

Master Thesis

The distribution of Skagerrak coastal cod (*Gadus morhua*) in relation to oxygen depletion, temperature and salinity, studied by acoustic telemetry in the Tvedestrand fjord in south-eastern Norway



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FRONT PAGE: Cod (*Gadus morhua*)

PHOTO SOURCE: Correiogourmand.com.br

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Abstract

Decreased oxygen levels in coastal waters due to human activities are receiving increased attention as a potential threat to marine biodiversity and harvestable resources. Hydrographic measurements and hydroacoustic single fish detections were used to study the horizontal and vertical distribution of Atlantic cod (*Gadus morhua*) in relation to oxygen, temperature and salinity in the Tvedestrand fjord in south-eastern Norway. Sampling was conducted from September to November in 2012. Movement of cod was inferred from hydroacoustic single fish detections (telemetry) and related to ambient environmental conditions.

Our data clearly showed that the Tvedestrand fjord experienced a long stagnation period. Oxygen concentrations decreased with depth and hypoxia occurred in the deepest water layers. Temperatures decreased with depth and stabilized at approximately 7 °C near 55 m depth. Salinity increased progressively from the surface and downwards. High-salinity water (> 34.5) was encountered close to the seafloor. Occurrence of cod was consistently highest in water depths between 2 and 14 m. The relative frequency of cod observations decreased with increasing depth and cod was nearly absent in water bodies under 35 m.

Generalized additive models (GAMs) suggested that oxygen was a key parameter influencing the vertical distribution of cod in the Tvedestrand fjord, where cod generally avoided low oxygen levels. However, a small proportion of cod observations were detected in water with less than 1 mL L⁻¹ oxygen. Cod also tended to avoid the coldest and most saline waters. Interpretation of the results from these statistical models was complicated by the fact that all three environmental variables were strongly correlated, but also somewhat aided by the fact that we had data from three different months and three fjord basins with variable hydrographic conditions. For instance, we found that there was an upward shift in the overall cod vertical distribution when the oxygen depleted layers expanded.

The results presented in this thesis illustrated how movement of cod in the Tvedestrand fjord may be influenced by several hydrographical variables, including temperature and oxygen concentrations. This presents a worrying situation because cod, already challenged by intensive fishing, may lose favorable habitats and spawning sites as a result of anthropogenic influence.

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1 Introduction

In recent years, decreasing oxygen concentrations and oxygen depletion (i.e. hypoxia) have been reported in many marine coastal areas around the world (Nixon 1995; Paerl 1995; Johannessen & Dahl 1996). Hypoxic bottom waters have long been a recognizable problem in the freshwater environment, and eutrophication has become increasingly common also in the marine systems (Rosenberg 1985). Hypoxia can be caused naturally in response to vertical stratification, such as formation of haloclines and thermoclines (Rosenberg et al. 1991; Pihl et al. 1992). More often however, hypoxia is due to excessive anthropogenic input of organic matter and nutrient from intensive farming, application of fertilizers and discharge of domestic wastewaters into systems holding poor circulation (Pihl et al. 1992; Peckol & Rivers 1995; Gamenick et al. 1996; Sandberg 1997; Wu & Lam 1997; Aarnio et al. 1998; Mason 1998). Recent studies have reported that conditions with oxygen depleted waters are more extensive and long-lasting than previously thought, persisting up to several weeks to months (Gilbert et al. 2005).

Hypoxia is a matter of concern because oxygen is essential for aerobic metabolic processes that most species rely on (Herbert et al. 2011) and its availability can potentially affect aquatic species on different levels (Wu 2002). Areas affected by hypoxia for a period of time are known to create inhospitable habitats, and result in mortality of fish and sedentary animals (Wu 2002). Some studies have reported that low oxygen concentrations can affect migration routes and distribution ranges of aquatic species (Murawski & Finn 1988; Perry & Smith 1994). For example, Baden (1990) documented mass mortality of bivalves (*Abra alba*) below the halocline in southeastern Kattegat and suggested that hypoxia was the main factor controlling this benthic community. Baden (1990) also registered dead and dying Norway lobster (*Nephrops norvegicus*) (up to 50 % of the total catch) after a trawling survey. In the same period, a considerable decline in catch per unit effort (CPUE) of Norway lobster was recorded, probably due to hypoxia that induced the lobster to leave their burrows.

The effects of low oxygen levels have also been well documented on certain fish species (Herbert et al. 2011). Hypoxic water bodies can induce stress (Herbert & Steffensen 2005), impair growth and reproduction (Thomas et al. 2007; Brandt et al. 2009) and there is a serious risk of death if hypoxic layers are not physically avoided (Plante et al. 1998). Avoidance is clearly an important survival mechanism, but accurate information on the degree of low oxygen avoidance differs between studies (Rose et al. 2009). For example, Schaber et al.

(2009) found that cod (*Gadus morhua*) avoided oxygen levels below 1.5 mL L⁻¹. Neuenfeldt (2002) reported that while the predator, cod, tolerated oxygen saturation levels down to 16 %, the prey, herring (*Clupea harengus*), generally avoided saturation levels below 50 %. Claireaux et al. (1995) and Neuenfeldt et al. (2009) also documented an avoidance reaction in cod from depleted water bodies. However, fish in these studies tended to enter extreme hypoxic conditions over short-term periods if food was offered. Such “hypoxic diving” behavior related to feeding has also been showed for the anchovy (*Anchoa spp.*) and the yellow perch (*Perca flavescens*) (Taylor et al. 2007; Roberts et al. 2009). Understanding how hypoxia avoidance behavior is controlled and to achieve a general knowledge on how low oxygen concentrations limit individual dispersion is critical since populations differ in intra-specific tolerance to hypoxic water volumes, meaning that populations are affected differentially across species ranges (Skjæraasen et al. 2008).

The distribution of marine fish is also influenced by other environmental factors, such as temperature and salinity. Several studies have documented that these factors interact with oxygen, to determine the availability of preferred habitat for different fish species (Murawski & Finn 1988; Perry & Smith 1994). Atlantic cod, among several other species, is influenced by a number of hydrographical factors. This has been documented in the Gulf of St. Lawrence (D'Amours 1993) and in the Baltic Sea (Tomkiewicz et al. 1998; Neuenfeldt 2002). In the Gulf of St. Lawrence, cod were strongly influenced by low oxygen levels (< 2.5 mL L⁻¹) and extreme temperatures (< 2°C). Both factors acted as barriers on cod movement, preventing them from entering the greatest depths. Studies from the Baltic Sea documented a highly stratified water column, consisting of a low salinity upper layer, and more saline deeper layers. The water column differed also in dissolved oxygen and temperature. Tomkiewicz et al. (1998) found that cod adapted to the intermediate layers were constrained by hypoxic bottom waters, and low salinity at the surface. It is interesting to note that other environmental factors, such as low temperatures in the deepest layers in the Gulf of St. Lawrence and low salinity upper layers, can truly prevent cod from entering preferable habitats with 100 % oxygen saturation. During certain times of the year, cod may be forced to stay in less saturated volumes of water because existing temperature- and salinity levels hinder access to full O₂ refuge areas.

Since 1927, hydrographical and chemical measurements have been conducted on annual cruises along the Norwegian Skagerrak coast (Dahl et al. 1987; Johannessen & Dahl 1996).

These studies have revealed deoxygenated water masses below sill levels among three well defined basins within the Tvedestrand fjord, Aust-Agder (Johannessen & Dahl 1996). The oceanographic conditions in the fjord depend mainly on the frequency and intensity of inflow from the Atlantic Ocean. However, deep water layers rarely get input of oxygenized water because sills reduce the fjord circulation. Renewal of bottom water and, thus, improvement of hydrographical conditions require special transport processes achieved by major intrusions (Aure et al. 1996; Schaber et al. 2009). *Advection exchange* occurs when sufficiently cold and dense water appears outside a sill. If these conditions persist for an extended period, considerable exchange could take place where “old” basin water gets flushed out. Inflow of new seawater will increase the content of dissolved oxygen, and improve the salinity conditions. Unfortunately, these events happen rarely. Exchange of basin water may also involve smaller volumes, a mechanism called *diffusive vertical exchange*. This more continuous process occurs when intermediate water masses get vertically mixed with less dense water from higher layers, due to turbulence.

In order to study the effects of hydrographical conditions on the distribution and movements of cod, a telemetry study was performed in co-operation with the Institute for Marine Research, Flødevigen, Arendal in the Tvedestrand fjord no-take marine reserve during a 3 month period in the autumn of 2012. Observations of individual fish horizontal and vertical positions were obtained from acoustic transmitters in combination with a network of acoustic receivers. Further, the utilization of the water column by the cod was studied in relation to ambient environmental conditions. Acoustic telemetry using a network of listening stations has been found to be a useful method to collect detailed information on fish behavior and habitat use (Olsen & Moland 2011). The listening stations consist of hydrophones that receive and store signals when fish equipped with transmitters are within listening range.

1.1 Research question

By using acoustic transmitters in combination with submerged receivers, this study aims to investigate whether oxygen, temperature and salinity influence the movement of Atlantic cod in the Tvedestrands fjord, in costal Skagerrak, south-eastern Norway. A working hypothesis is that cod avoid oxygen-depleted water. Furthermore, if tagged cod are observed to enter extreme hypoxic conditions, we expect that our individuals will only stay there for a short period of time since cod are known to require oxygen for metabolic processes (Herbert et al. 2011). Our second hypothesis is that cod avoid water masses containing low temperatures and high salinities.

2 Materials and Methods

2.1 Study species

Atlantic cod (*Gadus morhua*) is one of the most important commercial fish species in the world (FAO 2000). It is widely geographically distributed along coastlines and continental shelf areas in the North Atlantic, extending northwards to Disco Bay and Spitsbergen, southwards to Cape Hatteras and the Bay of Biscay. To the east, the species also enters the Baltic Sea (Knutsen et al. 2003). Coastal cod may attain a body length of more than 130 cm, weight up to 30 kg and may reach an age of more than 20 year (Bigelow & Schroeder 1953; Hutchings 1999). However, such large and old specimens are rarely encountered partly due to overfishing (Hutchings & Myers 1994; Beamish et al. 2006). Coastal Atlantic cod reach maturity at an age of 2 to 4 years (Olsen et al. 2004). Typically, coastal cod are stationary and complete much of their lifecycle within a restricted home range. In contrast, cod belonging to oceanic populations may migrate several hundred kilometers between spawning grounds and feeding areas. Spawning usually takes place from January to April. Under good nutritional conditions, a mature female may produce and release more than one million eggs per kilogram of somatic body weight, distributed over multiple spawning events (Wroblewski et al. 1999).

Genetic studies reveal that several distinct populations of Atlantic cod are present along the Norwegian coastline (Knutsen et al. 2003; Knutsen et al. 2004). Evidence suggests that the difference between the populations is small, but significant, where they inhabit areas only few tens of kilometers apart. Possibly, this fine-scale structure is maintained by the combined effect of spawning in sheltered inshore basins, protected against coastal currents, and site fidelity of older fish (Espeland et al. 2007; Ciannelli et al. 2010). Linked to this structure, there are evidence that the local populations have evolved different life history traits (Olsen et al. 2008).

2.2 Study site

The study was conducted in the central part of the Norwegian Skagerrak coast, near the town of Tvedestrand (Fig. 1). The Tvedestrand fjord is a semi-enclosed area with several sills and basins, extending 8 kilometers inland from the coastline (Ciannelli et al. 2010). The fjord system includes two main islands in the central part (Furøya and Hestøya), in addition to numerous skerries. Depth-wise the study area has shallower outer southern parts, while the inner northern sector is deeper (max 93 m, *see* Fig 1.1). Two river outlets along the northern

side of the fjord give a varying freshwater discharge, primarily to the surface layer. The Tvedestrand fjord has a great variation of habitats, such as eel grass beds, mud flats and kelp forest (Knutsen et al. 2010), which in turn contribute to several known inshore spawning and nursery sites for coastal cod (Knutsen et al. 2007).

Importantly, this study area was subject to a zoning plan where specific areas of the fjord were proposed as either no-take marine reserves or marine protected areas (MPAs) with varying degree of protection. This zoning plan was approved and implemented in June 2012. No-take marine reserves do not permit hook and line fishing, or other standing gear like gill net, fish-pots and traps (Pettersen et al. 2009). In the Tvedestrand fjord, no-take regulations apply north of Furøya and Hestøya, while fishing with hook and line are permitted in the southern part of the fjord. The goal of the establishment of marine reserves is to understand how cod populations develop within a restricted area where fishing is not permitted, as well as to test to what degree a marine reserve function in cod management. A previous acoustic tagging project revealed that 50% of all tagged cod were captured by leisure fishing within the first year (Olsen & Moland 2011). Capture will in turn reduce the amount of available data on cod behavior. With the establishment of no-take zones, this problem will be significantly reduced.

