

Temperature-associated habitat selection in a cold-water marine fish

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Summary

1. Habitat selection is a complex process, which involves behavioural decisions guided by the multiple needs and constraints faced by individuals. Climate-induced changes in environmental conditions may alter those trade-offs and resulting habitat use patterns.
2. In this study, we investigated the effect of sea temperature on habitat selection and habitat use of acoustically tagged Atlantic cod (*Gadus morhua*) at the Norwegian Skagerrak coast.
3. Significant relationships between ocean temperature and habitat selection and use were found. Under favourable sea temperature thresholds (< 16 °C), cod selected vegetated habitats, such as eelgrass and macroalgae beds, available in shallow areas. Selection for those habitats was especially high at night, when cod tended to ascend to shallower areas, presumably to feed. Selection and use of those habitats decreased significantly as temperature rose. Under increased sea surface temperature conditions, cod were absent from vegetated shallow habitats, both during the day and night, and selected instead non-vegetated rocky bottoms and sand habitats, available in deeper, colder areas.
4. This study shows the dynamic nature of habitat selection and strongly suggests that cod in this region have to trade off food availability against favourable temperature conditions. Future increases in ocean temperature are expected to further influence the spatial behaviour of marine fish, potentially affecting individual fitness and population dynamics.

Key-words: acoustic telemetry, location filtering, marine reserve, Norway, resource selection functions, vemco positioning system, VPS

Introduction

Adequate wildlife management requires knowledge of animal habitat requirements and how environmental variables influence their habitat selection. Habitat selection is a behavioural process by which animals choose the most suitable locations to maximize fitness (Fretwell & Lucas 1969). Habitat selection decisions involve trade-offs between multiple needs and constraints faced by individuals (Sih 1980; Werner *et al.* 1983; Orians & Wittenberger 1991). Often, energy intake will have to be balanced against exposure to predators or unfavourable climatic conditions. Terrestrial herbivores, for example, may alter

their habitat selection in the presence of predators (Creel *et al.* 2005; Fortin *et al.* 2009) or in response to changes in temperature (van Beest, Van Moorter & Milner 2012). In aquatic systems, animals often trade off food acquisition, safety, and thermoregulation by adjusting their depth on a diel basis (Mehner 2012). While diel vertical movements have been studied extensively (Neilson *et al.* 1990; Mehner 2012), habitat selection trade-offs in aquatic systems are less understood.

Habitat use and habitat selection are two important concepts used in behavioural studies. Habitat use refers to the set of habitat units that are encountered and used by an organism (see Buskirk & Millspaugh 2006; Lele *et al.* 2013). Habitat use may be quantified by the use distribution, which tells us in what proportion different habitat attributes are used, when considering only the set of used

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habitat units (Lele *et al.* 2013). Habitat selection, on the other hand, consists of quantifying for a given set of available resources, what animals ultimately choose to use (see Lele *et al.* 2013). The most common tool used to quantify habitat selection is the resource selection function (RSF), defined as any function proportional to the probability of use by an organism (Manly *et al.* 2002). RSFs link animal distribution to spatial patterns of habitat heterogeneity by comparing the characteristics of animal locations with a random selection of points reflecting habitat availability (Manly *et al.* 2002; Johnson *et al.* 2006).

In the marine environment, abiotic and biotic conditions may change dynamically over space and time. Such changes are expected to alter the cost and benefits of using particular locations. Ongoing warming of the upper ocean (0–700 m deep) (IPCC 2013) may pose additional challenges to marine fish as sea temperature may rise above the species' physiological tolerance (Pörtner & Farrell 2008). The Atlantic cod is a commercially important cold-water species, vulnerable to the warming tendency of the North Atlantic (Pörtner *et al.* 2008; McNeil & Chooprateep 2014), and especially so in its southern distribution range (Barceló *et al.* in press). Cod habitat use is known to change ontogenetically. Young juveniles are planktonic feeders (Pihl 1982; Keats & Steele 1992; Hüsey, St. John & Böttcher 1997). In coastal areas, these small fish are often associated with eelgrass meadows, which provide food and safety from predators (Gotceitas, Fraser & Brown 1997; Lilley & Unsworth 2014). Older juveniles and adult coastal cod feed mostly on benthic prey (Hop, Gjosaeter & Danielssen 1992; Hüsey, St. John & Böttcher 1997) and can be found in boulder, gravel, kelp, eelgrass, and sand habitats (Cote *et al.* 2001, 2003, 2004; Reubens *et al.* 2013). Their habitat selection varies both on a diel and seasonal basis (Cote *et al.* 2001, 2003, 2004; Reubens *et al.* 2013, 2014). Such diel and monthly shifts in habitat selection have been attributed to changes in the presence of predators and/or to foraging opportunities that vary over space and time (Cote *et al.* 2003). It is, however, possible that ambient temperature may pose an additional trade-off for cod habitat selection. A recent study indicates that wild-ranging cod tend to use deeper, colder waters when sea surface temperature increases in summer (Freitas *et al.* 2015). Cod can be found in waters ranging from –1.5 to 19 °C, but most observations occur in waters below 15 °C (Blanchard *et al.* 2005; Rindorf & Lewy 2006; Neat & Righton 2007; Righton *et al.* 2010). Experimental studies indicate that cod's thermal preference is in the range 3–15 °C (Petersen & Steffensen 2003; Lafrance *et al.* 2005; Behrens *et al.* 2012). Optimal temperatures for growth range between 9 and 16 °C (Jobling 1988; Björnsson & Steinarsson 2002; Björnsson, Steinarsson & Oddgeirsson 2007; Rogers *et al.* 2011; Bolton-Warberg, O'Keeffe & FitzGerald 2015).

