

Diel vertical migration patterns in juvenile cod from the Skagerrak coast

Sigurd Heiberg Espeland¹, Adine Guldborg Thoresen¹, Esben Moland Olsen²,
Leif Christian Stige¹, Halvor Knutsen², Jakob Gjørseter², Nils Christian Stenseth^{1,2,*}

¹Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway

²Institute of Marine Research Flødevigen, 4817 His, Norway

ABSTRACT: We demonstrated a clear year-round diel vertical migration pattern (DVM) of small (26 to 45 cm) Skagerrak coastal cod *Gadus morhua* on a small geographic scale. Generalized additive models (GAMs) were used to make inferences about depth movements from a large data set of repeated depth measurements of cod fitted with acoustical tags. The general pattern in vertical behaviour was closely linked to sunrise and sunset, and the timing varied with the length of the day. The absolute magnitude of vertical movement was seasonally variable and probably influenced by temperature and food availability. Cod constantly selected deeper residence depths during the day than at night, and during winter than in summer. This study uses flexible models to make generalisations of the varying nature of the diel vertical migration patterns in juvenile coastal cod.

KEY WORDS: Diel vertical migration · DVM · Generalized additive models · GAM · Coastal cod · *Gadus morhua*

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INTRODUCTION

Diel vertical migration (DVM) is a widespread phenomenon among aquatic organisms (Sims et al. 2009). Typical DVM behaviour involves a repeated shift between shallow water occupancy during the night and deep water occupancy during the day (Gliwicz 1986). DVM has ecological effects through the interaction between species and through direct physiological consequences for the individual organism. On the ecological scale DVM may affect the ecological effect of one species on others both through competition and/or predation (Hays 2003). Hunting strategies are often affected by light intensities, which vary with depth and time of day. Different species may thus experience varying hunting efficiencies and predation risks and, as such, induce DVM patterns. Furthermore DVM patterns in one species may induce DVM in either their prey or their predators. On the physiological scale the DVM patterns are important for food intake and meta-

bolic processes. This is due to both varying food availability and the associated environmental factors of the different depths (Hays 2003).

Potential nonexclusive explanations for DVM as an evolved strategy include: (1) a tradeoff between food availability and predation risk (Gliwicz 1986), where both are generally more pronounced in shallow water, while predation risk from visually hunting predators is reduced during nighttime, and (2) a thermoregulatory strategy allowing ectotherms to lower their metabolic rates in cold deep waters (Wurtsbaugh & Neverman 1988, Sims 1996).

Explanation (1) predicts that organisms with high predation risk should ascend at night to shallow waters to feed, but during the day descend to deeper waters where low light conditions reduce predator risk. This predator evasive behaviour is a strategy to avoid predators that use visual hunting strategies (Gliwicz 1986). Large predators, however, will move vertically to find food and optimise their foraging strategies.

DVM as a food driven pattern in prey species may therefore induce a similar vertical migration in the predator species.

Explanation (2) is based on the fact that temperature affects the metabolic processes of digesting food and growth (Imslund et al. 2005). Fish can regulate metabolic rate by actively choosing a depth with an optimal ambient temperature (Kristiansen et al. 2001); this 'hunt warm, rest cool' behaviour has been shown in many marine fish species (Sims et al. 2006, Mortensen et al. 2007).

Novel technology in data storage tags (DST) and acoustic transmitters with depth sensors have allowed detailed studies of the vertical positions of marine organisms. Given batteries with long lifetimes and good storage capabilities some of these tags may produce 100 000 to 200 000 depth observations from a single fish. Coupled with low cost, this provides the opportunity to acquire large data sets on DVM on aquatic species. Making inferences on 'typical' movement, excluding variable individual effects and abnormal behaviour, may be challenging for large data sets. Generalized additive models (GAM) are ideal for describing patterns in biological data sets with complicated structure. Instead of predefining particular linear or nonlinear functional forms, such models 'let the data tell' by fitting local piecewise polynomials to the data. This makes GAMs more flexible than parametric models as they do not require any a priori definition of the shape of the relationship between predictors and response (Hastie & Tibshirani 1990).

In this study, we observed the diel vertical migration of juvenile Atlantic cod *Gadus morhua* on the Norwegian Skagerrak coast and evaluated the factors influencing vertical movement in coastal cod. We expected the DVM patterns to be affected by the following factors: light intensity, ambient temperature and food availability. These factors exhibit large seasonal variations. We used GAMs as a tool for describing the vertical position of a typical fish and the temperature experienced. Predators may also affect the vertical migration, although numbers of possible predators are few.