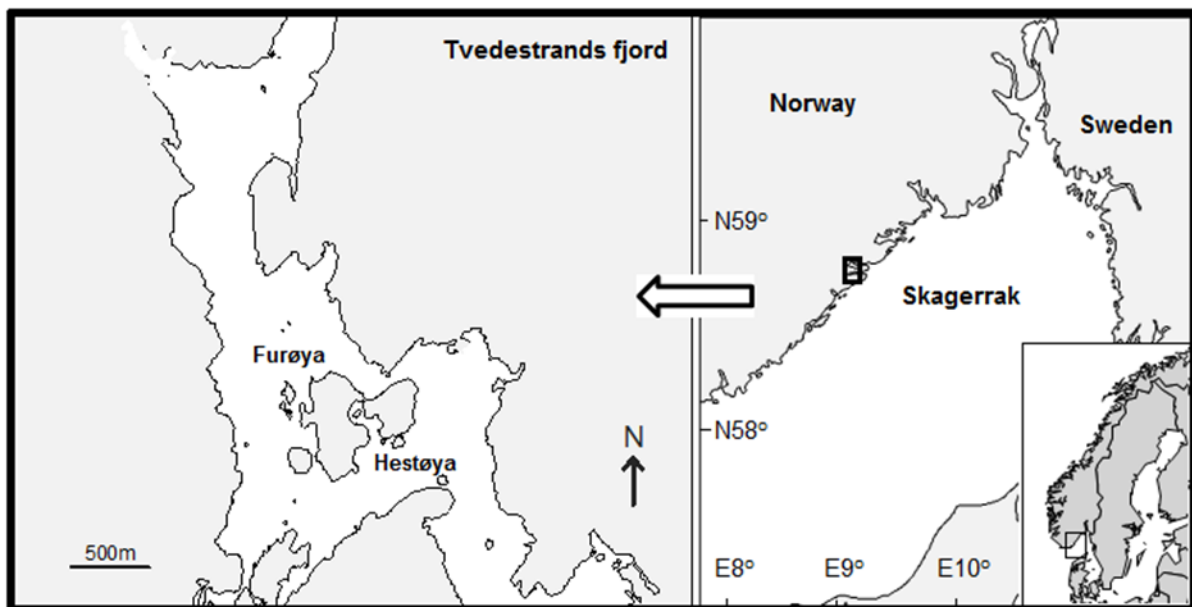


Fig. 1. Study area: The Tvedestrand fjord at the Norwegian Skagerrak coast.

2.2.1 Defining basins and sills

As previously mentioned, the study system contains several sills and basins (Ciannelli et al. 2010). Two basins are located north of the centered islands (Fig. 1.1). Basin 1 is found on the western side of the fjord, ranging south and all the way down to the defined sill. Basin 3 is situated on the eastern side of the fjord, delineated by a sill in the narrow channel opening north-east of Hestøya. Theoretically, these two basins may be viewed as one basin since a clear sill does not separate them. However, in this thesis we decided to divide the northern part of the fjord into two basins because the environmental conditions varied greatly between the western- and eastern side. Basin 2 is found south of the centered islands, towards the open ocean (Skagerrak).

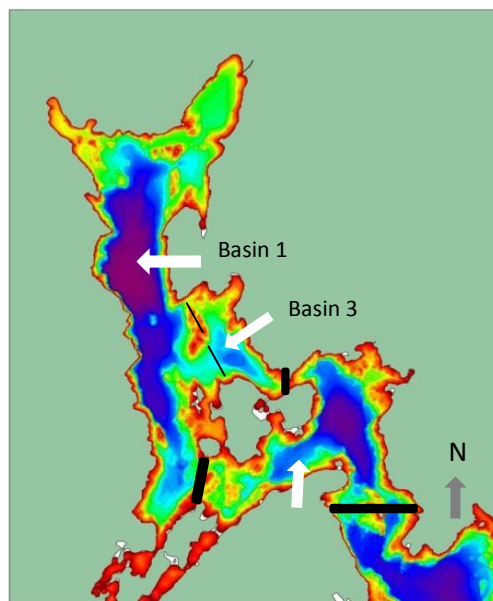


Fig. 1.1. Study area, showing the location of the present basins and sills within the Tvedestrand fjord. White arrows point in the direction of each basin. Black dotted lines indicate the boundary between the northern basins. Sills are marked by black solid lines. Depths are indicated by different colors; dark colors illustrate deeper depths and lighter colors illustrate shallow depths.

2.3 Sampling of cod for acoustic telemetry

During the spring of 2012 (April-May), 70 cod (*Gadus morhua*) were captured in the Tvedestrand fjord using traps (fyke-nets) (Fig. 2). Traps were set at different sites throughout the study area to ensure good spatial coverage, but at the same time set at known cod habitat locations to give a sufficient yield of individuals. The traps were left unchecked for a maximum duration of 2-5 days to ensure that minimal stress was exerted upon captured fish. This method of capture is thought to be relatively mild and causes no harm to the fish, if soak time is kept to a minimum (Olsen & Moland 2011). Captured individuals were measured to nearest cm (fork length). Catch position, trap depth and cod weight (g) was registered. Our

aim was to tag roughly the same number of fish throughout the available size-range (i.e., a flat length distribution). Other specimen caught in the traps were also identified and measured (cm) for further diversity studies (not included in this thesis). Individuals were then placed in a basin holding 40-50 l saltwater (present onboard the research vessel) between catch and the surgical procedure. To ensure optimal water temperature- and oxygen condition, the water was often replaced.



Fig. 2. Fyke-net used to capture cod in the Tvedestrand fjord.

Photo: otterspecialistgroup.org

2.4 Tagging cod with acoustic transmitters

An “outdoor surgery theatre” was set up at the pier on Furøya. Candidates were transferred one at a time to a tank containing saltwater supplied with clove oil for approximately 2-3 min. Clove oil anesthetizes the fish and reduce harmful effect while in surgery (King et al. 2005). Tools and transmitters were disinfected with ethanol before use to prevent possible bacterial infection. In addition, the transmitters were activated and their functioning checked with an ultrasonic receiver before implantation. A small incision was made posterior to the pelvic fin with the use of a scalpel. The fish were then equipped with a V9P-L transmitter (9 x 38 mm, weight in seawater <3g, Vemco Division, Amirix System Inc., Halifax, Canada), implanted in their abdominal cavity. A pressure sensor is built within the transmitter (accuracy ± 2.5 m when deployed at max. 50 m depth). It functions by transmitting the actual depth along with an identity code for each tag. Tags are programmed to transmit signals every 110-250 s at

random intervals in order to reduce code collision (i.e., two or more tags transmitting simultaneously to one receiver). Projected battery life time for these transmitters is estimated to 660 days. After surgical implantation, the wound was closed using absorbable suture material (Fig. 3). In addition to the acoustic transmitter, all candidates were equipped with an external T-bar anchor tag (TBA1, 30 x 2 mm, Hallprint Pty. Ltd, Holden Hill, South Australia) parallel to their anterior dorsal fin (Fig. 3). These tags hold printed information posting a reward of 500 NOK which would be paid if returned to the Institute for Marine Research, Flødevigen. Total handling time was approximately 5-8 min per candidate.

Individuals tagged with acoustic transmitters are most vulnerable during the first few days. Surgical intervention causes an unknown amount of stress upon the fish and may in the worst scenario cause mortality. However, Olsen & Moland (2011) reported that all fish survived after surgical procedure, and Espeland et al. (2007) found no indications that surgical procedure had any effect on cod behavior. To ensure full recovery, individuals were kept in a 40-50 l tank at the pier for up to 1 hour after surgery. All fish were then released at their position of capture in shallow water. Typically, released cod would spend a few seconds in shallow waters before they swam towards deeper water.



Fig. 3. Cod tagging and recovery. Left panel: Atlantic cod after surgical implantation of an acoustic transmitter (V9P-9 mm) in its abdominal cavity. The wound is being closed up using absorbable suture material. Right panel: after surgery, individuals were held in a 40-50 l basin to ensure full recovery. Note the pink external T-bar tag at the base of the anterior dorsal fin. **Photo:** Maren Duus Halvorsen

2.5 Monitoring cod movement

To track cod movement, a network consisting of 33 ultrasonic receivers (VR2W, Vemco Division, Amirix Systems Inc., Halifax, Canada) was placed in the Tvedestrand fjord (Fig. 4). The receivers function by recording signals emitted from the ultrasonic transmitters. The fjord system has one main channel in which tagged fish may leave the study area. Multiple receivers are placed along both sides of the channel to ensure that possible emigration of cod would be registered. Overall, the receivers are positioned approximately 3-400 m apart throughout the study area to ensure maximum monitoring capacity (i.e., ensuring overlap between listening ranges of receivers).

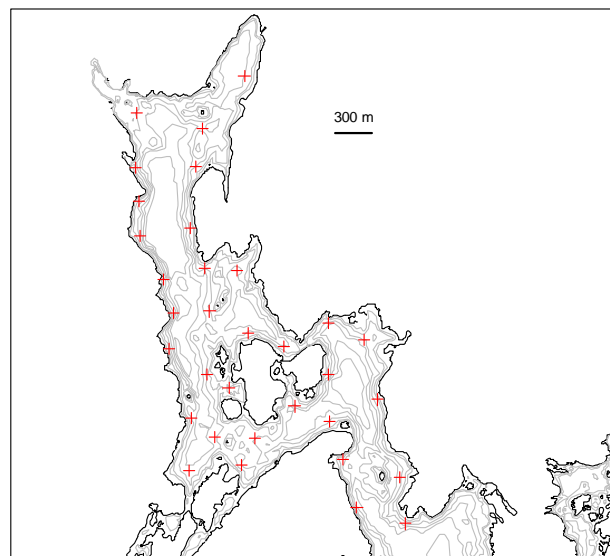


Fig. 4. Study area. The Tvedestrand fjord and the 33 ultrasonic receivers placed within it (red crosses). Grey lines denote the 5, 10, 15, 20, 30 and 50 m depth contours.

The ultrasonic stations are anchored at a fixed position at the bottom of the fjord by a mooring (50 kg). Receivers are deployed at 3 m depth, attached to a floater that keeps the device upright in the water column (Fig. 5). A smaller weight (9 kg) and 5 m extra rope allows the receiver to be hauled to the surface for downloading without moving the large main anchor.

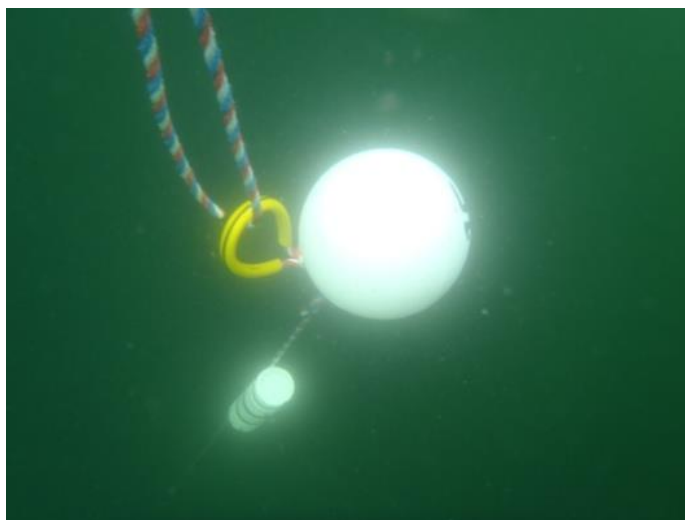


Fig. 5. One of the acoustic receivers during deployment in the Tvedestrand fjord, placed 3 m below the surface and held by a floater (at 2.5 m depth). **Photo:** Esben Moland Olsen

Data from the acoustic transmitters were downloaded from the receivers every 2-3 month during June to November. A GPS (Global Positioning System) was used to locate all the receivers within the study area. Each hydrophone was brought up manually to the surface by snorkeling and set in transmission mode with a magnetic key. Emitted data were transferred via Bluetooth to a field computer (Fig. 6). Receiver's logs (vrl files) were initially managed within a VUE data base (Vemco Division, Amirix Systems Inc., Halifax, Canada). Data were later imported into R software (version 2.15.2; R Development Core Team 2012) for statistical analysis. Receivers were reset and synchronized before they were put back in the water at the same position. In addition, ropes, hydrophones and buoys were rinsed for algae, barnacles and other fouling organisms. We also had to replace one missing receiver.



Fig. 6. Downloading data from a receiver to a computer in field. **Photo:** Karin Rötgers

2.6 Processing data on monitored cod movement

Receiver logs within the VUE-database, containing data on fish behaviour, were initially managed for each candidate. The vrl files were first exported into Microsoft Excel (2010), as csv files. Transmitted signals registered prior to, and after the hydrographical surveys, were deleted since we did not know the oceanographic state of the fjord at that time (*see* hydrographic measurements below). The data were further sorted into separate VUE-files according to month, meaning that each file contained monthly individual data on fish behaviour.

2.7 Investigation of cod fate

Horizontal activities were inferred from signals being transmitted from individual fish to multiple receivers over time, while vertical movements were inferred from obtained depth recordings (Olsen & Moland 2011). We expected that some of the tagged individuals would be lost after release. The fate of our candidate was determined on the percussion of movement - absent data, and tags received from local fishers. Fish was considered alive if data indicated a normal diel vertical migration pattern (DVM). Individuals were declared dead if they showed no sign of vertical or horizontal movement (i.e., when recorded signals were transmitted to the same receiver, at constant depths, over a longer period of time). Harvest mortality was inferred when the high-reward T-bar tag belonging to one of the individual was returned to the Flødevigen research station. Individuals were also considered harvested if fish were no longer transmitting to any of the telemetry receivers after a period of normal appearance. Dispersal out of the study area was inferred if the last recorded signal was received by a telemetry receiver situated at the outer edge of the channel opening, and no further recordings were done by any other receivers after that last registration.

