

YOU ARE WHAT YOU GET CAUGHT WITH: INTER-INDIVIDUAL VARIATION IN COASTAL ATLANTIC COD (*GADUS MORHUA*) BEHAVIOUR.

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MASTER THESIS 60 CREDITS 2013



This study would not have been possible without the help of many people:

A special gratitude to my main supervisor, Thron O. Haugen, for his invaluable enthusiasm, guidance and support throughout this process. Thank you for your endless patience, encouragement, and for your great humour that has made this learning process a highly enjoyable one. A special thanks to my second supervisor, Jonathan E. Colman, for your support and guidance in the field, and for providing the last input needed to finish this thesis.

I also wish to express my very great appreciation to Esben Moland Olsen at the Institute of Marine Research, for his invaluable help on the spatial analyses part of this study.

Thanks to all of you who offered your help and great company during the many, and often freezing cold hours of field work; Sondre A. Ski, Jeanette Thimamontri and Ronny Steen, and those who helped capturing the highly needed fish tagged in this study. I would also like to express my gratitude to Torbjørn H. Kornstad for his help during the final stages of my thesis.

Abstract

Consistent behavioural differences among individuals is a common phenomenon that has been demonstrated for a wide range of taxonomical groups. Such behavioural differences are expected to have ecological and evolutionary implications and has therefore received an increasing amount of attention during the past decade.

This study applies acoustic telemetry to explore intra-population variation in coastal Atlantic cod behaviour. Specifically, I explore whether consistent differences in cod (*Gadus morhua*) behaviour can be correlated to two *a priori* defined groups based on the type of gear that the individuals were caught with prior to tagging. The aim was to elucidate potential selectivity bias of fishing gear with respect to behavioural types. This was studied using acoustic telemetry within a small study area in the inner parts of Oslo fjord. A high level of among-individual variation in behaviour was identified, and the groups were significantly different with respect to temperature use and how they were distributed in the water column. The contrasting use of temperatures may have implications for growth and hence life-history characteristics, which in turn have the potential to provide the basis of fisheries-induced evolution. This suggests that the inclusion of a behavioural aspect in population management could be of high relevance.

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1 Introduction

Intra-population variation in behaviour has been demonstrated for a wide range of taxonomical groups. Behavioural differences among individuals in a population that exceeds the variation expressed by individuals over time or in different contexts, and which cannot be explained by differences in age, gender or discrete morphological group, is increasingly referred to as animal personality or behavioural specialization (Dall et al. 2012). Hence, much of the inter-individual variation in animal behaviour that has traditionally been treated as noise around an optimal population mean is now attributed to animal personalities or behavioural phenotypes (Conrad et al. 2011). Because behaviour fundamentally is expected to be flexible rather than constant, this phenomenon has puzzled scientists for many years (Bergmuller & Taborsky 2010). The observed differences may arise in multiple ways; differences in genotype, epigenetic effects (McGowan et al. 2008), adaptive phenotypic plasticity in combination with spatial heterogeneity (Angers et al. 2010), and learning (Werner et al. 1981) may cause individual differences in behaviour. Why this behavioural variability is maintained within populations is still poorly understood as, phenotypic traits should evolve towards an optimal mean (Dall et al. 2012). There is however general consensus that processes comprising density dependence and fluctuating selection pressures are likely to be involved. Differential behaviour in ecological relevant traits is nevertheless likely to have evolutionary and management implications, as outlined by Wolf and Weissing (2012): First of all, because differences in behaviour types are expected to result in differences in individual life-history characteristics as traits such as boldness, aggressiveness, activity or dispersal are directly related to mortality and fecundity which are key determinants of fitness. Also, different behavioural types will often occupy different habitats, hence causing differential exposure to resource densities, competitors and predators. And lastly; behavioural types within a population may affect population density and productivity because differences in activity patterns, habitat use and foraging strategies can be expected to increase carrying capacity due to more efficient use of resources (Wolf & Weissing 2012). Intra-population differences in individual behaviour is in terms of management is perhaps especially relevant for harvested species such as many fish populations, because behaviour is to a great extent a determining factor to an individual's susceptibility to harvest mortality (Uusi-Heikkilä et al. 2008).

During the past decade, developments in biotelemetry technology and analytical tools have provided an increasing amount of information about the presence of distinct behavioural types within natural fish populations connected to habitat use, (e.g., Hammerschlag-Peyer & Layman 2010, Kobler et al. 2009), foraging tactics, (e.g., Biro & Ridgway 2008), dispersal (Fraser et al. 2001) and movement patterns (e.g., Babcock et al. (2012), Olsen et al. (2012)). Field and laboratory research on fish has shown that such different behavioural types within a population can vary with respect to reproductive success and survival (Conrad et al. 2011). It is well established that fishery-induced evolution in life-history traits related to growth rate and maturation is important for harvested populations, but the role of behaviour has received less attention (Uusi-Heikkilä et al. 2008). This is despite the fact that certain aspects of behaviour such as movement patterns (Olsen et al 2012) and boldness/aggressiveness (Biro & Post 2008) have been demonstrated to increase susceptibility to fishing gear. Several studies of fish behaviour show that boldness, activity levels and exploratory tendencies also tend to covary (e.g., (Conrad et al. 2011)) in what is commonly referred to as behavioural syndromes (Sih et al. 2004). Such behavioural syndromes have been further connected to life-history trade-offs where bold individuals are generally more productive, but with the cost of higher mortality rates (Stamps (2007), Biro and Stamps (2008), Wolf et al. (2007)). Accordingly, fast growing individuals/genotypes are typically more active, bolder in the face of risk, and more aggressive than slow-growing individuals. Fish displaying these behavioural traits are therefore expected to have an

increased encounter rate to fishing gear, be less likely to detect and avoid them, and aggressively pursue gears and lures (Biro & Post 2008). A negative harvest selection on fish body size can therefore be an indirect effect of a behaviourally induced increase in harvest vulnerability (Uusi-Heikkilä et al. 2008). This suggests that the inclusion of a behavioural dimension in the management of fish populations is of high relevance.

This study applies acoustic telemetry to explore whether consistent differences in cod (*Gadus morhua*) behaviour can be correlated to two *a priori* defined groups based on the type of gear that the individuals were caught with prior to tagging. The aim of this group partitioning is to investigate whether or not different types of gear are biased with respect to the behavioural types they capture. Previous acoustic studies of cod have demonstrated repeatability (a standardized measure of among-individual differences) in individual movement patterns such as vertical position and horizontal movements (Olsen et al. (2012), Godo (1995)) in addition to considerable within-individual variation connected to vertical migration patterns. The latter has been connected to the species opportunistic feeding strategy, and is according to Neat et al. (2006) probably a characteristic of cod behaviour itself. Vertical migrations are generally explained as thermoregulatory-, antipredator- and foraging-efficiency strategies. Trade-offs are likely to exist between the three and may hence result in different manifestations of movement patterns with potential equal effects on fitness. In this study, I explore whether distinctions in behaviour connected to horizontal and vertical movement patterns as well as temperature use, can be identified between individuals caught with two types of gear that are expected to be very different in what types of behaviour they are more selective towards. Accordingly, one active and searching gear that fished only in the upper water stratum and one passive gear that fish only at the seafloor was chosen. The former is a floating stick bait, specifically a 13 cm Rapala® Original Floating Lure also called a “wobbler”, that imitates the movements of an injured fish. Fishing with wobbler was only performed in the tidal zone and in daytime, and vulnerability to capture by this gear depends on a fish’s willingness to be exposed in shallow waters during light hours and on its decision to attack the lure. The latter gear is a fyke net, and works by leading passing fish along a bottom net that directs into a department preventing escape. Vulnerability to this gear mainly depends on movement in the demersal zone and at any time during the day, as these can be deployed for days at a time. Hence, I assumed that gear type one would be more selective to bolder behavioural types compared to gear type two. A working hypothesis is thus that individuals caught by wobbler (hereby referred to as group W) should display a higher degree of boldness interpreted as greater occupancy at exposed depths during daytime, contrary to individuals caught by fyke nets (group F) which, compared to group W, are expected to show a more risk averse behaviour reflected in greater occupancy at deeper waters during daytime. A possible scenario is that the latter individuals have movement patterns more dominated by vertical migrations between the food-rich, but predator-exposed shallow waters during the safe hours of darkness and the deep, but safer waters during daytime, contrary to group W that is expected to show greater horizontal movements and search behaviour in the food rich littoral zone irrespective of daylight similar to a bold behavioural type syndrome. Because temperature can vary strongly along the vertical axis in stratified water bodies, movements between and within such temperature strata will affect the experienced temperatures and hence the bio-energetics of individual fish. Hence, water stratification may also be a contributing factor to movement behaviour in stratified water masses.

In order to test for consistent behavioural differences between the two gear groups, several behavioural elements will be defined based on positional and environmental data sampled by acoustic telemetry.

Measures of repeatability are also performed in an effort to quantify the magnitude of intra-population variation observed in the specified behavioural elements. Repeatability is a premise for individual behavioural specialization, and hence asserting its extent is therefore of interest in this context. Because personality structure often is more complex than consistency in a single behavioural component, a multivariate analysis with the different behavioural elements as responses will be performed in order to explore how the defined behavioural components are associated, and whether or not such association patterns differ between the groups.

The aims of the study can be summarized as follows:

- i. To test for consistent differences in movement patterns and temperature use between two *a priori* defined groups based on whether or not individuals were initially caught by one of two very different types of gear with respect to the behaviour they are expected to be more selective towards, and
- ii. to measure the extent of behavioural repeatability, i.e. the proportion of behavioural variance in movement patterns that is attributable to consistent differences between individuals, and
- iii. to search for consistent associations among multiple behavioural elements to test whether behavioural types can be distinguished objectively, and
- iv. to compare such potential personality types to the predefined groups in an objective evaluation of their explanatory power.

2 Materials and methods

2.1 Study system

The inner Oslo fjord is a semi sheltered system with a mean annual surface temperature of 7.5 degree °C (Baalsrud & Magnusson 2002). The boundary between the inner Oslo fjord and the outer Oslo fjord comprises a 1 km wide and 16 m deep sill located in the Drøbak strait. The width of the inner fjord ranges from 3 to 7 km and the maximum depth is 164 meters (Ibid). Multiple rivers and streams empty into the system, the largest of which are Lysakerelva, Akerselva and Sandvikselva. The main study site, the Bærum basin (Figure 1 B), has a mean depth of 30 meters and a volume of 103 mill. m³. Several islands and islets are located here. The river Sandvikselva empties into the basin and considerably influences the basin's abiotic conditions. The freshwater supply in the inner fjord is small with a yearly median of 27 m³/s (Ibid), but variations in surface water salinity are normal. The local river discharge yields an estuarine transport of low-salinity surface water out of the fjord, generating a deeper countercurrent of water with higher salinity from the outer fjord. The depth at which the thermocline is found varies, and temperatures below this threshold show little seasonal variation at 6-9 degrees °C (Figure 5). The near permanent temperature stratification is responsible for naturally low oxygen content in the deepwater layer. A determining factor for the physical and chemical properties of this layer is the near annual event of deepwater exchange caused by strong northern winds which produces a countercurrent of deep water masses from the outer Oslo fjord. In years when this water renewal fails, distinct events of near permanent occurrences of high hydrogen sulfide contents may occur. The marine environment of the inner Oslo fjord can be characterized as a dynamic system as the combination of freshwater input, different water transport mechanisms and a complex bathymetry, results in small, but substantial spatial and temporal variations in salinity, temperature and oxygen levels. This property yields a high temporal and spatial environmental heterogeneity that provides a broad set of habitat opportunities for non-sessile biota.

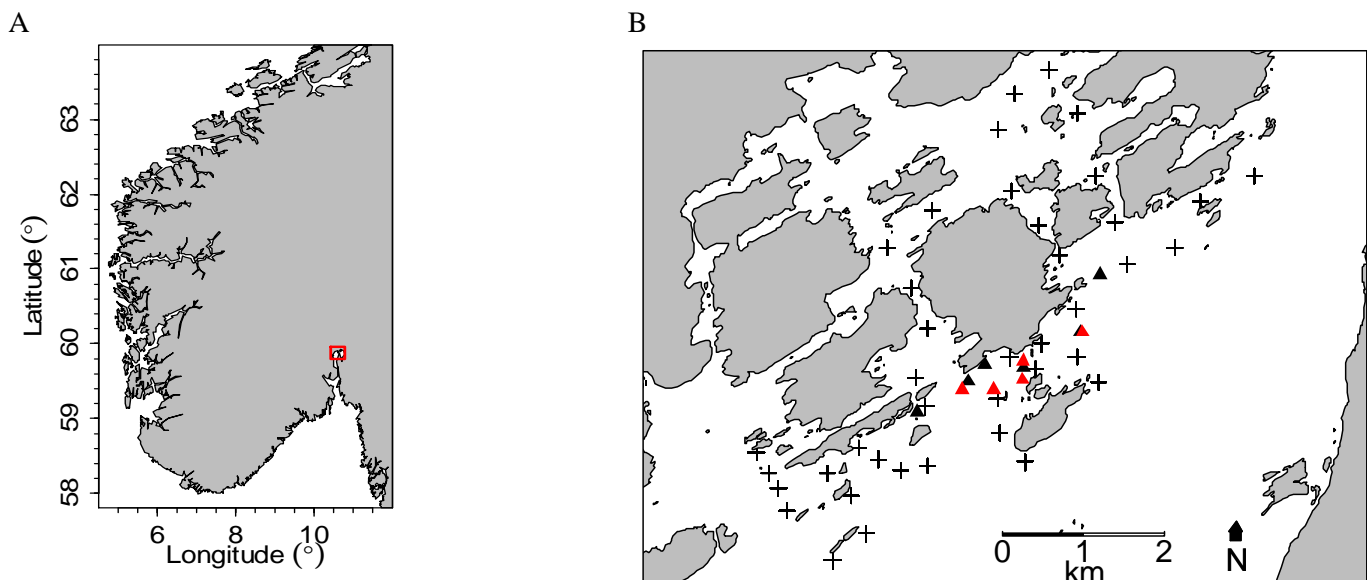


Figure 1. A) Study area with B) stationary acoustic receivers (black), positions in array of stations for CTD profiling and manual tracking (black cross), and stationary receivers included in triangulation procedure (red).

2.2 Study species

The coastal cod is a generalist groundfish predator that occurs at depths from 500 meters and up to the kelp zone. Spawning happens in the inner sections of fjords often related to partly isolated sites, especially in fjord basins (Johansen et al. 2009). This behaviour is believed to create and conserve genetic differentiation found among populations (Jorde et al. 2007). Based upon extensive release and recapture experiments, a sequence of studies have shown that the Norwegian coastal cod consist of several non-migratory populations subdivided into semi isolated local populations (Stenseth et al. 1999). Some of these populations differ in size and maturity at age, maturity at fork length (L_T), and survival (Olsen et al. 2004). The size at 50 % maturity has been estimated to 35 cm for cod in the Inner Oslo Fjord (Ibid). The diet of cod varies with age, juveniles in the size range 30-40 cm from the Skagerrak coast feed mainly on polychaetes in spring and small fish (mainly gobiids) and crustaceans (decapods and isopods) during winter (Hop et al. 1992). A major part of the diet in all age classes consists of demersal groups such as crustaceans, and a smaller part of pelagic fish (Gjøsæter et al. 1996). The maximum age recorded in the Norwegian Skagerrak populations is 12 years, but less than 2 % of those reaching an age of one year survive to an age of six years or more because of the high mortality rate of coastal populations due to harvesting (Ibid).

Several studies have applied telemetry to investigate the behaviour of coastal cod, such as movement patterns, home range sizes and habitat preferences. Previous studies has revealed that the coastal cod has a strong site fidelity (e.g., Bergstad et al. (2008), Espeland (2010) and Knutsen et al. (2003)), low migration rates, and a general pattern of diurnal vertical movements (DVM) connected to sunrise and sunset (e.g., Espeland (2010)). Tracking experiments on wild cod often show a “chaotic” diel vertical movement pattern with significant variations among and within individuals (e.g., Godo (1995)). According to Neat et al. (2006) this variation may be a “characteristic behaviour in itself, and may be connected to the cod’s predatory feeding strategy and opportunistic diet”. Recent studies on coastal cod from the inner part of Oslofjord demonstrate similar DVM patterns and strong site fidelity (Ilestad et al. (2012), Ski (2013)).