In this study, we evaluate the effect of sea temperature on habitat use and habitat selection of acoustically tagged

cod at the Norwegian Skagerrak coast. Optimal foraging theory predicts that when environmental conditions are favourable, animals should choose and use habitats based on food abundance (MacArthur & Pianka 1966). As such, we expect high use and selection of habitats that are rich in food and shelter, such as eelgrass and macroalgae beds (Persson *et al.* 2012). We hypothesize that changes in selection and use may occur if those shallow-water habitats become unfavourable during warm water periods. Alternatively, if the seasonal extremes occurring in coastal Skagerrak are tolerable to cod adapted to that system, the use of the most profitable habitats should continue unaltered.

Materials and methods

STUDY AREA AND HABITAT MAPPING

Our study was carried out in a marine protected area (MPA) located in Tvedestrand fjord, on the Norwegian Skagerrak coast (Fig. 1). The MPA, established in 2012, is closed to all fishing activities and this qualifies as a no-take marine reserve where fish behaviour can be studied in the absence of any disturbance from fishing gear such as baited hooks or traps. The reserve comprises waters ranging from 0 to 90 m depth. Bottom habitats in the area were mapped using video surveys, performed from a 7-m vessel equipped with a digital video drop camera. Surveys consisted of line transects perpendicular to the coastline, starting at \approx 30 m depth and continuing towards the shore (Fig. S1, Supporting information). Deeper areas were classified into soft and hard categories using backscatter data available for the area (see below). GPS positions and depth measurements were used to register limits of the different habitats defined during transects. In addition to transects, shallow areas (<7 m) were thoroughly searched for eelgrass presence using the drop camera, and the limits of eelgrass meadows were recorded in 3 dimensions (GPS location and depth – see Fig. S1, Supporting information). Surveys were performed in November 2013. Eelgrass beds showed some signs of winter die-off but were still easily identified. During post-processing of the recorded transects, habitat categories were refined based on visual assessment of survey film clips. A habitat map was then created using GIS tools (Fig. 1b). Habitats were drawn as polygons by connecting the GPS positions registered along the transects. Bathymetry and acoustic backscatter data, both available at 5-m resolution (Fig. S1, Supporting information), were used to complement the video transects information, that is, to aid drawing of the habitat polygons in between transects. Note that habitat margins generally occurred at consistent depths in adjacent transects. Backscatter data were useful to discern the transitions between hard and soft substratum, as high backscatter strength is usually obtained from hard features and weaker from soft substrates. The following habitat categories were defined (see Fig. 1b): *Eelgrass* (soft substrate covered by eelgrass *Zostera marina*; occurred in depths from 0 to 6 m); *H_Ve* (vegetated hard substrate, i.e. covered by macroalgae; occurred in areas shallower than 17 m approximately); *H_Nv* (non-vegetated hard substrate; present below 17 m depth approximately); *H_An* (steep rock wall covered by anemones and other invertebrates); *H_Co* (irregular rocky substrate with soft corals and patchy macroalgae); *H_Bo* (boulders, with no vegetation; present in the

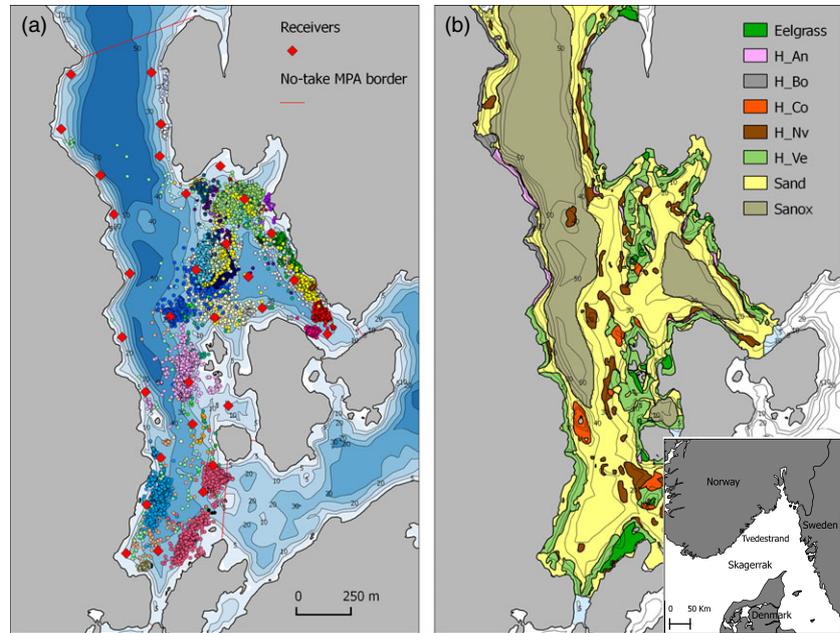


Fig. 1. (a) Map of the study area in Tvedstrand showing the network of acoustic receivers and post-filtered positions obtained from 40 tagged Atlantic cod (coloured dots). Original and post-filtered positions for each individual cod are presented on Fig. S3 (Supporting information). (b) Bottom habitat types in the study area. Abbreviations: H_An, rock wall with anemones; H_Bo, boulders, H_Co, Irregular hard substrate with soft corals; H_Nv, non-vegetated hard substrate; H_Ve, Vegetated hard substrate; Sanox, Soft anoxic substrate.

steep western margin of the fjord); *Sand* (soft, oxygenated substrate); and *Sanoxic* (anoxic soft substrate). Anoxic substrate in areas shallower than 30 m was defined based on the visual transects (visible as black patches/surfaces). In deeper areas, where video transects were deemed unsuitable, anoxic substrate was defined based on the depths where anoxia was consistently registered in the oxygen measurements performed by Halvorsen (2013).

