling in 2014 the water temperature was high in all of Skagerrak and the North Sea (Albretsen et al., 2015, p. 89). Accordingly, our egg sampling aiming for cod eggs should have initiated earlier. At March 15, probably close to the peak of cod spawning in 2014, the highest amount of cod eggs were collected and a drastic reduction in numbers appear later (fig 10). In 2015 the peak of cod spawning in Tvedestrand occurred early in March (Espeland, per comm[1]), while in 2001 the similar peak was assumed to occur in late March at a location in Arendal (Espeland et al., 2007), not far from our study area. This illustrates the year-to-year variation in spawning peak of cod within a relatively restricted geographical area. Regarding pollack, the egg

[1] Sigurd H. Espeland (IMR 2015) shared information about a dataset with cod eggs (collected in 2015) from a project in Tvedestrandsfjorden

sampling should probably have continued for a longer period to hit the spawning peak for this species. Because of very limited knowledge on pollack recruitment in the wild, our study assumes that eggs collected in March and April most likely are pollack, due to egg size and the high water temperature in Tvedestrandsfjorden in 2014 (see fig 21, Freitas pers comm[2]). Genetic investigations would have confirmed if egg size and water temperature during spawning are sufficient information to identify pollack (and cod) eggs in this area. That has not done in this study, due to high analytic cost and lack of experience in using the method on pollack.

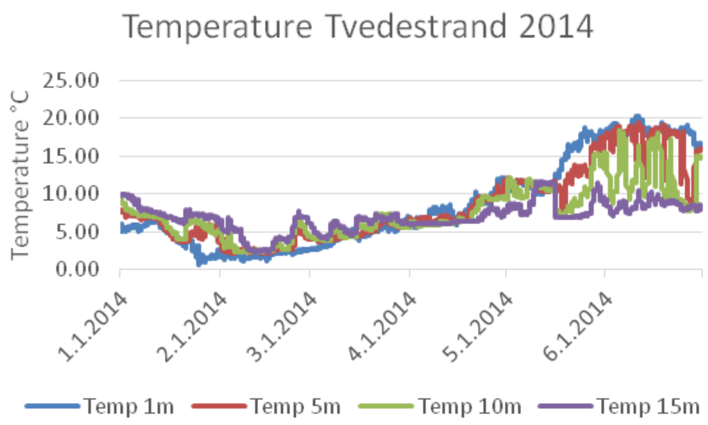

Figure 21 *Measured temperature (from one buoy) in Tvedestrandsfjorden from 17.01 – 01.07 2014 at 4 different depths (1m, 5m, 10m and 15m).*

The oceanographic current model (ROMS) is used widely within oceanography and marine biology (Myksvoll et al., 2011; Myksvoll et al., 2013; Vikebø et al., 2007). As an example ROMS has been used to estimate spawning fields along the coast in the Norwegian national program for mapping spawning fields (Espeland et al., 2013). There are some challenges with ROMS when trying to predict the drift routes of pelagic fish eggs and larvae. One big challenge is related to the vertical distribution (buoyancy of the eggs/larvae) and the potential vertical and horizontal active movement of pelagic larvae. Changes in distribution due to development and individual differences in density of the eggs can change the drift

[2] Carla Freitas (University of Agder/IMR) shared the temperature data from a project in Tvedestrandsfjorden in an e-mail 16.03.2015

route and the subsequent ending point. The particle-tracking simulations in this study was conducted by releasing eggs at multiple fixed depths, with the main portions released between 10 and 20m deep. During spring, fjord water is typically homogeneous, and even very small model errors in density fields in the water column or egg-density may cause the egg-particles to sink to unrealistic depths or rise to the surface. This can cause an unrealistically high amount of eggs at the surface and a massive drift out of the fjord (see fig 15). Using egg-density data (experiments) from eggs from other fjord or another year, may cause errors as it is assumed that cod adjust the buoyancy of their eggs with the changing oceanic environment (Asplin et al., 1999). As data regarding properties of pollack eggs is limited, this study assumes that pollack eggs have properties equal to cod. Our choice regarding the release of eggs in fixed depths empirically rely on earlier cod egg hauls from cruises in Norway implying that fjord cod eggs are located below the typical surface mixed layer (Stenevik et al., 2008).