2.3 Fish capture, handling and surgery

A total of 23 cod in the size range 42.5 to 65 cm (mean 51.1 ± 9.3 , SD) were captured in the study area from March 2012 to October 2012, i.e. in a size range where all individuals were likely to have reached maturity. The cod were captured by fyke nets or casting from land with a Rapala 13 cm original floating lure. The fyke net is a cylindrically shaped fish trap placed at the seafloor that works by leading passing fish along a bottom net that directs into a department preventing escape. The floating lure is designed to be retrieved no deeper than approximately 2 meters below the surface. In order to decrease stress imposed on captured fish, the maximum residence time of fyke nets in the water was kept below 5 days, and a minimum of 2 days to allow reasonable catches. In both procedures, the fish were released into dark containers with seawater after capture and the water was renewed on regular basis. Any fish showing signs of fatigue or bleeding was released without tagging due to raised risk of mortality. Fish were anaesthetized with clove oil or Aqui-S® at 5 ml/l in a separate container equipped with an airpump. Upon immobilization, the fish were placed with abdomen facing upwards in a V-shaped cradle that was covered with wet towels. An incision approximately 1 cm wide was made in the peritoneal cavity between the anal-, and pectoral fin and implanted with an acoustic transmitter (Figure 2 B). During surgery, the gills were irrigated with alternate doses of pure seawater and diluted anesthetic to ensure the fish was ventilated but remained unconscious (Parsons et al. 2003). The wound was sealed by 1-3 RESOLON®, DS24, 4/0 USP stitches. All cod were length measured

and tagged with external floy-tags. After the surgical procedure, the fish were placed in new containers and monitored until normal functionality was regained. All fish were then released close to the point of initial capture. The implantation protocol was approved by the National Animal Research Authority (Forsøksdyrutvalget Licence number 11/180321).

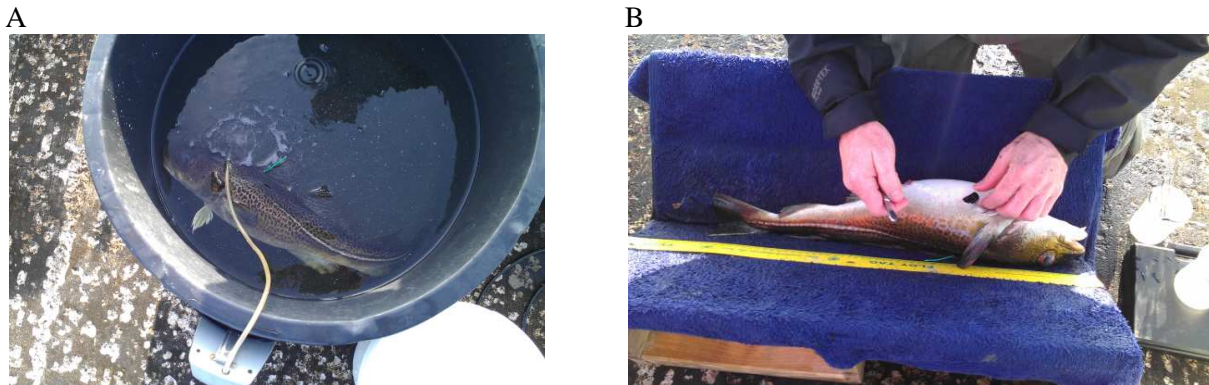


Figure 2. A) Anesthesia of cod, and B) Implantation of acoustic transmitter.

2.4 Tracking procedure

Fish sensor data was gathered using mobile tracking by boat (and by walking on surface ice in January) and logging by stationary receivers. The tracking was performed once a month with the exception of August, from June 2012 to January 2013. In this procedure, the presence or non-presence of fish was recorded on a gridded array of 50 fixed stations with an average distance of 500 meters between stations (Figure 1 B). This has been shown to be an optimal distance with respect to detection probability and performance of the handheld receiver in a similar environment (Ilestad et al. 2012). The tags used were VEMCO coded transmitters (V9TP – characteristics: 9x47 mm, 6.4 g, 153 dB output power) sending one code burst with random delays between 90 and 180 seconds at 69 kHz frequency (Figure 3 B). Each code burst contains a unique digital ID code, temperature or depth data. A hand held receiver (VEMCO VR100) (Figure 3 A) with two types of hydrophones was deployed during the mobile tracking; an omnidirectional hydrophone to detect the presence of fish within the receiver range, and a directional hydrophone to locate the position with the strongest signal. The ID number, depth and/or temperature code, and signal strength in dB were displayed on a screen. The fish location was logged by the VEMCO100 receiver-GPS and a hand held GPS device for cross validation.

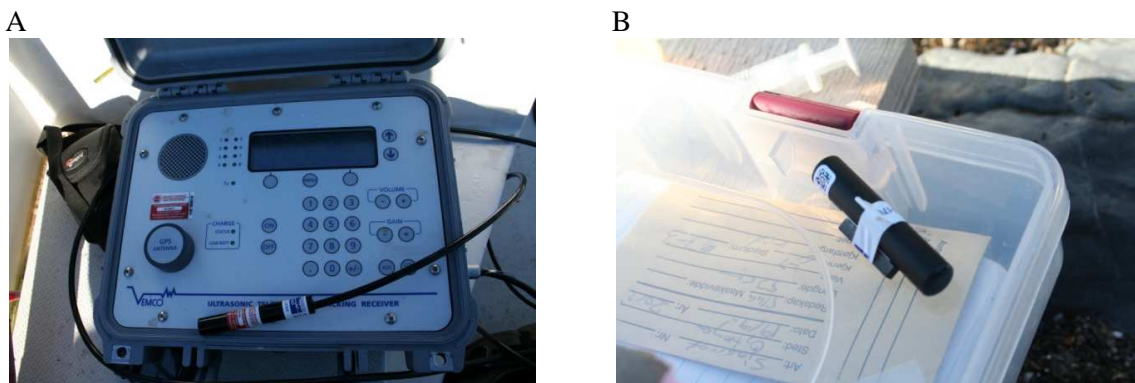


Figure 3. A) VEMCO VR100 receiver with omnidirectional hydrophone and B) acoustic transmitter.

Five stationary underwater omnidirectional VR2WW receiver loggers were mounted in May (hereby referred to as week nr 0) within the study area (Figure 1 B). These were attached to sub-surface buoys anchored at the bottom, at 4-3 m below the water line. The stationary receivers detect and store the ID number, depth and ambient temperature data of detected tags on flash memory devices. These data were transferred to ordinary lap top computers via Bluetooth connection in November 2012 and February 2013. From November and onwards, five additional receivers were placed in a triangulation array in the Bjørnerenna strait for continuous monitoring of sensor data and fish short-term center of activity after the method described in Simpfendorfer et al. (2002). This area was chosen because manual tracking detected the majority of individuals here, and is hence referred to as the core study site onwards. The receivers were positioned so that the signal reception range was partly overlapping to allow for detections of a single signal by multiple receivers. Only five of the originally mounted ten receivers were retrieved during the course of the study (Figure 1 B). In order to test the performance of the triangulation array and the manual tracking procedure, a detection range-test was performed. The manual hydrophones were tested by deploying two transmitters on a fixed location 2 m below the water line and tracked with increasing distance and resulted in a detection range of 850 meters. This was, however, under optimal conditions with no signal obstructions such as islets and shallows in the transmission pathway, and can therefore normally not be expected in the study area due to the bathymetric and topographic variation here. The stationary receivers were tested by deploying the transmitters at 20 different positions on a 2 km vertical line through the triangulation array and gave a maximum detection range of 850 meters, however at this distance, the probability of detecting a signal was significantly reduced (Figure 4 B). A logistic linear function was fitted to the range test data in order to estimate the probability of detection as a function of the distance between hydrophone and transmitter.

A



B

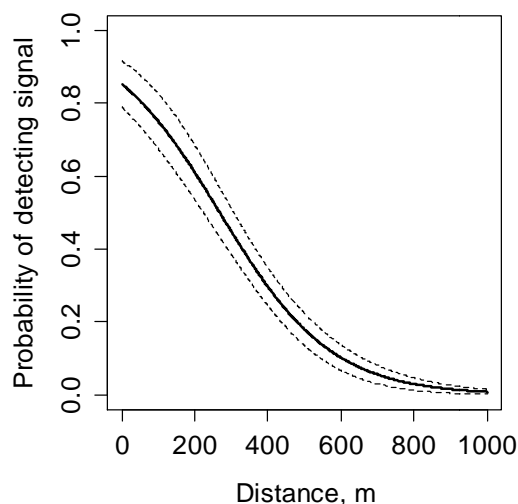


Figure 4. A) VEMCO VR2W stationary hydrophone, B) VR2W probability of detecting a signal (dashed lines: 95% confidence limits) estimated by range test (Dzadey In prep)

In the course of the study, all fish, except one individual from group F were detected by stationary receivers and/or by manual tracking. A total of 336 144 detections were recorded by the stationary receivers, on average 16 006 detections were made per individual (± 24970 SD, range: 8-80183). Three of the 5 receivers

that were retrieved accounted for 95 % of all detections, and these were the ones located the farthest to the south of the study area (Figure 1 B). Six individuals were recorded by the stationary receivers in a short time interval only (1 – 2 weeks) and were hence excluded from further analysis of VR2W data, leaving 70 % and 69 % of the originally tagged fish in the two groups. Their absence could be explained by permanent emigration, harvest mortality (though no recapture has been reported) or tag failure. The remaining detected transmitters showed variation in depth recordings that exceeded the tidal range, and all fish included in the analysis were accordingly assumed to be alive. Due to missing or sparse data in the time period before the triangulation array was deployed (Table 1), all statistical analysis based on VR2W data were performed on data after week number 24 of the study period (November). The length distribution of the fish in the remaining dataset ranged between 55.5 and 62.0 cm (mean 58.84 ± 2.7) for group W, and 42.5 and 57.5 cm (mean 46.2 ± 6.35) for group F.

Table 1. Summary of detections by stationary logging. Stationary receivers were deployed May 2012 and retrieved February 2013.

Month	Fyke net			Wobbler		
	Observed ind.	No. of detections	Fish w. tags	Observed ind.	No. of detections	Fish w. tags
5	1	7	5	3	186	5
6	2	21	5	3	321	5
7	2	33	5	2	86	5
8	2	90	5	3	65	5
9	1	25	5	1	8	5
10	2	72	5	0	0	8
11	7	13822	10	10	36820	13
12	7	29806	10	9	64625	13
1	5	35506	10	10	67062	13
2	6	38954	10	8	48635	13

Table 2. Summary of detections by manual tracking. *= no tracking was performed this month

Month	Fyke net			Wobbler		
	Observed ind.	No. of detections	Fish w. tags	Observed ind.	No. of detections	Fish w. tags
5	*	*	5	*	*	5
6	2	17	5	4	9	5
7	1	6	5	0	0	5
8	*	*	5	*	*	5
9	0	0	5	2	6	5
10	2	2	5	11	51	13
11	2	6	10	9	30	13
12	7	29	10	9	42	13
1	5	29	10	9	65	13
2	*	*	10	*	*	13

2.5 Environmental data

At each station in the gridded array (Figure 1 B), profiles of water temperature, salinity, depth, and oxygen saturation were taken using a SAIV 864 conductivity-temperature-depth logger with an oxygen sensor. A total of 316 CTD profiles were sampled from June 2012 to January 2013. Temperature variation above 20 meters depth was substantial during this period and ranged from -3 degree °C in February to 20 degree °C in July. At 20 meters depth and below, the temperature remained constant at 6 to 9 degrees. By November, an isothermal condition was reached and by December, this had been replaced by an inverse stratification. Onwards, the thermocline depth varied from 6 to 16 meters (mean 11.7 ± 3.1 , SD). The spatial variation in surface temperature was considerable with temperature differences ranging from 2.2 to 4.8 degrees between samples taken the same day. From November to January, the mean temperature recorded above 10 meters depth in the core study area dropped from 8.4 degrees to 4.2 degrees.

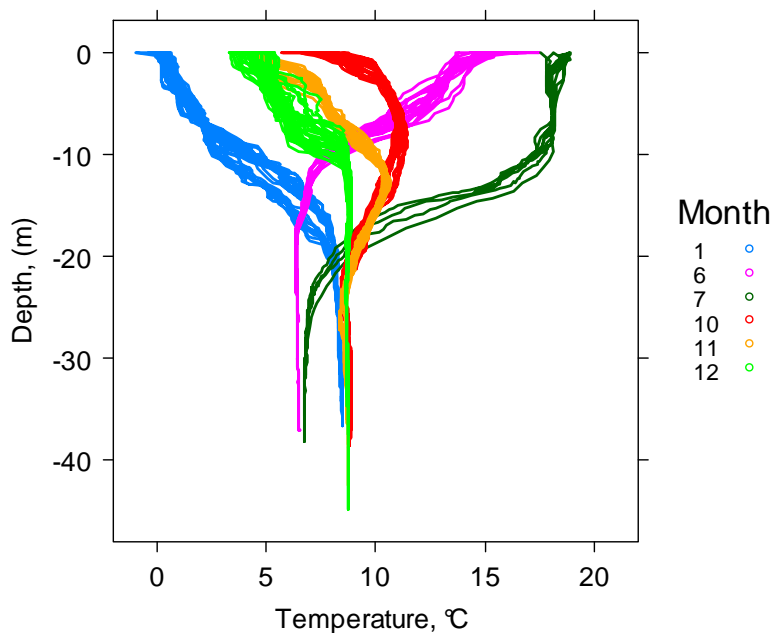


Figure 5. Temperature profiles sampled in the core study area from June 2012 to January 2013.

2.6 Triangulation

Because a signal reception at a given stationary receiver only provides information on whether or not an individual is present within the detection range, it was necessary to use a method that provided a more precise location estimate for the individual detections. Due to the near linear relationship between the distance between a receiver and transmitter, and the number of detections obtained (Figure 4 B), a location estimate can be calculated by weighing the mean of the respective receiver's coordinates by the number of detections obtained from a unique tag in a specified time period as described in Simpfendorfer et al. (2002). The precision of these location estimates increase with the number of receivers of which a signal is detected by within the given time slot, and will only yield positions inside the boundary of the minimal polygon surrounding the outermost hydrophones. Rather than providing point estimates, these estimates are better described as short time centers of activity (CA) (Ibid). Because the transmitters were programmed to transmit on average one signal within three minutes, thirty minutes were chosen as the time slot in which these CA's were estimated. This period is also within a small enough timeframe to expect the individual fish

not to perform any extensive movements. A total of 20097 CA's were obtained in this manner, excluding positions derived from only one receiver. Detections that included depth sensor data were used to calculate mean depth within the same time slot, providing a total of 17701 three dimensional CA positions (Figure 6).

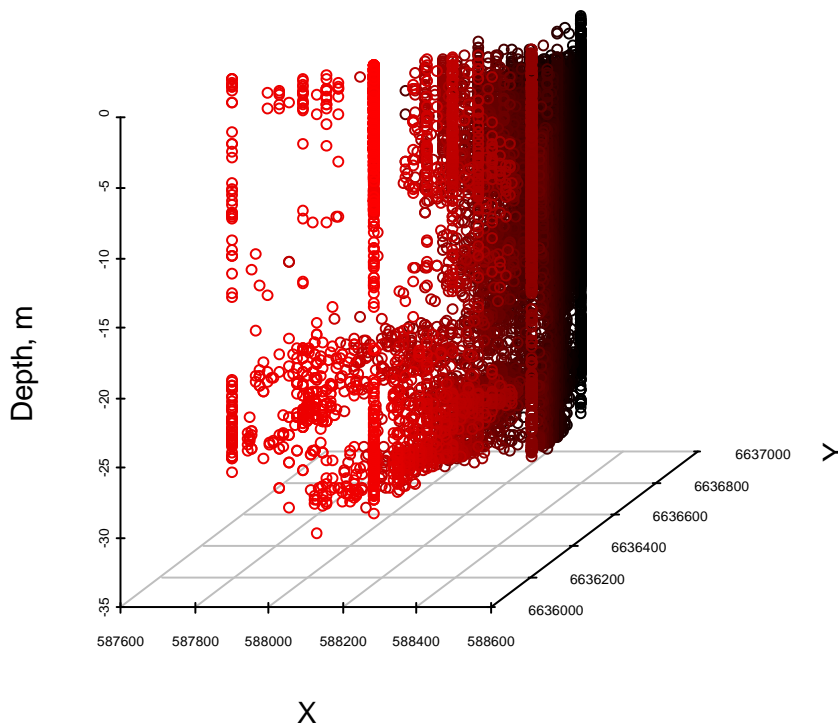


Figure 6. Triangulated position, or short term centers of activity, combined with mean depth (m) calculated in the same 30 minutes intervals.

2.7 Behavioural components

To compare the behaviour of the two groups, several behavioural variables were defined based on the sensor and positional data.

2.7.1 Vertical movement

Vertical position was defined as the individual mean depth recorded by the stationary receivers during a 24 h period. To examine diel patterns in vertical movements, mean depth was also calculated for nighttime and daytime separately. The night and day periods were retrieved from the sunset computer available from Mindspring (<http://www.mindspring.com/~cavu/sunset.html>). The maximum vertical distance measured (max. depth – min. depth) during a 24 h period provided a metric for individual daily depth-range. Individual temperature use was likewise determined as the mean ambient temperature recorded during day and night, respectively.

