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Acoustic tracking of juvenile cod (*Gadus morhua*) in Skagerrak: effects of body size on short-term movement patterns in nearshore habitats

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> The sea, once it casts its spell, holds one in its net of wonder forever
> - Jacques-Yves Cousteau

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Preface

A lot of people have helped me in the different phases of fulfilling this daunting task: to write a Master thesis. First of all I give many thanks to the Department of Biology and CEES and to my supervisors Nils Christian Stenseth, Esben Moland Olsen and Sigurd Heiberg Espeland for believing in me and giving me the opportunity to explore the magical world of science and research. Thank you for all your inspiration and help both in the field and in front of the computer.

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Blindern, June 2nd 2008

Abstract

The coastal cod is an important commercial and recreational resource for the local communities in the Skagerrak. The situation of this and neighbouring stocks has worsened for decades, promoting an imperative need for better knowledge of the fine-scale ecology and behaviour of the species. In this study, the home ranges and vertical movement pattern of nearshore juveniles (*n* = 20, length = 325 mm [mean]; 265 - 375 mm [range]) were investigated using acoustic telemetry and kernel density estimators. In addition, habitat preferences were estimated by use of resource selection functions. In concordance with the hypotheses, home range sizes increased with fish length, whereas bigger fish remained at shallower depths than smaller fish. Although inconclusive, results were indicative of smaller fish displaying greater variation in vertical movement than larger fish. The fish used habitats disproportionately to what was available, and although tests were not significant the results showed a clear trend of selecting barren habitats over more complex habitat structures. These behavioural patterns are thought to reflect a dynamic decision-making process where intra- and inter-specific competition and predation pressure drive the selection of the trade-off between shelter and forage. Further, these results show that the classification of important habitats for a commercially exploited species is a complex process that should be investigated on a broader scale.

Contents

1 Introduction

The coastal cod *Gadus morhua* has been of great economic and cultural importance to the maritime communities in the Skagerrak for centuries. Despite signs that the stocks are being overexploited, there is still a significant commercial and recreational fishing pressure on them (Gjøsæter, 2008). A large decrease in abundance and mean body size of several coastal species on the western coast of Sweden has been documented (Pihl *et al.*, 2006, Pihl and Ulmestrand, 1993, Svedang, 2003), leading scientists to speculate whether the historically rich local spawning grounds may have been eradicated. It is believed that many of the fish species found there today are mostly young recruits that have drifted in to the area from the North Sea with the North Atlantic circulation, which has been shown to be the case at least for the cod (Knutsen *et al.*, 2004, Pihl and Ulmestrand, 1993, Stenseth *et al.*, 2006). With the North Sea cod stocks currently being overexploited (ICES, 2007) and risking the same fate as their conspecifics in Newfoundland, where the stocks collapsed and a moratorium was enforced (Hutchings, 2004, Myers *et al.*, 1997), it is reason to assume that this may cause changes in the local cod communities in the Skagerrak. It is therefore crucial to have as much understanding as possible of the ecology and behaviour of the coastal cod, to be able to manage the species sensibly in the future. Restrictions on mesh size, seasonal closing of fishing grounds, construction of MPAs (Marine Protected Areas) and temporary moratoriums are proposed actions which may help to sustain a healthy cod population. However, to enforce these we need to increase our knowledge of the species and environment involved.

In this study, the main focus was to describe the movement patterns and habitat preferences of juvenile (1 year group) cod in a semi-sheltered area on the Norwegian Skagerrak coast, and, further, to link these behavioural characteristics to the body size of individual fish. Cod is known as a mass-spawner, with only a small fraction of the larvae being recruited to the spawning stock. To survive until reproduction of viable and competitive offspring is, according to evolutionary theory, the ultimate goal of any species and the basis of which the relative fitness of an animal is estimated. There are several phenotypic traits closely linked to survival and reproduction (e.g., birth size, age and size at maturity, life span), but one of the most important and well-studied of these is growth. An individual with an increased body size relative to conspecifics is considered to be less vulnerable to predation, have increased intra- and inter-specific competitive abilities, have better capability of storage of energy reserves and to mature sooner and have higher reproductive success (Lankford *et al.*, 2001, Metcalfe and Monaghan, 2003, Munch and Conover, 2003, Sundström *et al.*, 2005).

But despite having the capacity of continuous growth, fish rarely maximise their theoretical potential. This may be due to a variety of factors, both intrinsic (trade-offs between fitness correlated traits and the cost of somatic growth), and extrinsic (environmental factors, such as size of habitat, population density effects, predation risk and prey availability) (Freedman and Noakes, 2002, Stearns, 1992). Trade-offs are linkages between two or more life history traits that are selected for at the same time. Growth versus current reproduction is one such trade-off, where the animal must allocate its energy into one or the other but not both at the same time, if so it would face the risk of low-quality and -quantity offspring and poor body condition (Stearns, 1992). Growth versus future reproduction is another, in this case the animal must decide whether to invest in somatic growth or (in the case of cod) lipid liver reserves (Jørgensen and Fiksen, 2006). Moving on to extrinsic factors, there has been a wide reporting of different effects of body size on predation risk. While some have found predation mortality to increase with increasing body size (Dibattista *et al.*, 2007, Lankford *et al.*, 2001, Munch and Conover, 2003), others have found the opposite (Meekan *et al.*, 2006, Nielsen and Munk, 2004), showing that this trade-off may be dependent on different life history strategies between species and different effects in differing ecosystems. The size of the animal's habitat and prey availability and quality is also thought to affect the size of the animal. Pelagic species often grow larger than benthic ones, owing to their large cruising ranges in search of high-quality food. Benthic species, on the other hand, often rely on sedentary foraging strategies, which don't require the animal to be any bigger than what is needed to capture and process the prey (Freedman and Noakes, 2002).