2.8 Extraction of relevant data

It is important to note that each signal picked up by the receivers does not give the exact position of the fish, but simply tells that the fish were within the listening range of the receiver (Olsen & Moland 2011). Therefore, we used the method of position averaging (PAV) developed by Simpfendorfer et al. (2002) to estimate 30 min average horizontal positions for each fish through the study period. The more signals received by the more receivers, the more accurate is the position (Simpfendorfer et al. 2002). These average positions were then used when further analysing the data. For analyses on vertical position (depth use) we used the original detection data. Mean geographical position, min and max depth, including the

median, was extracted from all cod surviving in the system, from September through November. Relative frequency distribution were resolved to analyse utilized depth layers (1 m intervals). As the sampling period was shorter (i.e., fewer detections) for September and November compared with October, the total amount of detections was higher for October (n=412805) than for September (n=133997) and November (n=306422).

2.9 Hydrography measurements

To determine whether hydrographical conditions influenced the vertical distribution of cod, oxygen, temperature and salinity were measured at seven predetermined locations in the Tvedestrand fjord (Fig. 7). The measurements were carried out on monthly cruises during the latter half of September through November, which is usually the time of year when oxygen concentrations are at a minimum (Dahl & Danielssen 1992; Johannessen & Dahl 1996). The average starting date of the survey was the 19th each month (ranging from 19-23th). Water samples were collected with Niskin bottles, at 10 m intervals. The measurements in the bottom layers were taken ~1-2 m above the seafloor in order to prevent disrobement of the stratum. Oxygen was analyzed by the standard Winkler procedure after each sampling period (*see* Strickland & Parsons 1968). Vertical profiles of temperature and salinity were obtained using a CTD (acronym for conductivity, temperature and depth: model SD204). The CTD was lowered at 1-2 m/sec through the water column. Downcast values were used for later analysis.

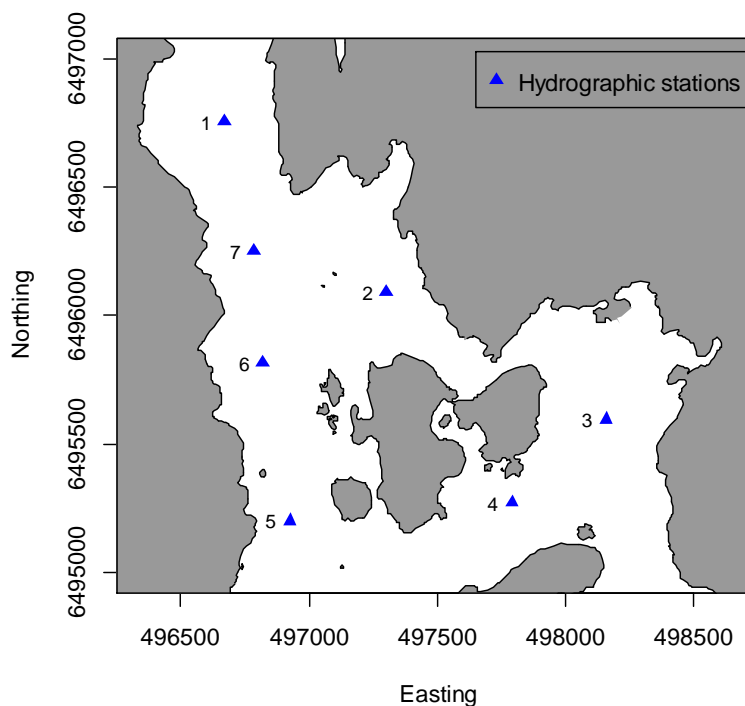


Fig. 7. Location of the seven hydrographic stations within the Tvedestrand fjord, marked with blue triangles.

2.10 Constructing horizontal maps

In order to present individuals along transects, a line profile (horizontal map) was constructed throughout the fjord using qgis (Quantum GIS) and the “python” script (*see* appendix 1). Depth data points were made every 5 m, starting in the northern sector of the fjord, going south and around the centered islands. The line was in total 5500 m long. Individual mean geographical position was replaced horizontally towards the line. Each cod’s new geographical position was registered in m from start and positioned along the transect.

2.11 Statistical analyses

Data on the distribution of cod was analysed in relation to ambient hydrography (oxygen, temperature and salinity). Since oxygen measurements were only taken at selected depths (0, 10, 20, 40, 50, 60, 70 and 80 m depth) once per month, Generalized Additive Models (GAM) was applied to the field observations of depth-specific oxygen concentration to predict oxygen concentrations at remaining depths for each month and fjord basin. This analysis was performed in the R software package *mgcv*. The smoothing parameter for calculation (k) was set to 3, 4 or 6, depending on the total number of samples taken at each hydrographical station. A new dataset with high resolution depths was constructed to obtain additional predicted oxygen values (interpolated within the depth range of observed oxygen measurements).

When studying the effects of environmental factors on the distribution of cod, data were first checked for normality. We log transformed those variables that did not meet the normality assumption. We also estimated Pearson-type correlations among environmental variables (oxygen, temperature and salinity), using the R package *corrplot*. Finally, we used GAMs to explore the potential influences of the environmental variables on cod depth use (vertical distribution), also accounting for differences in the number of cod observations among basins and months. The continuous exploratory variables, x , w and z was entered into the model as non-parametric smoothed function $s(x)$, $s(w)$, $s(z)$:

$$y \sim s(x) + \text{factor}(w) + \text{factor}(z)$$

where y is cod frequency and x is the abiotic factors (such as oxygen, temperature and salinity). The model also included the effect of basin (w) and month (z). GAM is a useful approach in cases where one has no *a priori* reason to choose one particular parametric form

over another for describing the relationship between the response variable and the explanatory variables (Crawley 2007). Note that the data on depth-specific observations of cod will involve some degree of pseudoreplication (Lazic 2010) since there are multiple observations of the same fish over a three month period (i.e. all observations are not statistically independent).

3 Results

3.1 Cod fate inferred from acoustic monitoring

In total, 70 cod were equipped with acoustic transmitters during the survey in 2012. However, tagged cod were harvested from the fjord system throughout the whole study period, with most cod being removed during May-September. Returned tags from individuals caught by fishers in combination with our telemetry data showed that 40 % of the cod disappeared from the fjord system throughout the study period (Fig. 8). Fifteen cod were registered harvested by local fishermen. Five candidates dispersed out of the study area without returning for as long as the study lasted. Three cod displayed a defect transmitter, while four individuals were declared dead based on a constant vertical and horizontal position for a long period of time. In addition, one cod was lost after the field work was terminated (human error). After six months, 42 tagged cod were left alive, transmitting to the telemetry receivers within the fjord system.

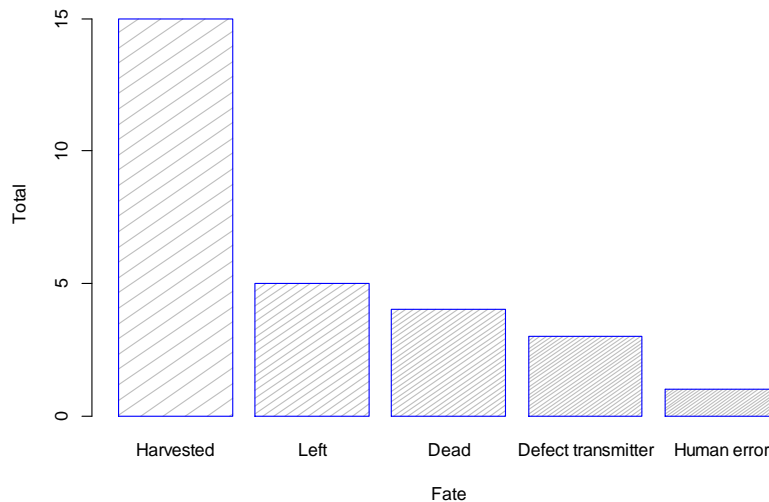


Fig. 8. Fates of lost tagged cod throughout the study period.

3.2 Hydrography

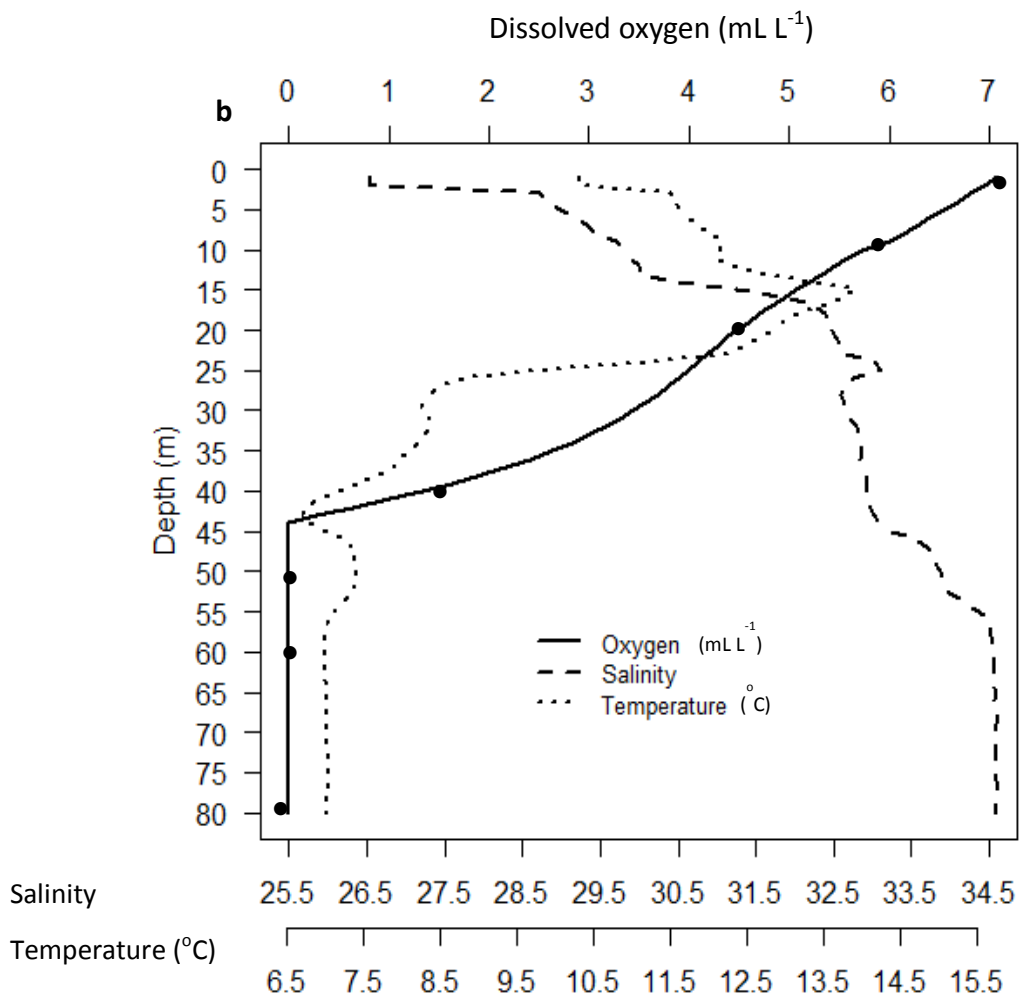
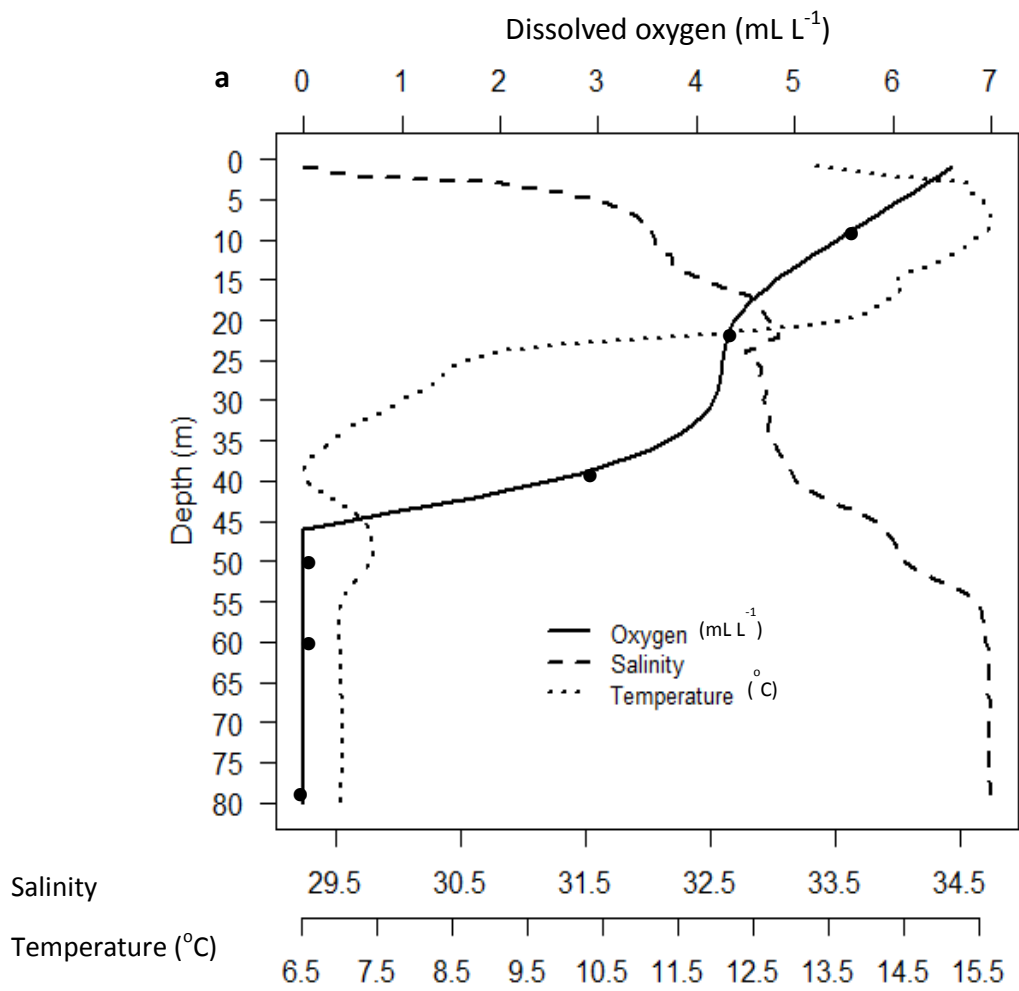
Oxygen concentrations decreased with depth and hypoxia occurred in the deepest water layers (Fig. 9, see appendix 2 for further results). Temperatures decreased near the surface during autumn, while an increase in salinity was observed at shallow depths (Fig. 9).