The vertical position of the fish does not provide information on where in the water column relative to the bottom it is located, and consequently, what type of habitat it experiences (i.e. pelagic zone vs. demersal zone). The individual vertical distance from the seafloor was therefore estimated by performing an overlay of the CA coordinates and associated mean depth recordings with a geo-referenced raster map providing 15 times 15 m depth data of the study area. The fish depth value of the given CA was hence subtracted from the estimated seafloor depth at the same position to provide an estimate of fish vertical distance from the seafloor. Accordingly, the relative vertical position with respect to local depth was calculated as fish depth

divided by local depth, giving a ratio from 0 to 1, where 1 represented maximum depth with respect to the seafloor. Because the CA coordinates are derived positions with a potential significant degree of error, some estimates of distance to seafloor were negative. Negative values were hence re-coded to 0.5 (0.5 meters above seafloor) and the associated RVP estimates were re-coded to 0.99.

The vertical position of a fish will in large part also determine the nature of the physical environment (i.e. temperature, oxygen, salinity, hydrostatic pressure, light) it experiences. Vertical gradients in the physical properties are also a determining factor in terms of the composition of food resource at a given depth. The thermocline represents the water layer where the rate of temperature change with respect to depth is at its greatest, and will often correspond to the position of the steepest gradient of other chemical components such as salinity and oxygen. When a fish is located at this depth it can access a broad range of biotic and abiotic factors over a small vertical distance (Bass et al. 2013). Cubic smooth spline curves were therefore fitted to the weekly pooled fish sensor data (mean individual depth and temperature per 30 minutes) in order to determine the depth of the thermocline center within a given week. The fish sensor data were aggregated to mean temperature per 1 meter depth to reduce 'noise' and facilitate curve fitting. The center point of a thermocline can be identified as the point on a third order polynomial where the curvature changes its sign, or, the point of inflection. This is determined by solving the root of the second derivative of the cubic curve (Figure 7). Comparisons with CTD data within the weeks where CTD profiles were available (October, November, December, January) showed that the sensor data corresponded well to the more objective CTD measurements. The individual mean vertical distance from the predicted thermocline depth could therefore be estimated. In addition, the binomial variables based on whether the mean distance to the center of thermocline depth was positive (above the thermocline depth) or negative (below the thermocline depth) was determined, providing another behavioural variable.

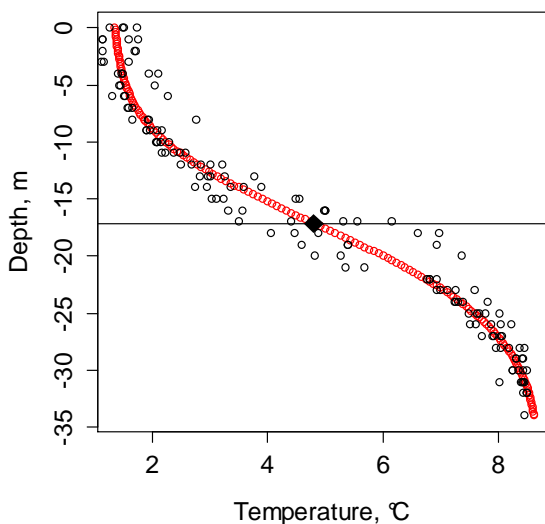


Figure 7. Predicted depth of thermocline center (horizontal line) derived from the point of inflection on a cubic curve (red) fitted to the fish sensor data (black points). Example from week 31 (December).

2.7.2 Horizontal movement

A home range is defined as the area an animal traverses during its daily activities (Burt 1943). In addition to providing knowledge about animal habitat requirement, it also provides information about individual

horizontal distribution patterns. To obtain a metric of individual area use, monthly horizontal activity areas were estimated using the manually tracked point location data, combined with point locations derived from the triangulation of stationary receiver detections. These areas were estimated using a minimum convex polygon (MCP) estimator (Mohr 1947) in the R package *adehabitatHR* (R Core Team 2012). The estimator was applied without the removal of extreme points to prevent the exclusion of the numerically limited tracked positions. Due to the low temporal resolution of these positions, the activity areas give a rough estimate of individual average distribution. Because the monthly manual tracking was only performed once at each station (50 in total), it seldom provided more than one location estimate per detected fish. To describe potential seasonal changes in individual horizontal distribution, activity areas were estimated for two consecutive time intervals; the summer to fall period (June 2012 to October 2012), and the fall to winter period (November 2012 to February 2013). These two periods were separated by the occurrence of isothermal conditions in the beginning of November, and the inverse temperature stratification from November and onwards. In addition, activity areas were also estimated using all locations obtained during the entire study period to get a metric of the maximum area traversed by each individual fish during the study period. Two-dimensional kernel densities were not applied so as to prevent the more temporally intense sampled CA positions to bias the result towards the triangulation area.

2.7.3 Volumetric space use

Besides providing information about horizontal distributions and habitat utilization, MCP based activity areas do not offer insight into the nature of the movements within this space. This horizontal representation is therefore especially limiting for organisms for which the vertical axis is an important dimension of their habitat. Instead, the use of three dimensional kernels can produce detailed representations of volumetric space use when geographic and depth data are available. Kernel density estimation is a non-parametric probabilistic estimation procedure where a smoothing function is used to produce a probability or density surface (Katajisto & Moilanen 2006). This method is often applied to telemetric data in habitat use analysis as it provides habitat utilization probabilities from locational observations. Kernel density approximations can be extended to estimate probability surfaces in three spatial dimensions. Accordingly, volumetric space use was estimated on the triangulated position and average depth data (R Core Team 2012)(Figure 6), using two probability estimates; a relative estimate of the space an individual occupies 95 and 50 % of the time. Some recordings were made on one receiver only, causing the triangulated position to equal the location coordinates of the receiver position. Thus, only triangulated positions that included recordings from two or more receivers were utilized in this procedure. This provided a metric of the three dimensional shape and volume of the space utilized by individual fish within the triangulation array and can outline the relationship between vertical and horizontal movement patterns. In this study, only the volume of the estimated kernel densities was calculated. These individual volumes were estimated for every month where CA's were available, in addition to total individual volumes over these four months. When using kernel density estimations, the amount of smoothing applied is of high relevance as it determines the complexity of the resulting area or volume estimate. Thus, a low level of smoothing reveals small-scale details of the data structure, whereas a higher level reveals the general shape of the distribution (Seaman & Powell 1996). Here, a plug-in smoothing factor selector was applied as suggested by Simpfendorfer et al. (2012). This smoothing factor matrix was further multiplied by 3 (Ibid) to reduce the amount of smoothing and hence better accommodate the level of precision of the triangulated data points.

2.8 Data analysis

Behavioural differences between the groups were examined by fitting linear models to each behavioural variable separately, and testing the statistical significance of group assignment as predictor variable. Each behavioural variable was initially modelled as a function of group category, week nr, and length. The latter term was included to correct for size bias in the two groups combined with a potential effect of allometry in the behaviour responses. Week number was treated as a factor to allow for different temporal trajectories between the groups, starting at zero in the calendar week of the deployment of the first receivers, ending at 39 in the week when the receivers were retrieved. Because of an imbalance of observations among receivers, data from all VR2W loggers were pooled. To allow for correlations of multiple observations per individuals in the VR2W data, the inclusion of random effects was applied. Mixed models can easily account for complex data structures within levels of aggregation and effectively deal with unbalanced data sets (van de Pol & Wright 2009). By including random effects one can investigate how much of the total variation in the dependent variable is explained by the fixed predictor variables while accounting for multiple measurements and between-subject variation in the response. Linear mixed models in this case were also an optimal tool because it allowed for partitioning of variance components into variation generated within and between the levels of a random factor (Dingemanse & Dochtermann 2013). When this random factor is subject ID, it allows for the estimation of behavioural repeatability, which is the fraction of the total random variation explained by differences between individuals, i.e. the among-individual variation. Because the data also included the longitudinal effect of time, a random structure was chosen *a priori* with fish ID nested under the nominal factor week, so that estimates of variance components could be performed within and between the time units. When measuring repeatability using linear mixed models, it is important to note that by including fixed effects and additional random factors, the variance component estimates will change, and the appropriate term in such cases are adjusted repeatabilities (Nakagawa & Schielzeth 2010). Adjusted repeatabilities implicitly assume that the repeatability is constant for all values of the covariate, and can be interpreted as the repeatabilities given that the level of the confounding factor or covariate is known (Ibid). In this case, the additional predictors are associated with individual data points, and so they will tend to reduce residual variance, hence the repeatability estimate will generally increase (Ibid). These adjusted repeatabilities represent the proportion of “phenotypic” variance not accounted for by fixed effects explained by differences between individuals (Dingemanse & Dochtermann 2013). Inclusion of between-individual fixed effects therefore results in the calculation of average within-class repeatability, in this case, the average repeatability within a group when the effect of length is adjusted for.

The behavioural traits were estimated as the individual mean daily value, and the datasets were balanced in terms of week. However, the number of days of observations within a week could vary between the individuals. For relative depth use, a logit transformation was applied to secure model predictions to be confined within the 0 and 1 interval. All covariates and interaction terms were included in the full model, and the optimal model structure (in terms of fixed effects) was chosen by comparing AIC values for models fitted with ML estimation. P-values were calculated for each term in the optimal model by performing a Log-Likelihood ratio test as suggested by Zuur (2009). The chosen model was then refitted with REML for better estimation of random effect and model validation (Ibid). If two models obtained did not differ by more than 2 AIC units, the most parsimonious model where all terms were significant according to the Log-Likelihood test was chosen. For the binomial variable of relative vertical position with respect to thermocline depth, a generalized linear mixed model with a logistic link function was fitted, and the significance of predictors was evaluated in a χ^2 -test. To test for differences between day and night in the

respective behavioural traits, an additional nominal predictor of day and night assignment for each data point was added to the most supported models. The residuals of the optimal models were examined for the presence of violation of independence.

For an objective test of the presence of distinct behavioural types, irrespective of *a priori* grouping, multivariate finite glm-mixture models (mvglmm) were fitted (Leisch 2004). In order to take data dependency into account, ID was included as a random repeated-measures effect. Based on findings from the univariate analyses, fish body length and month were included as fixed predictors. Mean depth, relative depth, temperature and daily depth range were included in the response matrix. The models were fitted using an Expectation-Maximization algorithm implemented in the FlexMix package in R (Leisch 2004). The models assign observations to k clusters that have cluster-specific glms fitted to all response variables included in the y -matrix (*i.e.*, the response matrix). If distinct clusters could be identified within the behavioural responses, this was interpreted as a behavioural 'type'. Here, weekly mean values for each variable were utilized, separated into night- and daytime values. The optimal number of clusters was assessed using both Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC). By constructing gear-group association vs cluster assignment contingency tables over-all χ^2 statistics could be estimated for testing whether the *a priori* gear group individuals are randomly distributed among the objectively fitted glm-mixture clusters.

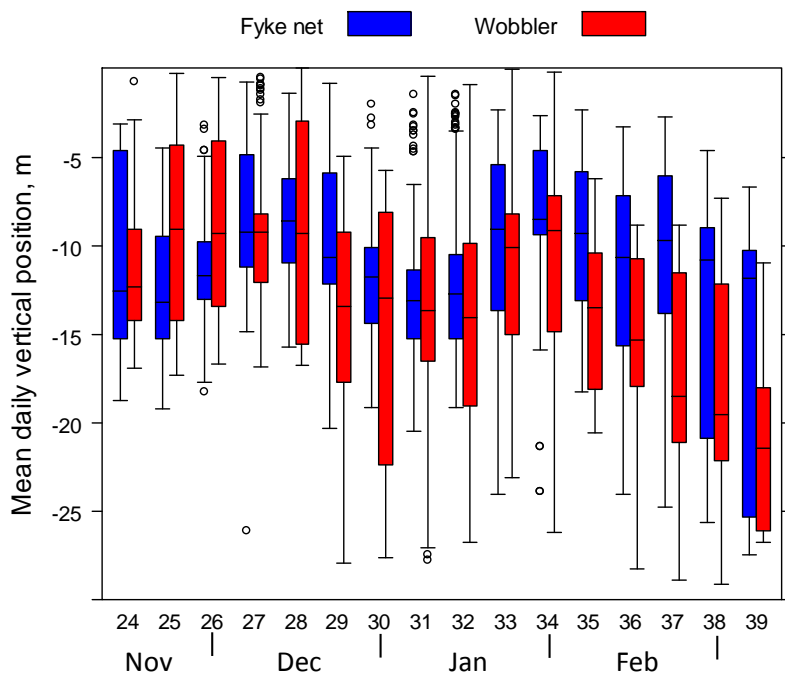
3 Results

3.1 VR2W data – Movement patterns and temperature use

3.1.1 Vertical position

Between November 2012 and February 2013, the recorded mean depth position occupied by group W and F was $-12.7 (\pm 6.8 \text{ m, SD})$ and $-11.2 (\pm 5.8 \text{ m, SD})$ meters in daytime and $-13.0 (\pm 6.2 \text{ m, SD})$ and $-10.9 (\pm 5.5 \text{ m, SD})$ meters during the night (Figure 8 A). The most supported model for mean daily vertical position was an additive model with gear and body length as predictors (Linear mixed effects model results Table 3, Model1). The second best model included week and an interaction between week and gear, but increased the AIC by 4 units and the term was not significant according to the Likelihood-ratio test. Gear type had a significant effect on vertical position ($p < 0.0001$, L.ratio=46.12) and group W were predicted to utilize a vertical position 10.5 meters deeper than fish in group F of equal size (Figure 9). Fish with larger body length occupied shallower waters compared to smaller fish ($p < 0.0001$, L.ratio= 45.34). When the nominal factor part-of-day (with respect to day and night) was added to the most supported model, it considerably improved the fit and reduced the AIC score by 25 units. There was a significant interaction between time-of-day and group ($p < 0.0001$, L.ratio= 18.48) and between time of day and fish length ($p < 0.0001$, L.ratio= 65.43) (Table 3). Larger fish were predicted to occupy deeper waters at night compared to smaller fish (Table 3, Model 1.1).

A



B

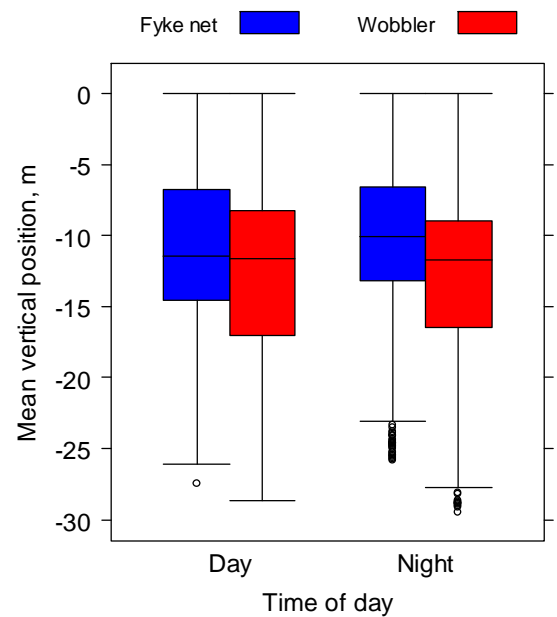


Figure 8.A) Distribution of weekly mean daily vertical positions for the two gear groups from November 2012 to February 2013. B) Boxplot of the pooled mean vertical positions during day and night of individual cod from November 2012 to February 2013. The boxes cover 50% of the observations and 90% of the observations are located between the whiskers. The thick horizontal line represents the median value (this will apply to all coming box plots)

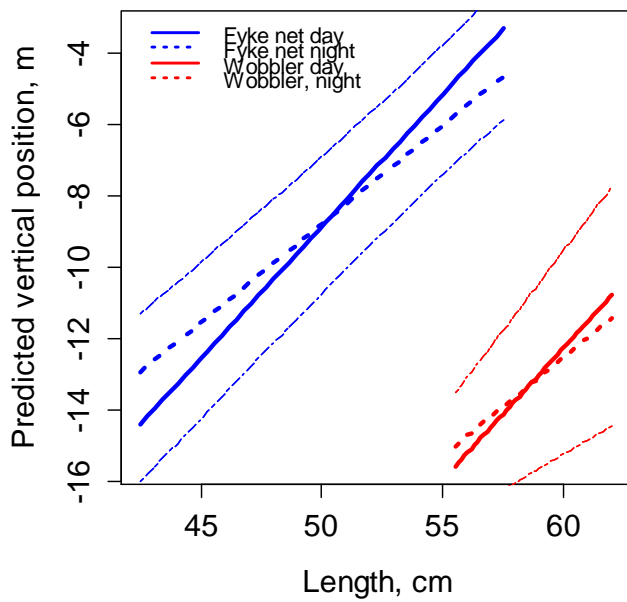


Figure 9. Predicted mean vertical position with associated confidence intervals (Model 1.1, Table 3.) as a function of part-of-day, gear and fish length.

The average among-individual difference (repeatability, R) in vertical position within a week was substantial, accounting for 78 % of the total random variation, whereas the average within-individual variation within a week constituted only 6 %, suggesting a consistency among-individual difference in vertical position over time (Table 3). The rest of the random variation was attributable to differences in mean vertical position among weeks.