FISH TAGGING

Cod used in this study were captured, tagged, and released inside the no-take marine reserve in May 2012 and May 2013 (Table 1). Cod were collected using fyke nets and taken to the nearest shore for tagging. There, they were anesthetized with clove oil and measured to the nearest cm (fork length). An ultrasonic transmitter (Vemco V9P-2L, 38 × 9 mm, weight in seawater <3 g) was then surgically implanted through a small incision on the ventral surface of the peritoneal cavity. The incision was closed with two absorbable sutures. All cod were also tagged with an external anchor T-bar tag (Hallprint TBA2, 30 × 2 mm) printed with a serial number, return address, and a reward notice. Fish were placed in a basin with sea water to recover from anaesthesia and were released at the site of capture after full recovery.

The transmitters were built with a pressure sensor. In 2012, we used transmitters having 100 m as max depth, 0.44 m resolution, and 5 m accuracy. In 2013, we used transmitters having 50 m max depth, 0.22 m resolution, and 2.5 m accuracy. They were programmed to emit the current depth and a unique identification code at random intervals every 110 to 250 s. Expected battery lifetime was 508 days.

ACOUSTIC POSITIONING SYSTEM

A Vemco positioning system (VPS) was used to obtain information on fish depth and horizontal location. The system was installed in June 2013, as an extension of a Vemco presence/

absence acoustic system already installed in the area. The VPS system consisted of 31 omnidirectional acoustic receivers (Vemco VR2W, 69 kHz; Fig. 1a). The VR2W receivers record the depth and id information emitted by the fish transmitters. Synchronization tags, 'Synctags' (Vemco V16-4x, random delay interval: 500–700 s), were moored along with each receiver to correct for clock drift between submerged receivers. Additional reference tags (three Vemco V13-1x and 1 Vemco V13T-1x, random delay interval: 500–700 s) were placed within the receiver grid in order to measure system performance during location estimation. The performance of the VPS system was further tested using a test transmitter (Vemco V9P-2x) with a transmission delay of 15 s. The test tag was attached to a cable and dragged behind a 5-m boat while driving through the receiver array at low speed (<2 knots). A handheld GPS unit was used to record the boat's track. GIS tools were used to compare VPS positions and the boat track (Fig. S2, Supporting information). Fish detection data, consisting of records of fish id, depth, detection time, and receiver id, were downloaded regularly from the receivers. This study used data collected from June 2013 (when the VPS system was installed) to December 2013. Several cod that had been tagged in 2012 and 2013 were detected during this study period (Table 1).

Data were sent to Vemco for post-processing of fish positions. Positions were calculated using hyperbolic positioning, which is a technique based on measuring differences in transmission detection times at pairs of time-synchronized receivers, and converting these to distance differences using the signal propagation speed (Smith 2013). A fish transmission needs to be detected by at least three receivers in order to produce a valid position. Most fish in this study provided valid positions (Table 1; Fig. S3, Supporting information). Calculated positions consisted of 3D positions with XY coordinates and depth. Calculated positions were filtered based on a trade-off between accuracy and quantity (see Appendix S1, Supporting information). Filtered positions had a median accuracy of 1.8 m to 4.4 m (Fig. S4, Supporting information). These were imported to GIS software where bottom depth and habitat-type information were extracted for each position.

Table 1. Summary data for 48 Atlantic cod tracked in Tvedestrand fjord in June to December 2013. Location data were obtained from 40 of them. Note that cod were tagged in May 2012 and 2013 and that the start of this study was defined by the date of installation of the VPS tracking system (see Materials and methods). Note that number (*n*) of depth records was calculated after removing repeated records received simultaneously by more than one receiver