In September, oxygen concentrations were up to 7 mL L⁻¹ in the upper layer. Oxygen decreased with depth and the water turned more or less anoxic close to the seafloor. Water layers below 46 m (\pm 10 m) were characterized by oxygen depletion with ambient oxygen concentration < 1 mL L⁻¹. Temperatures decreased from 13.5 °C at the surface to a minimum of 6.5 °C near 38 m. Below this layer, a slight increase in temperature occurred with depth

before it stabilized at approximately 7 °C near 55 m. Salinity increased progressively with depth down to 25 m with a slower increase to 55 m. At this depth, salinity stabilized and attained a salinity value of 34.75 close to seafloor.

By October, oxygen depletion in the deepest parts had progressed in all three basins with layers below 44 m (± 18 m) showing ambient oxygen concentration less than 1 mL L⁻¹. This was especially clear in the south-eastern basin where the hypoxic layer increased by 10.6 m (*see* appendix 2 and Fig. 11 for comparison). Temperatures decreased by a few degrees to 10 °C near the surface. There was an increase to 13 °C at 17 m, but deeper down, temperatures decreased progressively with depth and stabilized at 7 °C near 55 m. Salinity were close to 26.5 at shallow depths and increased down to 23 m. A less steep increase in salinity was observed below this depth before it obtained a maximum value of 34.5 near 55 m. Additionally, average temperature and salinity levels varied on the horizontal plane this month. Our data revealed higher temperatures and lower salinities at intermediate depths in basin 2. It should be kept in mind, however, that bottom depth and sill heights vary between basins.

An observation of particular interest was made in November. Here, a smaller volume of oxygen rich water seemed to have entered the fjord. This inflow was observed to replenish oxygen in shallow water layers. The intrusion was highly pronounced in basin 2 in connection with the open coast where “old” oxygen depleted water masses were replenished, but the oxygen conditions were only slightly improved in the innermost basins. Oxygen depleted layers (< 1 mL L⁻¹) were defined at 46 m (± 20 m). Temperatures dropped further to 8.3 °C in the uppermost part of the water column. Below, temperatures increased before it decreased progressively and stabilized at a temperature of 7 °C near 55 m. Salinity increased from 24.9 at the surface to 32.75 at 10 m this month. Below that, the salinity values were rather stable, reaching a maximum value of 34.5 at the bottom of the fjord.



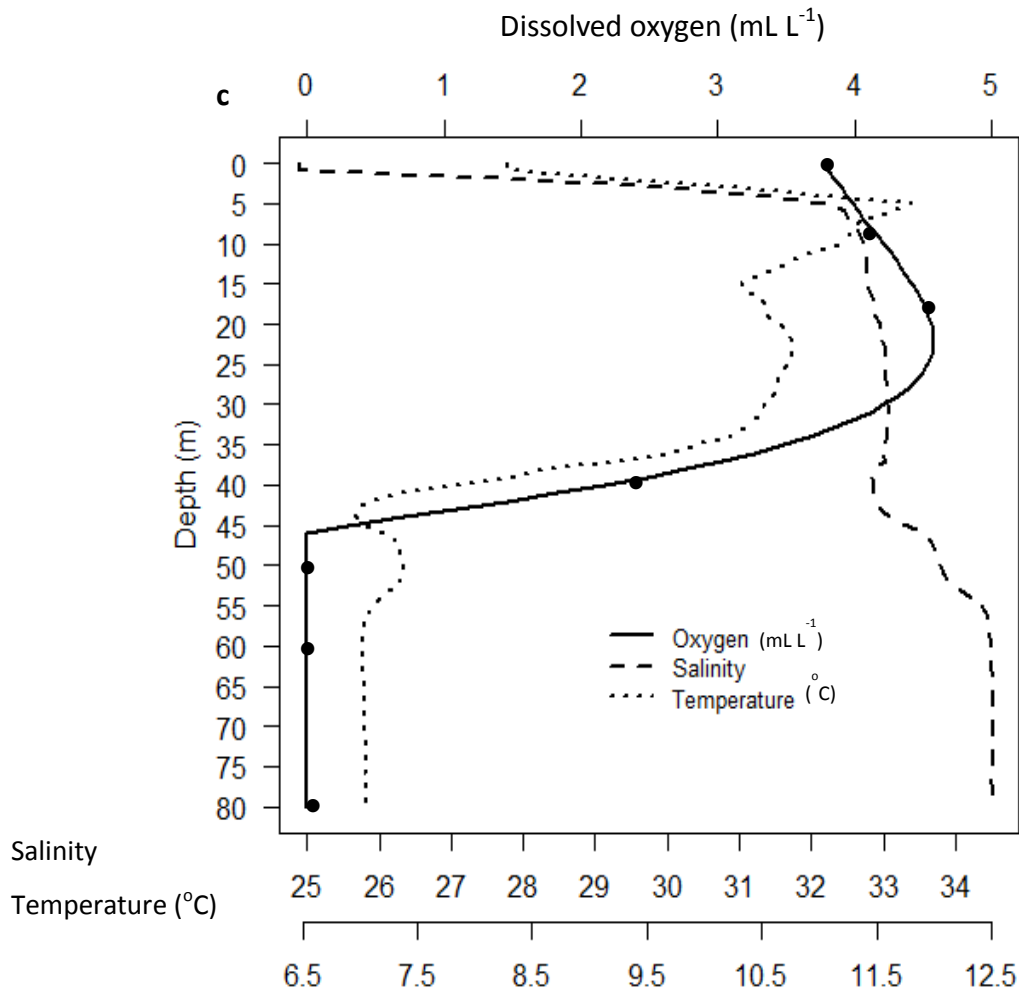


Fig. 9. The vertical profiles of oxygen, temperature and salinity in basin 1 in September (a), October (b) and November (c) 2012. Field observations are marked with black circles (at 0, 10, 20, 40, 50, 60 and 80 m depth). Be aware of that the axis differs. Solid line illustrates measured oxygen concentration (mL L^{-1}), dashed line salinity and dotted line temperature ($^{\circ}\text{C}$). Data points represent 1 m depth intervals.

All environmental variables were strongly correlated (Table 1). Oxygen was correlated negatively with salinity and positive with temperature. A negative correlation was also found between temperature and salinity. Based on this, the variables were tested separately for their potential influences on cod distribution.

Table 1. The results from the Pearson-type correlation test.

Variables	Frequency	Salinity	Temperature	Oxygen
Frequency	1.00	-0.56	0.69	0.79
Salinity	-0.56	1.00	-0.45	-0.78
Temperature	0.69	-0.45	1.00	0.74
Oxygen	0.79	-0.78	0.74	1.00

3.3 Spatial distribution of cod

Cod were almost exclusively found above 30 m depth (Fig. 10). The relative frequency decreased with increasing depth, and the abundance of cod was close to zero below 35 m. Occurrence of cod was consistently highest in water depths between 2 and 14 m. There was also an upward shift in median depths from September to October (Fig. 10) Cod was observed to aggregate in shallower depths in basin 3 compared to basin 1 (Fig.10). Data on fish movement in basin 2 was sparse and therefore not presented here (all fish were tagged in connection with either basin 1 or 3).

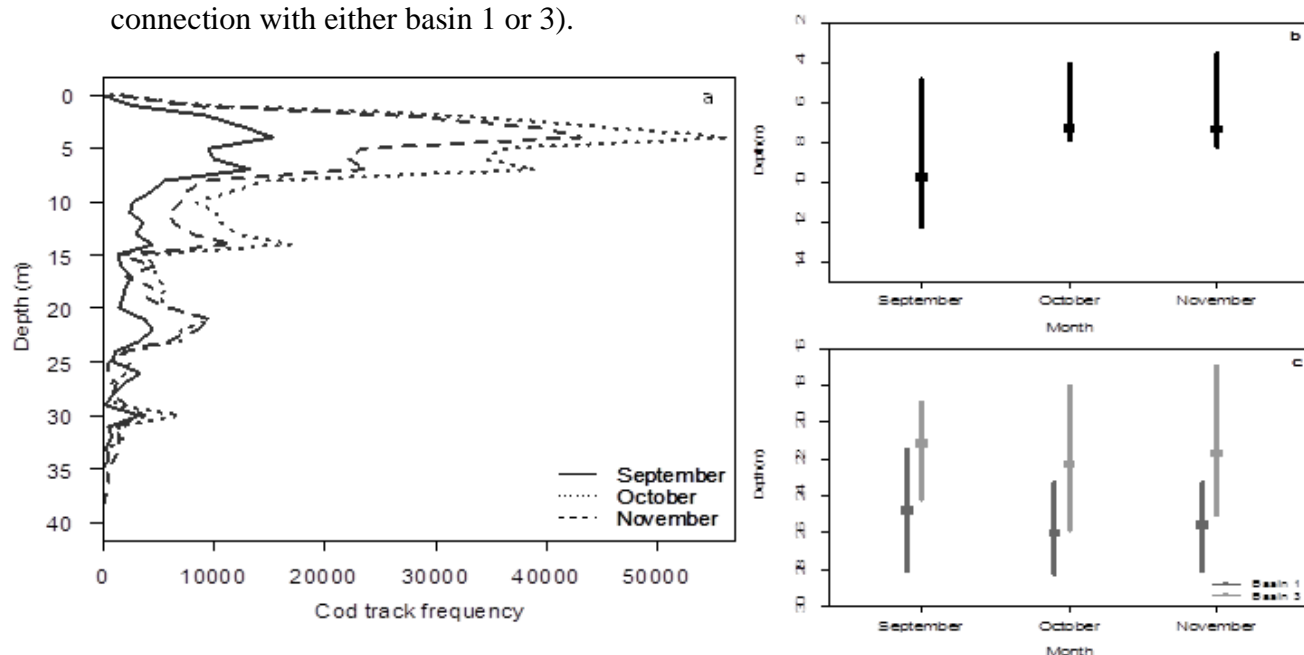


Fig. 10. The distribution of cod at different depth in September (a, solid line), October (dotted line) and November (dashed line), showing the change in median depth during the study period (b) and between basins (c).

The statistical model applied (GAM) confirmed that there were significantly more signals received in October and November compared with September (Table 2). The model also confirmed that significantly more signals were recorded in basin 3 compared with basin 2.

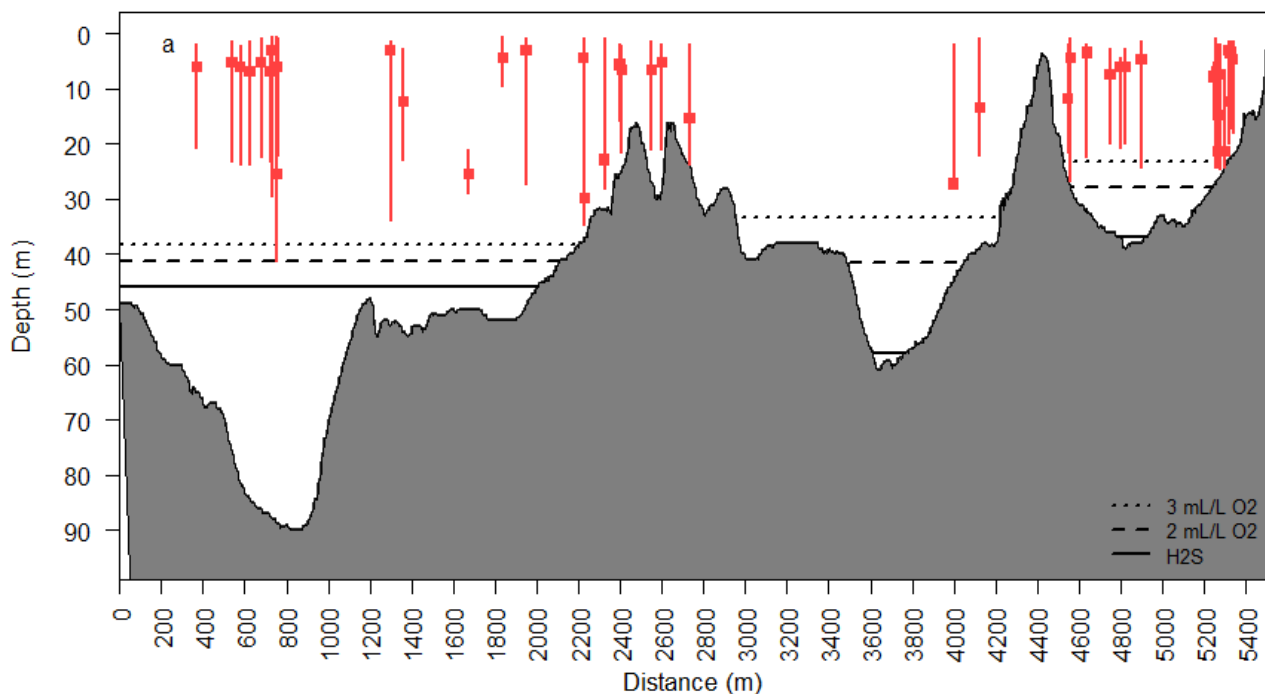
Table 2. Effects of study month and fjord basin on the frequency of cod observations. September and basin 1 were set as reference levels.