Several studies discuss factors affecting the buoyancy of cod eggs and larvae. Saborido-Rey et al. (2003) showed that the buoyancy changed significantly with season, development stage, egg size and maternal condition. Late season cod larvae in their investigation was less buoyant compared with earlier in the season. When the larvae perform active horizontal and vertical movement in the water column, the distribution pattern is even more complicated to model (Leis, 2006). The degree of diel vertical migration of larvae affects the drift route and survival. It is a behavioral trade-off between being more exposed to predators by food motivated migration into brighter, shallower areas and staying in a safer place (Fiksen et al., 2007). Vikebø et al. (2007) claimed that the most successful individuals of Northeast Arctic cod where the ones that performed vertical migration, prioritizing growth in the beginning, before taking less risk. As this study was implemented in more exposed areas compared with our study site in Tvedestrandsfjorden, this behavior trade-offs may necessarily not affect the drift routes or survival in the same way.

Mapping movement and behavior of older stages of fish, mark-recapture (Rogers et al., 2014) or acoustic telemetry (Freitas et al., 2015; Olsen and Moland, 2011) are the most widely used methods. These methods are difficult to use on cod eggs and larvae because they are very small, and both the numbers of pelagic individuals and the mortality are high. In a dispersal study from Papa New Guinea all larvae of a population of clownfish were marked with tetracycline and traced (Jones et al., 2005). The study was partially successful but very costly and less applicable to fish populations with a large home range, like the gadoids. Oceanographic models, combined with advanced genetic techniques, meta-population models and fish otolith chemistry are today the most used methods to predict movement of the pelagic stages, dispersal, retention and connectivity (Jones et al., 2007).

Regarding fish recruitment, there seems to be no published studies where the outcome of particle drift models have been crosschecked with field studies, at least not in sheltered fjord areas. Thus, it is difficult to compare our results with other studies. Using particle drift models on cod-eggs is common, but to our knowledge, there are no scientific articles where particle drift models have been used on pollack eggs and larvae.

In this study, the majority of cod and pollack eggs were found at the 6-7 innermost stations, in the most protected part of the fjord where there are less wind and current (figure 10). The findings suggest this area to be important spawning sites for cod and pollack in the fjord. The oceanographic model show high retention of the particles released from these stations (fig 16). After releasing egg-particles (based on the field data) in the oceanographic model and modelling drift for 30 days, the areas with the highest modelled density of eggs were in the inner basin of Tvedestrandsfjorden, and the innermost area of Eikelandsfjorden (fig17 and 18). Field data from Eikelandsfjorden was unfortunately not collected during this study. When adding the current regime from 2013 into the oceanographic model, the same high density of particles was not present in Eikelandsfjorden after drift, as with the 2014 current regime. This documents the importance of variations in environmental conditions as essential factor for the geographical distribution of eggs in Tvedestrandsfjorden (see fig 16).

The interesting results from the beach seine survey in June was the very low numbers of juvenile cod in Tvedestrandsfjorden, e.g. only 3 cod in the whole fjord at three different stations (fig 11). The catch corresponded to 0.2 cod/haul. In the annual autumn beach seine survey conducted by the Institute of Marine Research along Skagerrak, no cod was caught in the Oslofjord-area (Berglihn, 2014; Espeland and Knutsen, 2014), 0.8 cod/haul in the east region of Skagerrak (east of Kragerø to the Swedish boarder) and 2.3 cod/haul in the west region of Skagerrak (from Kragerø to Lindesnes) in 2014. All these catches are very low compared with earlier years and indicates a very low recruitment of coastal cod in the whole area of Skagerrak (Bakketeig et al., 2015, p 201). Because of the very low number of 0-group cod caught in our beach seine hauls, no further analysis were conducted of the relationship between the recruits, the modelled drift, habitat (flora) and flora coverage at the stations. The autumn beach seine survey mentioned above, reported an average of 0.45 pollack/haul along all of the Skagerrak coast and 0.9 pollack/haul in the western region in 2014 (Espeland and Knutsen, 2014; Espeland pers comm[3]). The number of pollack caught in the beach seine in June 2014 were 2,6 pollack/haul (fig 11), and most of the catch were taken in areas where the current model predicted a quite high density of particles after drift (fig 18 and 20). Most pollack were caught in the innermost area of Tvedestrandsfjorden (12 at one station, see fig 11), this station had full coverage of eelgrass (fig 14, table 1). There is also indications that spawning fields around the island Furøya and in the inner basin have contributed to the pollack juveniles caught in the beach seine in June (when modelling the origin of the eggs with the starting point being where the juveniles were caught, see fig 19). The available field data correspond quite well with the modelling results, although none of the investigated factors had a significant effect on the number of recruits (table 2).