3.1.2 Vertical distance to seafloor

From November 2012 to February 2013, the average vertical distance from the local seafloor depth was 7.5 and 8.2 meters (± 6.3 and ± 6.8 m, SD) for group W and F, respectively (Figure 10 A). At night, this distance was 7.4 meters (± 5.6 m, SD) for group W and 8.1 meters (± 5.8 m, SD) for group F. In February, the mean vertical distance to the seafloor depth at daytime decreased for both groups and was reduced to 3.4 meters (± 3.7 m, SD) for group W and 6.7 meters for group F (± 5.3 , SD) (Figure 10 A). The nominal effect of week was not included in the most supported model, which only contained the additive effects of gear group and fish body length. There was a strong positive correlation between length and vertical distance to seafloor ($p < 0.0001$, L.ratio 65.28) (Table 3, Figure 11, Model 2). Group W were predicted to stay 11.5 meters closer to the seafloor depth than group F (length adjusted for) ($p < 0.0001$, L.ratio=52.26). The model with the second lowest AIC value included week and an interaction between week and length, however, the models only differed by 0.5 units, and the interaction term was only weakly significant ($p = 0.0031$, L.ratio=28.15) hence the simpler model was chosen. When the nominal factor time-of-day was added to the most supported model, it resulted in a decrease of AIC value by 14 units. Here, the most supported model included an interaction between time-of-day and length, as well as time-of-day and gear (Table 3, Model 2.1). The among-individual difference in vertical distance to seafloor depth was considerable, accounting for 71 % of the total random variation (R , Table 3).

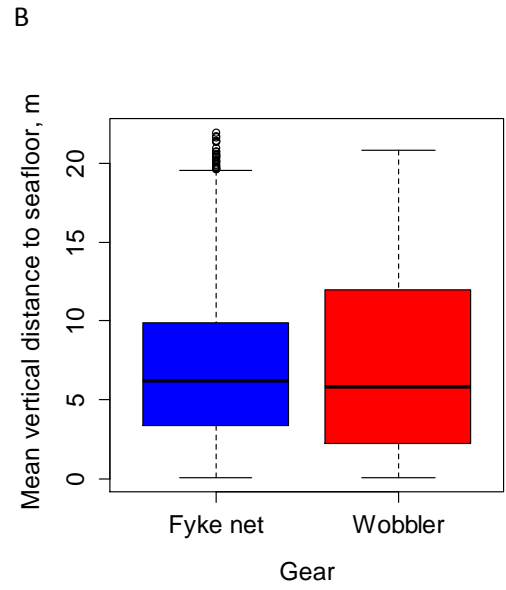
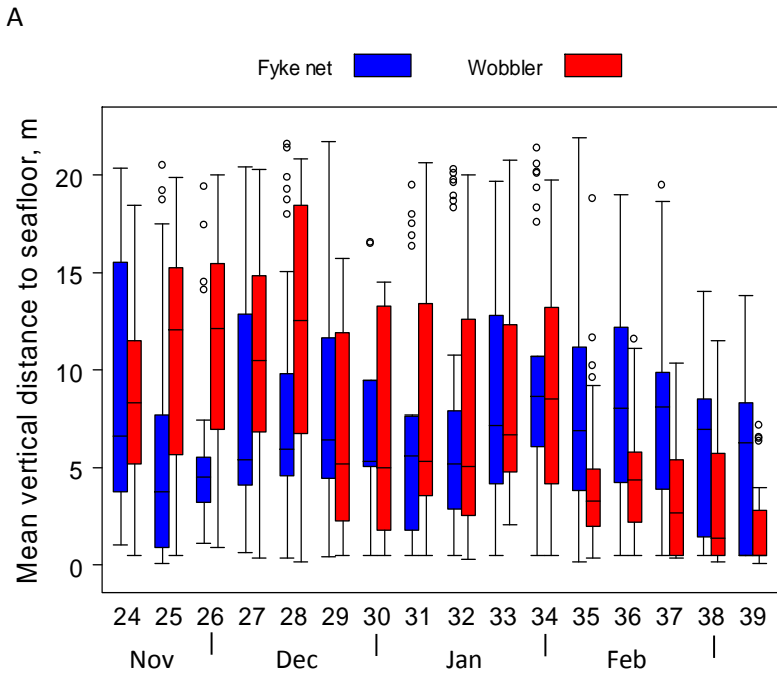


Figure 10 A) Boxplot over mean daily vertical distance to seafloor depth from November 2012 to February 2013 B) Mean daily distance to seafloor depth.

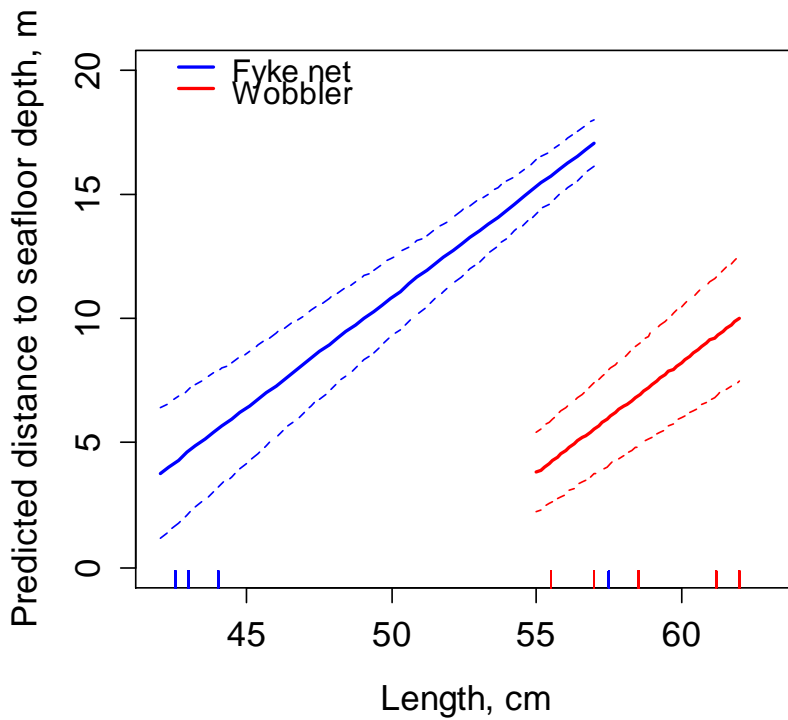


Figure 11. Predicted vertical distance to seafloor as a function of gear group and fish length, with associated 95% confidence intervals (Table 3, Model 2).

3.1.3 Relative depth use

The model selected was an additive model with gear group and length as predictors. This model predicted fish of length 55 cm in group W to utilize a depth-ratio of 0.86, whereas fish of the same length in group F were predicted to occur at a depth-ratio of 0.27 ($p < 0.0001$, L.ratio 37.67) (Figure 12 B). The correlation between fish length and relative depth was negative so that smaller fish were predicted to utilize greater relative depths compared to larger fish (Figure 12 B) ($p < 0.0001$, L.ratio=45.36). The second best model included the additional effect of week as well as an interaction between gear and length. These two models only differed by 0.4 AIC units, but the interaction term in the more complex model was not significant. Adding the predictor part-of-day to the most supported model led to a decrease of 21 AIC units. There were significant interactions between part-of-day and gear group ($p < 0.0001$, L.ratio= 16.44), as well as part-of-day and length ($p < 0.0001$, L.ratio= 25.15) (Table 3, Model 3.1). The average among-individual variation within a week accounted for 73 % of the total random variation.

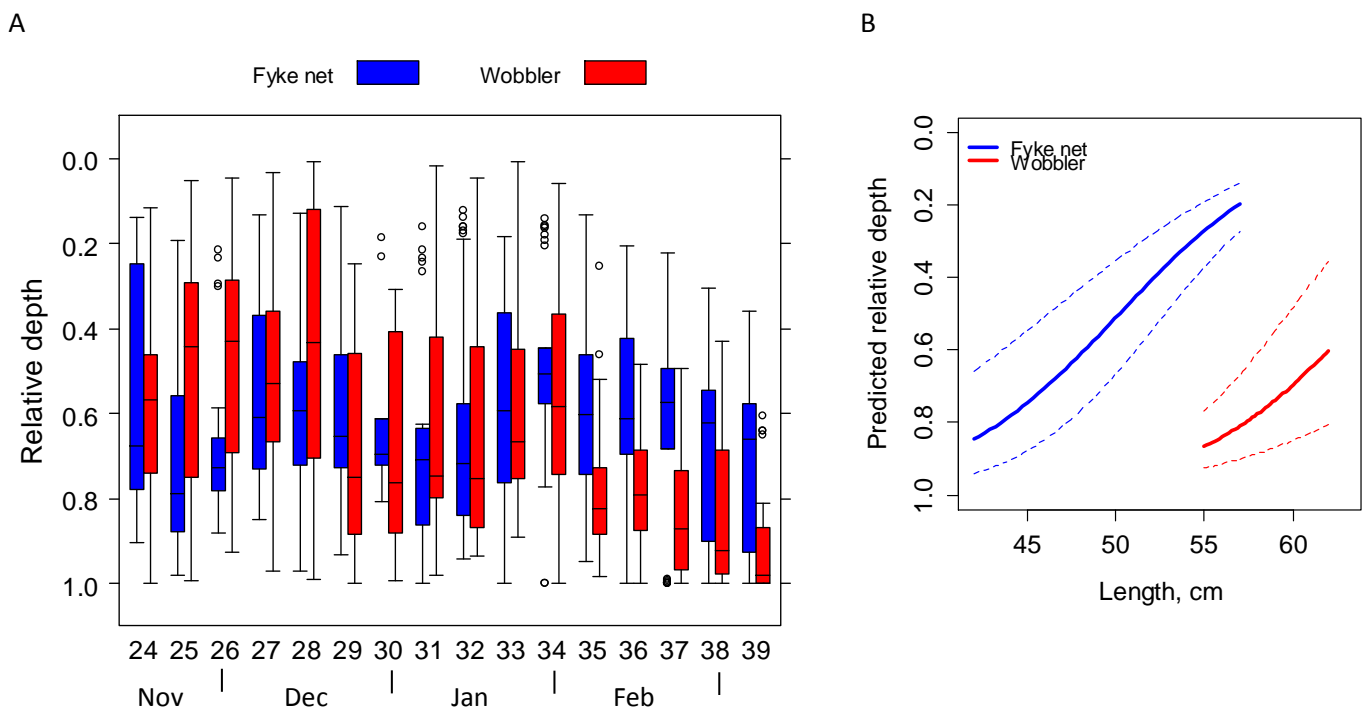


Figure 12. A) Boxplot over mean daily relative depth use from November 2012 to February 2013 and, B) predicted relative depth use as a function of gear group and fish length (Table 3, Model 3).

3.1.4 Vertical migration

The mean daily vertical migration amplitude, or depth-range, for group W was 6.5 meters (± 4.7 , SD) and for group F, 8.6 meters (± 4.6 , SD) (Figure 13 B). The daily vertical migration amplitude ranged from 0.2 to 24.6 meters for both groups throughout the study period. Model selection based on AIC values gave no support for any changes in depth-range over the weeks, nor could any clear differences between the two groups be identified. The most supported model included length only as dependent variable and predicted smaller individuals to have a larger vertical migration amplitude than larger fish ($p < 0.0001$, L.ratio=25.05) (Figure 14, Table 3). The second best model included the additive effect of gear in addition to length, but increased the AIC by 1.5 units and the term was not significant ($p = 0.375$, L.Ratio= 0.78). The among-

individual variation in depth-range accounted for 57 % of the total variation, demonstrating that the within-individual variation in depth-range was greater for this behavioural element.

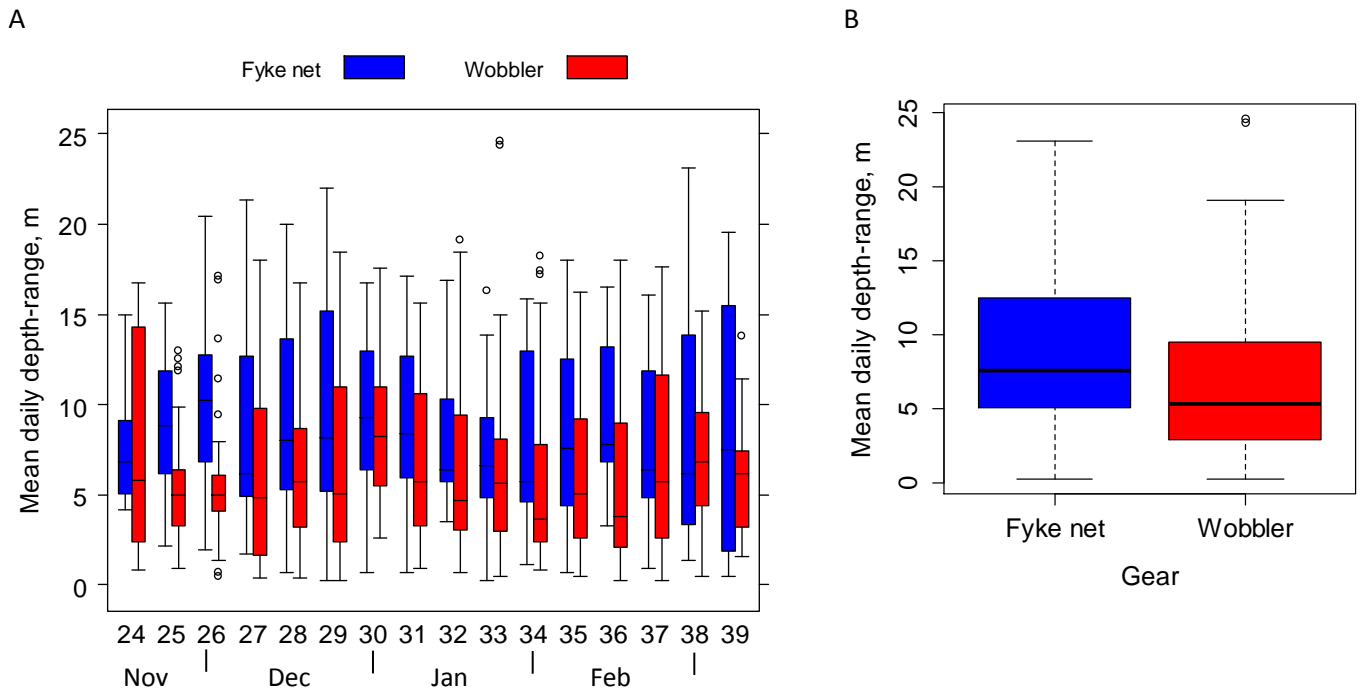


Figure 13. A) Boxplot of average daily depth-range from November 2012 to February 2013, B) Boxplot of daily depth-range.

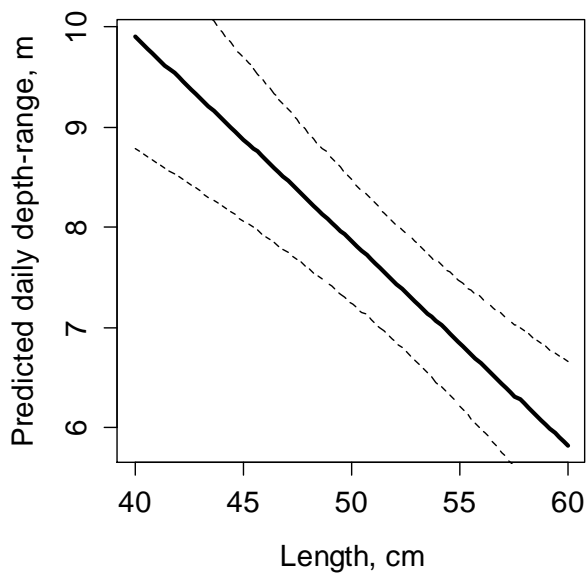


Figure 14. Predicted daily depth-range as a function of fish body length (**Feil! Fant ikke referansekilden.**Table 3, Model 4).

3.1.5 Vertical distance -, and relative position with respect to, -the estimated thermocline depth

The estimated depth of the thermocline centre varied with 10 meters in the winter half (mean -11.7 ± 3.1 , SD). During this period, the fish stayed in close proximity to the depth where the temperature gradient was at its steepest (mean wobbler $-1.6 \text{ m} \pm 7.6 \text{ SD}$, fyke net 0.9 m , ± 6.16 , SD). Beyond week 36 (February 2013), the average daily distance to the thermocline decreased in both groups for the beyond week 36 period (i.e., February 2013; Figure 15 A). The two groups were significantly different, both in the magnitude of distance from the thermocline ($p < 0.0001$, L.Ratio = 46.03) and in the position relative to ($p < 0.0001$, $\chi^2 = 45.19$) the thermocline depth. The probability of occupying depths below the thermocline center in a given week for fish of similar length was 90 % higher for group W than for group F (Figure 15 A), which on average (length and week adjusted for) stayed 10 meters shallower than the former with respect to the thermocline depth (Figure 15 B). There was a positive association between body size and distance to thermocline where larger fish tended to be located farther above the thermocline depth compared to smaller individuals ($p < 0.0001$, Log.lik 41.7). Likewise, the probability of staying above the thermocline increased with body length of the fish ($p < 0.0001$, $\chi^2 = 42.86$) (Figure 16 A). The model with the second lowest AIC value (0.4 units more than the most supported model) also included an interaction between gear group and length, however this term was not significant ($p = 0.1922$, L.ratio = 1.7). Adding time-of-day as predictor reduced the AIC by 18 units. The most supported model with this additional predictor included an interaction between time-of-day of and length as well as time-of-day and gear (Table 3, Model 6.1). Likewise, adding part-of-day to the model 5 resulted in a decrease of 24 AIC units, here the most supported model included the additional effect of time, and an interaction between part-of-day and group ($p < 0.001$, $\chi^2 = 15.84$) (Table 3, Model 5.1).

