

# Cod migration patterns in relation to temperature: analysis of storage tag data

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Bivariate time-series of depth (pressure) and temperature with two-hour intervals from 19-data storage tags (DST) attached to adult Northeast Arctic cod (*Gadus morhua* L.) released from mid-March are analysed. Interplay between migration behaviour, physiological limitation factors, environment, and ecology in the Barents Sea is investigated using geometrical and statistical methods. Thermo-stratification is identified using  $r(t)$ , the ratio between temperature and depth change over each record interval. Vertical activity,  $act(a)$ , in relation to physiological limitations to pressure change is measured with the ratio of the daily depth range to the free vertical range. Cycles are detected by spectral analysis. The analysis supports conclusions from large-scale studies. Cod migrate along stable thermal paths until they reach a front area (or feeding ground), where the vertical activity increases and the records of depth, temperature, and  $r(t)$  change pattern, level and range. The (semi-) diurnal vertical migration (DVM) occurs seasonally in some fish, mainly in areas with large temperature gradient. In 11 out of 12 tags where DVM is detected, this occurs during summer and autumn. In seven out of 11 tags where semi-diurnal tidal cycles are detected in the temperature series together with a significant reduction in vertical migration, this occurs during April. In some tags diurnal or semi-diurnal cycles appear in both depth and temperature series.

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## Introduction

Numerous studies on cod migration behaviour based on fishery data, tag experiments, and surveys conclude that foraging and spawning are the main reasons for cod to migrate over a long distance. Preferred migration is along stable thermal paths, but the cod will diverge from the norm to pursue prey concentrations of high density (Konstantinov, 1965; Cushing, 1981; Rose and Leggett, 1989; Rose, 1993; Rose *et al.*, 1995).

The March–April and January–March survey data show that vertical distribution and catch rates of Northeast Arctic cod (*Gadus morhua* L.) vary substantially with day and night (Engås and Soldal, 1992; Michalsen *et al.*, 1996; Hjellvik *et al.*, 1999; Aglen *et al.*, 1999; Korsbrekke and Nakken, 1999). The latter two studies stress that the vertical migration is size dependent. These studies are mainly in agreement with a study of demersal

fish in the Northwest Atlantic (Beamish, 1966). Their purpose is to understand the vertical migration behaviour of cod, since this influences the survey stock assessment (Aglen, 1994; Godø, 1994).

Knowledge of seasonal and spatial distribution and behaviour in relation to environment, such as when, where and why these occasionally rhythmic vertical migrations of the fish occur, could also improve the survey stock assessment. If the rhythm is size dependent and different between species, it is plausible that the survey will exhibit a variable bias from year to year according to the big difference in year-class strength. To the extent that diurnal vertical migration (DVM) in cod is a feeding response, e.g. preying on species with DVM (Brunel, 1965; Turuk, 1973), the picture gets more complicated, as the cod's activity will be influenced by changes in behaviour and availability of important prey species. Data-storage tags (DST) contain detailed

information on different vertical migration patterns, which may help to understand the migration process and the variability in bottom-trawl catch and acoustic target strength (Harden Jones and Scholes, 1981).

Using acoustic tags, Arnold *et al.* (1994) observed that cod migrate horizontally by selective tidal stream transport, and found one cod with DVM. Analysis of DST records show that some individual cod occasionally, for short periods, exhibit DVM (Stensholt, 1998; Steingrund, 1999; Godø and Michalsen, 2000). Godø and Michalsen (2000) studied the seasonal trends of depth and temperature, range, speed and repeatability of vertical movement in relation to the cod's swimbladder physiology and buoyancy status. They conclude from their study that cod are negatively buoyant most of the time, and that cod seek higher temperatures in winter and spring than in summer and autumn, in agreement with Lee (1956), Trout (1957), Woodhead and Woodhead (1959) and Midttun (1965). In this paper we use the ratio of the daily depth range to the free vertical range (Harden Jones and Scholes, 1981) to measure the vertical activity in relation to physiological limitations to change of pressure.

Throughout a migration, each cod experiences a change of temperature distribution as a consequence of changing depth level and area, but so far the depth and the temperature series have been analysed separately. By means of  $r(t)$ , the ratio of temperature change to depth change over a two-hour interval, Stensholt and Stensholt (1999) related the depth and temperature data using geometrical analysis of the fish move vector in the temperature gradient vector field. The  $r(t)$  series is used to identify thermo-stratification. Stensholt (1998) and the present paper apply these ideas together with spectral analysis to DST data to investigate the seasonal migrational behaviour in relation to environmental conditions. By incorporating other known information about behaviour and spatial density distribution of cod and its prey species, as well as general knowledge on physical oceanography, it is possible to discuss what areas the cod will possibly migrate to during different seasons and possible influences on the migration patterns.