MATERIALS AND METHODS

Data collection. During fall 2006 (11 October to 4 November), 20 cod (mean length, 325 mm) were captured in the Sømshilen area west of Arendal on the Norwegian Skagerrak coast (Fig. 1) and brought to the Institute of Marine Research, Flødevigen. The fish were tagged with acoustic transmitters (V9P-2L, Vemco; Lokkeborg 1998, Lindholm & Auster 2003, Espeland et al. 2007) and released back to the same area where they were caught. During April 2007,

another 10 cod (mean length, 405 mm) were tagged and released in the same area using the same procedure as for the first 20 cod (for a complete overview of all 30 tagged cod see Table 1).

Transmitters were 9 × 30 mm in size and set to transmit a signal every 20 to 60 s, with a random interval to reduce code collision (i.e. 2 or more fish simultaneously transmitting a signal to the same receiver). The projected battery life of these transmitters was 230 d. The depth of the fish was transmitted along with an identity code for each cod. Transmitters were surgically implanted in the abdominal cavity. Fish were anesthetized with clove oil (King et al. 2005), a small incision was made posterior to the pelvic fins and the transmitter inserted. The wound was closed with absorbable suture material. The fish were kept from 3 to 13 d in captivity before release to ensure they recovered from the surgical procedure. All fish were released close (<100 m) to the point from where they were captured.

Several genetically distinct populations of cod (Knutson et al. 2003, Jorde et al. 2007) are found along the Skagerrak coast where fish generally display a high degree of site fidelity (Espeland et al. 2008). The Skagerrak cod are subject to intensive fishing pressure (Julliard et al. 2001), which induces skewed age and size structure, with few, old, large fish and reduced phenotypic diversity (Olsen et al. 2004, 2009). The Skagerrak cod reach maturity at the age of 2 to 4 yr (Olsen et al. 2004). Due to their relatively small body size, we expected the fish in our study were immature (see Olsen et al. 2008), so they would not display any spawning behaviour.

The area of Sømshilen, where all fish were released, is a semisheltered basin with several small islands and rocks (Fig. 1). The surface area is ~3 km², excluding permanently dry land. Sømshilen is influenced by the River Nidelva, which has one of its outlets in the northern sector of the basin (Fig. 1). The freshwater discharge into Sømshilen is variable, but limited to the surface layer. The minimum salinity at 2 m depth was 18.8. The water column from 2 to 30 m depths had salinities ranging from 18.8 to 37.8 (mean 31.5). The island of Jerkholmen is part of a moraine extending obliquely across the basin from the southwest, at Hasseltangen, towards the northeast (Fig. 1). This creates a shallow, but passable, barrier sheltering the area from the open ocean. The southwestern part of the basin extends down to 10 m depth while the northeastern parts are somewhat deeper (maximum depth ~30 m).

Salinity, temperature and depth (STD) data were taken weekly at 5 different locations (Fig. 1) by lowering a mini STD probe. The STD measurements started 21 December 2006 and continued to 17 November 2007.