Some important factors likely to affect the recruitment success will be discussed here with Tvedestrandsfjorden especially in mind, because of the low recruitment of cod seen in 2014. When trying to explain the low cod recruitment in our area, and other nearby areas, there are many factors to consider which might affect the size of cohorts in fish populations. Both indirect and direct effects of

[3] Sigurd H. Espeland (IMR 2014) shared information about pollack from the same dataset published in (Espeland and Knutsen, 2014)

environmental, anthropogenic and biological origin can cause oscillatory changes (Fromentin et al., 1997). Firstly there has to be a spawning generation in the area. Events of low recruitment will reduce the future spawning generations with severe long-term effects on population level. A broad spatial distribution and large age distribution will reduce the possibility of recruitment failure and overfishing. Regarding age, it is well known that older females contribute with more eggs and better egg quality and have a longer spawning period than younger spawners (Berkeley et al., 2004). A large part of the study area in Tvedestrandsfjorden, is a MPA (Marine Protecting Area), which have included a no-catch zone since 2012. Cod is one of the target species within this MPA, but all other species also benefit from this regulation. Commercial and recreational fishing have been blamed for the decreasing coastal cod populations in this area, but these pressures can now be excluded as declining factors for the fish populations in Tvedestrandsfjorden. At present, no recovery of the cod population have been registered (Moland pers comm[4]). Other areas with collapsing populations of predator fish, like cod, have struggled to recover. By removing a top predator the structure of the ecosystem changes (a regime shift), leading to an unbalance, which can take a long time to revers (Frank et al., 2011). Annual test fishing in spring with fish traps has been performed in Tvedestrandsfjorden since before the MPA area was established in 2012, but still it is too early to evaluate the outcome of the protection. In 2014 average size of cod 50.9 cm, was larger than in 2011 (40.4 cm) and 2012 (39.5 cm), but the difference was not statistical significant. The CPUE (Catch per unit effort, here the average amount of fish caught per fish trap per day) was 0.2 cod/trap/day in 2014 and has been fluctuating all the investigated years without any significant trend. Average size of pollack was 31.0 cm in 2014 compared with 37.9 cm in 2011 and 21.5 cm in 2012. The CPUE for pollack was 0.3 pollack/trap/day in 2014. The amount of pollack caught during test fishing in Tvedestrand was almost twice the amount of cod (141 cod/263 pollack), a

[4] Even Moland (IMR 2014) shared the dataset from the ongoing test fishing project in the MPA in Tvedestrandsfjorden and gave permition for the use in this thesis.

domination of pollack has not been seen during earlier investigated years (Moland pers comm[4]). This corresponds well with the domination of pollack over cod (3 cod/39 pollack) in the beach seine survey in June. The reason why the pollack are quite small, with most individuals being under 30 cm (fig 22, Moland pers comm[4]), might reflect good recruitment during the latest years and/or migration out of the fjord by the largest individuals. If so, the MPA in Tvedestrandsfjorden might act as a good spawning and nursery site which can benefit areas outside by spillover (movement of juveniles and adults) and/or export of eggs and larvae (Gell and Roberts, 2003). More years of monitoring is needed to obtain reliable time trends, but cod along Skagerrak is known to respond positively to protection quite fast (Moland et al., 2013). While fisheries target the largest individuals in a population, natural selection favor the large ones and therefore the size distribution is likely to change within an MPA (Olsen and Moland, 2011). If the size of the cod in Tvedestrand have increased, as suggested by the test fishing (Berglihn, 2014), it might be a weak indication of an initial recovery of the cod population, and thus a potential respond to the harvest restrictions. If so, the cod spawning capacity should have increased the latest year resulting in more recruits, this was not confirmed by our beach seine catch in June 2014, but the egg hauls in March 2014 did have cod eggs (fig 7 and 10). This indicates high mortality between spawning and settling of the recruits, or extremely low catchability in June. The highest abundance of both cod and pollack juveniles in the beach seine is normally in June, later in the season the abundance is much lower due to high mortality rates after settling (Johannessen, 2014, p 45).