## Material and methods

### Data collection

The DSTs were attached to 200 adult Northeast Arctic cod of length 50–100 cm and released from mid-March 1996. The experiment focussed on the physiological limitations of cod to maintain neutral buoyancy under pressure changes (Godø and Michalsen, 1997, 2000). There were two release sites: Lofoten (site L) for 42 mature cod and off North Cape (site N) for 158 mainly immature adult cod. A tag gives no direct information

on position in the time between release and recapture. Recorded hours are in GMT. Many tagged cod were recaptured along the coast of Finnmark to Kola Peninsula and southwest of Novaya Zemlya (Figure 1; Godø and Michalsen, 2000). Southwest of Novaya Zemlya the sea is shallow with high surface temperature and a strong vertical gradient in summer and autumn, and with fronts from the outflow of cold arctic water and big rivers.

The data from 19 tags, each with time-series longer than three months, were selected for analysis. Tag numbers 33, 38, 39, and 44 were released at site L, the rest at site N. In eight tags, 39, 44, 117, 131, 191, 204, 206, 246, the records are longer than ten months. In tags 39, 191, and 206 recording had terminated before recapture so the location of the last record is unknown. The data record from the two weeks of acclimatisation after release were not used in the analysis focusing on fish migration behaviour (Godø and Michalsen, 2000), but it may be used in the analysis of temperature gradient distribution.

The spatial distribution of temperature during autumn (Figure 1) is derived from CTD data of the 0-group survey 21 August–9 September 1996. The CTD stations were generally 35 km apart, and at each station data was collected at every 5 m along the depth. For comparison, the swimming speed varies with conditions (Cushing, 1981; Arnold *et al.*, 1994; Rose *et al.*, 1995; Winger *et al.*, 2000), but the speed commonly used is one fish-length per second. Vertical movement is seldom more than 50 m in two hours (Figure 4).

### Data treatment

Each tag recorded the depth (pressure) and temperature every other hour for six days and every twelfth hour on the seventh day. To have values at regular intervals, the ten unobserved values on the seventh day are replaced by interpolated values (cubic splines method, SAS, 1993, Proc Expand) before spectral analysis (Jones, 1971), and otherwise by repetitions of the last observation. With two-hour resolution a highest frequency of a four-hour cycle may be detected (Nyquist frequency, Priestley, 1981).

Temperature is recorded in degrees Celsius with one decimal and accuracy 0.2°C. Pressure is recorded step-wise and converted to depth in metres with one decimal and accuracy one bar (10 m). The calibration of the pressure unit  $d$  used in converting pressure into depth depends on the tag (e.g.  $d=1.976$  m in tag 44, 1.553 m in tag 246). All observed depths are of the type  $I \cdot y + K \cdot x$ , with integers  $I$  and  $K$  and increments  $x$  or  $y$ , e.g.  $x=1.9$  or  $y=2.0$  when  $d=1.976$  m. This particularly affects the record of small changes in depth or temperature, and therefore also the distribution of values of  $r(t)$  introduced below as the ratio of temperature change to depth