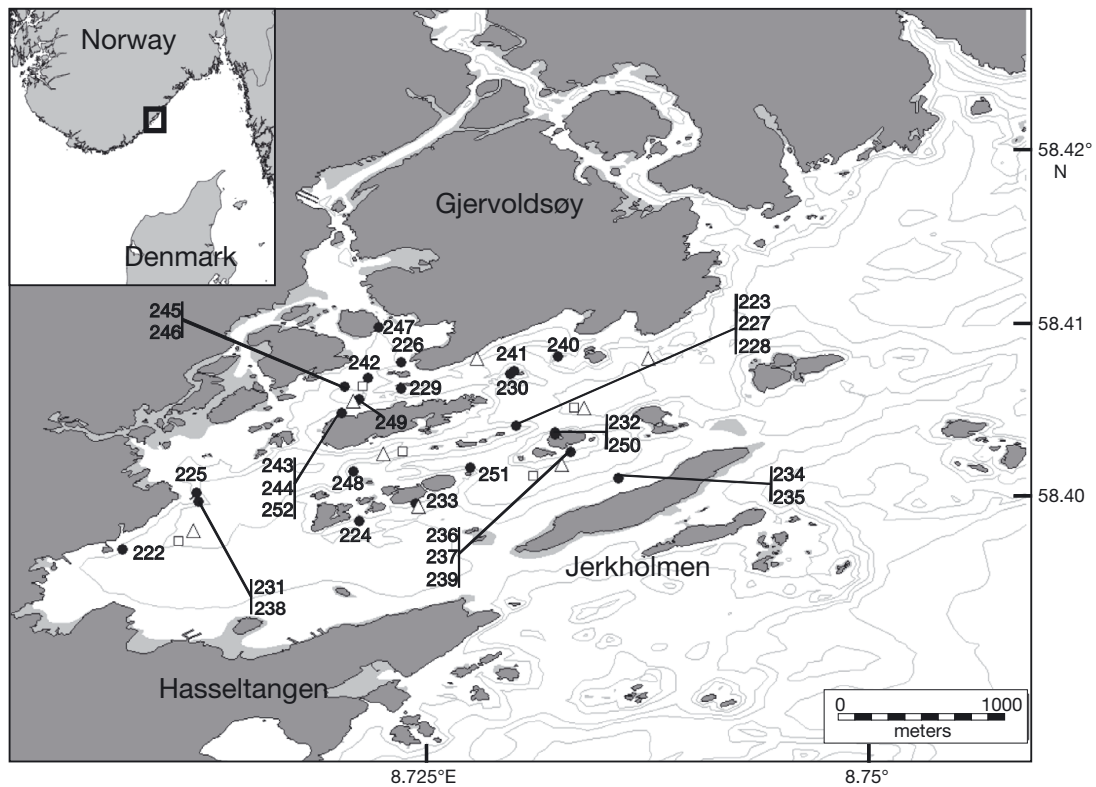


Fig. 1. The study area of Sømskilen. Grey shaded areas: dryfall (<0.5 m depth); light grey lines: 5 m depth contour intervals. The island of Gjervoldsøy splits the river Nidelva into 2 separate outlets. (●) Release point for the cod. The serial number of each fish is given. (△) VR2 receiver buoy position. (□) Station where salinity, temperature and depth measurements were made weekly. Inset: location of study area at the Norwegian Skagerrak coast

General habitat category mapping was performed in the area and divided into 2 sediment types (rocky or fine) and 2 macrophotosynthetic community types (sparse and lush). The habitat categorization was done based on remotely operated vehicle (ROV) video film from 20 transects (total length 2.7 km) and 30 fixed stations in a grid net pattern. The upper 1 to 2 m were usually rocky habitat inhabited by several species of macroalgae. The depths between 5 and 3 m were either rocky or sandy, but usually lush with respect to macrophytes. Several large eelgrass beds dominate the shallow (<5 to 7 m depth) flat areas. Photosynthetic communities became gradually sparser down to 10 m and were more or less absent farther down, so the deeper basins were barren muddy flats.

Ultrasonic receivers (VR2, Vemco) were used to register signals emitted from the ultrasonic transmitters. Two receivers were anchored in the area on 27 October 2006, 4 more were deployed on 29 November 2006, while an additional 2 were deployed in the area on 13 February 2007. These 8 buoys marking the receivers (Fig. 1) were anchored with the receiver positioned 1 to 2 m below the surface.

Since there were times when many fish were present in a small area, signals from the codes had a tendency to collide even though they had a random interval delay. This would sometimes lead to the erroneous recording of a transmitted signal. Furthermore, some transmitters started to send erroneous signals after a period of time turned off. These signals were usually easily detected and removed from the data set (e.g. signals indicating depths greater than the maximum depth of the area). Observations were plotted for every fish and inspected for erroneous signals, such as singleton signals with no other signals present for days before or after.

Data analysis. Manual STD measurements resulted in ~15 000 recordings. Since changes in temperature through the year were not assumed to be linear in the periods between days of observations, a GAM (Hastie & Tibshirani 1990, Hastie et al. 2001) was fitted to the STD data. The model was created with the GAM function in the mgcv library (v. 1.3-31) in the statistical package R (R-2.7.0; R Development Core Team 2006). With this function the optimal degrees of freedom for each smooth function is estimated by minimising the

generalized cross validation score (Wood 2006). The STD model was given by the equation:

$$T_{ilr} = \beta_l + s_1(D_i, P_r) + \varepsilon_{ilr} \quad (1)$$

Predicted temperature (T_{ilr}) at day i , location l (Fig. 1) and depth r was determined by a nonlinear interaction effect of day and depth (D_i, P_r) and a location-specific intercept β_l . The depth was modelled as a negative number to allow for more intuitive presentation of the data; shallow depths are represented by small numbers and, therefore, are positioned higher on the vertical scale in the figures. The error term ε_{ilr} is assumed to be identically and independently distributed (iid). The s_1 term is a 2-dimensional smoothing function modelled as a tensor product of 2 natural cubic spline basis functions (Wood 2006). The D and P basis functions had 9 and 19 maximal degrees of freedom (df), respectively (i.e. 10 and 20 knots). We allowed for relatively high df in order to be able to capture the steep temperature gradient in the upper part of the water column.