The Skagerrak coastal cod is considered a benthic species, showing signs of site fidelity and discrete population structures within distances < 30 km (Bergstad *et al.*, 2008, Espeland *et al.*, 2007, Jorde *et al.*, 2007, Knutsen *et al.*, 2003). In literature, adult cod is often shown to undertake migrations to deeper water as winter sets in, while younger cod seem to remain stationary (Cote *et al.*, 2004, Godø, 1984, Pihl and Ulmestrand, 1993). This segregation during winter time is thought to be a result of differing physiological abilities between juvenile and adult cod, with juveniles being better adapted to shallow, cold waters than adults, which need to migrate to warmer water (Goddard *et al.*, 1992). On a smaller temporal scale, juvenile cod is known to sometimes have diel migrations in the water column (Anderson *et al.*, 2007, Grant and Brown, 1998, Gregory and Anderson, 1997). There is some confusion as to why this pattern is seen, but it is mainly thought that the juveniles move vertically to avoid predators during the day, or to feed during the night. The different life stage groups also seem to have somewhat different habitat preferences; while juvenile cod often select habitats that provide shelter from predators (such as coarse bottom substrates that match their skin colouration and habitats with high vegetation cover), older cod tend to associate more with single habitat structures that provide predation cover from which they stray to forage (e.g. high bathymetric relief, boulders and little vegetation) (Chan *et al.*, 2003, Cote *et al.*, 2004, Cote *et al.*, 2003, Dalley and Anderson, 1997, Gotceitas and Brown, 1993, Gotceitas *et al.*, 1997, Gregory and Anderson, 1997, Lekve *et al.*, 2006, Riley and Parnell, 1984).

There are numerous studies on the behavioural patterns of juvenile cod reported in the literature. While a few of these deal with individuals within the body length range used in this study (e.g. Cote *et al.*, 2003, Gregory and Anderson, 1997), most of them focus on the young of the year; the 0 year group (e.g. Anderson *et al.*, 2007, Grant and Brown, 1998, Linehan *et al.*, 2001). The latter age group may experience radically different selection pressures from what larger individuals do. In addition, few behavioural studies have been done on the movement patterns and habitat preferences of nearshore cod in the Skagerrak, compared to the literature that exists on cod from e.g. Newfoundland and surrounding areas. As life history traits have been shown to vary among populations only a few hundred kilometres apart (Olsen *et al.*, 2004), it is reason to assume that behavioural responses of the Skagerrak cod may differ from their conspecifics studied elsewhere. This study thus aims to investigate the habitat selection and effects of body size on home ranges and movement patterns of nearshore juvenile cod, using acoustic telemetry and resource selection functions.

Previous studies have shown that at about age 3 (total length = 590 mm [mean]), 50 % of the stocks close to the study area have reached maturity (Olsen *et al.*, 2004). Based on length-at-age relationships available for cod from this area, the study animals used here were sampled so that it was unlikely that any of them would mature within the time frame of the study and show signs of an eventual spawning migration. I hypothesise that the animals will select habitats that maximise shelter from predators (H1), preferring coarse bottom substrates (H1a) and dense vegetation (H1b). I also hypothesise that movement patterns of the fish will depend on the size of the fish within the age group (H2). Here I predict that larger fish will be competitively superior to smaller fish, reflected in larger home ranges (H2a). Smaller fish will show greater variation in their vertical distribution (H2b), due to predator avoidance and differing foraging strategies. I also predict that mean depth will be negatively correlated with the size of the fish, as smaller individuals will seek refuge from predators closer to the bottom than larger ones (H2c).

2 Materials and methods

2.1 Study area

The study area consists of a 2.5km^2 semi-sheltered archipelago located at the Norwegian Skagerrak coast close to the city of Arendal (Fig. 1). The river Nidelva, with a mean annual water discharge of 123 m^3 s^{-1} (Thorstad *et al.*, 2003), has one of it's three outlets in the northern part of the locality, making the area an estuarine system. Most parts of the area are quite shallow, with depths of 10-15 meters predominating. Maximum observed depth was about 30 meters.

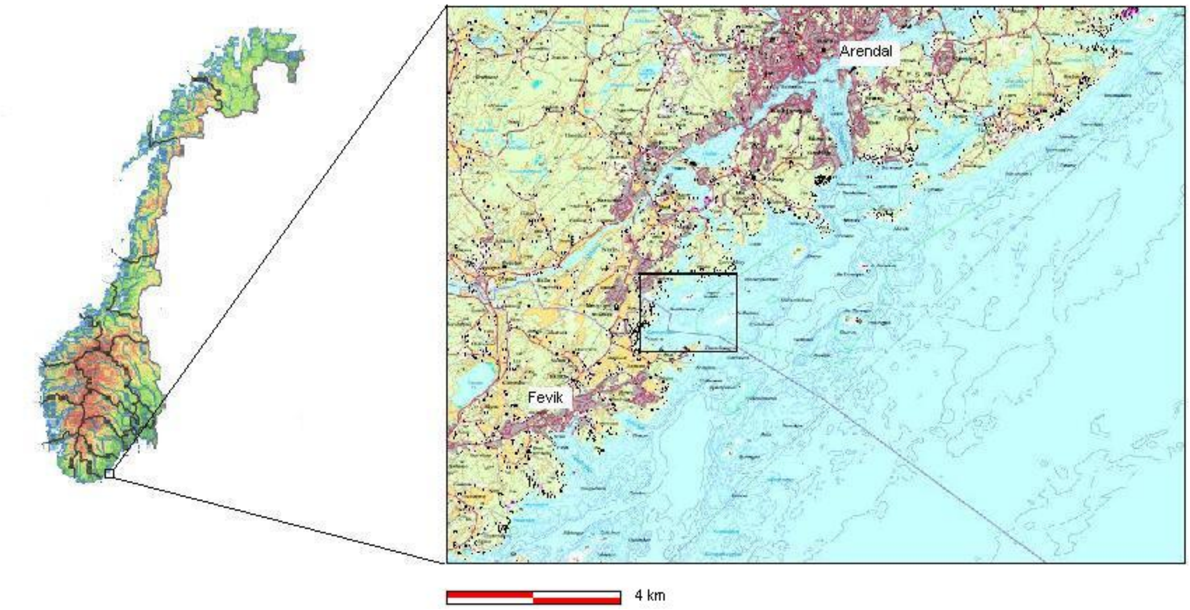


Figure 1. Map of the study area located in the southern part of Norway.