| Fish ID | Tagging year | Length (cm) | Data range (start) | Data range (end) | <i>n</i> days with depth data | <i>n</i> depth records | <i>n</i> positions |
|----------|--------------|-------------|--------------------|------------------|-------------------------------|------------------------|--------------------|
| Cod_6755 | 2012 | 47 | 28/06/2013 | 06/10/2013 | 101 | 21 860 | 284 |
| Cod_6761 | 2012 | 32 | 28/06/2013 | 10/10/2013 | 105 | 12 241 | 0 |
| Cod_6765 | 2012 | 46 | 28/06/2013 | 10/10/2013 | 105 | 17 651 | 411 |
| Cod_6766 | 2012 | 45 | 28/06/2013 | 28/09/2013 | 93 | 18 133 | 616 |
| Cod_6773 | 2012 | 59 | 28/06/2013 | 12/10/2013 | 107 | 27 407 | 29 |
| Cod_6776 | 2012 | 31 | 28/06/2013 | 03/07/2013 | 6 | 1414 | 215 |
| Cod_6778 | 2012 | 68 | 28/06/2013 | 19/08/2013 | 53 | 12 038 | 202 |
| Cod_6779 | 2012 | 48 | 28/06/2013 | 02/12/2013 | 158 | 31 418 | 1431 |
| Cod_6780 | 2012 | 47 | 28/06/2013 | 12/10/2013 | 107 | 22 236 | 920 |
| Cod_6783 | 2012 | 57 | 28/06/2013 | 16/10/2013 | 111 | 10 899 | 0 |
| Cod_6784 | 2012 | 62 | 28/06/2013 | 16/10/2013 | 85 | 6552 | 0 |
| Cod_6785 | 2012 | 59 | 28/06/2013 | 16/10/2013 | 111 | 26 393 | 593 |
| Cod_6787 | 2012 | 60 | 28/06/2013 | 16/10/2013 | 95 | 28 840 | 212 |
| Cod_6791 | 2012 | 33 | 28/06/2013 | 16/10/2013 | 111 | 34 516 | 0 |
| Cod_6793 | 2012 | 56 | 28/06/2013 | 16/10/2013 | 111 | 28 507 | 800 |
| Cod_6795 | 2012 | 50 | 28/06/2013 | 16/10/2013 | 111 | 20 126 | 41 |
| Cod_7266 | 2012 | 41 | 28/06/2013 | 18/10/2013 | 110 | 17 762 | 20 |
| Cod_7267 | 2012 | 43 | 28/06/2013 | 18/10/2013 | 113 | 27 060 | 330 |
| Cod_7270 | 2012 | 51 | 28/06/2013 | 19/10/2013 | 114 | 19 921 | 26 |
| Cod_7272 | 2012 | 40 | 28/06/2013 | 18/10/2013 | 101 | 2628 | 0 |
| Cod_7274 | 2012 | 53 | 28/06/2013 | 23/07/2013 | 26 | 5604 | 88 |
| Cod_7279 | 2012 | 37 | 28/06/2013 | 23/10/2013 | 116 | 9688 | 50 |
| Cod_7280 | 2012 | 41 | 28/06/2013 | 03/12/2013 | 159 | 53 272 | 69 |
| Cod_7282 | 2012 | 52 | 28/06/2013 | 01/09/2013 | 58 | 17 703 | 3874 |
| Cod_7283 | 2012 | 56 | 28/06/2013 | 23/10/2013 | 118 | 13 571 | 195 |
| Cod_7285 | 2012 | 75 | 28/06/2013 | 20/09/2013 | 65 | 11 432 | 465 |
| Cod_7286 | 2012 | 58 | 28/06/2013 | 25/10/2013 | 91 | 6622 | 0 |
| Cod_8981 | 2013 | 47 | 28/06/2013 | 13/10/2013 | 108 | 34 045 | 7933 |
| Cod_8982 | 2013 | 64 | 28/06/2013 | 20/08/2013 | 54 | 14 782 | 1137 |
| Cod_8984 | 2013 | 55 | 28/06/2013 | 03/12/2013 | 159 | 21 677 | 221 |
| Cod_8985 | 2013 | 40 | 28/06/2013 | 30/11/2013 | 156 | 39 834 | 5657 |
| Cod_8986 | 2013 | 49 | 28/06/2013 | 03/12/2013 | 159 | 32 222 | 1093 |
| Cod_8987 | 2013 | 51 | 28/06/2013 | 25/08/2013 | 49 | 15 297 | 4134 |
| Cod_8988 | 2013 | 51 | 28/06/2013 | 03/12/2013 | 159 | 38 244 | 1247 |
| Cod_8999 | 2013 | 49 | 28/06/2013 | 24/07/2013 | 27 | 7970 | 0 |
| Cod_9000 | 2013 | 50 | 28/06/2013 | 03/12/2013 | 159 | 45 317 | 1625 |
| Cod_9002 | 2013 | 53 | 28/06/2013 | 31/08/2013 | 65 | 15 573 | 606 |
| Cod_9003 | 2013 | 41 | 28/06/2013 | 03/12/2013 | 158 | 31 035 | 137 |
| Cod_9004 | 2013 | 43 | 28/06/2013 | 03/12/2013 | 159 | 35 929 | 2370 |
| Cod_9005 | 2013 | 53 | 28/06/2013 | 03/12/2013 | 159 | 35 288 | 2479 |
| Cod_9031 | 2013 | 51 | 28/06/2013 | 03/12/2013 | 159 | 49 963 | 4998 |
| Cod_9032 | 2013 | 49 | 28/06/2013 | 03/12/2013 | 159 | 34 269 | 4164 |
| Cod_9034 | 2013 | 31 | 28/06/2013 | 03/12/2013 | 159 | 47 893 | 728 |
| Cod_9035 | 2013 | 32 | 28/06/2013 | 19/09/2013 | 84 | 23 951 | 3134 |
| Cod_9043 | 2013 | 52 | 28/06/2013 | 03/12/2013 | 159 | 31 246 | 319 |
| Cod_9044 | 2013 | 40 | 28/06/2013 | 03/12/2013 | 159 | 45 548 | 140 |
| Cod_9045 | 2013 | 46 | 28/06/2013 | 07/10/2013 | 102 | 20 454 | 759 |
| Cod_9046 | 2013 | 30 | 28/06/2013 | 03/12/2013 | 73 | 3808 | 0 |
| Total | | | | | | 1 129 839 | 53 752 |

DATA ANALYSIS

Depth use relative to sea temperature

Sea temperature was monitored in the study area using temperature loggers deployed at 6 different depths: 1, 5, 10, 15, 20, and 33 m (Table S1; Fig. S2, Supporting information). Temperature

at 1 m depth is hereafter referred to as sea surface temperature. Temperatures at 1–20 m were recorded hourly and later averaged daily. Temperatures at 33 m were recorded each 500–700 s (see Table S1, Supporting information) and also averaged daily. Temperature profiles were generated from the daily temperature data, using linear interpolation in between measurements (Fig. 2).