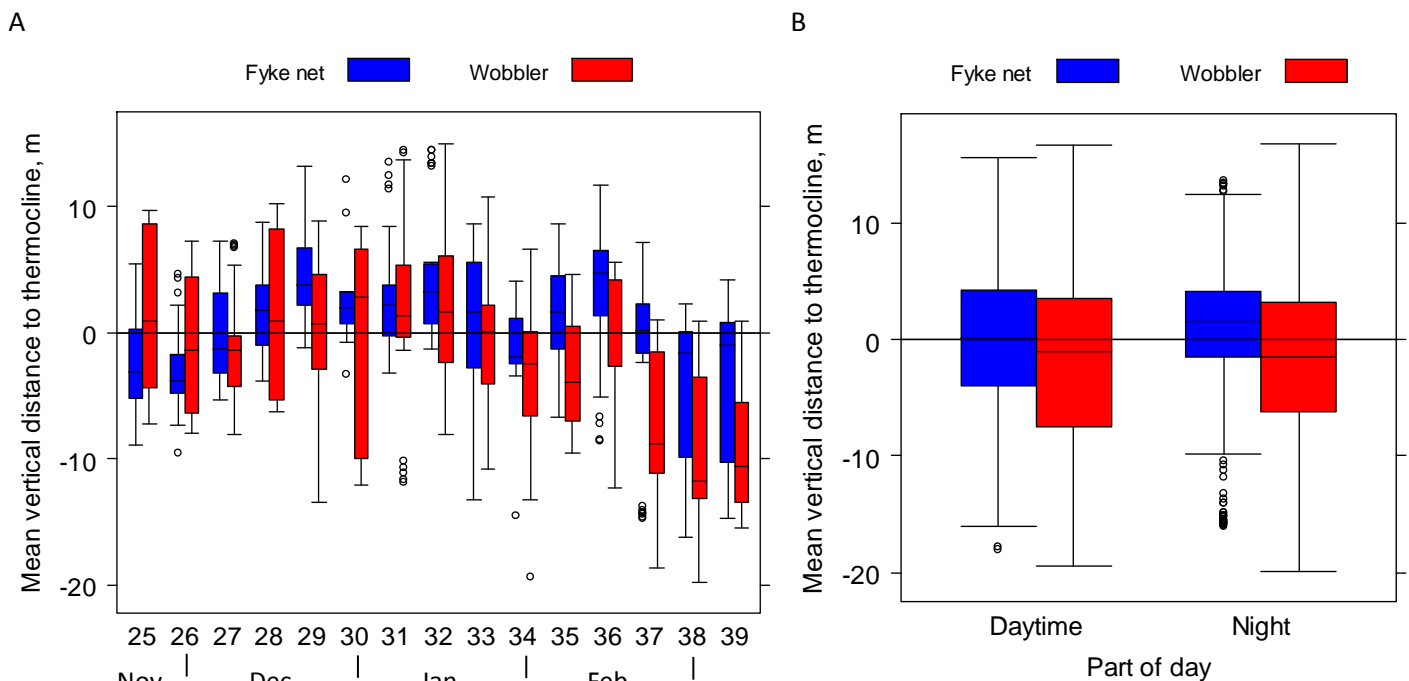


Figure 15. A) Boxplot over mean daily vertical distance to thermocline depth, and B) Boxplot over mean daily vertical distance to thermocline depth.

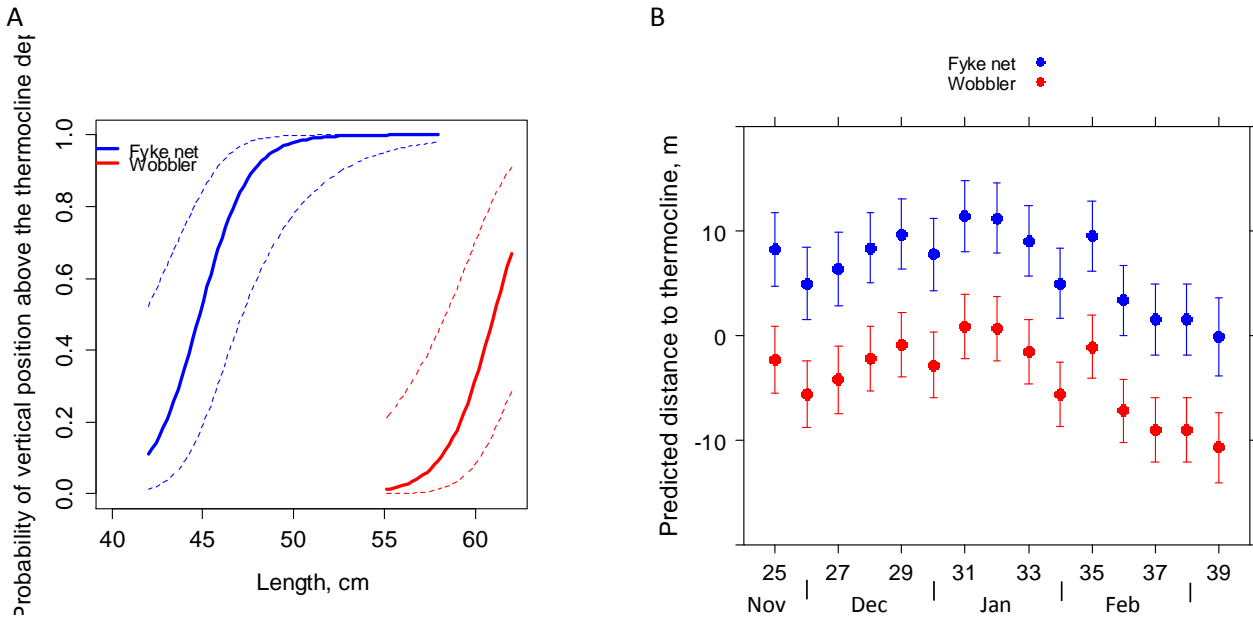


Figure 16. A) Predicted probability (Table 3, Model 5) of staying above the centre of the thermocline depth as a function of gear group and fish length, and B) predicted distance to thermocline (Table 3, Model 6) as a function of gear group and week for fish of body length 55 cm.

3.1.6 Temperature use

The mean ambient temperature from November 2012 to February 2013 for group F and W were 5.1 and 5.9 °C respectively (± 2.6 and 2.5 , SD) during daytime. At night, the mean temperature was 4.7 and 6.0 °C for group F and W (± 2.6 and 2.5 , SD) (Figure 17 A). There was a significant difference in temperature use between the two groups ($p < 0.0001$, L.ratio = 26.84). According to the most supported model, group W consistently experienced a higher ambient temperature which deviated from group F by + 3 °C, week and length adjusted for (Figure 17 B). There was a negative correlation between temperature use and fish size ($p < 0.001$, L.ratio = 16.67) (Table 3, Model 7).

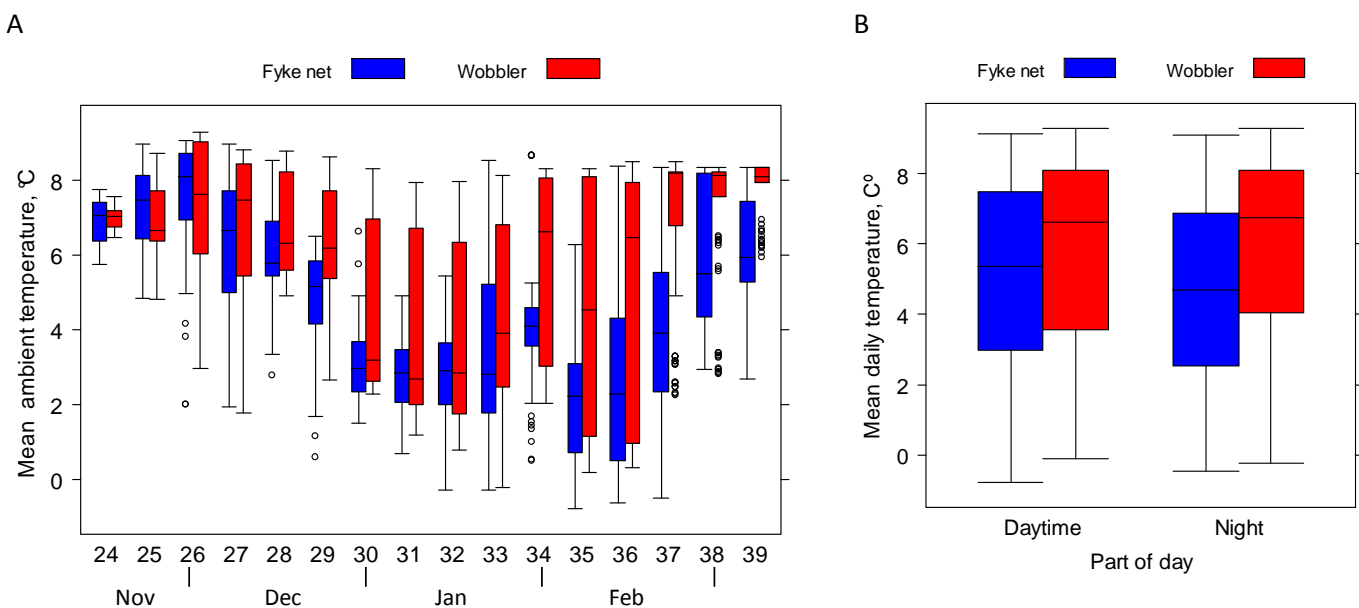


Figure 17. A) Distribution of weekly mean individual daily (24 h) ambient temperatures (°C) used by cod from November 2012 to February 2013, and B) Mean daily temperature use for group wobbler and fyke net during day and night

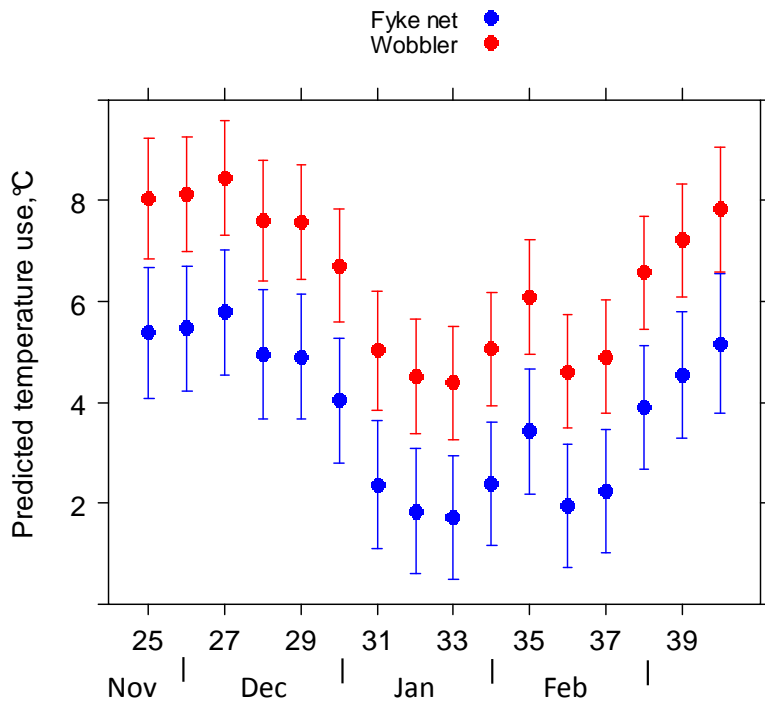


Figure 18. Predicted temperature use for fish in group W and F of size 55 cm (Table 3, Model 7).

When the predictor time-of-day was added to the most supported model with respect to temperature use, it resulted in a decrease of 148 AIC units. The most supported model including the predictor time-of-day had significant interactions between time-of-day and week ($p < 0.0001$, L.ratio= 62.37), time-of-day and length ($p < 0.0001$, L.ratio= 99.98, Figure 19), as well as time-of-day and group ($p < 0.0001$, L.ratio= 28.54) (Table 3, Model 7.1, Figure 19). The among-individual variance in temperature use accounted for 62% of the total random variation.

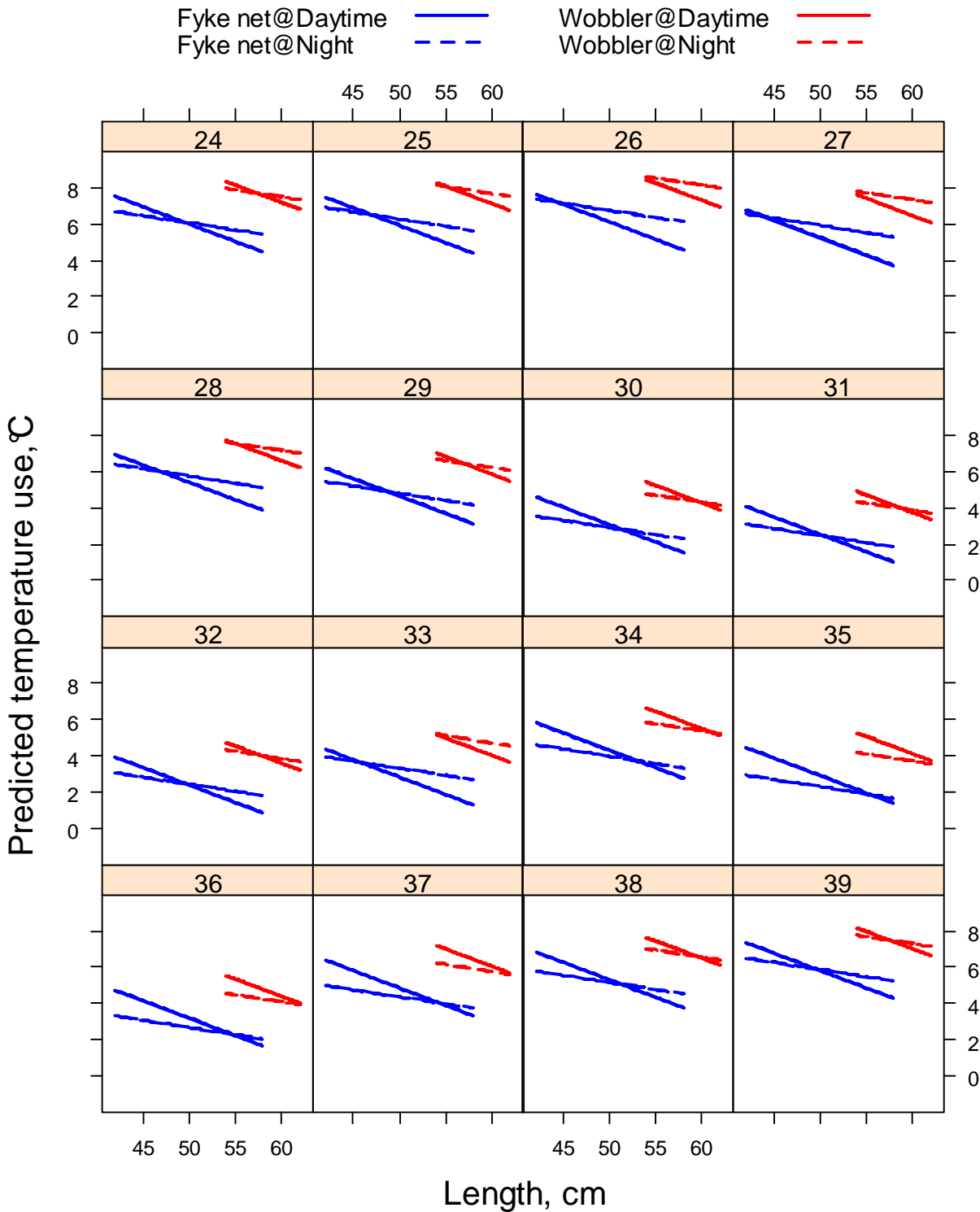


Figure 19. Predicted temperatures as a function of fish length, week, and part-of-day (Table 3, Model 7.1)

3.1.7 Volumetric space use

The mean monthly individual 95 % kernel volumetric space use was 46 and 19 ha³ for group W and F respectively (± 23.5 and ± 9.9 , SD) (Figure 20 A and B) from November 2012 to February 2013. The most supported model included length only as predictor ($p < 0.0001$, L.ratio=10.95) (Figure 21 B, Table 3). This model was only 0.8 AIC units lower than the second best model which also included the additional effect of

group, however this term was not significant ($p=0.2717$, $L.ratio= 1.21$). The repeatability of this trait was low, as among-individual variation only accounted for 14 % of the total random variation.