2.2 Tagging and tracking

2.2.1 Capture and selection

The study was carried out in the period October-December 2006. A total of 20 cod were caught by eel pots left overnight scattered around in the study area (Fig. 2a). Based on previous studies on cod caught in the vicinity (unpublished data, Jakob Gjøsæter, Institute of Marine Research Flødevigen), only specimens assumed to be at age 1 were brought back to the Flødevigen research station; other animals were released back to the sea (see Appendix I, Table A1 and Figure A1 for estimated length at age). During the sampling, cod of various sizes (100 - 600+ mm) and ages (0 - 3+) were frequently caught. The total lengths (L_t) of the specimens chosen for the study (Table 1), measured at the capture site, were well within the length-range of the 1 year group. All research animals were equipped with a unique T-bar tag, showing its identification number, the name of the research station and a capture reward (NOK 50,-) in case the fish should get caught by local fishermen.

2.2.2 Tag implantation

At the research station, each individual was anaesthetised in a 40 L seawater bath containing a mixture of 0.36 ml ethanol/L and 0.04 ml concentrated clove oil/L as described by Cooke *et al.* (2004) and Cote *et al.* (1999). Comparative experiments have shown clove oil to be an efficient sedative, with minimum stress impact on the test animals and low mortality rates, in addition to having antibacterial and antiviral effects (King *et al.*, 2005, Munday and Wilson, 1997, Soto and Burhanuddin, 1995, Tort *et al.*, 2002). When the fish no longer responded to visual stimuli and lost equilibrium, it was taken out of the bath and placed on a sterilised bench. A small incision (10-12 mm) was made mid-ventral posterior to the pelvic fin, through which a V9P coded acoustic transmitter (40 mm [length] x 9 mm [diameter], 2.6 g [in water]; Vemco Ltd, Halifax, Canada) was passed and gently inserted in the body cavity. The transmitter sends a unique ID code and pressure measurement at random intervals every 30 to 60 seconds. The wound was then closed using absorbable sutures (Dexon* II™, Tyco Healthcare Group, Mansfield, MA, USA) and a liquid tissue adhesive (Vetbond™, 3M Company, St. Paul, MI, USA). During the surgery, a small tissue sample was taken from the tail fin for DNA profiling useful for further studies.

After the procedure, the fish was put in a 3000 L holding tank and manoeuvred back and forth to stimulate respiration and to clear the gills of the anaesthetic. The time elapsed from total anaesthesia to full control of equilibrium varied from 5 to 15 minutes. All of the fish used in this experiment made a full recovery, and the surgeries were conducted by experienced personnel from the Flødevigen research station.

2.2.3 Acoustic tracking

The tagged individuals were kept in the holding tanks for observation for 1-3 days, before they were released at their respective capture sites. Immediately after release, the fish were tracked using an omnidirectional hydrophone (VH165) and a directional hydrophone (VH110), connected to a receiver on board (VR100; all from Vemco Ltd, Halifax, Canada). The position of the fish was estimated to be where the directed signal was strongest at the lowest possible gain, and a coordinate was assigned to the position in addition to the tracked depth.

When tracking the fish, a portable CTD (Conductivity-Temperature-Depth) recorder was deployed at five regular locations within the study area to measure the temperature and salinity in the water column. The CTD stations represent a gradient from inshore (close to the river mouth) to more exposed areas (far from the river mouth). For each relocation of a fish, the temperature and salinity at the tracked depth measured at the nearest CTD station were used to describe the variation of the environment experienced by the fish during the study period. The difference of these variables over the inshore-exposed gradient was minimal (temperature: 13.3 °C [mean inshore], 13.1 °C [mean exposed]; salinity: 33.3 ‰ [mean inshore], 33.4 ‰ [mean exposed]). A summary of the measurements are given in Appendix II, Table A2.

The tracking and CTD measurement procedure was repeated at daytime every 1 to 10 days from October 11th to December 21st, giving the total number of relocations for each fish listed in Table 1.

Table 1. Number of relocations and total length (L_t) of each individual. Mean, median and standard deviation are given at the bottom.

Tag ID	Relocations	L_t (mm)
233	13	315
234	13	340
235	13	325
236	13	350
237	13	330
238	13	305
239	13	295
240	14	320
241	14	320
242	14	375
243	18	320
244	18	353
245	19	319
246	17	335
247	17	358
248	22	265
249	15	348
250	27	285
251	27	298
252	18	350
Median	15	323
Mean	17	325
SD	4	27

2.2.4 Habitat types

Using a portable ROV (Remote Operated Vehicle), the bottom substrate of the study site was video taped at 28 equally interspersed stations (Fig. 2b). The vehicle was deployed at predetermined coordinates and manoeuvred in a 360° circle at the bottom in a radius of 5 m. The video clips were then analysed and bottom substrate and vegetation cover (mainly eel grass (*Zostera marina*), sea lace (*Chorda filum*) and sugar kelp (*Laminaria saccharina*)) for each station was quantified. The bottom substrates were categorised into “fine” and “coarse”, as there were no medium grained substrates among the ROV samples. The vegetation cover was divided into “little” (0 % - 20 % cover) and “lush” (> 20 % cover). The available combinations of these categories made up a total of 3 different habitat types (a – c) in the study area, given in Table 2. For a more detailed view of the ROV samples, see Appendix III, Figure A2 and Table A3.