This model explained 96.9% of the variation in the temperature data. There was generally little difference between sampling locations; only the station closest to the river outlet was significantly different with an effect of -0.06°C .

The data set of depth observations for all fish, as recorded by the VR2 buoys, consisted of a total of ~ 2.2 million recordings. To reduce the amount of data the mean depth for each 10 min interval (10 min mean depth) was calculated for all fish and all time periods during which fish were observed, which resulted in 363 000 mean depth values for all fish. The CTD model (1) was used to predict the ambient temperature associated with each mean depth observations for each fish (C_{ijk} in Eq. 3). Water temperatures for the fish were predicted according to the CTD station effect of the station closest to the buoy recording the signal. To obtain a more balanced data set 1000 data points for each fish were randomly selected from the mean depth data set, giving a total data set of 30 000 recordings for all fish.

To describe the depth movement of fish throughout a year, we constructed a GAM based on the subsampled depth observations data set. The model is described by the equation:

$$-P_{ijk} = s_1(D_i, M_j) + \beta_k + \varepsilon_{ijk} \quad \varepsilon_{ijk} \sim N(0, \sigma^2) \quad (2)$$

where $-P_{ijk}$ represents the negative value of the depth of fish k at day i at time j . The term β_k is the fish-specific intercept. The D_i and M_j terms are the day and time of day associated with the 10 min mean depth. Day was defined as day of the year (i.e. Day 1 is 1 January and Day 365 is 31 December). The time of day was defined in decimal hours, from 0 to 23.99. S_1 is a 2-dimensional smoothing function mapping the nonlin-

ear interaction effect of day and time. In this case the smoother was modelled as a tensor product of 2 cyclic cubic spline basis functions (Hastie & Tibshirani 1990). Cyclic basis functions allowed effects to be continuous at the upper and lower bounds of the covariates. The smoother was modelled with 13 and 12 maximal df for the D and M basis functions, respectively. ε_{ijk} is an iid error term. The model did not account for positive temporal autocorrelation; this is not expected to have large influence on the estimation of the mean response, but nominal p-values and CIs tend to be overly optimistic and are therefore not shown. To indicate the representativeness of model predictions compared with among-individual variation in behaviour, we plotted model predictions along with observed 10 min mean depths of individual fish at 3 representative dates (see Fig. 3).

To describe the predicted ambient temperature experienced by each fish a GAM of temperature experienced for a given time of day and day of year was constructed.

$$C_{ijk} = s_1(D_i, M_j) + \beta_k + \varepsilon_{ijk} \quad \varepsilon_{ijk} \sim N(0, \sigma^2) \quad (3)$$

Here the ambient temperature C_{ijk} for fish k at day i and time j , is given by the fish-specific intercept β_k and the interaction between day (D_i) and time (M_j). The s_1 term is the smoothing function modelled as a tensor product of cyclic cubic spline basis functions of D and M (maximal df 13 and 12, respectively). ε_{ijk} is an iid error term. The predicted ambient temperatures for the fish were compared with the predicted available temperature range from the STD model from Eq. (1).

All models were computed using the TITAN computer cluster at University of Oslo (available at www.biportal.uio.no).

RESULTS

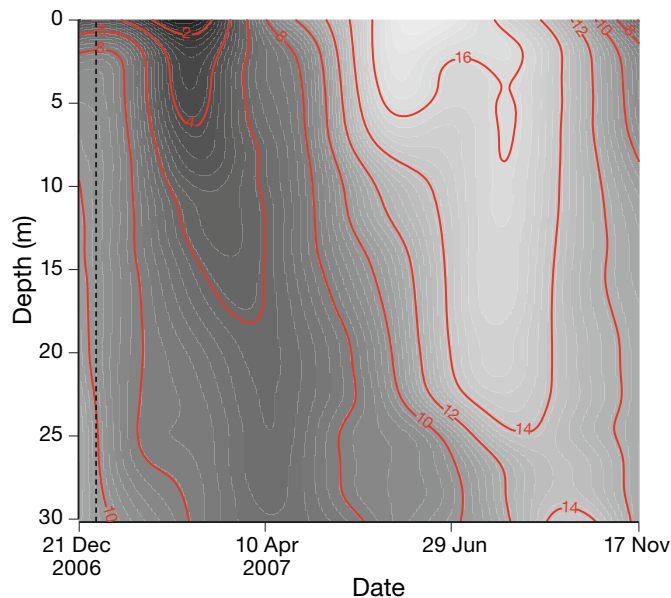
All 30 fish recovered from surgery and were successfully released in the study area. During the first 100 d 8 fish were lost after release (Table 1). This could be due to permanent emigration, transmitter failure or unreported harvest mortality. Two fish were declared dead as they ceased to show any vertical activity and were manually tracked to the exact same location on several occasions. Three of the fish were harvested by fishers and reported to us, while one transmitter clearly malfunctioned producing spurious measurements. A total of 12 fish stayed in the area until either the battery expired or the study ended.