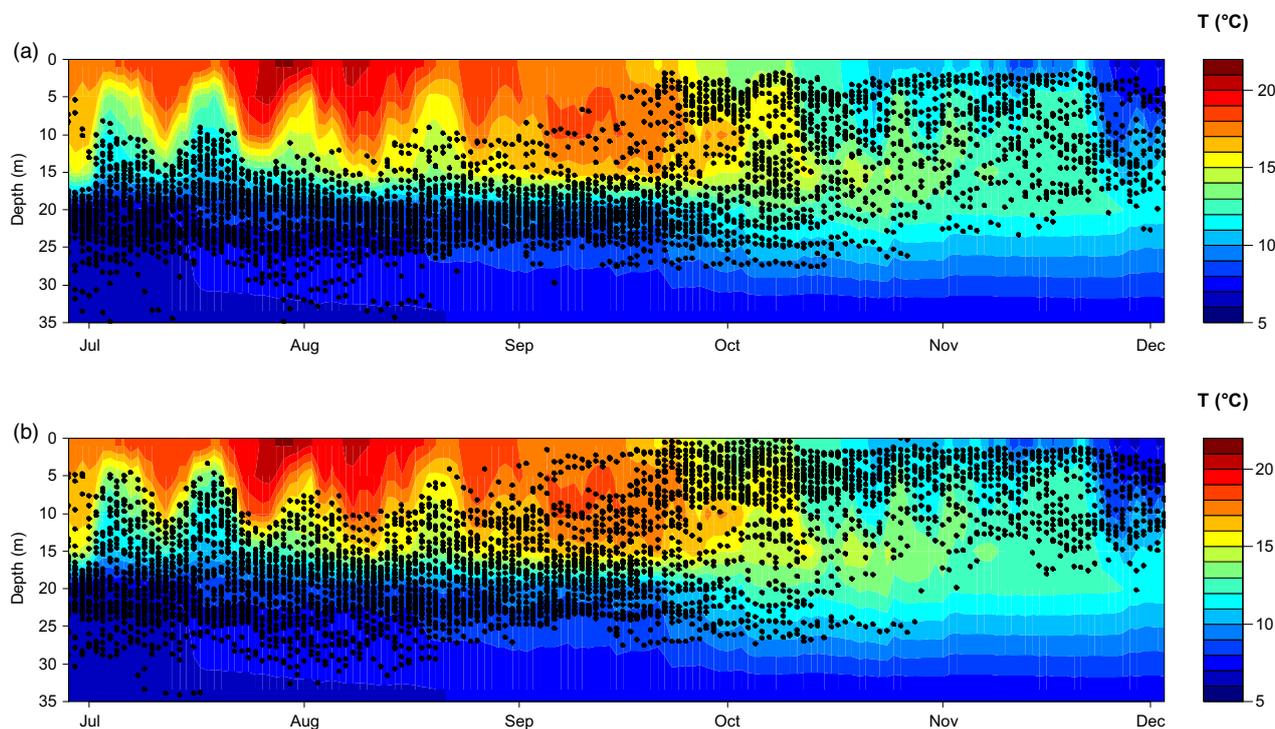


Fig. 2. Water temperature recorded in Tvedestrand in June–December 2013 and average depth used by individual cod ($N = 48$) during the day (a) and night (b). Each black dot corresponds to an individual on a given day.

Average depth used by cod during the day and night was estimated for each cod for each day. These were estimated from the original depths recorded by the receivers, as depths obtained from the location data set were a subset of these (see Table 1). Repeated depth transmissions (received by different receivers at the same time) were removed from the data set to eliminate pseudoreplication in the data. For a given day, average depth during the day was calculated as the average of all depths recorded between sunrise and sunset (i.e., when solar elevation was ≥ 0). Average depth during the night was calculated as the average of all depths recorded from sunset in the previous day to sunrise of that day. Two linear mixed-effects models were used to test whether there was a significant effect of sea surface temperature on depth use during the day and during the night, respectively:

$$\text{Depth}_{ij} = \alpha + \beta \text{Temp}_j + \alpha_i + \varepsilon_{ij}$$

where Depth_{ij} is the average depth used during daytime or nighttime by individual i at day j and Temp_j is the average sea surface temperature at day j . The random intercept α_i allows for a random variation around the intercept α and is assumed to be normally distributed with mean 0 and variance δ^2_i . The random intercept ensures that observations between the same individuals are allowed to be correlated. The term ε_{ij} is independently normally distributed noise. An autoregressive process of order 1, corAR1 (see Zuur *et al.* 2009), was added to the random structure of the model to take temporal autocorrelation into account. Models were fitted in R software (R Core Team 2012) using the package *NLME*.