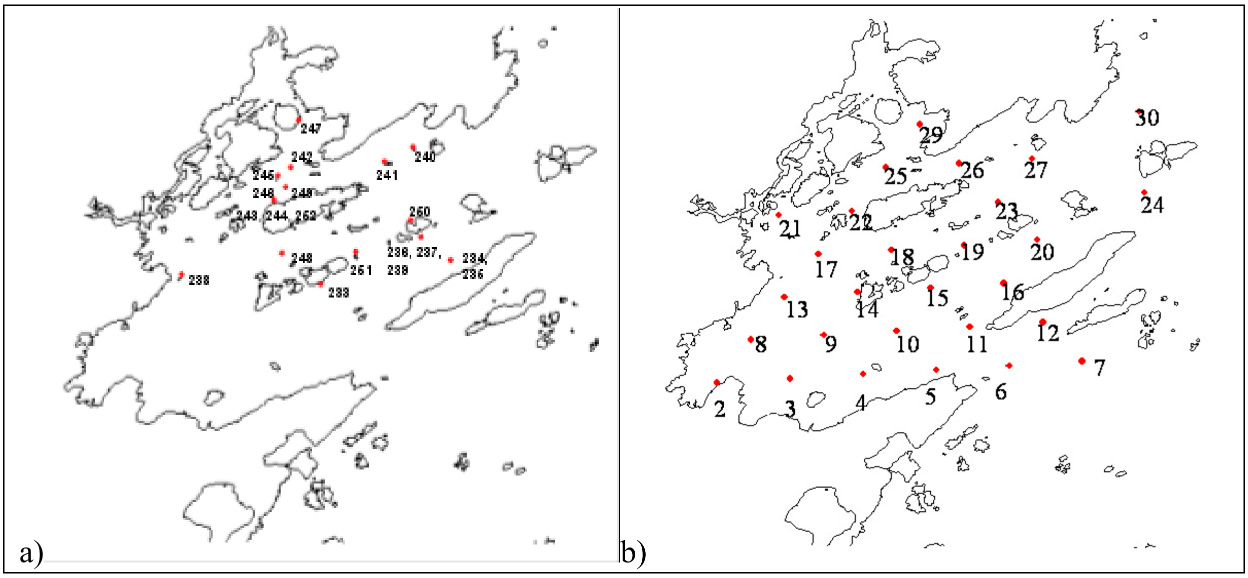


Figure 2. a) The capture sites of the study animals. Tag ID is annotated next to the coordinate (●). b) ROV sampling stations in the study area (●). Stations number 1 and 28 were not sampled and left out of the map.

Table 2. Combinations of bottom substrates and vegetation cover in the study area.

Habitat type	**Habitat category**
Fine bottom substrate, little vegetation	a
Fine bottom substrate, lush vegetation	b
Coarse bottom substrate, lush vegetation	c

2.3 Data analysis

2.3.1 Initial screening of data

Immediately after tracking the study animals in the field, all coordinates, depth recordings and CTD measurements were stored in an excel spreadsheet. The coordinates were then exported to a mapping software (Google Earth, Google Inc) to check if any positions ended up on land or other unlikely locations. This was never the case. Whilst tracking, any unlikely depth recordings (depths above surface or far below the maximum depth of the study area) were ignored and attributed to poor communication between the transmitter and the receiver. At two occasions, a fish was tracked at the same position and depth over 2-3 consecutive days. After examining the immediate area, eel pots were found and hauled after notifying the owners. Both times the fish were found trapped inside the gear in good condition, and released. The consecutive tracked positions from these incidents were not included in the spreadsheet.

2.3.2 Home range analyses

The telemetry observations for each fish were imported to the statistical software R (R Development Core Team, 2006). Using the adehabitat package (Calenge, 2006), the home range probability densities were estimated with both h_{LSCV} and h_{ref} kernels. The home range probability levels from 20 - 95 % with 5 % increments were also estimated.

Estimating the home range area of an animal based on tracking data can be confounded by several factors. First of all, the tracked estimated positions may be considered a small sub-sample of the animal’s true movements, and with few data points the estimated home range may reflect probability distributions far from the true values. Secondly, tracking an animal will inherently result in spatially and temporally autocorrelated data, since an animal does not move randomly. The usual statistical demand of independence may therefore result in heavily truncated data sets (if one decides to remove data points to achieve independence), or data points with inflated degrees of freedom (De Solla *et al.*, 1999). A way to cope with this problem is to use methods that are less sensitive to autocorrelation when estimating home ranges. Kernel probability density estimators are non-parametric and estimate the probability density in an animal’s home range by constructing scaled-down probability density functions, or kernels, over each relocation of the animal, based on the estimated positions used in the analysis. The amount of variation used in each kernel estimation is determined by the smoothing parameter, h (Worton, 1989). With the least square cross validation (h_{LSCV}) method this parameter is found by minimizing the estimated error between the unknown true density function and the kernel density estimate. With the reference (h_{ref}) method, h is estimated from the number of relocations and the standard deviation of the coordinates (Blundell *et al.*, 2001, Hemson *et al.*, 2005). Several studies have found the kernel density methods to be reliable estimators of home ranges, even with small sample sizes and autocorrelated data points (Blundell *et al.*, 2001, Borger *et al.*, 2006, De Solla *et al.*, 1999).

2.3.3 Effects of fish size on home range size and depth

To investigate potential effects of fish size on home range and depth, simple linear models (LM) were applied. These were used to test the size of the fish against the size of its 90 % probability level home range (as recommended by Borger *et al.* (2006)) and against mean depth. In addition, the coefficients of variation of the tracked depths (D) were calculated using:

$$D_i = \sigma * 100 / \mu \tag{1}$$

where σ denotes the standard deviation of the data, and μ denotes the mean tracked depth of each fish. The coefficients of variation were also analysed against fish size with LMs.

2.3.4 Resource selection functions

Habitat selection was analysed by comparing the telemetry observations and estimated home ranges to the ROV mapping of bottom habitats. For each individual, I visually examined which ROV stations were covered by its 90 % probability level h_{ref} kernel. These stations were then categorised according to Table 2, and a proportional use of each habitat category (U) was calculated:

$$U_i = a_i / b_i \tag{2}$$

where a is an individual's number of use of the habitat category and b is the sum of the individual's number of use of all the habitat categories. In addition, the proportional availability (A) was calculated as:

$$A_i = c_i / e \tag{3}$$

where c is the number of ROV stations consisting of the habitat category and e is the total number of ROV stations (= 28). The proportional availability was hence assumed to be the same for all individuals. The used and available proportions were then imported to R and RSFs (resource selection functions) were fitted using the widesII function in the adehabitat package (Calenge, 2006). Chi-square tests of identical habitat use at the individual level and overall habitat selection at the population level were run, and the mean selection ratios with 95 % confidence limits were plotted. Selection ratios above 1 indicate that the specific habitat type is selected, whereas selection ratios below 1 indicate avoidance. Selection ratios equal to zero represent no use. The test of the hypothesis that animals are on average using resources in proportion to availability was also run by subtracting the individual level test statistic from the population level test statistic.

RSFs are useful for testing whether there exist any significant selection of specific habitats, based on the proportional use versus the proportional availability of habitat categories. There are three different types of RSF data, based on what sort of study has been conducted. I used the type fitted for estimating selection of the home range within the study area when the availability of the habitat categories are the same for all animals, the design II data (Manly *et al.*, 1993).