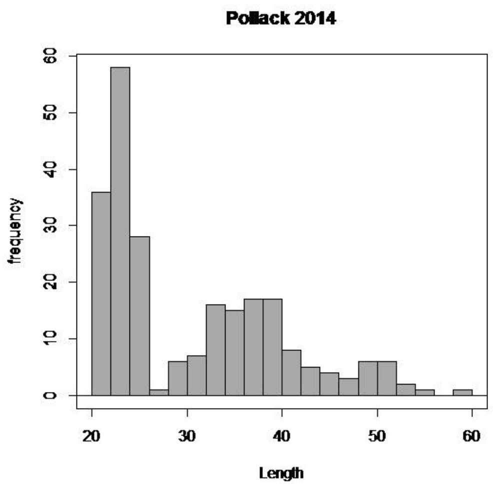

Figure 22 *The length (cm) distribution of pollack caught in fish traps in Tvedestrandsfjorden 09.05 – 02.06 2014. The height of the bars indicate the number of individual at each length.*

Earlier recruitment collapses of cod in the Skagerrak area is linked to changes in the habitat, e.g. disease and dieback on eelgrass, eutrophication leading to changes in the food availability and changes in the plankton community (Johannessen, 2014, p 35). Destruction of the kelp forest along the Norwegian coast has resulted in less juvenile cod, due to reduction of habitat (Bodvin et al., 2015). Fromentin et al. (1998) investigated if the long term changes in abundance of cod and pollack along Skagerrak was linked to the abundance of the zooplankton *Calanus Finmarchicus*, and the North Atlantic Oscillation (NAO) index, they found no significant relationship between these factors. However they found a correlation between the abundance of sea grass coverage (eelgrass) and fish abundance. Changes in the primary producers, both species composition and abundance, have also been documented during the last decade and might be one explanatory factor for the low recruitment of cod in 2014 (Falkenhaug, 2015, p. 98). There have been fluctuations in the recruitment of gadoids along the Skagerrak coast several times, in addition to the general decrease in amount of 0-group cod and pollack. A general decrease is thought to be caused by environmental changes and anthropogenic influences. Fromentin et al. (1997) suggested a 2 – 2.5 year fluctuation cycle for recruitment of gadoids caused by density-dependent survival due to cannibalism and competition. This is only documented in years with high recruitment, and subsequent cascade effects is revealed the following years.

A relevant environmental factor worth discussing is global warming, as rise in seawater temperature can affect cod and pollack in many ways. The stationary fjord cod, might be affected to a greater extent than offshore populations because they lack the option of going into deep and colder water, suiting their temperature preferences. The basins in Tvedestrandsfjorden have an anoxic bottom water from about 30-40 meters deep (varying with the depth of the different basins), an unsuitable habitat which excludes the cod from the deepest parts of the fjord

(Olsen pers comm[5]). Increase in water temperature can limit the available habitat and food for the populations within the southern range of the distribution of Atlantic cod (Freitas et al., 2015), while for the cod in the Barent Sea and other northern cod populations a rise in water temperature have had a positive effect (Kjesbu et al., 2014; Sundby, 2000). In addition, increasing water temperature means increasing metabolic rates with subsequent need of more energy (food). Early development stages of cod and pollack are especially sensitive towards changes in diet, which is one possible consequence of a climate change. The cod larvae in Tvedestrandsfjorden might have experienced a mismatch with their preferred diet in 2014, due to the warm water. Rogers et al. (2011) suggested that Skagerrak may become ill-suited for Atlantic cod if temperatures rise. Warmer spring may increase growth, while warmer summers limit the growth of juveniles. The negative effects of warmer summers might outweigh positive effects of warmer spring. Pollack might be better suited for the Skagerrak area when water temperature rise, because they have a more southern distribution pattern and the upper temperature limit for successful reproduction is higher for pollack than cod (Suquet et al., 2005). In addition juvenile pollack seems to have a high capacity to recover from a period of little growth induced by high temperature (Person-Le Ruyet et al., 2006).

[5] Esben Moland Olsen (professor at UiA /IMR); “Coastal degradation and recovery”, lecture at UiA, BIO401, 23.01.2015

5 Conclusion

Our results cannot disprove that there is a relationship between the geographical position of the spawning site, the currents in the fjord and the geographical pattern of settled recruits. Neither of the investigated factors could explain the spatial pattern of recruits. Data available indicates active spawning of cod and pollack in the fjord, with the most important spawning areas being inside the island Furøya, where the retention of particles are high. The cod population in Tvedestrandsfjorden had low recruitment in 2014, the reason is probably not related to the oceanographic conditions. The low number of juveniles makes it hard to analyze to which extent the currents affect habitat choice and whether the oceanographic model predicts the correct potential nursery areas after drift. For pollack, the highest density of egg-particles after drift correlates with the geographical position of the settled recruits caught in the beach seine, although the effect is not significant. The results suggest that the fjord is an important area for pollack recruitment, independent of the juveniles belonging to a local fjord population or being a part of an offshore population. The study also points out the knowledge-need about pollack recruitment and their biology.

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