Habitat selection

Habitat selection was quantified using RSFs. A RSF estimates the relative probability of selecting one habitat with a particular

set of characteristics relative to another with different characteristics (Manly *et al.* 2002; Johnson *et al.* 2006). We estimated RSFs using a use-availability design and used logistic regression to compare the habitat selected by cod (used locations, coded as one) to what was theoretically available (random locations, coded as zeros) – see Johnson *et al.* (2006). To represent availability, we drew random points from the area detectable by our array of receivers, using the same number of points as in the sample of used locations. Following the recommendations in McDonald (2013), RSFs were estimated from the logistic regression coefficients, using an exponential link:

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_z x_z)$$

In the equation, $w(\mathbf{x})$ is the RSF and β_1 represents the coefficient for the variable x_1 in a vector, \mathbf{x} , of z covariates. In order to account for differences in sampling intensity and random variation between individuals, random intercepts for each individual were added to the logistic model. Telemetry location data are often autocorrelated, which does not influence estimates of model coefficients but can deflate standard errors (Fieberg *et al.* 2010). In order to minimize temporal autocorrelation, we added Julian day, nested within individual, to the random-effects structure.

We fitted 4 RSFs, representing different combinations of diel period (day vs. night) and seasons. Based on the analysis of the temperature profiles (Fig. 2), two seasons were defined: summer (28 June to 15 September, when surface temperatures were above the thermal preference for cod; see introduction) and autumn (16 September to 3 December, when temperatures were within the thermal preference for this species). Models were fitted using the package *LME4* in R.

Environmental drivers of habitat use

Following Lele *et al.* (2013), the habitat use distribution, denoted by $f^U(x)$, can be used to quantify the probability that a used habitat unit is of type x , that is, $p(x)$. Considering only the set of used locations, we quantified p for four key habitat types (eelgrass, vegetated hard substrate, non-vegetated hard substrate, and sand), using generalized mixed-effects models, with a binomial link:

$$\text{logit}(p_{ij}) = \alpha + \beta_1 \text{Temp}_j + \beta_2 \text{Diel}_j + \alpha_{ij}$$

In this model, p_{ij} denotes the probability that a used habitat unit is of type x . Surface temperature (Temp) and diel period (Diel) were included as explanatory variables. Models were fitted using the above-mentioned package LME4 in R. Similar to the RSFs, individual id and Julian day, nested within individual, were used as random effect variables (α_{ij}) to account for individual variability and for temporal autocorrelation.

Results

THERMAL ENVIRONMENT

Sea temperature in the study area ranged between 6–21.5 °C at 1 m depth and 7.6–19.2 °C at 10 m depth. Surface waters were in general warmer than deeper water masses during summer, while a gradual surface cooling was observed towards the end of the year (Fig. 2). An alteration of the thermal stratification, mainly in July and August, is clearly seen during subsurface cooling events (Fig. 2), induced by coastal upwelling where offshore winds force warm surface waters to be replaced by the colder waters below.

DEPTH USE RELATIVE TO OCEAN TEMPERATURE AND BATHYMETRY

Cod were detected at depths from 0 to 54 m. Average daytime and night-time depths were in general shallower than 30 m (Fig. 2). Cod were detected in deeper water when surface temperatures increased, rarely using waters above 16 °C (Fig. 2). The use of shallower waters at night was evident, especially during cooler surface temperature periods (Fig. 2). Linear mixed-effects models fitted to these data showed that the positive relationship between cod depth and sea surface temperatures was statistically significant (effect of surface temperature on (i) daytime depth: $\beta = 0.69$, SE = 0.05, d.f. = 5087, $P < 0.001$; (ii) night-time depth: $\beta = 0.77$, SE = 0.05, d.f. = 5113, $P < 0.001$).

Cod were located close to the sea floor most of the time. Average (\pm standard deviation) distance to the substrate was 0.2 ± 1.7 m at night and 0.1 ± 1.6 m during daytime ($n = 40$ fish).

HABITAT SELECTION AND USE

Resource selection functions revealed changes in habitat selection between the two thermal periods analysed.

During summer, when surface temperatures were above 16 °C, cod selected mainly non-vegetated hard substrate, avoiding both eelgrass beds and vegetated hard substrate (Fig. 3). Conversely, during autumn, when water temperatures were lower (Fig. 2), cod selected mostly vegetated hard substrate and eelgrass beds, especially during the night, while avoiding sand and non-vegetated hard substrate (Fig. 3). In addition, anemone rock walls and soft coral rock substrates were also selected more than sand, especially during night-time. Anoxic areas were avoided, irrespective of diel period or temperature scenario (Fig. 3). In general, the probability that a used habitat unit was eelgrass or vegetated hard substrate increased when sea surface temperature decreased, especially during night-time (Table 2). In contrast, the probability of using non-vegetated hard substrate and sand habitats, which are available in deeper areas, increased as surface temperature increased (Table 2). The probability that a used habitat was sand, the habitat available in the deepest areas, decreased at night, probably as a consequence of night-time diel vertical movements.

Discussion

This study found that habitat selection of Atlantic cod in coastal Skagerrak was highly dynamic and associated with changes in ocean temperature. Under favourable sea surface temperature conditions (<16 °C), cod selected shallow-water habitats such as eelgrass and macroalgae meadows. However, during warm sea surface temperature conditions, individual cod were observed in significantly deeper waters, where they selected non-vegetated hard bottom and sand habitats.