Sea surface temperature in the area ranged from nearly 0°C during February up to 18°C during July (Fig. 2). Bottom temperatures (30 m depth) varied somewhat less; the coldest bottom temperatures occurred late in March (6 to 8°C), whereas warmest bot-

Table 1. *Gadus morhua*. Release and tracking information on coastal cod tagged and released in the study area of Sømskilen. ID: transmitter serial number identifying all depth codes; release date: the date the fish was released after surgery; fish length: total body length measured during surgery; end date: the day when the last valid signal was recorded; days at sea: number of days between release and the last signal; no. obs.: number of valid depth measurements made during the period the fish was at sea; no. 10 min: number of 10 min mean observations calculated from the raw data

ID	Release date	Fish length (mm)	End date	Days at sea	No. obs.	No. 10 min
233	04 Nov 2006	315	20 Mar 2007	108	60 541	10 380
234	04 Nov 2006	340	04 Apr 2007 ^a	241	84 981	12 967
235	04 Nov 2006	325	28 Aug 2007 ^b	297	193 422	28 564
236	25 Oct 2006	350	21 Apr 2007 ^c	179	117 629	17 614
237	25 Oct 2006	330	20 Jul 2007 ^b	268	252 870	31 557
238	25 Oct 2006	305	25 Dec 2006 ^d	61	19 875	2 283
239	25 Oct 2006	295	31 Mar 2007	157	85 146	14 704
240	25 Oct 2006	320	16 Nov 2007 ^e	387	55 345	15 236
241	25 Oct 2006	320	05 Mar 2007	131	19 051	6 112
242	16 Oct 2006	375	23 Jan 2007	99	15 549	3 762
243	16 Oct 2006	320	01 Jan 2007	83	15 210	3 524
244	16 Oct 2006	353	21 Jan 2007	97	47 043	8 968
245	16 Oct 2006	319	03 Apr 2007	169	152 479	21 195
246	16 Oct 2006	335	22 Jan 2007	98	29 808	5 445
247	16 Oct 2006	358	11 May 2007 ^d	208	96 408	18 289
248	11 Oct 2006	265	03 Jan 2007	79	11 086	2 497
249	16 Oct 2006	348	05 Mar 2007	140	19 439	4 885
250	11 Oct 2006	285	17 Apr 2007 ^b	188	72 596	15 237
251	11 Oct 2006	298	04 Sep 2007 ^b	328	96 946	21 255
252	16 Oct 2006	350	27 Apr 2007 ^c	198	87 783	12 679
223	27 Apr 2007	400	16 Nov 2007 ^e	203	18 522	3 623
224	27 Apr 2007	440	16 Nov 2007 ^e	203	151 492	14 415
225	27 Apr 2007	445	27 Oct 2007	183	142 683	18 063
226	27 Apr 2007	435	22 Jun 2007 ^c	56	107 900	8 155
227	27 Apr 2007	435	16 Nov 2007 ^e	203	46 583	9 203
228	27 Apr 2007	400	19 Aug 2007	114	73 873	11 161
229	27 Apr 2007	375	30 Jun 2007	64	63 737	5 667
230	27 Apr 2007	355	16 Nov 2007 ^e	203	49 414	8 009
231	27 Apr 2007	395	15 Jul 2007	69	29 928	4 125
232	27 Apr 2007	370	05 May 2007	8	13 091	1 246

^aTransmitter malfunction after given day. ^bBattery assumed expired during study. ^cFish removed from area by fishers. ^dDeclared dead by given date. ^eTransmitter present in the area at the end of study



tom temperatures occurred in mid-August (12 to 14°C). Some periods in spring and autumn exhibited narrow temperature ranges.

Overall, the tagged cod were observed throughout most of the depth range available within the study area. The deepest available habitat (25 to 30 m) was occupied only during the winter months of January through March. The cod generally stayed in deep layers during the day and then ascended to more shallow areas at night (Figs. 3 & 4). Furthermore, there were clear seasonal tendencies in the extent and timing of the vertical movements of the 30 fish (Fig. 4).

Model (2) describing the 10 min mean depth of a fish as a function of the interaction between time of day (h) and time of yr (day number) explained 57% of the variation and had a generalized cross validation (GCV) of 15.318. Modelling day and time as additive effects instead of an interaction increased the GCV to 19 and only explained 46% of the variation.