3 Results

3.1 Habitat selection

Opposed to what was predicted in H1a and H1b, there was a strong, although not significant, trend of selection of habitat category *a*; fine grained bottom substrates with little or no vegetation cover. There was also an opposite, negative trend of avoidance of habitat category *b*; fine grained bottom substrates with lush vegetation cover. This habitat category was the most available habitat in the study area (proportion = 0.50), but had a mean use proportion of only 0.18 (Table 3). Habitat category *c*, which was expected to be selected for (predictions H1a and H1b), was avoided by all of the fish. The test of average use in proportion to availability was highly significant (p = <0.001), showing that although the overall habitat selection was not significant at the level of the specific habitats (p = 0.98), there was a clear discrepancy between the mean availability and the mean use. The individual level test statistic was not significant (p = 1) (Table 4). A visual inspection of the different habitat categories within each individual's home range revealed that many of the animals used a variety of different habitats. A total of 8 of the 20 individuals used substrates with both high and low vegetation cover, whereas 7 of 20 individuals had stations with dense eel grass beds within their home range. One individual used only habitats with fine bottom substrates and high vegetation cover.

Table 3. Availability and usage proportions for each habitat category, and their respective selection ratios ± 95 % confidence intervals (CI). Selection is marked either as "Positive" or "Negative".

Habitat type	Habitat availability (proportion)	Mean use (proportion)	Selection ratio (use/ availability)	95% CI	Direction of selection
a	0.43	0.82	1.92	1.60, 2.24	Positive
b	0.50	0.18	0.35	0.08, 0.63	Negative
c	0.07	0.00	0.00	0.00, 0.00	Negative

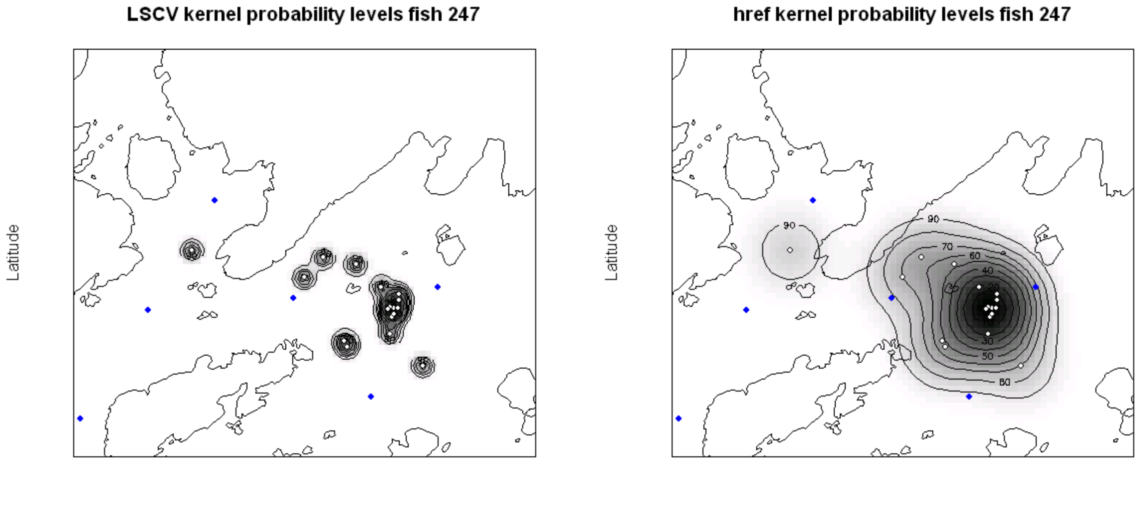
Table 4. The chi square test statistics (χ^2), degrees of freedom (df) and *p*-values of the tests of habitat selection at the individual and population level, as well as the test of whether mean use is proportional to the availability of habitat categories.

	X^2	df	*p*
Individual level	9.09	38	1.00
Population level	23.23	40	0.98
Use vs. availability	14.14	2	<0.001

3.2 Home ranges

The sizes of the 90 % home ranges varied greatly between the animals (range: 0.93 – 117.09 ha) (Table 5). Many of the fish that relocated over longer distances within the study area, moved to areas within established home ranges of other individuals. This trend became more and more common during the study period (personal observation).

A visual inspection of the home ranges estimated by the least square cross validation (h_{LSCV}) method showed that they were consistently overfragmented. I therefore decided to use the reference (h_{ref}) method for all further analyses, although the h_{ref} home ranges tended to be overestimated. According to Borger *et al.* (2006), a means to mend this problem is to discard the 95 % probability levels and instead base the analyses on the 90 % probability levels, which I did. An example of the under- and overestimation of h_{LSCV} and h_{ref} home ranges is given in Figure 3.



a) b)

Figure 3. h_{LSCV} (a) and h_{ref} (b) home ranges for fish ID 247. The smoothing parameter (h) was 17.5 and 72.6, respectively.

Table 5. The estimated 90 % h_{ref} home range areas (ha) for each fish. Mean, median and standard deviation values are given at the bottom.

Tag ID	90 % home range area (ha)
233	40.85
234	57.37
235	25.46
236	117.09
237	5.72
238	50.00
239	7.39
240	3.75
241	6.72
242	78.86
243	67.17
244	51.11
245	4.59
246	56.97
247	19.89
248	0.93
249	36.66
250	6.13
251	4.16
252	36.03
Median	30.74
Mean	33.84
SD	31.42

3.3 Home range size, depth and fish length

Confirming prediction H2a, there was a highly significant, positive effect of fish size on the size of the home ranges ($p = <0.001$, $R^2 = 0.51$) (Fig. 4a). The mean depth was also significantly correlated with the length of the fish, although in the opposite direction ($p = 0.02$, $R^2 = 0.26$), confirming prediction H2c (Fig. 4b). The coefficients of variation of all the tracked depths were slightly negatively correlated with fish size, but this result was not significant ($p = 0.34$, $R^2 = 0.05$) (Fig. 4c).