The use of deeper, cooler waters by Atlantic cod under increased sea surface temperatures corroborates with the results recently found in a nearby coastal area (Freitas *et al.* 2015). It is well known that ambient temperature can deeply affect cod physiology (Jobling 1988; Brander 1995; Claireaux *et al.* 2000; Pörtner *et al.* 2001; Björnsson & Steinarsson 2002; Lannig *et al.* 2004; Yoneda & Wright 2005). Deviations in temperature beyond thermal limits induce a progressive mismatch between oxygen supply and oxygen demand, which will, in turn, firstly cause a decrease in whole organism performance and finally become lethal towards extreme temperatures (see Pörtner *et al.* 2008). Laboratory studies indicate that the thermal preference of Atlantic cod varies between 3 and 15 °C, depending on factors such as body size, reproductive state, and haemoglobin genotype (Petersen & Steffensen 2003; Lafrance *et al.* 2005; Righton *et al.* 2010; Behrens *et al.* 2012). During the present study, surface temperatures during summer raised considerably above those thresholds. Although we found some individual variability in depth use in relation to temperature profiles, interestingly, most individuals avoided temperatures above 16 °C. Negative effects on growth of juvenile cod in waters

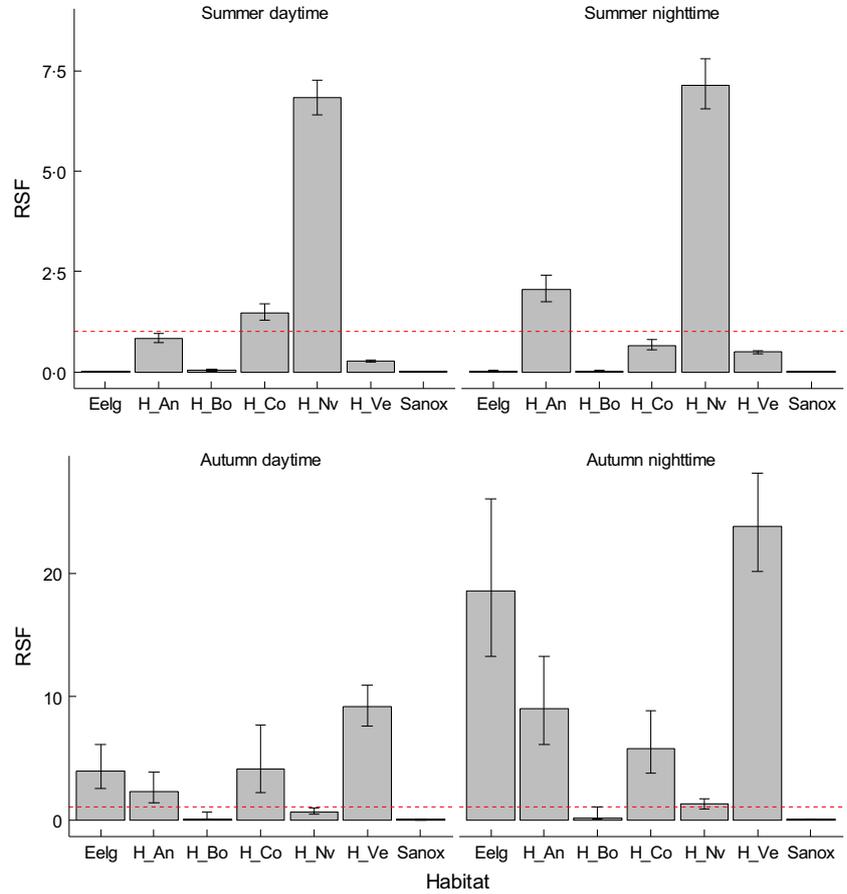


Fig. 3. Resource selection functions (RSFs) for cod in coastal Skagerrak, showing the relative probability of using a habitat, during summer (upper panels) and autumn (lower panels). Sand habitat was used as comparison level. Error bars denote 95% confidence intervals. Abbreviations: Eelg, eelgrass; H_An, rocky wall with anemones; H_Bo, boulders; H_Co, Irregular hard substrate with soft corals; H_Nv, non-vegetated hard substrate; H_Ve, Vegetated hard substrate; Sanox, Soft anoxic substrate.

Table 2. Estimated coefficients (β) and corresponding standard errors (SE) and significance levels (P value), describing how the probability that a used habitat unit being of type x , $p(x)$, was affected by sea surface temperature (Temp) and diel period (Diel). Daytime was used as comparison level in all 4 models

| Response | Covariate | β | SE | P value |
|----------------------|-------------------|---------|-------|-----------|
| $p(\text{Eelgrass})$ | Temp | -0.695 | 0.052 | <0.001 |
| | Diel (day, night) | 1.162 | 0.189 | <0.001 |
| $p(\text{H_Ve})$ | Temp | -0.470 | 0.019 | <0.001 |
| | Diel (day, night) | 0.655 | 0.044 | <0.001 |
| $p(\text{H_Nv})$ | Temp | 0.375 | 0.022 | <0.001 |
| | Diel (day, night) | 0.073 | 0.027 | 0.006 |
| $p(\text{Sand})$ | Temp | 0.325 | 0.017 | <0.001 |
| | Diel (day, night) | -0.351 | 0.025 | <0.001 |

H_Nv, non-vegetated hard substrate; H_Ve, Vegetated hard substrate.

above 16–17 °C, most likely also affecting survival, were shown using a nine-decade-long time series (Rogers *et al.* 2011). Freitas *et al.* (2015) showed that behavioural responses to temperature in wild-ranging cod depend on fish body size, where smaller cod appeared less sensitive to warm summer temperatures. Other individual traits such as reproductive state and genotype may also cause individual differences in physiological and behavioural responses to ocean temperature. Reproductive state is not known for the cod being monitored in this study, but

since the range of body length spanned from 30 to 75 cm, it is highly probable that both juvenile and sexually mature individuals were represented (Olsen *et al.* 2004).