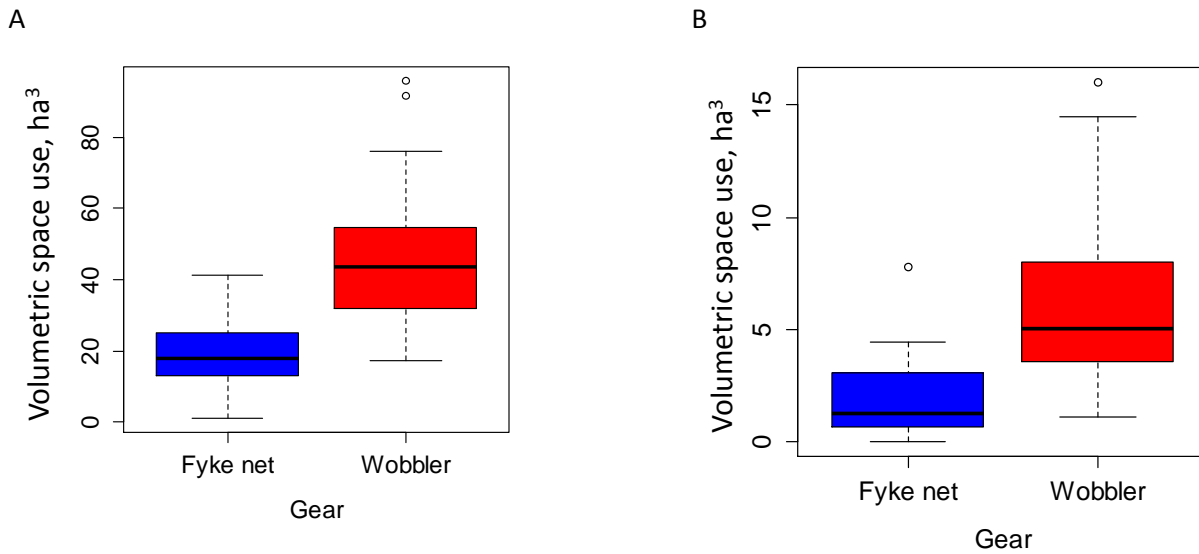


Figure 20. A) Three-dimensional monthly 95 % kernel utilization distributions, and B) monthly 50 % kernel utilization distributions.

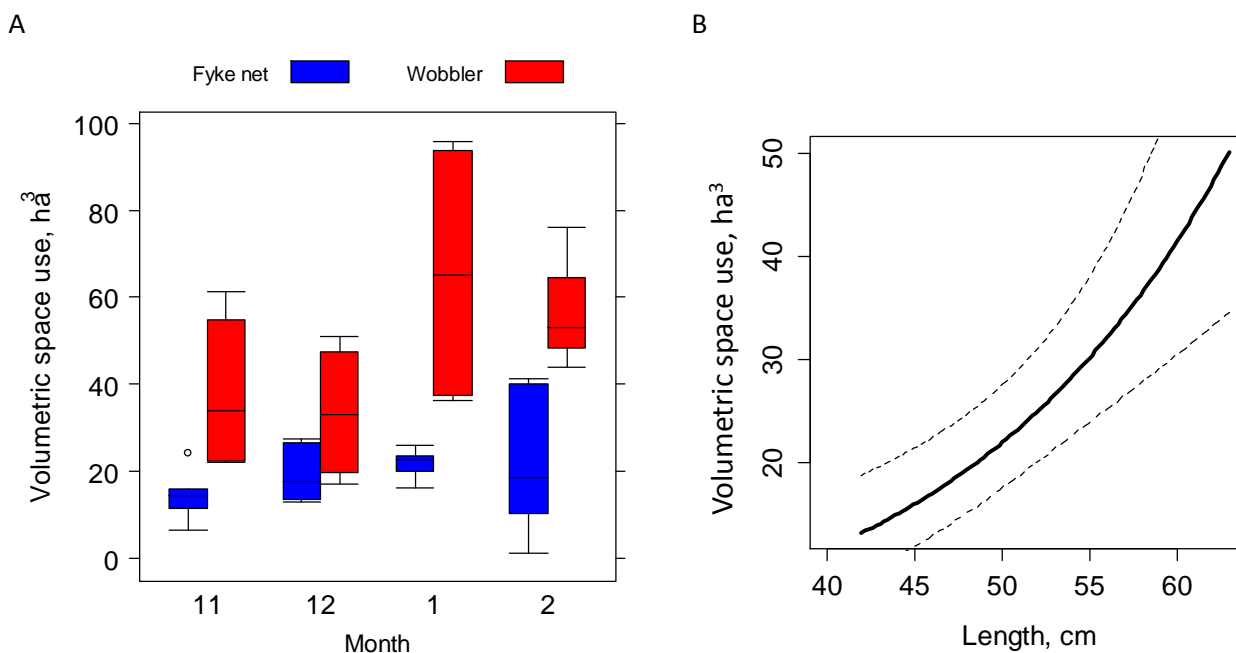


Figure 21. A) Monthly volumetric space use (95 %), and B) Predicted monthly volumetric space use (95 %) as a function of fish length (Model 8, **Feil! Fant ikke referansekinden.**).

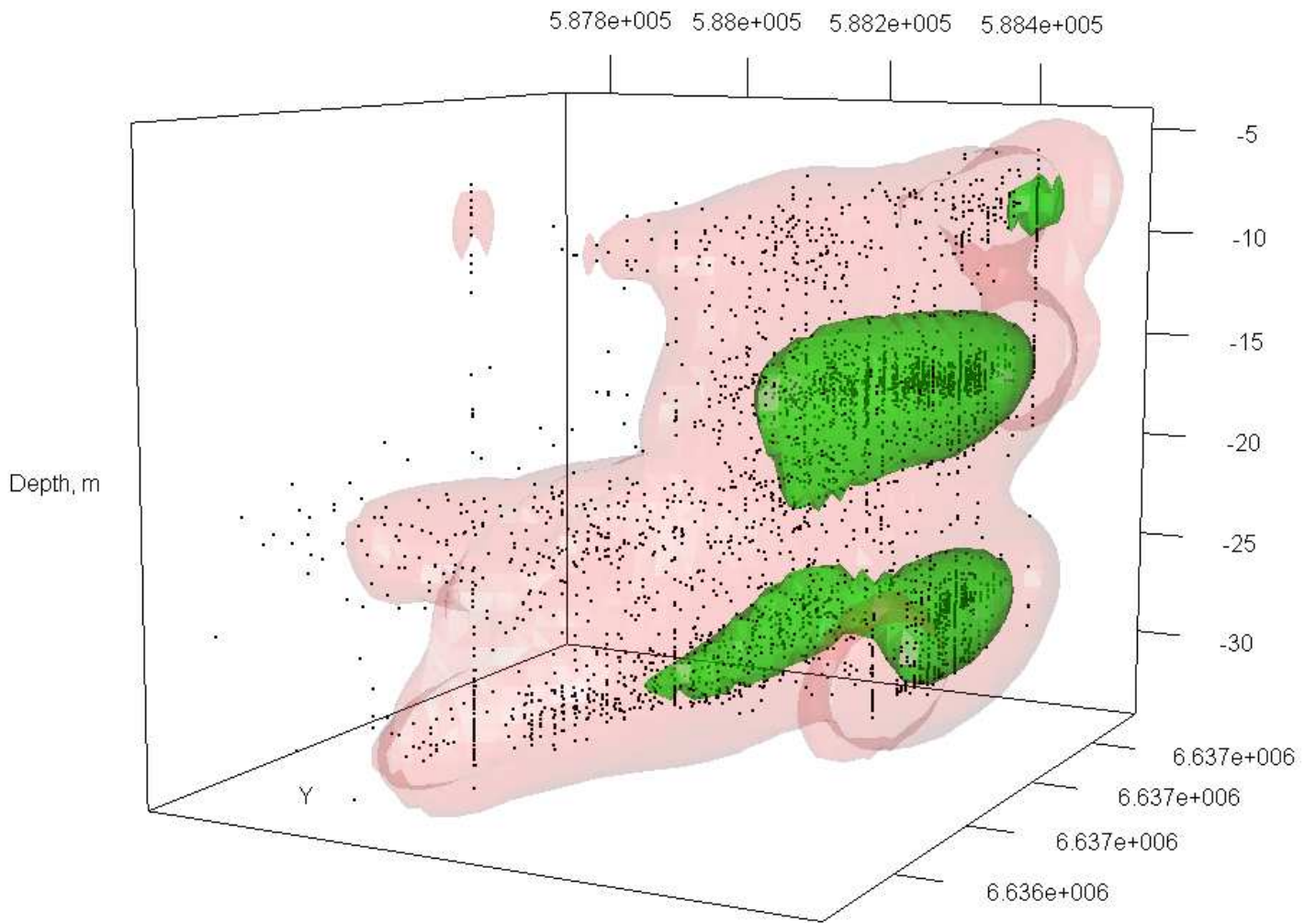


Figure 22. Volumetric space use for ID 23 (group W) from the period November 2012 to February 2013. Green contour outline the 50 % utilization volume and pink contour outline the 95 % utilization volume. The mean vertical migration distance of this individual was 11.2 meters ± 4.9 , SD.

Table 3. Linear mixed effects model results for univariate analyses of VR2Ww-data. The factor levels for the various parameter estimates are provided in square brackets in the “Term” column (F=Fyke net; W=Wobbler; DT=Daytime; NT=Night time). Coefficients for the predictor week are not given, but these week-effect models all intercept to week 25, see figures.

Model	Response	No.fish	Term	β -parameter	SE	p-value	L.ratio χ^2	Random effect	Random variance	Residuals	R ²
1	Vertical position	10	Intercept[F]	-40.9	4.15			week	1.67	4.57	0.78
			Group[W]	-10	1.37	<.0001	46.12	week/ID	22.63		
			Length	0.64	0.08	<.0001	45.34				
1.1	Vertical position		Intercept[F,DT]	-45.77	4.17			week	1.66	4.31	0.79
			Group[W]	-10.77	1.37			week/ID	22.56		
			Length	0.74	0.08						
			Time[NT]	9.39	1.06						
			Group:Time[W,NT]	1.52	0.35	<.0001	18.48				
			Length:Time[NT]	-0.18	0.02	<.0001	65.43				
2	Distance to seafloor	10	Intercept[F]	-30.47	3.52			week	0.66	5.85	0.71
			Length	0.82	0.07	<.0001	65.28	week/ID	15.81		
			Group[W]	-10.98	1.17	<.0001	52.26				
2.1	Distance to seafloor		Intercept[F,DT]	-33.95	4.13			week	0.64	5.74	
			Group[W]	-11.83	1.37			week/ID	15.82		
			Time[NT]	6.79	1.54						
			Group:Time[W,NT]	1.67	0.51	<.0001	19.25				
			Length:Time[NT]	-0.14	0.03	0.0011	10.71				
3	Relative depth use		Intercept[F]	11.2	1.43			week	0.15	1.02	0.69
			Group[W]	3.09	0.47	<.0001	37.67	week/ID	2.66		
			Length	-0.22	0.03	<.0001	45.36				
3.1	Relative depth use		Intercept[F,DT]	12.54	1.46			week	0.15	1	
			Group[W]	3.44	0.48			week/ID	2.66		
			Length	-0.25	0.03						
			Time[NT]	-2.67	0.51						
			Group:Time[W,NT]	-0.69	0.17	<.0001	16.44				
			Length:Time[NT]	0.05	0.01	<.0001	25.16				
4	Depth-range	10	Intercept[F]	18.06	2.08			week	0	9.21	0.57

			Group:Time[W,NT]	-0.9	0.17	<.0001	28.54		
			Length:Time[NT]	0.11	0.011	<.0001	99.89		
			Week:Time[NT]	<.0001	62.37		
8	Volumetric space use (log transformed)	10	Intercept	9.12	0.8		ID	0.06	0.36
			Length	0.06	0.016	<.0001	10.95		0.14

3.2 VR100 data- Horizontal movements

During the course of the study, no detections were made more than 3 km outside the core study site, reflecting a high degree of stationarity of the individuals included in the home range estimation. From June 2012 to February 2013, the mean individual activity areas for group F and W were 24.6 and 53.9 ha (± 10.8 and ± 69.03 , SD) (Figure 24 D), respectively. One individual (ID 22, Figure 23) in group W had an estimated activity area of 250.7 ha which accounted for the largest activity area observed. This fish had moved approximately 2.5 km north of its previous detected location in the core study site, when it was relocated in January. When this observation was removed, the mean activity area for group W decreased to 34.3 ha (± 23.8) (Figure 24 D). Similarly, individual nr 6 (Figure 23) in the same group had moved approximately 2 km north from its previous point of detection in November when it was relocated in December. Both fish had moved to areas that were covered by ice at the time of the relocation. For both groups the mean individual activity areas increased from the summer/fall to fall/winter period (Figure 25 B).

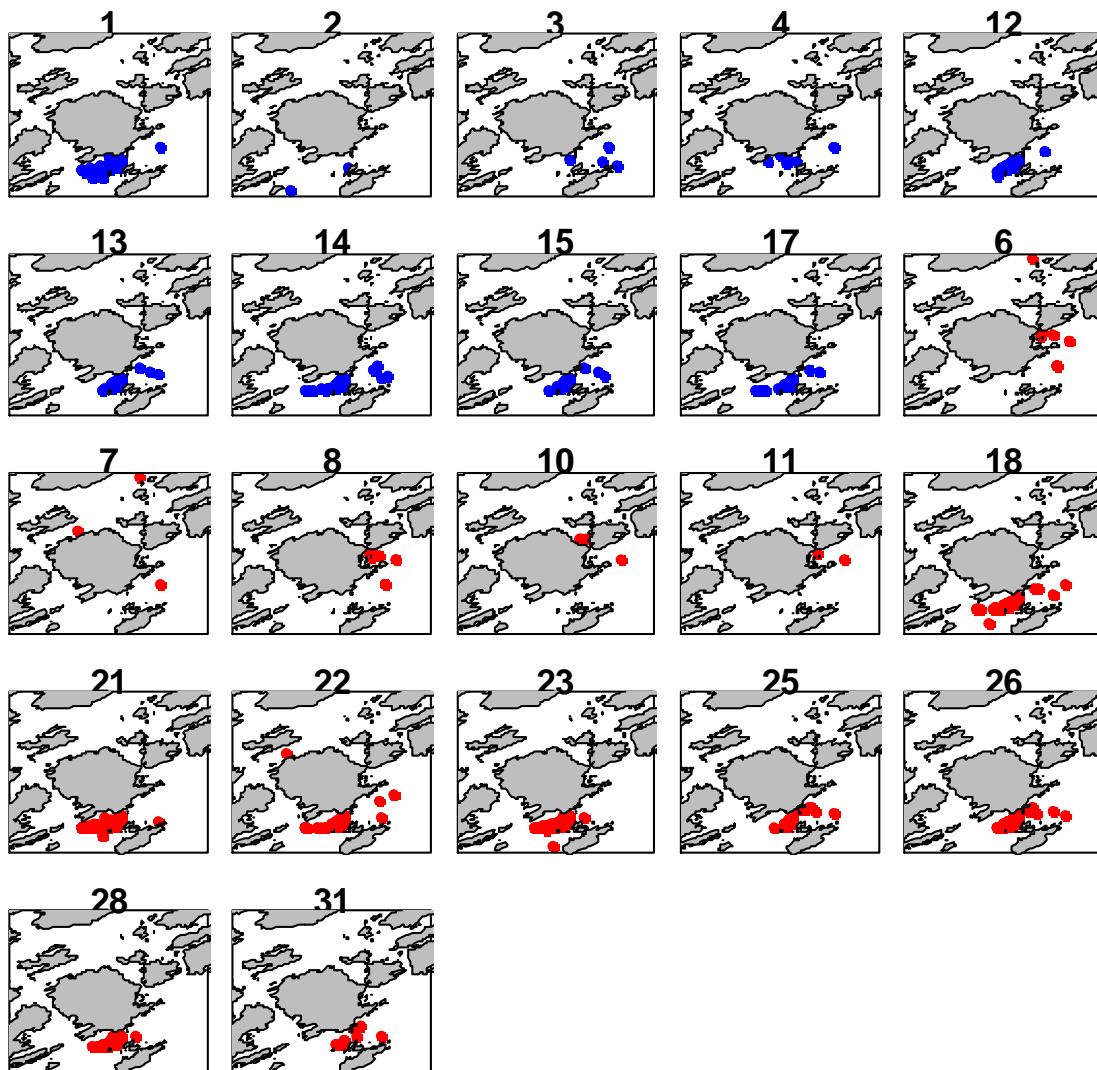


Figure 23. Individual locations detected by triangulation and manual tracking.