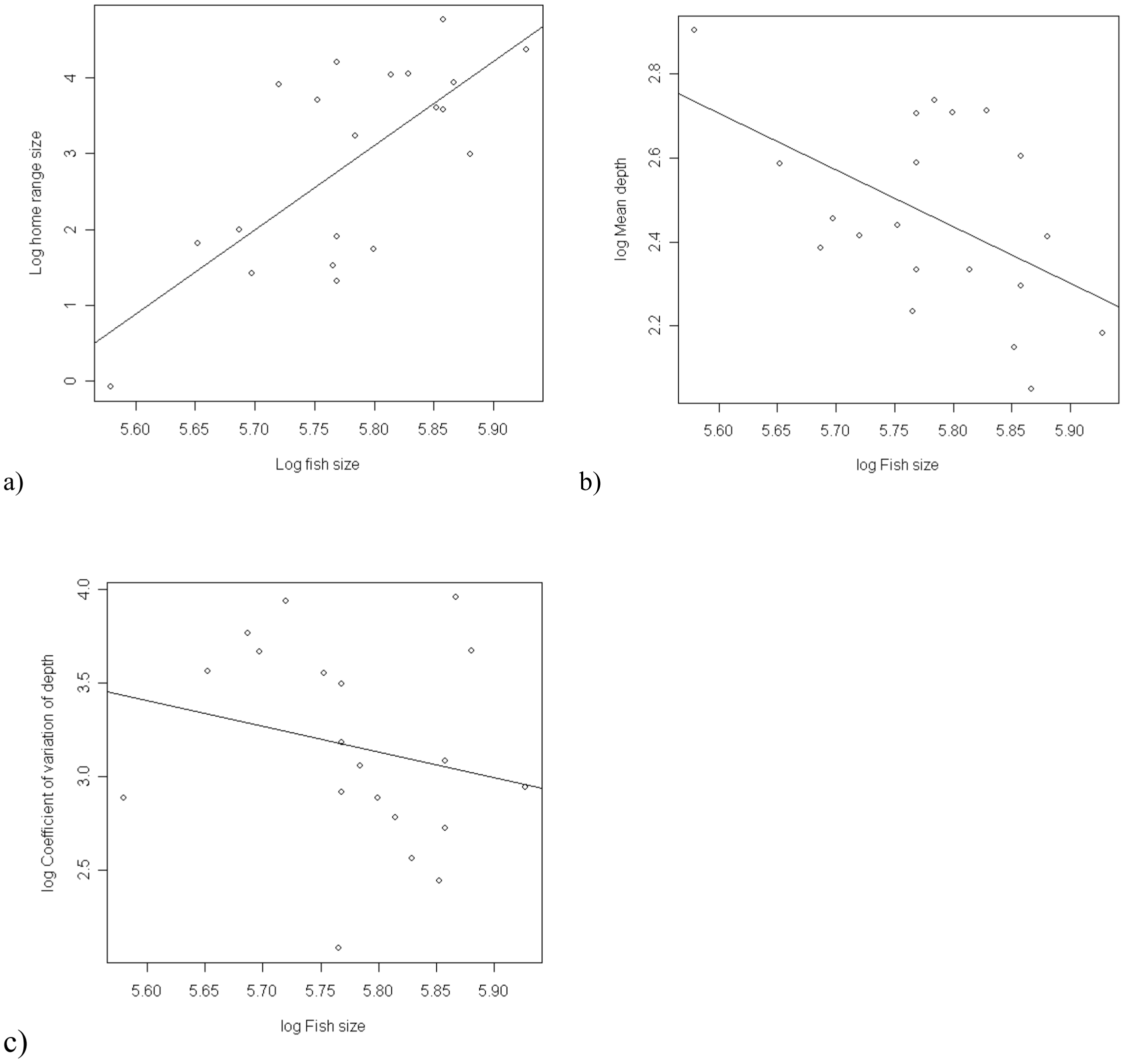


Figure 4. Linear relationship between the lengths of the fish and a) the 90 % home range sizes; b) the mean tracked depth, and c) the coefficients of variation of the tracked depths. All variables are log transformed for better fit of the models.

4 Discussion

The main purpose of this study was to investigate habitat preferences and size-dependent movement patterns of juvenile cod in a nearshore environment. Due to their young age and relatively small size, behaviour strategies were expected to be driven mainly by predator avoidance. Habitats that were structurally complex, such as with high vegetation cover and coarse bottom substrates were thought to be preferred over bare sediments. I also expected that the variability of total lengths between the individuals would be reflected in independent movement strategies. Larger fish are known be competitively superior to smaller fish (Tupper and Boutilier, 1995), and they were such thought to occupy larger areas in this study. Smaller fish were thought to show signs of avoidance both from predators and larger conspecifics, reflected in a more flexible use of the water column and a preference for deeper habitats than bigger fish.

4.1 Habitat selection

Contrary to what was expected, the fish studied in my work tended to prefer habitats with few structures. It is commonly accepted that species diversity and abundance increases in areas rich with vegetation. Several investigations have also shown foraging success over such habitats to be affected not only be the mere abundance of prey but also by the quality and quantity of the vegetation. Gotceitas & Colgan (1989) estimated that the response of habitat use on habitat complexity by both predators and prey was non-linear and that above a certain threshold level of vegetation density, foraging success decreased significantly. It seems both from this study and from others (Cote *et al.*, 2003, Gotceitas and Brown, 1993, Gregory and Anderson, 1997) that the habitat preferences of the prey often depend on the presence of predators. In manipulated experiments, responses of juvenile cod have been investigated when exposed to a predator (Fraser *et al.*, 1996, Gotceitas *et al.*, 1997). In many of the trials, the juveniles prefer fine bottom substrates with no vegetation prior to an encounter with a predator, but quickly seek out patches of coarse bottom substrates and/or vegetation when a predator is introduced. Comparisons of habitat selection between the predators and the prey revealed that in most cases the juvenile cod choose habitats because of predator avoidance. This may be indicative of low predation pressure for the fish studied in my work. Although no tests of size-specific habitat selection were run, it was clear that habitat structures associated with low protection from predators were chosen over structures that provide good shelter. It may be that the habitat samples that contained high degrees of vegetation cover and coarse bottom substrates were not above the threshold value proposed by Gotceitas & Colgan (1989), thereby not providing enough shelter for the animals to seek them out. It may also be that these types of habitats were not equally available to all the animals, as assumed in the test.