	Estimate	Std. Error	Pr(> t)
(Intercept)	3.27	0.14	< 0.0001
factor(mo) 2	1.17	0.16	< 0.0001
factor(mo) 3	1.04	0.16	< 0.0001
factor(basin) 2	-1.77	0.16	< 0.0001
factor(basin) 3	0.49	0.18	< 0.001

3.4 Distribution of cod in relation to ambient oxygen concentration

Comparisons of oxygen concentration and cod abundance strongly indicated that our individuals avoided low oxygen levels (Fig. 11). Fewer than 5 % of the cod were found associated with oxygen levels $< 4 \text{ mL L}^{-1}$. Still, a small proportion of cod was detected in oxygen concentration of less than 1 mL L^{-1} .

In September, more than 96 % of the cod observations were found in oxygen levels between 4 and 7 mL L^{-1} , with the highest occurrence between 4 and 6 mL L^{-1} . Only one observed cod were associated with oxygen levels below 2 mL L^{-1} . By October, the cod were found mostly in oxygen levels from 4 to 7 mL L^{-1} (73.2 %), with a clear peak at 6 and 7 mL L^{-1} oxygen, but a small proportion of cod observations were detected in oxygen concentrations $< 1 \text{ mL L}^{-1}$. Six cod was observed to enter hypoxic water masses and five of these belonged to basin 3. Also in November, cod tended to accumulate in oxygen concentrations between 4 and 7 mL L^{-1} . Most of the cod was detected in layers with 4 mL L^{-1} oxygen. Fewer than 2 % of the cod were observed in water masses holding less than 3 mL L^{-1} with one observation in $< 1 \text{ mL L}^{-1}$ oxygen.



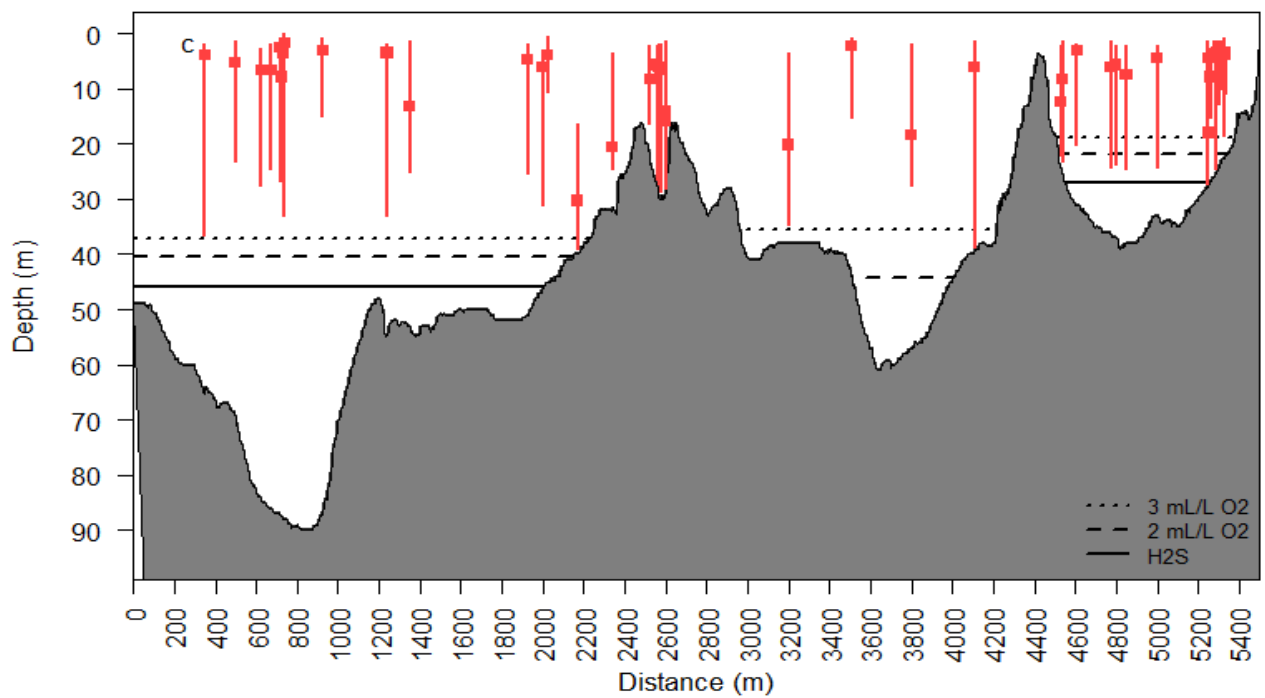
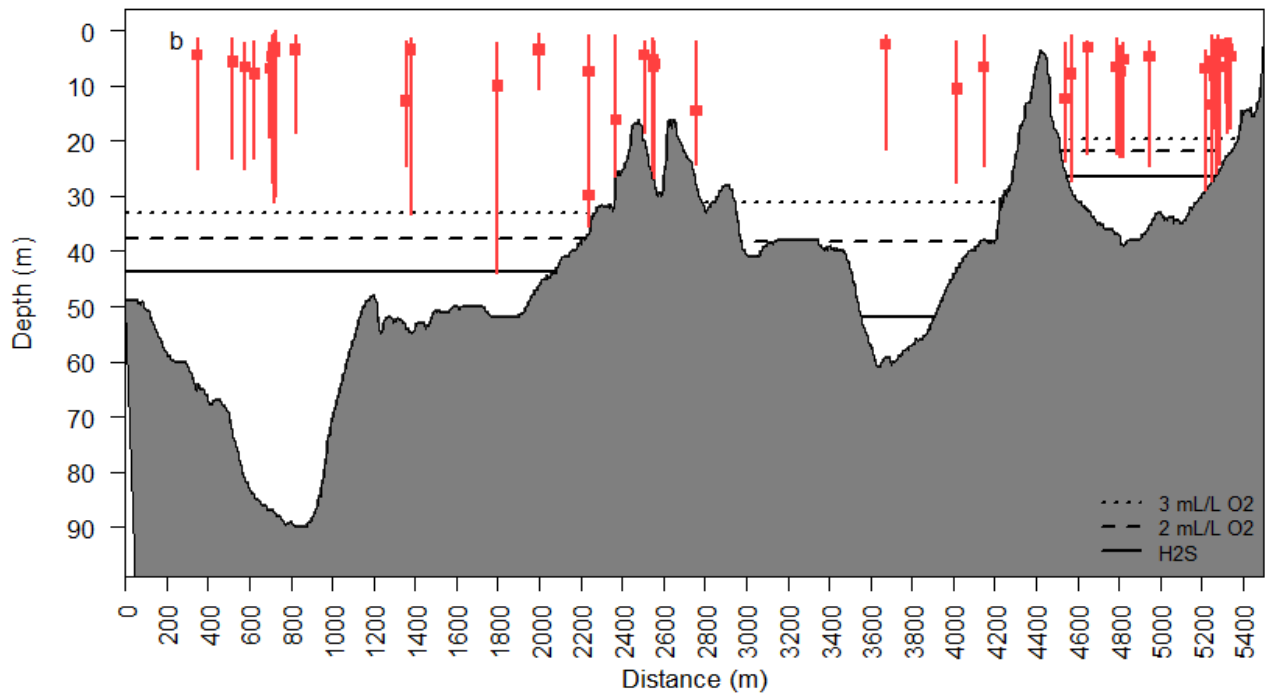


Fig. 11. The vertical and horizontal distribution of cod along a line transect (m) curved through the Tvedestrand fjord in September (a), October (b) and November (c). The vertical red lines represent individual cod and their depth distribution each month. The red rectangles marked in each line show each cod's median position. Individuals are placed according to their mean geographical position along the constructed line profile through the fjord. Dotted line illustrates the oxygen 3 mL L^{-1} boundary, dashed line 2 mL L^{-1} , while the area under the solid line indicates anoxic bottom water (hydrogen sulfide).

3.5 Distribution of cod in relation to temperature

Cod were observed throughout most of the available temperatures. However, our data showed that low temperatures were avoided by our tagged individuals with less than 1 % of the cod found in temperatures below 8.5 °C (Fig. 12).

In September, cod was observed in temperatures between 15.6 and 6.5 °C, with a clear peak between 14 and 15.5 °C (80 %). Cod observations decreased as temperature declined. Cod tended to aggregate at higher temperatures this month compared with the following two months. In October, over 90 % of the cod were found in water with temperatures between 10 and 13.5 °C with dominating temperatures from 11.5 to 12 °C. Cod abundance sunk as temperatures decreased and only a small proportion (0.23 %) was detected in temperatures below 8.5 °C. By November, cod were mostly registered in water temperatures between 9.5 and 11.5, accounting for nearly 90 % total time. A clear temperature preference was observed between 10.5 and 11 °C. No cod was present in water layers with less than 8.5 °C.

3.6 Distribution of cod in relation to salinity

Tagged cod did not utilize the whole available salinity range observed in the study area and were virtually absent from high-salinity bottom water with less than 1 % associated with salinities higher than 33 (Fig. 12).

In September, almost 90 % of the cod were registered in salinities between 31 and 33, with the highest amount observed in salinities between 31.5 and 33. The abundance of cod decreased with increasing salinities. Individuals did not progress above salinities of 33.19 this month. In October, most of the cod were found in salinities between 29 and 30.5. Similarly, cod were absent from high salinity waters where none of the individuals were observed in salinities above 32.94. By November, water masses containing salinities between 30 and 33 accounted for over 90 % of the observations with highest abundance between salinities of 31 and 33. No cod were found above salinities of 33.40.

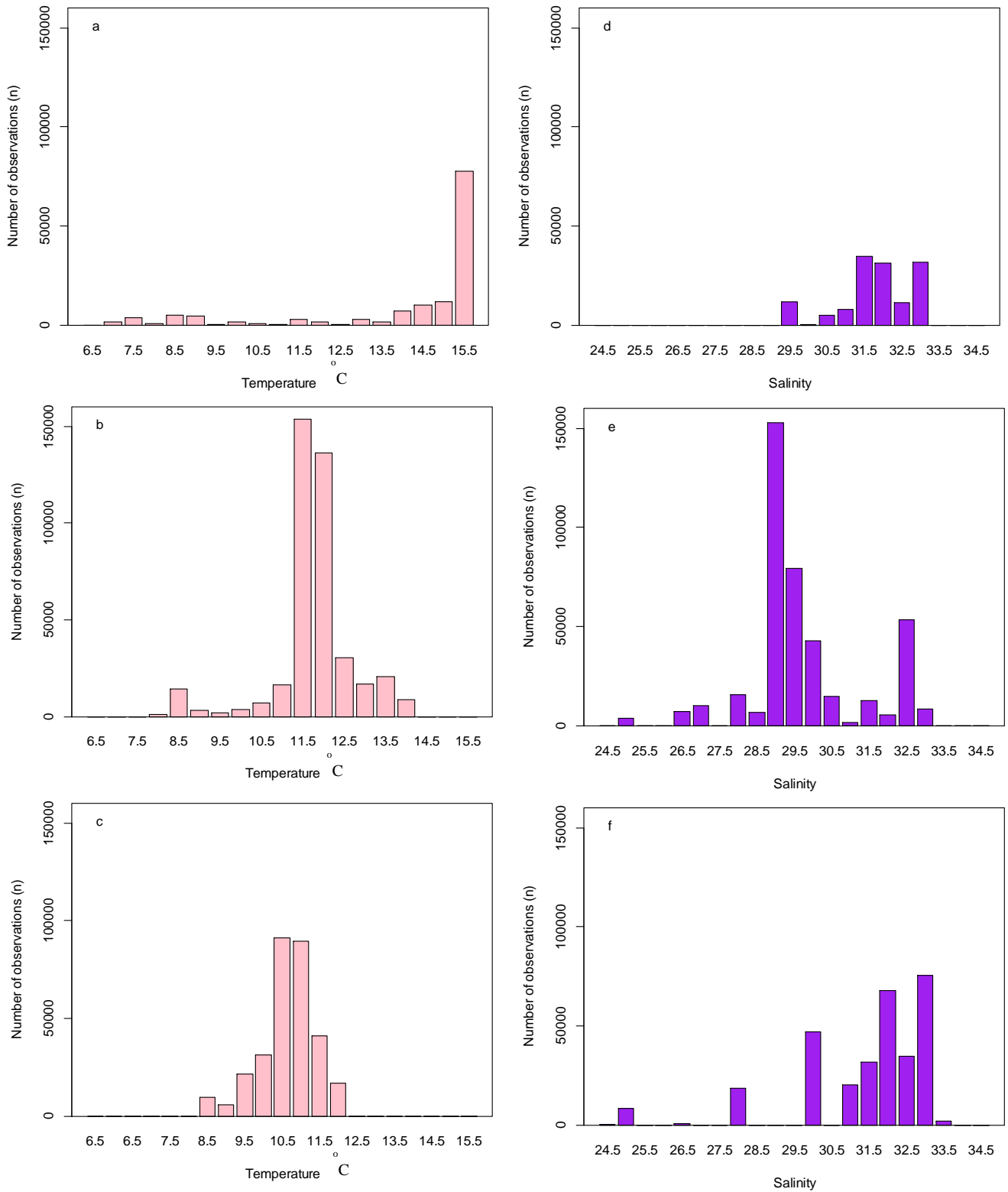


Fig.12. The distribution of cod in September (a, d), October (b, e) and November (c, f) in relation to ambient temperature °C (pink) and salinity (purple).