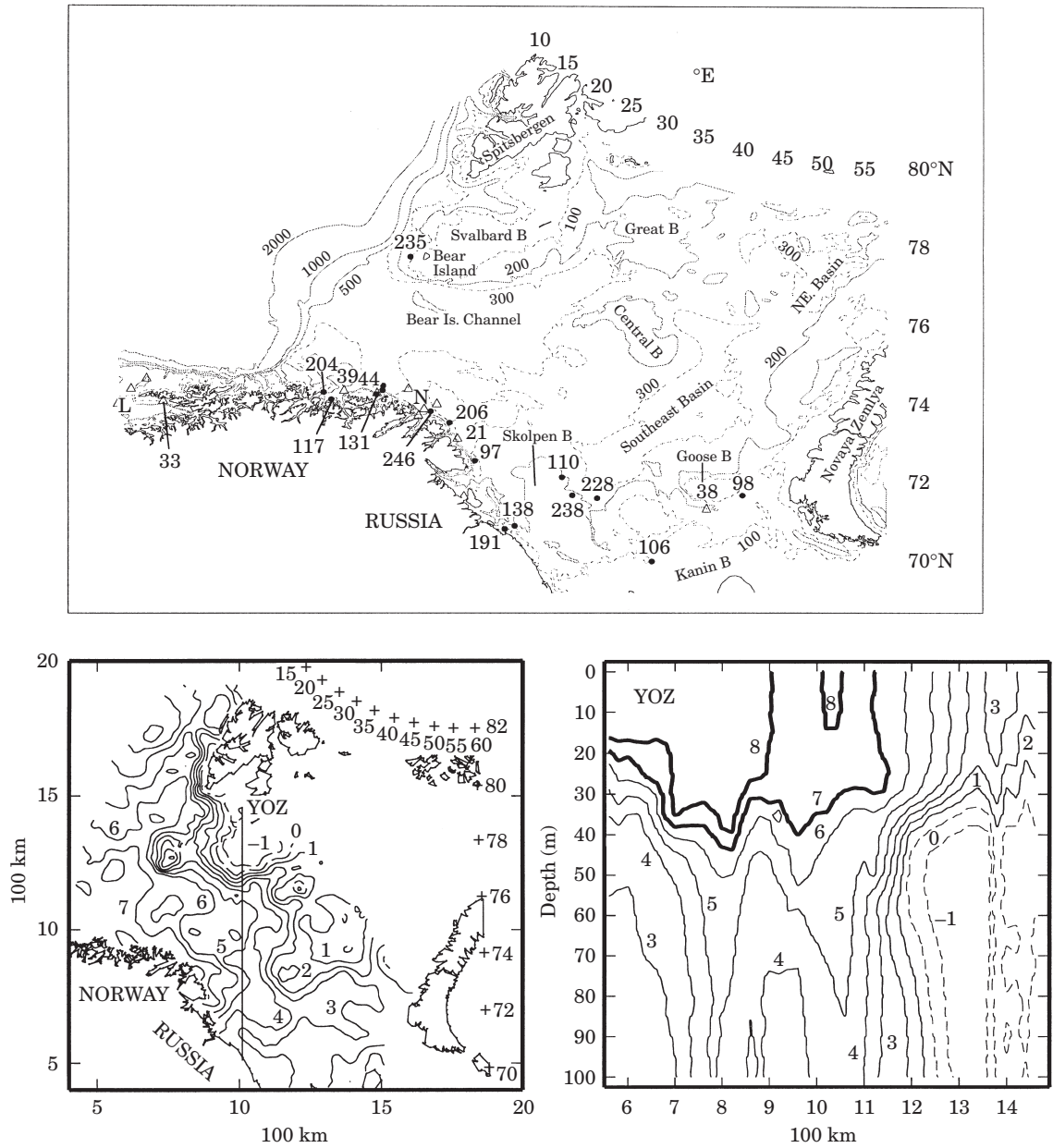


Figure 1. Bottom topography of the Barents Sea with the release sites L and N. Triangle ( $\Delta$ ) and dot ( $\bullet$ ) mark sites of the 31 recaptured cod released from site L and N respectively, with tag number for analysed tags. Temperature distribution in horizontal (at 50 m) and vertical (YOZ) sections shows Polar Front and thermocline (from August–September 1996 CTD sampling survey).

change. An  $r(t)$ -value will be recorded as undefined [0] when a small depth [temperature] change is recorded as zero. This should be kept in mind in the interpretation of  $r(t)$  patterns.

Data analysis

Time-series data analysis (Priestley, 1981) both on discrete time domain and on frequency domain (spectral

analysis) is employed for analysing trend, cyclical pattern and cross-correlation in the bivariate time-series of depth and temperature. Concepts in spatial data analysis (Cressie, 1991), e.g. spatial continuity, are central for the discussion, analysis, estimation and interpretation of the temperature and its gradient spatial distribution.

Let  $d(t)$  and  $c(t)$  be the depth and temperature record at time  $t$ ,  $t=1, 2, 3, \dots$ ,  $dd(t)$  and  $dc(t)$  be the first difference of depth and temperature, e.g.

$dd(t)=d(t) - d(t - 1)$ , and  $dmax(a)$ ,  $dmin(a)$ ,  $cmax(a)$ ,  $cmin(a)$  be the daily maximum and minimum values of  $d(t)$  and  $c(t)$  during day  $a$ . Seasonal trend and daily range of temperature in relation to the daily range of depth can be observed through the time-series plot of  $dmax(a)$ ,  $dmin(a)$ ,  $cmax(a)$ ,  $cmin(a)$  (Figure 2).

*Spectral analysis*

Spectral analysis is applied to detect and estimate the frequency of depth and temperature cycles, and also to estimate the linear relationship between the two variables. It is suitable to detect the frequency when the regular cyclical pattern persists for some time. If the time-series has one dominant frequency it may be clearly visible from the time-series plot. When there are mixed frequencies the spectral analysis becomes an important tool in identifying the frequencies. The methods assume the time-series to be stationary over the investigated duration (Table 1). First-order differences are sufficient to remove the stochastic trend in the tag data (see Results).