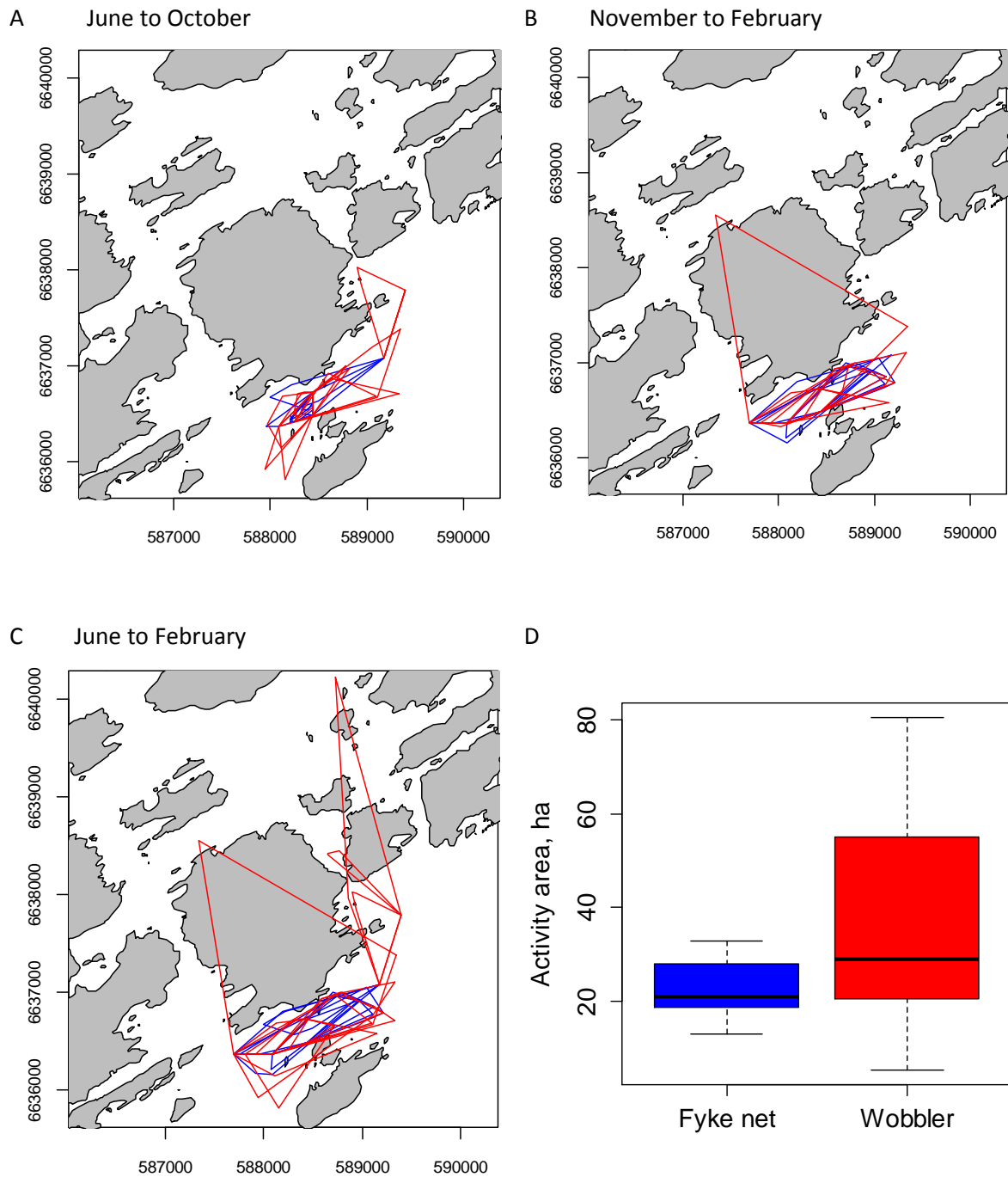


Figure 24. Estimated activity areas as 100 % minimum convex polygons. Positional data (UTM32 coordinates) from manual tracking and triangulation in the periods A) June to October, B) November to February and C) June to February. D) Boxplot over individual activity areas with positional data from June to February, ID no 22 removed.

There was a weak, but significant, correlation between activity area and length (Figure 25 A), and fish length explained 17 % of the observed variation in individual activity areas, (log linear model, $p_{\text{length}}=0.0028$).

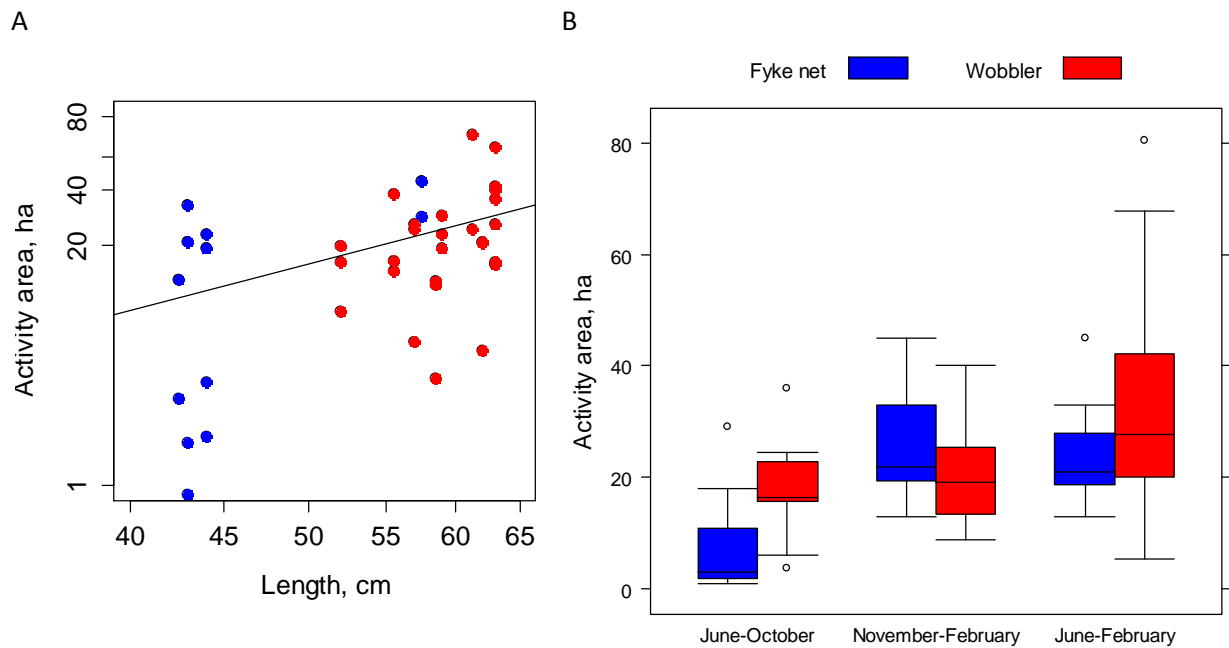


Figure 25. A) Log activity area over log length, and B) Activity areas before (June to October) and after (November to February) the occurrence of isothermal conditions in early November and activity area for the complete study period (June to February). ID 22 removed.

3.3 Multivariate behaviour types

For both daytime and night analyses, the most supported flexmix model (mvglmm) had five glm mixture clusters. The daytime model had an additive length and month prediction structure for the four behavioural components included in the response matrix, whereas the prediction structure in the night model comprised an interaction between length and month. The most supported model was more than 50 AIC units lower than the second-best model. Similar results were obtained when using BIC as model selection metric.

Individual assignments to the five daytime flexmix-clusters produced significant among-gear-group distributions ($\chi^2=64.21$, $df=4$, $p<0.0001$). In particular, cluster 4 included group F individual assignments only and cluster 5 only included group W, whereas the other glm clusters did not separate the two gear types to any extent (Table 4). The cluster 4 and 5 model predictions are presented in Figure 26.

The individual assignments to the five night-time flexmix-clusters produced significantly different between-gear-group distributions ($\chi^2=65.16$, $df=4$, $p<0.0001$). Here, clusters 2 and 5 included group W individual assignments only, whereas cluster 1 (in particular) and cluster 3 had predominantly group F individual assignments (Table 5). The cluster 1 and cluster 5 glm predictions are presented in Figure 27

Table 4. Group-specific individual cluster assignment contingency table for the most supported daytime flexmix model. Expected (Exp) number of individuals (over four months) are provided together with observed (Obs) number of individuals with the corresponding grand χ^2 statistics.

Group		Cluster				
		1	2	3	4	5
Fyke net	Exp	23.6	18.6	20.7	13.9	7.2
	Obs	15	19	17	33	0
Wobbler	Exp	32.4	25.4	28.3	19.1	9.8
	Obs	41	25	32	0	17

$\chi^2 = 64.21, df = 4, p < 0.0001$

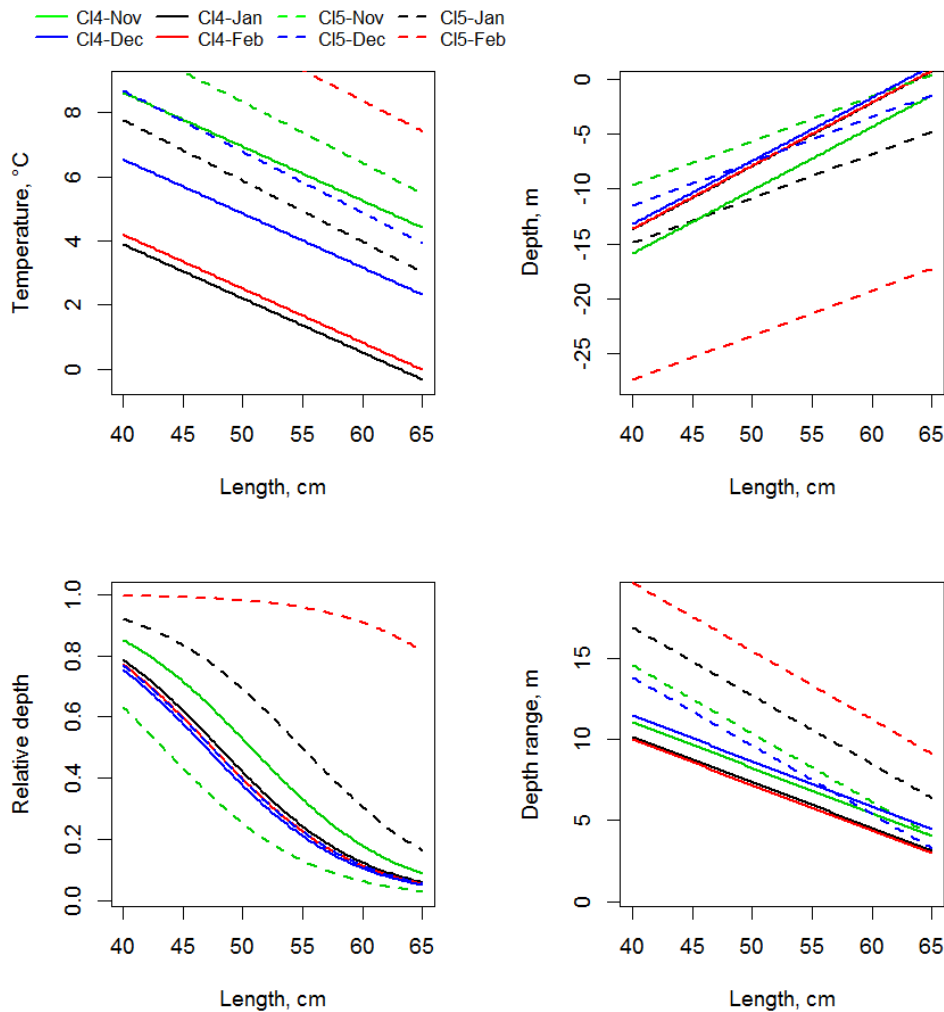


Figure 26. Daytime predictions of month-specific length effects from the most supported flexmix model mgfmm. Cluster 4 (solid lines) and cluster 5 (dashed lines) predictions are plotted only, as these two clusters completely separates the two gear groups (Table 4).

Table 5. Group-specific individual cluster assignment contingency table for the most supported night-time flexmix model. Expected (Exp) number of individuals (over four months) are provided together with observed (Obs) number of individuals with the corresponding grand χ^2 statistics.

Gear		Cluster				
		1	2	3	4	5
Fyke net	Exp	31.9	10.8	9.1	16.2	14.1
	Obs	51	0	13	18	0
Wobbler	Exp	45.1	15.2	12.9	22.8	19.9
	Obs	26	26	9	21	34

$\chi^2 = 65.16, df = 4, p < 0.0001$

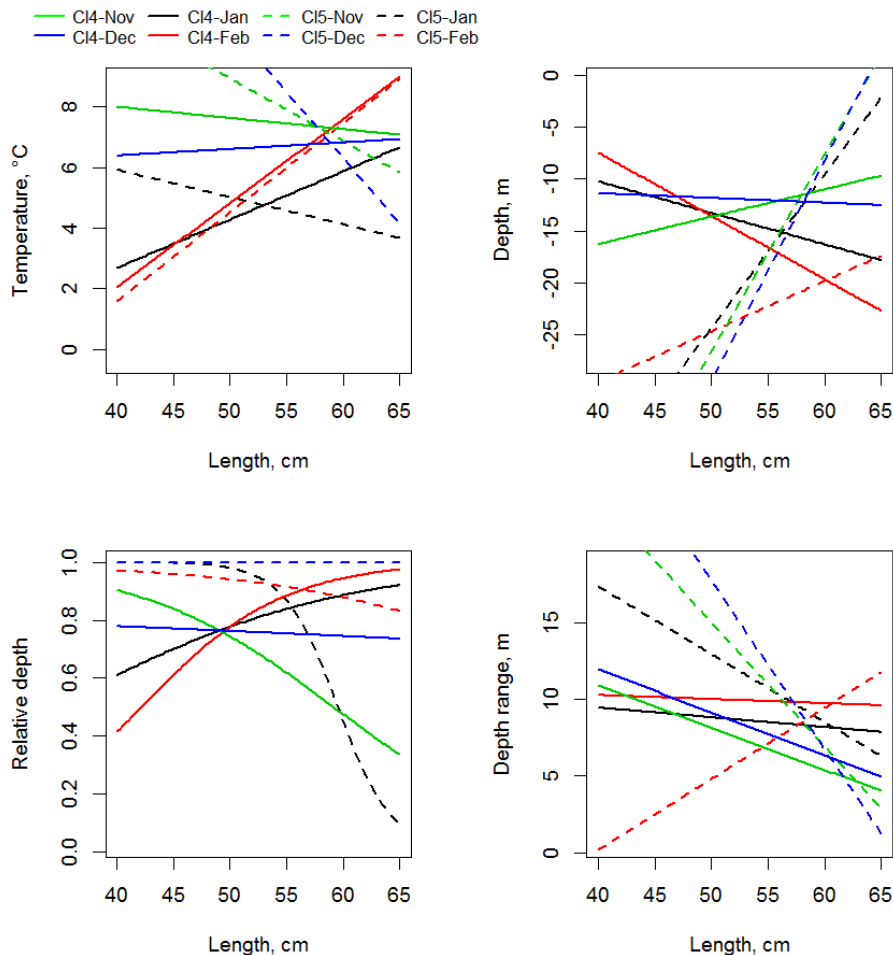


Figure 27. Night-time predictions of month-specific length effects from the most supported flexmix model mvglmm. Cluster 1 (solid lines) and cluster 5 (dashed lines) predictions are plotted only, as cluster 1 mostly loads fyke net cod and cluster 5 only loads wobbler cod (Table 5).

4 Discussion

4.1 Are they really different?

This study has demonstrated significant differences in behaviour between fyke-net-caught and wobbler-caught cod. This result is coherent for the univariate analyses of separate behavioural components and the multivariate analyses assessing the presence of distinct behavioural clusters. The multivariate analyses supported the presence of distinct mixtures of behavioural types, where 5 significantly different clusters distinguished by the length-specific behaviours were identified. The gear groups were non-randomly distributed between these mixtures and were completely separated in four of them. Analyses of the separate behavioural components revealed that the average among-individual differences within each group were consistent, which further supports the presence of behavioural specialization. The group-specific differences in behaviour demonstrate that gear type does not capture a random sample from the population but are biased with respect to behavioural types. Differences were identified in vertical distribution, temperature use, and distance and position relative to the thermocline center. There was also a trend of considerably larger horizontal and volumetric activity areas in group W, but this was not statistically supported. Contrary to the working hypothesis, individuals in group W consistently utilized greater depths, associated with higher temperatures, throughout the November to February period. Although the two groups were different in terms of their respective day and night-time behaviours, the difference was nevertheless so small the biological relevance can be considered negligible (Figure 9 and Figure 19). Assuming residency in shallow waters during daylight can be considered a bold behaviour, the results gave no indication of any group specific differences in this respect. Concerning the fact that all fish were captured in late spring or early fall, it is possible that the behaviour expressed at the time of capture is not representative with respect to their behaviour during the altered conditions in winter. If temperature rather than risk was a main driver for vertical distribution and horizontal movement patterns, then the inversed stratification present in the November to February period is likely to cause a different behaviour compared to summer stratification. The altered temperature conditions will also likely contribute to changes in the quality, quantity, and distribution of food resources. Because of the limited knowledge about the intrinsic and extrinsic factors that the behaviours respond to, characterizing the observed behavioural differences further than a description of the observable symptoms is challenging. Field and laboratory studies of Atlantic cod do support that the species may adopt a vertical movement cycle that optimize the balance between energy expenditure and energy gain and hence maximize growth (e.g., Espeland et al. (2010), Claireaux et al. (1995), Clark and Green (1991)). This balance is again a function of metabolic,- and food intake rates, the former which depends on temperature. Because of the strong correlation between depth and temperature in stratified water bodies, it is difficult to separate the unique effect of these two factors, as fish depth in this context could either be a result of temperature choice or food resource availability, and isolating the relative contribution of each would require a controlled experimental setting. The fact that individuals in one group were predicted to have a higher probability of being located below the centre of the thermocline and hence at depths of which temperatures were increasing, may however indicate that temperature selection is at play. Irrespective of the ultimate causations, the result

of the behavioural differences is that the gear groups were unequally distributed in two different temperature conditions. Because temperature is the key factor for metabolism and energy expenditure in poikilotherms like cod, this will inevitably be of ecological relevance due to its effect on growth and accordingly life history characteristics (e.g. Roff et al. (2006)). Age-determining structures, or other biological data except body length, were not collected in this study and so comparison of growth trajectories and reproductive states could not be compared. Although it is out of the scope of this study, linking the behavioural differentiation to variations in life-history characteristics in order to explore the potential presence of alternative life-history strategies would be of high relevance here, specifically in the context of fisheries-induced evolution.