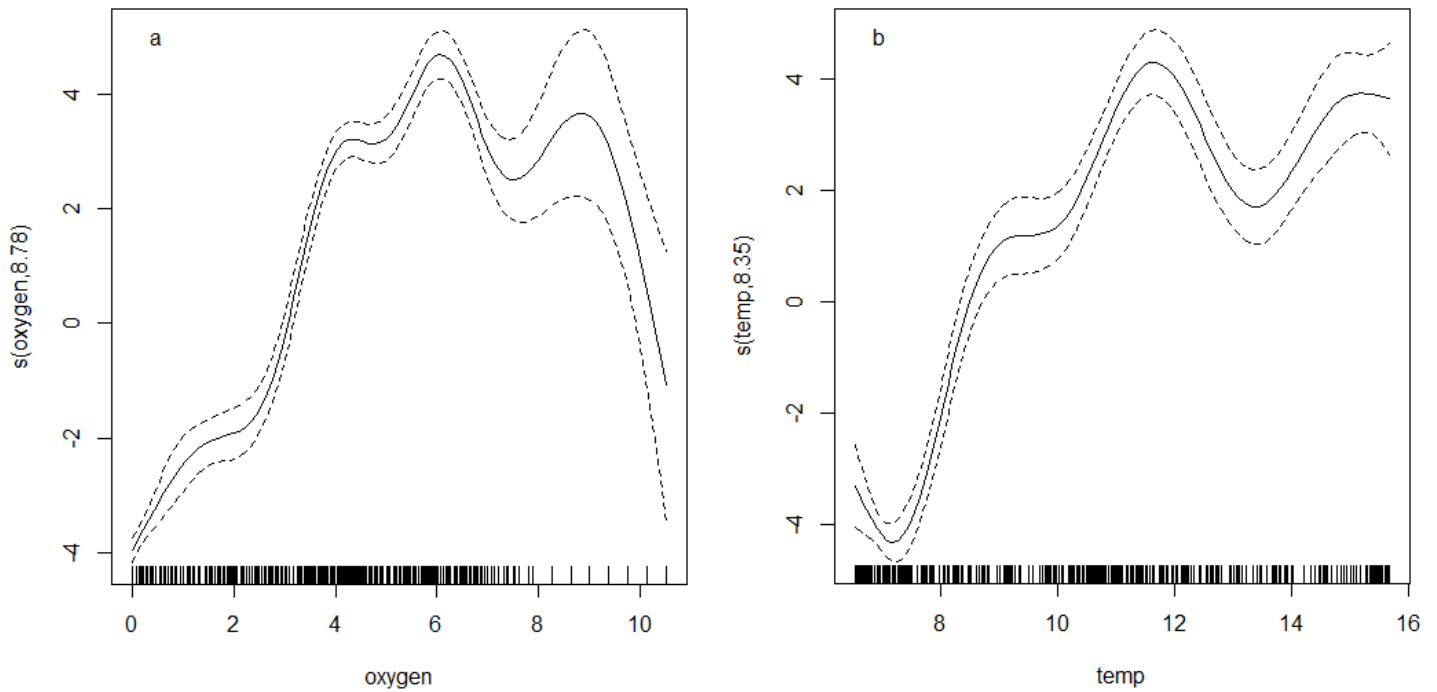
3.7 Environmental effects on cod spatial distribution

Both oxygen, temperature and salinity had statistically significant effects on the spatial distribution of cod (Table 3). Model comparisons using the GCV-score indicated that cod distribution was better explained by oxygen, as compared to temperature and salinity (Table

3). The effect of oxygen was strongly negative for levels below 3 mL L⁻¹ (Figure 13). Further, two separate models indicated a clear negative effect of low temperature and high salinity on cod distribution (Fig. 13). Salinity was the variable influencing cod distribution the least (GCV score = 4.51).

Table 3. GAM modeling of cod distribution in relation to oxygen, temperature and salinity. The variables were tested in three separate models and compared using the GCV score.

Variable	R-sq.(adj)	GCV score	Pr(> t)
Oxygen	0.82	2.44	< 0.0001
Temperature	0.70	4.05	< 0.0001
Salinity	0.67	4.51	< 0.0001



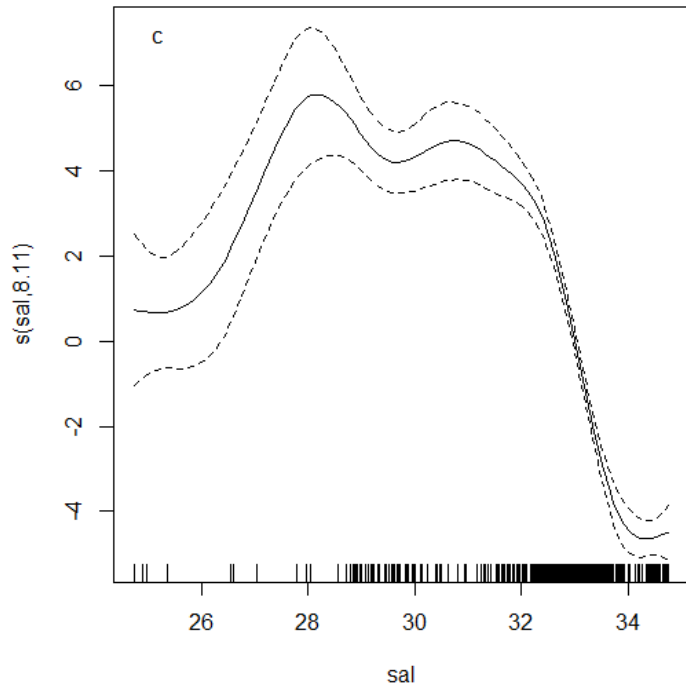


Fig. 13. Predicted (GAM) effects of oxygen (a), temperature (b) and salinity (c) levels on cod distribution, showing the mean prediction (solid line) and 95% confidence limits (dashed line).

4 Discussion

This study investigated the influence of fjord environmental conditions on the habitat use (spatial distribution) of cod, specifically exploring the potential detrimental effects of oxygen depletion on habitat availability. Oxygen depletion in coastal waters may be a considerable issue in many parts of the world (Wu 2002, Herbert et al. 2011).

The hydrographical conditions observed in the Tvedestrand fjord were typical for sill fjords along the Norwegian Skagerrak coast, with low levels of oxygen in the deep water layers (Aure et al. 1996; Johannessen & Dahl 1996). The highly saline- and oxygen depleted water close to seafloor indicated that the Tvedestrand fjord experienced a long stagnation period prior to our survey in 2012. Atlantic cod was almost exclusively found above 30 m, with highest abundance in layers > 14 m depth, i.e. above low levels of oxygen. This study is the first to observe the movement of cod in the Tvedestrand fjord.

We note that factors other than oxygen, temperature and salinity are likely to affect the movement of cod in this study area (indicated by unexplained variance in cod distribution in the GAM models). Possible explanations may include diel vertical migration which is a widespread phenomenon observed among many aquatic species (Sims et al. 2009) where individuals occupy deep bottom water during daytime and return to shallow water at night (Gliwicz 1986; Clark & Levy 1988; Loose & Dawidowicz 1994). This behavior has probably evolved as a tradeoff between food availability and predator risk. The influence of bottom depth on the distribution of cod have been shown where the abundance of cod significantly increased with shallow depths (Tomkiewicz et al. 1998). In addition, organisms have preferable habitats where the choice of habitat depend on what requirements is to be satisfied, i.e., habitat structure and availability, food supply, inter- and intraspecific competition (Gjøsæter 1987a; Menge & Sutherland 1987), shelter from predation and finding a mate (Adams 1976). Some studies have found a linkage between rich vegetation's and the faunal community structure (Wheeler 1980; Carr 1989; Sogard & Able 1991), meaning that i.e., diverse sea grass meadows support more vertebrates and invertebrates compared with unvegetated habitats (Orth et al. 1984). For instance, cod are known to utilize such rich feeding grounds at very shallow depths (1-2 m) (Pihl 1982).

We also note that, since all are variables were strongly correlated, it may be difficult to tease out their relative importance on cod distribution. However, the comparison across months and

basins somewhat reduces this problem, showing for instance that cod shifted to more shallow waters during a period of extending hypoxia and in the basin with the poorest oxygen concentration.

4.1 Distribution of cod in relation to ambient oxygen concentration

Accounting for significant month-basin effects, our models supported the hypothesis that oxygen concentration is an important environmental variable affecting the distribution of cod. In particular, oxygen levels below 3 mL L⁻¹ showed a marked negative effect on the occurrence of cod. Similar results were found by D'Amours (1993) in the Gulf of St Lawrence where cod avoided oxygen levels below 3.4 mg L⁻¹ (equivalent to 2.4 mL L⁻¹). Furthermore, a study in the Bornholm basin (Baltic Sea) found that cod mainly occupied water layers with oxygen levels above 2.5 mL L⁻¹ (Tomkiewicz et al. 1998). Since populations are thought to differ in intra-specific tolerance to hypoxia (Skjæraasen et al. 2008), this may explain why slightly different results were found in my study.

Further findings supporting our hypothesis that cod avoid low levels of oxygen were found when comparing vertical movement of cod among months and basins. In October, oxygen depletion in the deepest parts progressed throughout the whole system with layers below 44 (± 18 m) showing ambient oxygen levels < 1 mL L⁻¹. The overall median distribution of cod was shallower than in the other months. Additionally, cod was found to aggregate at shallower depths in the south-eastern basin compared with other parts of the fjord where the water body was more oxygenized. Similar findings have been observed in the Baltic Sea (Schaber et al. 2012) where progressive oxygen depleted water induced an upward shift in cod depth use.

In captivity, cod are known to exhibit physiological reactions to low oxygen concentrations. Sundnes (1957) reported that oxygen levels below 3.5 mL L⁻¹ led to rapid decline in the normal metabolic rate of fish. Saunders (1963) performed further analysis on cod respiration and suggested that oxygen levels below 3 mg L⁻¹ induced stress since the oxygen consumption rate would not keep pace with the increasing metabolic cost of irrigating the gills. More recently, cod was observed to hyperventilate in mild hypoxic conditions with oxygen conditions below 4 mg L⁻¹ (Claireaux & Dutil 1992). These publications elucidate mechanisms behind field observations of cod avoiding low levels of oxygen.

In October and November, however, a minor fraction of cod was detected in water bodies with $< 1 \text{ mL L}^{-1}$ oxygen. This behavior have been observed under laboratory experiments where cod in general avoided low oxygen levels ($< 16 \%$ saturation), but voluntarily entered hypoxic water if food was offered (Claireaux et al. 1995). Cod could also swim into hypoxic water to reduce osmotic stress (Neuenfeldt et al. 2009), or to display courtship and mating behavior (Rose 1993; Lawson & Rose 2000).

Fish exhibit a well-developed sensing capacity to the external environment (Burluson 1995; Perry & Gilmour 2002). Both internal and external oxygen receptors on their gills play an important role to modulate cardiorespiratory reflexes during hypoxia. It would therefore appear that cod not necessarily avoid dangerous regions, but rather intentionally perform “hypoxic diving” to access for instance rich feeding areas.

Moreover, cod possess excellent survival strategies under the influence of hypoxia. In order to increase duration during visits to hypoxic waters, cod may reduce its swimming speed (Schurmann & Steffensen 1994; Herbert & Steffensen 2005) or increase gill ventilation (Randall 1982). However, Herbert et al. (2011) reported that cod actually swam *faster* on the more hypoxic side of an experimental chamber and suggested that this behavior represented an escape reaction. Previous studies have actually not presented fish with the choice or opportunity to escape under progressive hypoxia. Short-term forays would probably only occur if cod had access to full O_2 refuge areas. This appears reasonable since O_2 refuge areas would ultimately allow cod to regulate their total time under hypoxia within safe physiological limits.

4.2 Distribution of cod in relation to temperature

In this study, cod was found to avoid low temperatures. Specifically, less than 1 % of the cod observations were associated with temperatures below $8.5 \text{ }^\circ\text{C}$.

Temperature effects on cod habitat use have been reported for a number of stocks (Tomkiewicz et al. 1998). For example, in the Gulf of St Lawrence, cod avoided temperatures below $2 \text{ }^\circ\text{C}$ (D'Amours 1993). More recent studies from in the Gulf of St Lawrence found that cod selected temperatures in relation to age (Swain & Kramer 1995). Smith & Page (1996) reported highest abundance of cod in the intermediate cold-water layers. They also found age- and area-specific associations with temperature and salinity. Lastly, Tomkiewicz et al. (1998)

found that adult cod tended to aggregate in warmer water than immature cod. This behavior might be a pattern of selection, related to changes in temperature preference during spawning (Rose 1993).