In the coastal fjord area studied herein, cod was located close to the bottom most of the time, both during day and night. This is in contrast to the behaviour seen in some offshore cod populations (Hobson *et al.* 2007, 2009) and implies that night-time ascents to shallower waters involved horizontal movements along the sea floor slope rather than pelagic vertical movements. A similar finding has been reported for benthic sharks (Sims *et al.* 2006). Olsen *et al.* (2012) documented a human-induced fitness cost associated with these diel vertical migrations performed by coastal cod, where fish suffered increased mortality from fixed fishing gears such as gillnets and fyke nets when utilizing near-shore shallow waters.

Previous studies have underscored that habitat use in cod may vary in a diel and seasonal context (Cote *et al.* 2001, 2003, 2004). Such diel and monthly shifts in habitat selection have been attributed to changes in the presence of predators and/or to foraging opportunities that vary over space and time (Cote *et al.* 2003). While this is likely to be true also for our study area, we show that changes in habitat selection were significantly linked to changes in water temperature. Under unfavourable surface temperatures observed during summer, cod selected non-vegetated hard substrates, as well as sand habitats. Conversely, dur-

ing more favourable temperature conditions, cod selected mostly vegetated hard substrates and eelgrass beds. In addition, anemone-covered rock walls and soft coral-covered rock substrate features were also selected more than sand habitats, especially during night-time. Anoxic habitat was avoided (i.e., was selected less than oxygenated sand habitat) irrespective of diel period or temperature scenario. Juvenile and adult cod (>30 cm length) in Skagerrak feed on a variety of benthic invertebrates (e.g. crabs, shrimps, gastropods, and polychaetes) and fish (Hop, Gjosaeter & Danielssen 1992). Eelgrass beds and vegetated hard substrates are known to be more favourable in terms of food resources for cod compared with non-vegetated substrates, at least during spring and autumn (Persson *et al.* 2012). Our study strongly suggests that cod in this region have to trade off food availability against physiologically benign temperature. By moving to deeper, less prey-rich habitats, cod may sacrifice energy intake in favour of tolerable temperature conditions. In fact, there is evidence that cod in coastal Skagerrak show signs of reduced somatic growth during late summer (Gjosaeter & Danielssen 2011), opposite to what is found in more northern latitudes.

The limiting effect of sea temperature on cod habitat selection is likely to become increasingly apparent as climate changes. The upper layers of the oceans have warmed during the last decades (IPCC 2013). Sea surface temperature is predicted to increase further, with rises between 2 and 4 °C being predicted by the end of the century in the Skagerrak and shallow southern North Sea (Ådlandsvik 2008; Dye *et al.* 2013). Such increases in summer temperature may exacerbate the trade-offs between favourable temperature and optimal feeding areas, likely to affect growth rates and condition. Such temperature-induced effects may become detrimental for cod and other cold-water marine fish in their southern areas of distribution. Such effects may become particularly evident in small, genetically distinct fish populations (Knutsen *et al.* 2003, 2011; Jorde *et al.* 2007). Local populations may vary in their potential to adapt to temperature changes and are in addition especially vulnerable to impacts of other external stressors such as overfishing and pollution (Myers, Hutchings & Barrowman 1997).

Our study substantiates the dynamic nature of habitat selection and illustrates the importance of ocean temperature in shaping habitat selection in the marine environment. Recent terrestrial studies have pinpointed the importance of ambient temperature as a limiting factor during habitat selection (Aublet *et al.* 2009; van Beest, Van Moorter & Milner 2012; Sunde *et al.* 2014). Similar to our study, foraging decisions in moose seem to be guided by conflicting needs for thermal conditions and forage availability (van Beest, Van Moorter & Milner 2012). The effects of temperature constraints in habitat selection on individual fitness and population dynamics remain largely unexplored. However, individual fitness and population dynamics can be strongly dependent on

habitat selection (McLoughlin *et al.* 2006; Van Moorter *et al.* 2009; Hodson *et al.* 2010; DeCesare *et al.* 2014; Matthiopoulos *et al.* 2015). We therefore expect that temperature-mediated changes in habitat selection may have individual and population-level outcomes. For marine fish in particular, predicted increases in ocean temperature may further influence their habitat selection, likely to affect individual fitness and population dynamics.

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Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.j78p5> (Freitas *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. VPS location data filtering.

Figure S1. Maps showing the transects, bathymetry and acoustic backscattering data used in the mapping of sea bottom habitats.

Figure S2. Map showing the GPS track and calculated positions of the range test tag.

Figure S3. Individual positions obtained from 40 Atlantic cod in Tvedestrand.

Figure S4. Median, mean and distance root mean squared (2DRMS) error of calculated positions.

Table S1. Temperature sensors used in this study.