4.2 Potential mechanisms underlining the behavioural differences

The behavioural difference observed may have arisen in multiple ways. The different behaviours can be adaptive and maintained in the population by means of frequency-dependent selection driven by fluctuating environmental conditions (*sensu e.g.* Wolf and McNamara (2012)); Residing in warmer temperatures may for example be a profitable behaviour when food resources are sufficient so that growth and subsequently fecundity can be maximized, while a more conservative behaviour of higher occupancy in colder temperatures resulting in lower metabolic rates could be an adaptation to less favourable environmental and limited food resources. Another possibility is that the behaviours result from different life-history strategies within the same environmental context: One strategy might be to invest more in present growth and fecundity resulting in a preference for higher temperatures that increases the scope for activity levels, food intake rates and hence growth potential. Such a strategy would potentially include a raised risk of mortality because it would involve an increased predator exposure caused by higher levels of foraging activity. The other strategy might then invest more in survival and future reproduction, and result in behaviours that reduce exposure to predators, hence avoiding temperatures that increase food demand, resulting in a “slower” but “safer” strategy. Different behavioural types are increasingly linked to different life-history strategies (Reale et al. (2010), Biro and Stamps (2008)), hence it is suggested that consistent individual differences in behaviour within a population could be maintained by life-history trade-offs, integrated within a pace-of-life syndrome (Reale et al. (2010), Careau and Garland (2012)) and the fast-slow life-history continuum (Gaillard et al. 1989 in Real 2010) at the within population level. Another possibility is adaptive phenotypic plasticity in combination to spatial variability; Phenotypic plasticity can be adaptive if environmental fluctuations are predictable and expected within a generation. Within a heterogeneous environment, phenotypic plasticity could result in the expression of different behavioural phenotypes due to residency in different sets of habitats (e.g. Herczeg and Valimaki (2011)). Another option involves the stochastic influence of epigenetic effects, or molecular modifications that alter the expressions of genes during early stages of ontogeny. An increasing body of evidence supports that such changes in gene expression can cause long-term changes in neurobiological mechanisms and behaviour (e.g. Jones et al. (2010)). For example, it can be envisaged that increased growth in early ontogeny might affect metabolism later in life with consequent behavioural implications such as foraging activity and abiotic preferences (Fonseca & Cabral 2007). This scenario can result

in inter-cohort behavioural differentiation if rearing-environment is variable over time, or intra-cohort differences if rearing-environment is variable in space. Another potential mechanism also involves differential regulation of gene expression; maternal effects occur when the maternal environment affects offspring gene regulation. Such transgenerational plasticity have been demonstrated to cause inter-individual behavioural variation (e.g., Keiser and Mondor (2013), Graff and Mansuy (2008)), some of which have been connected to offspring anti-predator behaviour in fish (Roche et al. 2012). Behavioural differences can also arise due to state dependence and not be stable for a lifetime but be affected by factors such as social status or condition (Dall et al. 2012): Competitive exclusion may for example generate behavioural differences as a result of behavioural compensation due to exclusion of competitively inferior individuals into suboptimal habitat, i.e. 'doing the best out of a bad situation'. Learning can also be a contributor to the development of behavioural types. Hatchery-reared fish often show reduced antipredatory responses compared to wild fish (Patten 1977). A similar scenario can be envisaged in the wild when habitat variability causes differential exposure to different stimuli, for example; development in different microhabitat can cause differential exposure to prey items and affect the development of search images due to individual differences in prey encounters.

There are many candidate mechanisms which can cause intra-population differentiation, only some of them listed here, many of which can act in concert or antagonistically. Delineating these sources of variation or their interactions requires controlled experiments such as relevant common-garden experiments. This would foremost help to distinguish genetically-determined variation from other effects.

4.3 Management implications

The presence of intra-population variation in ecologically relevant behaviours is likely to have ecological and management implications. If a managed population is characterized by high levels of heterogeneity it suggests that the unit of management should be revised because the targeting of broad generalities may harm a subset of the population and in turn ecologically relevant diversity. For harvested populations, the differential susceptibility to fishing gear between behavioural variations, as demonstrated in this study, have the potential to selectively diminish or remove a subgroup of the population with the potential for fisheries induced evolution assuming the behaviours are genetically controlled. This might in turn have cascading effects due to selection on correlated traits (Biro & Post 2008). Although the empirical evidence is limited, it is suggested that intra-population behavioural variability may increase population stability through improved resilience to environmental fluctuations (Bolnick et al. 2003), similar to the portfolio effect witnessed with population diversity on the species level (i.e., Schindler et al. (2010)). Accordingly; populations that contain a diversity of behavioural types may be more likely to survive as conditions change because some behavioural types will thrive in new environmental conditions, while others will not (Conrad et al. 2011). Similarly, differentiation in behaviours connected to activity patterns, habitat use and resource use can be expected to enhance the carrying capacity and productivity of a population (Wolf & Weissing 2012). This suggests that behavioural diversity in ecological relevant traits can be subject to protection by its own right, in a 'phenotype

management' approach (Conrad et al. 2011). Another dimension is that using population "averages" in ecological modelling will have a negative impact on the predictive power in terms of population dynamics and responses to anthropogenic and non-anthropogenic changes in the environment. In terms of surveillance programs, not accounting for individual-level variability may lead to problems with lack of representativeness. The potential impact of individual-level behavioural diversity on harvest-induced selection, population productivity and resilience hence suggests a need to determine the presence, nature and extent of inter-individual behavioural variation for an improved population and species management. In addition to providing a more integrative approach, this will also lead to a better theoretical foundation for understanding the dynamics of populations.

4.4 Study limitations

In addition to the effect of group, body length (as measured at the time of capture) had a significant effect on each of the behavioural elements included in the statistical analyses (Table 3). Smaller fish utilized greater depths, higher temperatures, were more associated to the seafloor depth, had a higher probability of occurring below the thermocline, and displayed larger vertical migration distances. Size dependence was also identified in the horizontal (Figure 25 A) and three-dimensional movement metrics. Allometric and size-scaling relationships are important factors in animal behaviour (Dial et al. 2008), for example, respiration rates and energy expenditures depends on body size in fish (Clarke & Johnston 1999), and risk of predation is more pronounced for smaller size classes. There is a strong correlation between size and age within fish populations, and hence behavioural differences that arise as a consequence of differences between age groups do not conform to the concept of intra-population behavioural differences. If the size differences of the fish in this study were due to differences in age, then a general note of caution here is the size bias in the two groups used in the analyses (mean group W $58.8 \text{ cm} \pm 2.7$ and group F $46.2 \text{ cm} \pm 6.35$). Consequently, the confounding effect of body length may not have been completely distinguished from the effect of group assignment. Although random effects in mixed models can account for between-subject variation in the dependent variable, they do not automatically account for possible among-subject variation in the independent variables (van de Pol & Wright 2009). Nevertheless the unanimous result of several models and two different statistical approaches strongly suggest that the size-independent differences were highly realistic. It should also be added that smaller than 46 cm individuals do get caught on floating wobblers, but due to under-communication and a bit of bad luck (small individuals tended to get off the hook prior to landing!) I ended up not having tagged any smaller fish in group W. A final note of caution is the small sample size of this study. While this does affect the generality of the result in terms of whether or not the observed behaviours can be considered as "typical" for individuals captured by the respective gear types, it does not reflect on the validity that the group-specific differences documented for this particular sample of cod.

4.5 Conclusions

This study has demonstrated that consistent intra-population differences in coastal cod behaviour exist in the Inner Oslo fjord. Specifically, the individuals differed in temperature

use and how they were distributed in the water column. These differences were related to the gear type that the individuals were captured by prior to tagging, which demonstrates that different capture techniques do not necessarily sample randomly in a population but rather are biased in terms of behavioural types. The differential temperature use is likely to affect individual life-history characteristics due to the effect of temperature on ectotherm metabolism and growth. Differential susceptibility to harvest gear types induced by among-individual behavioural variation may have implications for fisheries-induced evolution if the behaviours are genetically determined. Because intra-population variation in ecologically relevant behavioural traits may affect population resilience and carrying capacity, the inclusion of a behavioural aspect in population management may be of high relevance

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6 Appendix

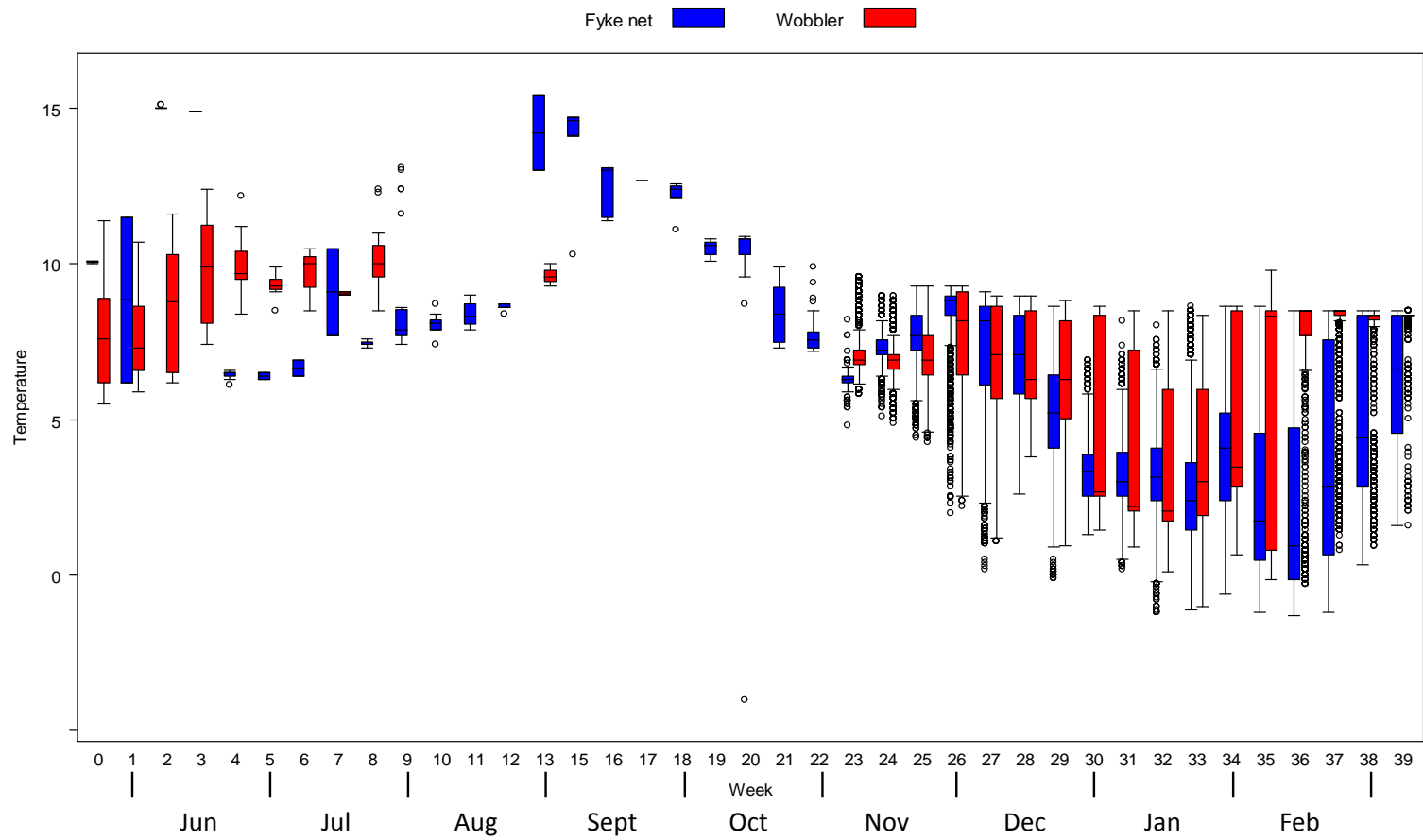


Figure A 1. Boxplot of weekly distribution of daily mean ambient temperature (°C) use of cod in inner Oslo fjord from June 2012 to February 2013.

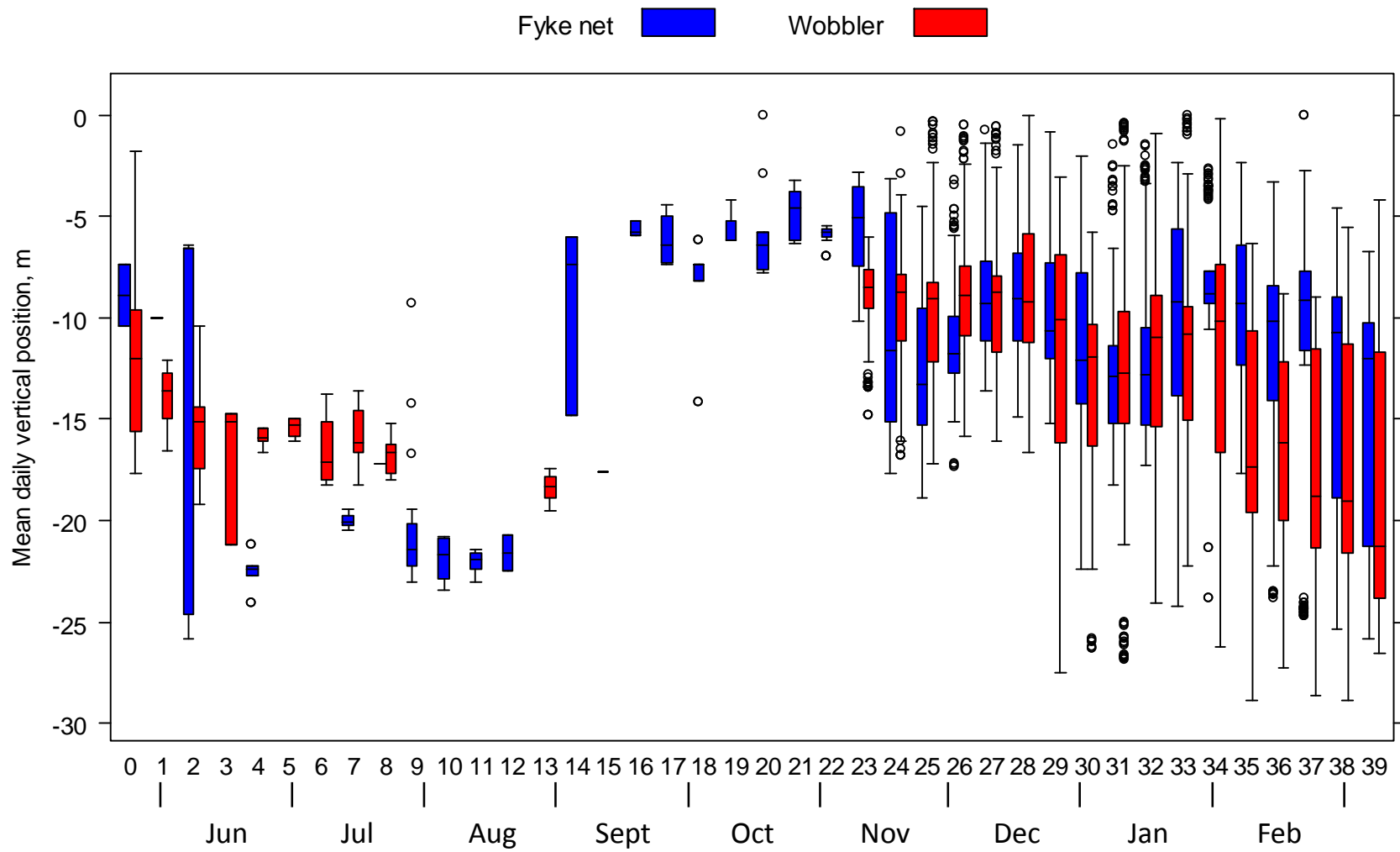


Figure A 1. Boxplot of weekly distribution of daily mean vertical position (m) of cod in inner Oslo fjord from June 2012 to February 2013.