The effects of temperature have also been studied in relation to incubation of cod egg (Alderdice & Forrester 2011). In the natural environment, temperature was suggested as the major factor to controlling successful egg development. Cod egg in temperature ranges of 3-5 °C was shown to tolerate a wide variety of salinities and dissolved oxygen. The development of egg was found to decrease below 3°C.

High temperatures function by increasing the metabolic rate in fish which further enhance oxygen consumption (Schurmann & Steffensen 1997). Increasing temperatures also reduce available oxygen by decreasing its solubility (Benson & Krause 1984). Thus, if the severity and frequency of hypoxic events increase, areas affected by eutrophication might become exacerbated as temperatures around the world increases by global warming (Grottoli et al. 2006; Schiermeier 2006). This may place additional pressure on the marine stocks already at historical lows, like the Atlantic cod population in the North Atlantic (Hutchings & Baum 2005).

4.3 Distribution of cod in relation to salinity

In our study, cod tended to avoid water masses with high salinity, and were virtually absent from high-salinity bottom water. In the other end of the scale, cod in the Borholm basin avoided salinities < 11 (Tomkiewicz et al. 1998). The authors suggested that salinity functioned as an upper boundary, preventing cod from entering shallow waters. Since cod tended to aggregate near the surface, no restricted upper boundary was evident in this study. This might be explained by the fact that our salinity values did not range by the extreme from shallow- to deeper depths; as an effect of limited freshwater discharge along the northern sector of the fjord.

Claireaux et al. (1995) studied the behavior of free-swimming cod in the laboratory under the impact of fluctuating salinities. Cod were observed to select low-salinity upper layers if given choice was provided and were reluctant to leave this layer. When fully strength sea water was added to the tank, an escape reaction towards the approaching high-salinity water was observed. However, when food was introduced to the high-salinity layers in the tank, fish did

not hesitate to dive in and feed. The individuals remained there for as long as food could be found. When no more food was available, cod immediately returned to low salinity layers. These findings support our hypothesis that in general cod avoid high-salinity levels.

Few studies have actually investigated the impact of acute salinity on the metabolic rate of cod (Claireaux et al. 1995). However, Dutil et al. (1992) studied the effect of osmoregulation on cod and found no severe disturbance in low salinities (7) during the first 24 hours in diluted seawater. Furthermore, Claireaux et al. (1995) found no changes in cod behavior during acclimation in salinities from 28 to 7.

The ability for cod eggs to maintain neutral buoyancy and thereby survive varies between years, spawning area and prevailing conditions (Nissling et al. 1994). Between 1976 and 1977, the Bornholm basin experienced a major inflow from the North Sea (Fonselius 1988). Favorable conditions resulted in successful spawning amongst the local cod population where nearly all egg batches observed managed to maintain neutral buoyancy. In the following years (after a long stagnation period) deep water bodies were dominated by low levels of oxygen and high salinities. The spawning success was then low with only a few egg batches able to maintain neutral buoyancy. Fonselius (1988) concluded that egg survival depended on inflow of oxygenated saline water.

The growth of cod has also been observed under the impact of various environmental salinities. Lambert et al. (2011) found higher growth rate among cod present in low salinity water and suggested that cod increase their food conversion efficiency when within preferable salinity levels.

Conversely, Claireaux & Dutil (1992) found in a laboratory experiment that salinity had little influence on the tolerance of cod towards low oxygen levels.

5 Conclusion

This study found that the distribution of Atlantic cod (*Gadus morhua*) within a small fjord is likely strongly influenced by prevailing hydrographical conditions. Most notably, telemetry-tagged individuals avoided deep waters with low oxygen concentration. I put this forward as an important topic for future research, because severe hypoxia is becoming increasingly common in coastal areas all around the world (Diaz & Rosenberg 2008; Kidwell et al. 2009). This presents a worrying situation because cod is already facing additional threats from intensive fishing pressure and climate change (Claireaux et al. 1995). As a result, the overall vertical range of favorable habitats may diminish, which can further lead to reduction in successful spawning and feeding opportunities (Schaber et al. 2012). In the future, we should continue to monitor cod distribution in relation to environmental variables and work together as a nation to reduce total anthropogenic impact on the environment.

6 References

- Aarnio, K., Bonsdorff, E. & Norkko, K. (1998). Role of *Halicryptus spinulosus* (Priapulida) in structuring meiofauna and settling macrofauna. *Marine Ecology Progress Series*, 163: 145-153.
- Adams, S.M. (1976). The ecology of eelgrass, *Zostera marina* (L), fish communities. I. Structural analysis. *Journal of Experimental Marine Biology and Ecology*, 22: 269-291.
- Alderdice, D.F, Forrester, C.R (2011). Effects of salinity, temperature and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). *Journal of the Fisheries Research Board of Canada*, 28: 883-902.
- Aure, J., Danielssen, D. & Sætre, R. (1996). Assessment of eutrophication in Skagerrak coastal waters using oxygen consumption in fjordic basins. *ICES Journal of Marine Science*, 53: 589-595.
- Baden, S.P., Loo, L.O., Pihl, L. & Rosenberg, R. (1990). Effects of eutrophication on benthic communities including fish: Swedish west coast. *Royal Swedish Academy of Sciences*, 19: 113-122.
- Beamish, R.J., McFarlane, G.A. & Benson, A. (2006). Longevity overfishing. *Progress in Oceanography*, 68: 289-302.
- Benson, B.B. & Krause Jr, D. (1984). The concentration and isotopic fractionation of oxygen dissolved in freshwater and seawater in equilibrium with the atmosphere. *Limnology Oceanography*, 29: 620-632.
- Bigelow, H.B. & Schroeder, W.C. (1953). Fishes of the Gulf of Maine. *Fish Bull*, 53: 182-196.
- Brandt, S.P., Gerken, M., Hartman, K.J. & Demers, E. (2009). Effects of hypoxia on food consumption and growth of juvenile striped bass (*Morone saxatilis*). *Journal of Experimental Marine Biology and Ecology*, 381: 143-149.

- Burleson, M. (1995). Oxygen availability: sensory systems. In: Hochachka PW, Mommsen TP (eds) Environmental and Ecological Biochemistry, Elsevier, New York, pp: 1-18.
- Carr, M.H. (1989). Effects of macroalgae assemblages on the recruitment of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology*, 126: 59-76.
- Ciannelli, L., Knutsen, H., Olsen, E.M., Espeland, S.H., Asplin, L., Jelmert, A., Knutsen, J. A. & Stenseth, N.C. (2010). Small-scale genetic structure in a marine population in relation to water circulation and egg characteristics. *Ecology*, 91: 2918-2930.
- Claireaux, G. & Dutil, J. D. (1992). Physiological response of the Atlantic cod (*Gadus morhua*) to hypoxia at various environmental salinities. *Journal of Experimental Biology*, 163: 97-118.
- Claireaux, G., Webber, D.M., Kerr, S.R. & Boutilier, R.G. (1995). Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating salinity and oxygenation conditions. *Journal of Experimental Biology*, 198: 61-69.
- Clark, C.W. & Levy, D.A. (1988). Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *The American Naturalist*, 131: 271-290.
- Crawley, M.J (2007). *The R Book*. Wiley Publishing, Imperial College London at Silwood Park, UK. ISBN:0470510242 9780470510247.
- Dahl, E., Dahl, F.E. & Danielssen, D.S (eds). (1987). Resipientundersøkelser i Tvedestrandsfjorden 1985. Flødevigen meldinger 1. (In Norwegian).
- Dahl, E. & Danielssen, D.S. (1992). Long-term observations of oxygen in the Skagerrak. *ICES Marine Science Symposia*, 195: 455-461.
- D'Amours, D. (1993). The distribution of cod (*Gadus morhua*) in relation to temperature and oxygen levels in the Gulf of St. Lawrence. *Fisheries Oceanography*, 2: 24-29.

- Diaz, R.J. & Rosenberg, R. (2008). Spreading dead zones and consequences of marine ecosystems. *Science*, 321: 926-929.
- Dutil, J.D., Munro, J., Audet, C. & Besner, M. (1992). Seasonal variation in the physiological response of the Atlantic cod *Gadus morhua* to low salinity. *Canadian Journal of Fisheries and Aquatic Science*, 49: 1149-1156.
- Espeland, S.H., Gundersen, A.F., Olsen, E.M., Knutsen, H., Gjørseter, J. & Stenseth, N.C. (2007). Home range and elevated egg densities within an inshore spawning ground of coastal cod. *ICES Journal of Marine Science*, 64: 920-928.
- FAO, 2000. United Nations Food and Agricultural Organization. FAO agricultural data bases are obtainable on the world wide web: <http://www.fao.org>
- Fonselius, S. (1988). Long-term trends of dissolved oxygen, pH and alkalinity in the Baltic deep basins. Intern Counc Explorer Sea Community Meeting (Hydrography Comm.), 23:1-6.
- Gamenick, I., Jahn, A., Vopel, K. & Giere, O. (1996). Hypoxia and sulphide as structuring factors in a macrozoobenthic community on the Baltic Sea shore : colonisation studies and tolerance experiments. *Marine Ecology Progress Series*, 144: 73-85.
- Gilbert, D., Sundby, B., Gobeil, C., Mucci, A. & Tremblay, G.H. (2005). A seventy-two-year record of diminishing deep-water oxygen in the St. Lawrence estuary: The northwest Atlantic connection. *Limnology and Oceanography*, 50: 1654-1666.
- Gjørseter, J. (1987a). Habitat selection of juvenile cod (*Gadus morhua*), whiting (*Merlangus merlangius*) and some littoral fish in an aquarium. *Flødevigen Rapport Series*, 1: 17-26.
- Gliwicz, M.Z. (1986). Predation and the evolution of vertical migration in zooplankton. *Nature*, 320:746-748.
- Grottoli, A.G., Rodrigues, L.J. & Palardy, J.E. (2006). Heterotrophic plasticity and resilience in bleached corals. *Nature*, 440: 1186-1189.

- Herbert, N.A. & Steffensen, J.F. (2005). The response of Atlantic cod, *Gadus morhua*, to progressive hypoxia: fish swimming speed and physiological stress. *Marine Biology*, 147: 1403-1412.
- Herbert, N.A., Skjæraasen, J.E., Nilsen, T., Salvanes, A.G.V. & Steffensen, J.F. (2011). The hypoxia avoidance behaviour of juvenile Atlantic cod (*Gadus morhua* L.) depends on the provision and pressure level of an O₂ refuge. *Marine Biology*, 158: 737-746.
- Hutchings, J.A. & Myers, R.A. (1994). What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 2126-2146.
- Hutchings, J.A. (1999). Influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 1612-1623.
- Hutchings, J.A. & Baum, J.K. (2005). Measuring marine fish biodiversity: temporal change in abundance, life history and demography. *Philosophical Transactions of The Royal Society B*, 360: 315-338.
- Johannessen, T. & Dahl, E. (1996). Declines in oxygen concentrations along the Norwegian Skagerrak coast, 1927-1993: A signal of ecosystem changes due to eutrophication? *Limnology and Oceanography*, 41: 766-778.
- Kidwell, D.M., Lewitus, A.J., Jewett, E.B., Brandt, S. & Mason, D.M. (2009). Ecological impacts of hypoxia on living resources. *Journal of Experimental Marine Biology and Ecology*, 381: 1-3.
- King, W., Hooper, B., Hillsgrove, S., Benton, C. & Berlinsky, D.L (2005). The use of clove oil, metomidate, tricaine methanesulphonate and 2-phenoxyethanol for inducing anaesthesia and their effect on the cortisol stress response in black sea bass (*Centropristis striata* L.). *Aquaculture Research*, 36: 1442-1449.

- Knutsen, H., Jorde, P.E., André, C. & Stenseth, N.C. (2003). Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. *Molecular Ecology*, 12: 385-394.
- Knutsen, H., André, C., Jorde, P.E., Skogen, M.D., Thuróczy, E. & Stenseth, N.C. (2004). Transport of North Sea cod larvae into the Skagerrak coastal populations. *Proceedings Royal Society B*, 271: 1337-1344.
- Knutsen, H., Olsen, E.M., Ciannelli, L., Espeland, S.H., Knutsen, J.A., Simonsen, J.H., Skreslet, S. & Stenseth, N.C. (2007). Egg distribution, bottom topography and small-scale cod population structure in a coastal marine system. *Marine Ecology Progress Series*, 333: 249-255.
- Knutsen, J.A., Knutsen, H., Rinde, E., Christie, H., Bodvin, T. & Dahl, E. (2010). Mapping Biological Resources in the Coastal Zone: An Evaluation of Methods in a Pioneering Study from Norway. *Ambio*, 39: 148-158.
- Lambert, Y., Dutil, J.D. & Munro, J. (2011). Effects of Intermediate and low salinity conditions on growth rate and food conversion of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Science*, 51: 1569-1576.
- Lawson, G.L. & Rose, G.A. (2000). Small-scale spatial and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. *Canadian Journal of Fisheries and Aquaculture Science*, 57: 1011-1024.
- Lazic, S.E. (2010). The problem of pseudoreplication in neuroscientific studies: is it affecting your analysis? *Lazic BMC Neuroscience*, 11: 1471-2202.
- Loose, C.J. & Dawidowicz, P. (1994). Trade-offs in diel vertical migration by zooplankton: The costs of predator avoidance. *Physiological Ecology*, 75: 2255-2263.
- Mason Jr, W.T. (1998). Macrobenthic monitoring in the Lower St. Johns River, Florida. *Environmental Monitoring and Assessment*, 50: 101-130.