The predicted depth of the fish in response to day and time is shown in Fig. 4. During winter (January to February), the day residence depth (given as the area in the middle of Fig. 4 above sunrise and below sunset) was much deeper than during early summer (May and June). Also the nightly residence depth varied, with somewhat deeper depths occurring during winter than in summer. The deepest overall depths occupied by cod occurred in the middle of the day during February.

In winter and early spring the ambient day temperatures were in the warm end of the available temperature range and were higher than the ambient night temperatures (Fig. 5). In late spring and during summer the ambient temperatures at night were higher than the ambient temperatures at day, however both were in the warm end of the available temperature range.

Fig. 2. Modelled temperature throughout the year at different depths. The surface plotted is the interaction effect between depth and day as given by the GAM from Eq. (1). Isolines connect day and depth combinations with equal predicted temperature. Moving vertically in the figure indicates how temperature changes with depth at a given day. Moving horizontally describes how temperature at a given depth varies throughout the year. The black dotted line indicates 1 January 2007

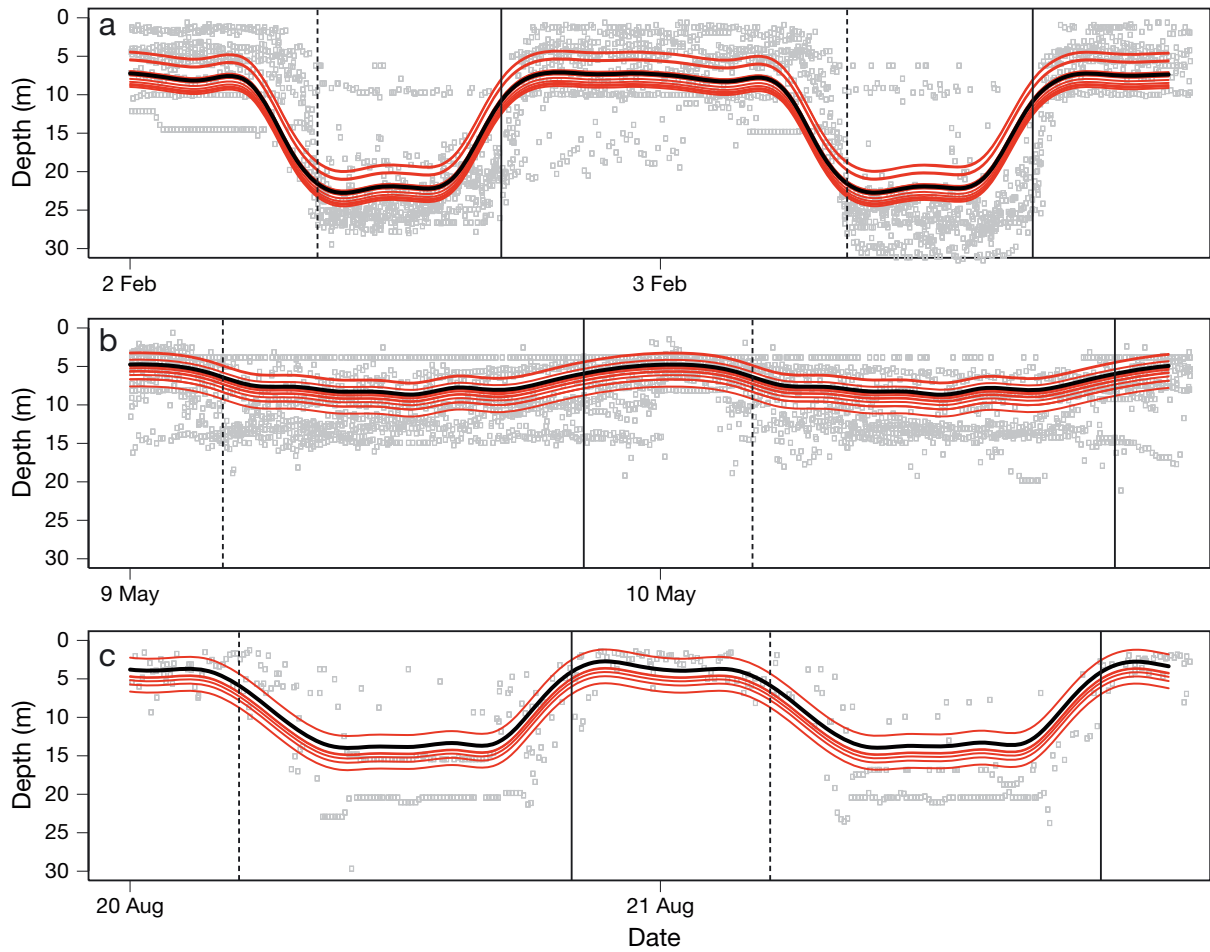


Fig. 3. Comparison of model predictions and data for three 2 d periods: (a) early February; (b) mid-May and (c) late August. Points in panels: 10 min running mean depths for cod present during the period. The number of fish present varied ($n = 14$ during 2 and 3 February, 13 during 9 and 10 May, 6 during 20 and 21 August). Red lines: model predictions for the same fish. Thick black line: predictions from the average fish (predictions with average fish specific offset). Vertical lines: time of sunrise (dashed) and sunset (continuous)

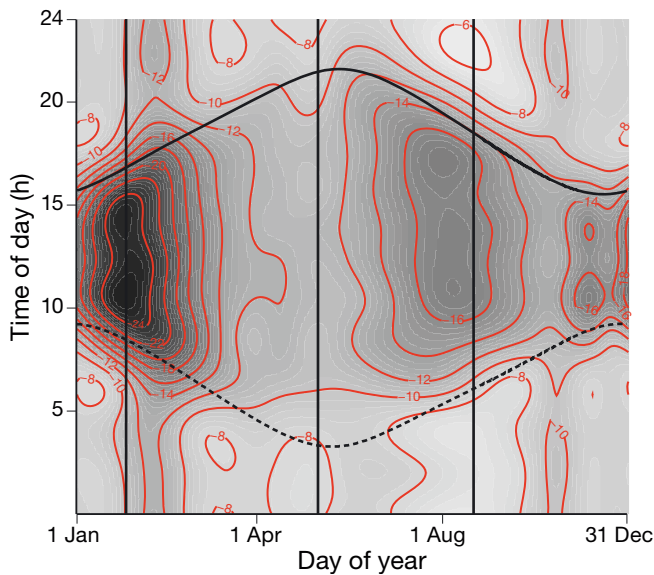