Although being of only age 1, the study animals used here probably do not have many natural predators. Most common are probably older conspecifics, humans and marine birds, of which the true aquatic animals are thought to be the main force to induce changes in movement strategies. During the sampling of the animals, a wide variety of size- and age groups of cod were caught, indicating that the study area consists of a heterogeneous mixture of age classes. The selection of relatively barren habitats may therefore be the result of a trade-off between foraging and shelter, as the animals are not available as prey to a large number of species. This may also be reflected by the fact that almost half of the study animals used one or more habitat samples that contained dense vegetation cover. More often than not, this vegetation consisted of eel grass (*Zostera marina*) (personal observation; Appendix III, Table A3), a plant species known to be of great importance as nursery habitats for marine species (Joseph *et al.*, 2006, Tveite, 1984). The animals may therefore utilise these sites for shelter, as foraging success has been seen to decrease over eel grass beds (Gotceitas *et al.*, 1997), while they use the open spaced structures for hunting prey. Gregory & Anderson (1997) also speculate whether the difference in skin colour between young and old juveniles may affect the choice of preferred habitats. Younger cod have more mottled skin colouration than older cod, which would provide them shelter in habitats that match their colour patterns, such as gravel, if they rely on crypsis from predators. However, all of the fish sampled in this study had very similar skin colour and -pattern, so it is unlikely that this would cause any difference in habitat selection here.

Caveat. In addition to the results of the habitat selection tests not being statistically significant, it is also worth considering the nature of the data used in this analysis. First of all, all of the home ranges estimated here are based on day time relocations. There might be different habitat preferences during the diel cycle, which might explain why I did not see the expected pattern of substrate selection. In addition, the 28 ROV samples are small sub-samples of the true substrate and vegetation of the study area. Outside of each roughly 30 m^2 sample, I cannot justify any interpolation of the nature of the environment. A large-scale mapping of marine biotopes along the Norwegian coast is currently being conducted (personal communication, Torjan Bodvin, Institue of Marine Research Flødevigen), but data from this project were not available at the time of my study. Such habitat data will in the future give much more predictive power when analysing resource selection than what is currently available.

4.2 Movement patterns and size-dependent variation

There was a strong relationship between the sizes of the fish and the sizes of their home ranges in this study. This is indicative of intra-cohort competition among the individuals, where larger fish will out-compete smaller fish over important resources such as shelter and foraging grounds. During a visual inspection of juvenile cod in St. Margaret's Bay, Nova Scotia, Tupper & Boutilier (1995) documented that larger individuals had significantly larger home ranges ($p < 0.001$, $R^2 = 0.95$) than smaller sized conspecifics. They also observed that encounters between different sized individuals were generally aggressive, with the bigger fish driving away the smaller ones. In their study, which lasted from June to December, none of the smallest sized individuals had high enough growth rates to out-grow their bigger counterparts. This may reflect a negative feedback in which small sized individuals are inferior competitors of food and shelter, and thus grow even slower than bigger fish.

Resource competition is not restricted to interactions between individuals of the same species. In a survey of stomach contents of young-of-the-year cod, whiting (*Merlangius merlangus*) and other littoral fishes outside of Flødevigen, Fjøsne & Gjøsæter (1996) documented a high degree of dietary overlap between cod and whiting. Both species mainly foraged for actively moving prey (such as fish and copepods), indicating that these two species might be competitors of food. This may be reflected in the trend for smaller fish to utilise larger portions of the water column than bigger fish, as shown in my study. Individuals that are inferior competitors may need to be less specialised when it comes to prey preferences, and thus utilise larger parts of the surrounding three-dimensional area. In addition, small and large cod occupied significantly different depths in my study, which may indicate that the smaller individuals experience different predation pressures than the bigger ones. Laurel & Brown (2006) found that juvenile cod tend to change their relative position to a predator dependent on the type of predator and habitat characteristics. Over sandy bottoms and eel grass beds cod remained below cruising predators, such as older conspecifics. Ambush predators, such as short-horned sculpins (*Myoxocephalus scorpinus*), did not provoke any change in movement patterns over sand, but when juvenile cod entered the eel grass beds they preferred the upper part of the vegetation and maintained a larger distance between themselves and the sculpins. The tendency for smaller cod to inhabit deeper areas than larger ones was also documented by Gregory & Anderson (1997) during a habitat preference survey in Placentia Bay, Newfoundland. The authors dismissed that this segregation of vertical distribution was biologically meaningful though, as they observed small and large cod coexisting on many of the depths studied. It is worth mentioning that this latter study was conducted in the spring, when ambient water temperatures were about - 1 °C. The individuals seemed to be in what Gregory & Anderson referred to as a “winter mode”, moving slowly and possibly infrequently compared to warm water behaviour. As the cod studied in my work experienced much higher temperatures (Appendix II, Table A2), it is unlikely that this shift in activity patterns due to temperature would be apparent.

Throughout the study period, many of the individuals relocated over longer distances within the study area. More often than not, they moved from an area with low density of tagged individuals, to areas within established home ranges of other individuals. Typical “hot spots” of aggregation of fish were close to the capture sites of fish ID 250 and 241 (see Fig. 2a), which both represent relative barren habitats. At the end of the study in late December, more than half of the study animals were tracked within 50 m of at least two other individuals. This pattern of aggregation over sandy habitats is something that is recognized as an anti-predator strategy among juvenile cod (Anderson *et al.*, 2007, Laurel and Brown, 2006, Laurel *et al.*, 2004). In the absence of structural shelter, schooling behaviour may confuse visual predators so that they will have trouble in stalking and capturing a prey. In addition there is safety in numbers, and although individuals that aggregate may have to compete more intensively for food, they will have a lower probability of being caught.

5 Conclusion

This study has shown that behavioural strategies are dynamic and can vary even within single individuals. The type of available habitats, density of animals and size- and species composition may all affect the determination process of choosing the optimal habitat. For juvenile nearshore cod, both predation pressure and inter- and intra-specific competition appears to be the driving forces when selecting movement strategies. The behavioural selection process was shown to vary within the age group, dependent on the relative body lengths of the fish. Bigger fish had large home ranges and showed little variation in vertical distribution, indicative of high competitive abilities and a lowered predation risk. Small fish on the other hand, behaved in ways thought to represent high predation pressure. They generally stayed at deeper depths than their larger conspecifics, but also tended to show a more flexible distribution in the water column. This may be the result of changing anti-predator strategies over different habitats. In addition, smaller individuals had smaller home ranges, which may indicate that they are not capable of competing for the optimal resources in the same way that bigger fish do. The cod seemed to prefer open habitats that provided little shelter over more structurally complex habitats. This may be explained by the fact that many of the fish were observed to aggregate with conspecifics, a known anti-predator strategy when sheltered habitats are unavailable.