- Menge, B.A. & Sutherland, J.P. (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*, 130: 730-757.
- Murawski, S.A. & Finn, J.T. (1988). Biological bases for mixed-species fisheries: Species co-distribution in relation to environmental and biotic variables. *Canadian Journal of Fisheries and Aquatic Sciences*, 45: 1720-1735.
- Neuenfeldt, S. (2002). The influence of oxygen saturation on the distributional overlap of predator (cod, *Gadus morhua*) and prey (herring, *Clupea harengus*) in the Bornholm Basin of the Baltic Sea. *Fisheries Oceanography*, 11: 11-17.
- Neuenfeldt, S., Andersen, K.H. & Hinrichsen, H.H. (2009). Some Atlantic cod *Gadus morhua* in the Baltic Sea visit hypoxic water briefly but often. *Journal of Fish Biology*, 75: 290-294.
- Nissling, A., Kryvi, H. & Vallin, L. (1994). Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. *Marine Ecology Progress Series*, 110: 67-74.
- Nixon, S.W. (1995). Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia*, 41: 199-219.
- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. & Dieckmann, U. (2004). Maturation trends indicative of rapid evolution preceded the collapse of Northern cod. *Nature*, 428: 932-935.
- Olsen, E.M., Knutsen, H., Gjørseter, J., Jorde, P.E., Knutsen, J.A. & Stenseth, N.C. (2008). Small-scale biocomplexity in coastal Atlantic cod supporting a Darwinian perspective on fisheries management. *Evolutionary Applications*, 1: 524-533.
- Olsen, E.M. & Moland, E. (2011). Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. *Evolutionary Ecology*, 25: 695-710.

- Orth, R.J., Heck, K.L. & Montfrans, J.V. (1984). Faunal communities in seagrass beds: a review of the influence of plant structures and prey characteristics on predator-prey relationships. *Estuaries*, 7: 339-350.
- Paerl, H.W. (1995). Coastal eutrophication in relation to atmospheric nitrogen deposition: Current perspectives. *Ophelia*, 41: 237-259.
- Peckol, P. & Rivers, J.S. (1995). Physiological responses of the opportunistic macroalgae *Cladophora vagabunda* (L.) van den Hoek and *Gracilaria tikvahiae* (McLachlan) to environmental disturbances associated with eutrophication. *Journal of Experimental Marine Biology and Ecology*, 190: 1-16.
- Perry, R.I. & Smith, S.J. (1994). Identifying Habitat Associations of Marine Fishes Using Survey Data: An Application to the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 589-602.
- Perry, S.F. & Gilmour, K.M. (2002). Sensing and transfer of respiratory gases at the fish gill. *Journal of Experimental Zoology*, 293: 249-263.
- Pettersen, A.R., Moland, E., Olsen, E.M. & Knutsen, J.A. (2009). Lobster reserves in coastal Skagerrak – an integrates analysis of the implementation process. Pages 178-188 in E. Dahl, E. Moksness, & J. Støttrup, editors. Wiley-Blackwell Scientific Publications, London.
- Plante, S., Chabot, D. & Dutil, J.D. (1998). Hypoxia tolerance in Atlantic cod. *Journal of Fish Biology*, 53: 1342-1356.
- Pihl, L. (1982). Food intake of young cod and flounder in a shallow bay on the Swedish west coast. *Netherlands Journal of Sea Research*, 15: 419-432.
- Pihl, L., Baden, S.P., Diaz, R.J. & Schaffner, L.C. (1992). Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea. *Marine Biology*, 112: 349-361.

- Randall, D.J. (1982). The control of respiration and circulation in fish during exercise and hypoxia. *Journal of Experimental Biology*, 100: 275-288.
- Roberts, J.J., Höök, T.O., Ludsin, S.A., Pothoven, S.A., Vanderploeg, H.A. & Brandt, S. B. (2009). Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. *Journal of Experimental Marine Biology and Ecology*, 381: 132-142.
- Rose, G.A. (1993). Cod spawning on a migration highway in the north-west Atlantic. *Nature*, 366: 458-461.
- Rose, K.A., Adamack, A.T., Murphy, C.A., Sable, S.E., Kolesar, S.E., Craig, J.K., Breitburg, D.L., Thomas, P., Brouwer, M.H., Cerco, C.F. & Diamond, S. (2009). Does hypoxia have population-level effects on coastal fish? Musings from the virtual world. *Journal of Experimental Marine Biology and Ecology*, 381: 188-203.
- Rosenberg, R. (1985). Eutrophication – the Future Marine Coastal Nuisance? *Marine Pollution Bulletin*, 16: 227-231.
- Rosenberg, R., Hellmann, B. & Johansson, B. (1991). Hypoxic tolerance of marine benthic Fauna. *Marine Ecology Progress Series*, 79: 127-131.
- Sandberg, E. (1997). Does oxygen deficiency modify the functional response of *Saduria entomon* (Isopoda) to *Bathyporeia pilosa* (Amphipoda)? *Marine Biology*, 129: 499-504.
- Saunders, R. L. (1963). Respiration of the Atlantic cod. *Journal of the Fisheries Research Board of Canada*, 20: 373-386.
- Schaber, M., Hinrichsen, Hh., Neuenfeldt, S. & Voss, R. (2009). Hydroacoustic resolution of small-scale vertical distribution in Baltic cod *Gadus morhua*—habitat choice and limits during spawning. *Marine Ecology Progress Series*, 377: 239-253.

- Schaber, M., Hinrichsen, H.H. & Gröger, J. (2012). Seasonal changes in vertical distribution patterns of cod (*Gadus morhua*) in the Bornholm Basin, central Baltic Sea. *Fisheries Oceanography*, 21: 33-43.
- Schiermeier, Q. (2006). The costs of global warming. *Nature*, 439, 374-375.
- Schurmann, H. & Steffensen, J. (1994). Spontaneous swimming activity of Atlantic cod *Gadus morhua* exposed to graded hypoxia at three temperatures. *The Journal of Experimental Biology*, 197: 129-142.
- Schurmann, H. & Steffensen, J.F. (1997). Effects of temperature, hypoxia and activity on the metabolism of juvenile Atlantic cod. *Journal of Fish Biology*, 50: 1166-1180.
- Simpfendorfer, C.A., Heupel, M.R. & Hueter, R.E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movement. *Canadian Journal of Fisheries and Aquaculture Science*, 59: 23-32.
- Sims, D.W. (2009). Satellite tracking of the world's largest bony fish, the ocean sunfish (*Mola mola* L.) in the North East Atlantic. *Journal of Experimental Marine Biology and Ecology*, 370:127–133.
- Skjærraasen, J.E., Nilsen, T., Meager, J.J., Herbert, N.A., Moberg, O., Tronci, V., Johansen, T. & Salvanes, A.G.V. (2008). Hypoxic avoidance behaviour in cod (*Gadus morhua* L.): The effect of temperature and haemoglobin genotype. *Journal of Experimental Marine Biology and Ecology*, 358: 70-77.
- Smith, S.J. & Page, F.H. (1996). Associations between Atlantic cod (*Gadus morhua*) and hydrographical variables: implications for the management of the 4VsW cod stock. *ICES Journal of Marine Science*, 53: 597-614.
- Sogard, S.M. & Able, K.W. (1991). A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine, Coastal and Shelf Science*, 33: 501-519.

- Strickland, J.D.H. & Parsons, T.R. (1968). A practical handbook of seawater analysis. Bulletin of Fisheries and Research Board Canada. 167.
- Sundnes, G. (1957). On the transport of live cod and coalfish. ICES Journal of Marine Science, 22: 191-196
- Swain, D.P. & Kramer, D.L. (1995). Annual variation in temperature selection by Atlantic cod *Gadus morhua* in the southern Gulf of St. Lawrence, Canada, and in its relation to population size. Marine Ecology progress Series, 116: 11-23.
- Taylor, J.C., Rand, P.S. & Jenkins, J. (2007). Swimming behavior of juvenile anchovies (*Anchoa* spp.) in an episodically hypoxic estuary: implications for individual energetics and trophic dynamics. Marine Biology, 152: 939-957.
- Thomas, P., Rahman Md. S., Khan, I.A. & Kummer, J.A. (2007). Widespread endocrine disruption and reproductive impairment in an estuarine fish population exposed to seasonal hypoxia. Proceedings Royal Society / Biological Sciences, 274: 2693-2702.
- Tomkiewicz, J., Lehmann, K.M. & St. John, M. (1998). Oceanographic influences on the distribution of Baltic cod, *Gadus morhua*, during spawning in the Bornholm Basin of the Baltic Sea. Fisheries Oceanography, 7: 48-62.
- Wheeler, A. (1980). Fish-algal relations in temperate waters. In: The shore environment. Edited by J.H. Price., D.E.G. Irvine & W.F. Farnham. Academic Press, London, 677-698.
- Wroblewski, J.S., Hiscock, H.W. & Bradbury, I.R. (1999). Fecundity of Atlantic cod (*Gadus morhua*) farmed for stock enhancement in Newfoundland bays. Fisheries oceanography, 171: 163-180.
- Wu, R.S.S. & Lam, P.K.S. (1997). Glucose-6-phosphate dehydrogenase and lactate dehydrogenase in the green-lipped mussel (*Perna viridis*): Possible biomarkers for hypoxia in the marine environment. Water Research, 31: 2797-2801.

Wu, R.S.S. (2002). Hypoxia: from molecular responses to ecosystem responses. *Marine Pollution Bulletin*, 45: 35-45.

Web references:

Correiogourmand.com.br. Localized 19.05.2013

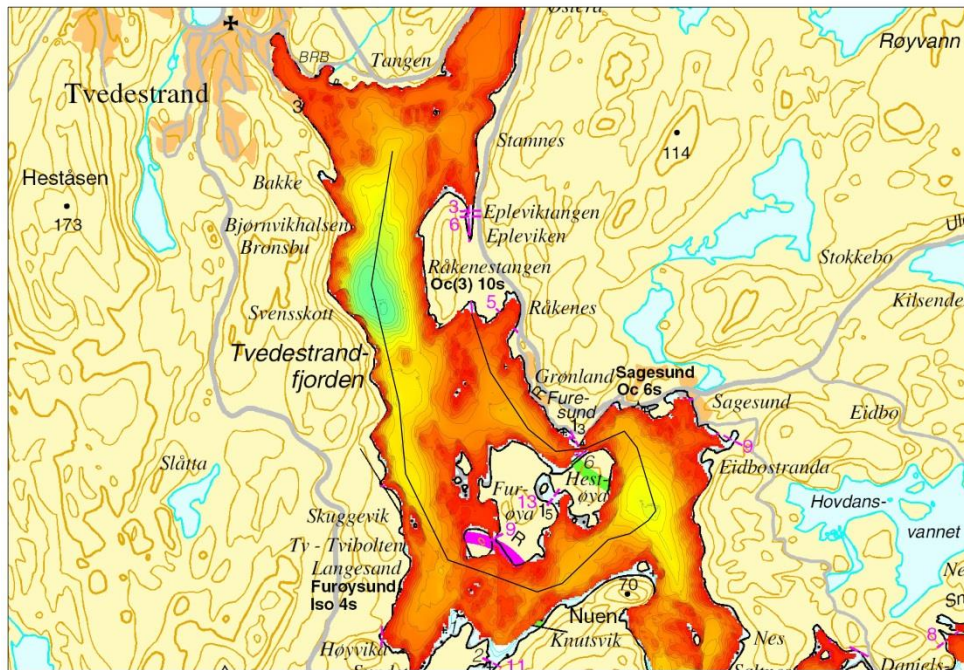
http://correiogourmand.com.br/info_03_dicionarios_gastronomicos_alimentos_carnes_pescados_peixe_bacalhau_01_o_peixe_fotos.htm

Otterspecialistgroup.org. Localized 19.05.2013

<http://www.otterspecialistgroup.org/OM/causes.html>

7 Appendix 1

Line profile constructed through the Tvedestrand fjord. Depth data points were made every 5 m, starting in the northern sector of the fjord, going south and around the centered islands. The line was in total 5500 m long. Individual mean geographical position was replaced horizontally towards the line. Each individual's new geographical position was registered in m from start and position along transects (Result section, Fig. 11).



8 Appendix 2

The vertical profiles of oxygen, temperature and salinity in basin 2 (September (a), October (b) and November (c)) and basin 3 (September (d), October (e) and November (f)). Data from September is shown in text (*see* the Hydrography section). Field observation are marked with black circles (at 0, 10, 20, 40, 50 and 60 m depth). Be aware of that the axes differ. Solid line illustrates measured oxygen concentration (mL L^{-1}), dashed line salinity and dotted line temperature ($^{\circ}\text{C}$). Data points represent 1 m depth intervals. Further, vertical profiles comparing the environmental factors between basins in September through November (g-o). In the oxygen graphs (September (g), October (h) and November (i)) the black line illustrates basin 1, purple line basin 2 and the grey line indicates the oxygen levels in basin 3. The temperature graphs (September (j), October (k) and November (l)), blue line illustrates basin 1, light grey line basin 2 and the dark grey line shows the temperature profile in basin 3. Lastly, in the salinity graphs (September (m), October (n) and November (o)), grey line indicates basin 1, turquoise line basin 2 and the orange line basin 3.