Fig. 4. Depths occupied by a typical cod through the day and year. Contour lines show how predicted depth varies in response to day and time and represents a 2-dimensional surface estimated by the model from Eq. (2). Moving vertically through the figure indicates how the occupied depth at a given time of year varies through the day. Fig. 3 shows predictions for the dates represented by the 3 vertical lines. Moving horizontally indicates how the occupied depth at a given time of day varies throughout the year. Dark areas in the figure correspond to periods when the fish occupy deep waters and light areas correspond to shallow waters. Red contour lines connect day and time combinations of equal predicted depth. Negative numbers: depth (m) below the surface. Black curves: time of sunset (continuous) and sunrise (dashed). Predictions are shown for a cod with near average mean depth; predictions for other cod differ by fixed constants

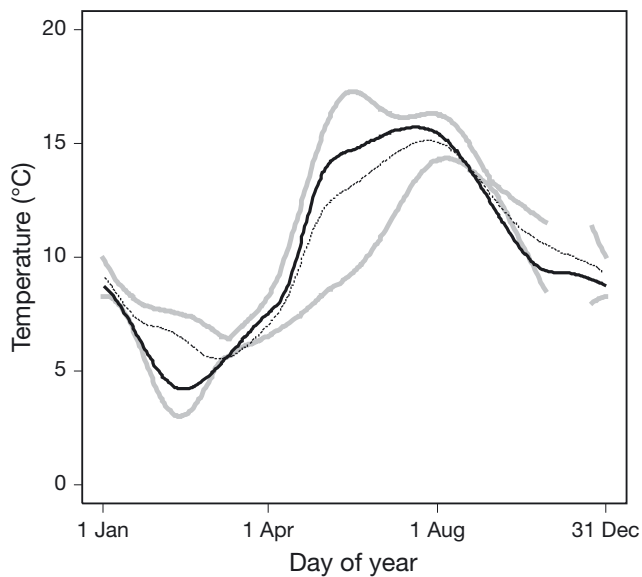


Fig. 5. Predictions of temperature experienced by a typical cod through the year. The continuous black line is the predicted temperature experienced (from Eq. 3) during the night at 0 h, while the dotted line is the predicted temperature experienced (from Eq. 3) during the day at 12 h. The 2 grey lines are the maximum and minimum temperatures in the area as predicted by Eq. (1). Since salinity, temperature and depth (STD) measurements were not done for a complete year and model (Eq. 1) does not use a cyclic smoother, no estimate is presented for the period from 17 November to 21 December

DISCUSSION

In this study we investigated both depth preferences and ambient temperatures for wild juvenile cod in a semisheltered natural basin. The cod displayed a consistent diel vertical migration pattern within a limited geographic area, moving from deeper areas during the day to shallow water habitats, such as kelp and eelgrass beds, at night. We discuss potential proximate and ultimate factors influencing this behaviour. Specifically, the habitat use is compared with temperatures experienced by the fish.