As a species that is currently under great fishing pressure, I suggest that further studies on a larger scale should be done on the behaviour and habitat selection process of cod in the Skagerrak. This is needed to identify the different importance of various habitats not only to specific life stages but also across the relative body size gradient, so that we will have a better knowledge of which areas are more vulnerable to exploitation than others.

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Appendices

Appendix I Estimated length at age

The data used in the estimation of length-at-age (Fig. A1, Table A1) are part of an annual autumn survey of biodiversity along the Norwegian Skagerrak coast. The cod are sampled with the same trammel gillnets at regular stations each year (mesh size = 45 mm). The gillnets are set in the evening and hauled in the morning at shallow, near-shore sites. Among the characters measured are total length and age, determined by otoliths (unpublished data, Jakob Gjøsæter, Institute of Marine Research Flødevigen; Olsen *et al.*, 2008). The data used here stems from the station sampled medio December 2006 located outside of the Flødevigen research station, considered to be representative of the study animals used in this work.

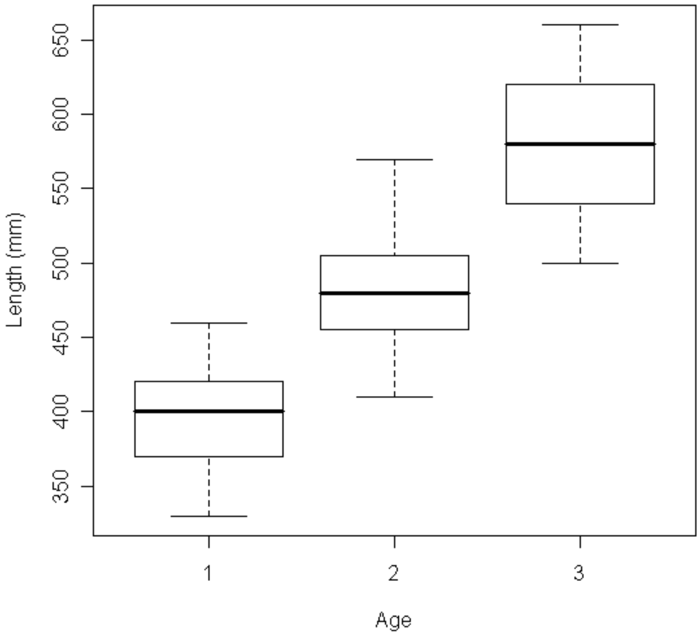

Figure A1. Length (mm) at age, calculated from the reading of otholits.

Table A1. Median and mean (± SD) length at age, calculated from *n* individuals in each age group.

	n	**Median L_t (mm)**	**Mean L_t (mm)**	**SD**
Age 1	43	400	396	34
Age 2	12	480	482	44
Age 3	3	580	580	80

Appendix II Salinity and temperature

Measurements of salinity and temperature were taken each day the fish were tracked, at regular stations. The stations represent a supposed gradient from close to the river outlet to away from the outlet in the study area. The measurements reported in Table A2 are taken at the nearest CTD station from a fish's estimated location at its tracked depth.

Table A2. Minimum, mean and maximum salinity and temperature in the study area over time and distance from the river outlet, based on the variables measured at each fish's estimated position.

	Salinity (‰)			**Temperature (°C)**		
	Min	**Mean**	**Max**	**Min**	**Mean**	**Max**
October						
Close to river outlet	30.3	32.6	33.7	14.1	14.9	15.3
Away from river outlet	24.4	31.9	33.4	13.5	14.9	15.5
November						
Close to river outlet	32.2	33.6	34.5	11.1	13.7	14.6
Away from river outlet	28.9	33.6	34.6	10.7	13.4	14.4
December						
Close to river outlet	33.3	33.5	33.7	10.7	10.7	10.7
Away from river outlet	32.2	33.5	33.8	10.4	10.6	10.7

Appendix III ROV samples

The ROV samples were categorised according to the different bottom substrates available in the study area, which were mud or silt, fine grained sand and large rocks or bedrock. The coverage of vegetation was split into eel grass (*Zostera marina*) and other vegetation, and were categorised into “none” (absent), “sparse” (< 20 %), “patchy” (20 % - 50 %) and “covered” (> 50 %) (Table A3). The locations of the ROV sampling stations are given in Figure 2b in the main text. Examples of the habitat categories used in the analyses are given in Figure A2.

Figure A2. Snapshots of the three different habitat categories sampled in the study area. From left to right: category a, fine bottom substrate without vegetation; category b, fine bottom substrate with dense vegetation; category c, coarse bottom substrate with dense vegetation.

Table A3. Overview of the bottom substrates and vegetation cover for each ROV sampling station. The corresponding habitat categories used in the analyses (see Table 3 in the main text) are given to the right. See text for explanation of cover categories.

ROV station	Bottom substrate	Eel grass	Other vegetation	Habitat category
2	Mud/silt	None	Covered	b
3	Mud/silt	None	Covered	b
4	Sand	Covered	Patchy	b
5	Sand	Patchy	Covered	b
6	Sand	None	Patchy	b
7	Rocks/bedrock	None	Covered	c
8	Mud/silt	None	None	a
9	Mud/silt	None	None	a
10	Mud/silt	None	None	a
11	Sand	None	Covered	b
12	Sand	None	Covered	b
13	Mud/silt	None	Sparse	a
14	Sand	Covered	Covered	b
15	Sand	None	Covered	b
16	Sand	Covered	Patchy	b
17	Mud/silt	None	Sparse	a
18	Sand	Covered	Patchy	b
19	Mud/silt	None	None	a
20	Mud/silt	None	None	a
21	Sand	None	Covered	b
22	Mud/silt	None	Patchy	b
23	Sand	None	Sparse	a
24	Rocks/bedrock	None	Covered	c
25	Mud/silt	None	None	a
26	Mud/silt	None	Sparse	a
27	Sand	None	Sparse	a
29	Mud/silt	None	Patchy	b
30	Sand	None	None	a