Studies of DVM in cod have been ambiguous and inconclusive as large regional, seasonal and individual differences have been found (Righton et al. 2001, Neat et al. 2006, Svedäng et al. 2007). Cod feed both during the night and the day (Gregory & Anderson 1997, Løkkeborg 1998) and select depths to regulate body temperature (Clark & Green 1990, 1991, Righton et al. 2001). Coastal cod in Newfoundland, Canada, hunt in shallow warm water and rest in cool deep water when the water column is stratified. When the column is isothermic, they consistently prefer shallow waters rich in prey (Clark & Green 1990, 1991). In the North Sea vertical behaviour is closely linked to horizontal movement (Hobson et al. 2007, 2009).

We found that the seasonal shift in the timing of DVM was highly correlated with the seasonal shift in sunrise and sunset; i.e. throughout the year, the fish ascended from deep waters close to sunset and descended from shallow waters close to sunrise. Fish may partly select ambient temperature by selecting a given depth. When considering ambient temperature, the temperature at night closely follows the surface temperature; i.e. it is cold during winter and warm during summer (Fig. 5).

Previous studies on the feeding ecology of cod in the area indicate regional and seasonal differences in stomach contents. Fish in this size range preferred small fish (mainly gobiids) and crustaceans (decapods and isopods) as their primary food source during winter. During spring the proportion of polychaetes increased to more than 50% with a corresponding reduction in decapods (Hop et al. 1992, 1993). Crustaceans and small fish are expected to be more numerous in the shallower habitat from 10 m depth and upwards.

Cod behaviour with regard to vertical position varied between day and night. Vertical position during the day showed the largest seasonal fluctuation. The deepest occupied daily depths were found from January to March (20 to 24 m depths). This is the period when temperatures are at their lowest overall and the fish occupy the warm end of the available temperature range (Fig. 5). These depths lack macrophotosynthetic communities and have low prey densities, consisting mainly of echinoderms (ophiurans) and polychaetes.

During the day in May and June the fish usually occupied intermediate depths (8 to 12 m). During this period the water column is nearly isothermic. These deeper depths contain macrophotosynthetic communities and may include variable numbers of food items. Later in the summer (August) the fish use slightly deeper depths during the day.

Vertical positions at night had less variation through the year, but were constantly shallower than depths occupied during daylight. The deepest vertical positions during the night were found in February and March (10 to 14 m) while during the rest of the year they varied from 2 to 8 m. These depths represent the middle and the lower zones of the lush coastal macrophotosynthetic communities and are usually inhabited by small fish and invertebrates. The temperature experienced by fish during the day closely follows the surface temperature except in February and June when the fish may avoid the extreme ends of the temperature range.

From this and previous studies on cod feeding it appears that night is the primary foraging period. Cod may avoid waters with very low temperatures during February as the night foraging depths ranged from 6 to 12 m, instead of the shallower cooler water. This study

suggests that daytime is used for resting, but feeding may also occur especially during spring when there is little variation between day and night vertical positions and cod are feeding on polychaetes.

Some of these vertical behaviours could be driven by predator risk. Cannibalism is known to play a role in cod biology; however, in this area there are few large conspecifics. For these fish the most numerous predators would be cormorants and gulls. However, when the cod reach a size of 30 to 40 cm (as in this study), they are too large to be taken by birds. Also during the period around mid-June when the night is short and daylight is extended, they prefer shallower depths than during the rest of the year. If vertical migration was linked to predator avoidance behaviour, shallow depths would be most dangerous during this period.

This study suggests that the fine scale diel vertical migration is influenced by food availability and temperature. Night is the primary feeding period in unfavourable temperatures at shallow depths, whereas daytime is the resting period in deeper waters. Due to the lack of accurate observations of fish behaviour (resting or feeding) and because we only have data on depth, we are prevented from drawing strong conclusions on causality of vertical movement. An extension of this study could specifically examine feeding in the wild (Bestley et al. 2008, Fossette et al. 2008).

We have shown how large data sets on vertical behaviour may be analysed using GAM models. Using these models we specifically demonstrated how the typical pattern in vertical behaviour is closely linked to environmental cues. The timing of the vertical behaviour was closely linked to sunrise and sunset. However, the overall behaviour is flexible and the total depth use may be affected by other factors in addition to temperature and food availability.

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