*Univariate time-series.* The spectral data-analysis method is an analysis in the frequency domain. The method involves partition of the total variation in the series  $\{Y_t\}$  over the frequency  $\omega$ . Consider a stationary random sequence  $\{Y_t\}$  with autocovariance function  $\gamma_k = cov\{Y_t, Y_{t-k}\}$ . We define the spectrum of  $\{Y_t\}$  as the Fourier transform of  $\gamma_k$ :

$$f(\omega) = \sum_{k=-\infty}^{\infty} \gamma_k e^{-ik\omega} = \gamma_0 + 2 \cdot \sum_{k=1}^{\infty} \gamma_k \cos(k\omega)$$

The periodogram  $I(\omega)$ , the discrete Fourier transform of the sample auto-covariance function  $g_k$ , is defined similarly as

$$I(\omega) = g_0 + 2 \cdot \sum_{k=1}^{n-1} g_k \cos(k\omega)$$

Thus in the application of this method to stationary time-series data we estimate the spectrum of  $\{Y_t\}$  by taking an average of the periodogram  $I(\omega)$  of the time-series, e.g.

$$\hat{f}(\omega_j) = (2p + 1)^{-1} \sum_{l=1}^p I(\omega_{j+l}), \text{ for some integer } p.$$

It involves the decomposition of the total variation in the time-series  $\{Y_t\}$  of length  $n$  into harmonic components at the Fourier frequencies  $\omega_j = (2\pi \cdot j)(n)^{-1}$ ;  $j=1, \dots, n(2)^{-1}$ .

The graph of  $\hat{f}(\omega)$  as a function of  $\omega$  can be used to detect which frequency components that contribute large discrete variations in the time-series. The peaks in  $\hat{f}(\omega)$  correspond to the variation contributed from cyclical patterns at frequency  $\omega$ . The confidence interval is:

$$l_j \leq \hat{f}(\omega_j) \leq u_j, \text{ where } l_j = [2(2p+1)] \cdot \hat{f}(\omega_j) \cdot (c_2)^{-1} \text{ and } u_j = [2(2p+1)] \cdot \hat{f}(\omega_j) \cdot (c_1)^{-1},$$

and  $P[\chi_{2(2p+1)}^2 \leq c_1] = P[\chi_{2(2p+1)}^2 \geq c_2] = \alpha$ , where  $\chi_{2(2p+1)}^2$  is the Chi-square distribution with  $2(2p+1)$  degree of freedom (Diggle, 1990).

*Bivariate time-series.* The cross-spectrum of a bivariate stationary process  $(X_t, Y_t)$  is the discrete Fourier transform of its cross-covariance function  $\gamma_{xy}(k)$ .

$$h_{xy}(\omega) = \sum_{k=-\infty}^{\infty} \gamma_{xy}(k) e^{-ik\omega}$$

This is a complex-valued function and can be represented in complex polar coordinates as:

$$h_{xy}(\omega) = a_{xy}(\omega) \cdot \exp\{i\phi_{xy}(\omega)\}$$

The cross-amplitude spectrum is defined as  $a_{xy}(\omega) = |h_{xy}(\omega)|$ , this represents a form of covariance between the aligned frequency components of  $X_t$  and  $Y_t$  at frequency  $\omega$ . Consequently the complex coherency between  $X_t$  and  $Y_t$  at frequency  $\omega$ ,

$$b_{xy}(\omega) = h_{xy}(\omega) \cdot [\sqrt{h_{xx}(\omega) \cdot h_{yy}(\omega)}]^{-1},$$

represents the correlation between the corresponding frequency components of  $X_t$  and  $Y_t$ .

The coherency is defined as  $|b_{xy}(\omega)|$ , and the graph of  $|b_{xy}(\omega)|$  as a function of  $\omega$  is called the coherency spectrum.  $|b_{xy}(\omega)|$  may be interpreted as the correlation coefficient (in the frequency domain) between the random coefficients of the components in  $X_t$  and  $Y_t$  at frequency  $\omega$ . Hence  $|b_{xy}(\omega)|$  over all  $\omega$  determines the extent to which the processes  $X_t$  and  $Y_t$  are linearly related.

The phase spectrum  $\phi_{xy}(\omega)$  will measure the phase-shift between the two processes, i.e. how much they are out of phase, at frequency  $\omega$ .

The cross-spectrum was estimated using the cross-periodogram:

$$I_{xy}(\omega) = \sum_{k=-(n-1)}^{n-1} g_{xy}(k) e^{-ik\omega}$$

where  $n$  is the length of the observed series  $\{X_t\}$  and  $\{Y_t\}$ , and  $g_{xy}(k)$  is the sample cross-covariance.

In this application a high coherency over all frequencies indicates a high correlation between depth and temperature. If they are out of phase by half a cycle [phase =  $\pm\pi$ ] or in phase [phase=0] the temperature respectively decreases or increases with increasing depth. This gives us an idea about the spatial distribution of temperature in the area where the cod migrates. When the fish moves into waters with a different temperature

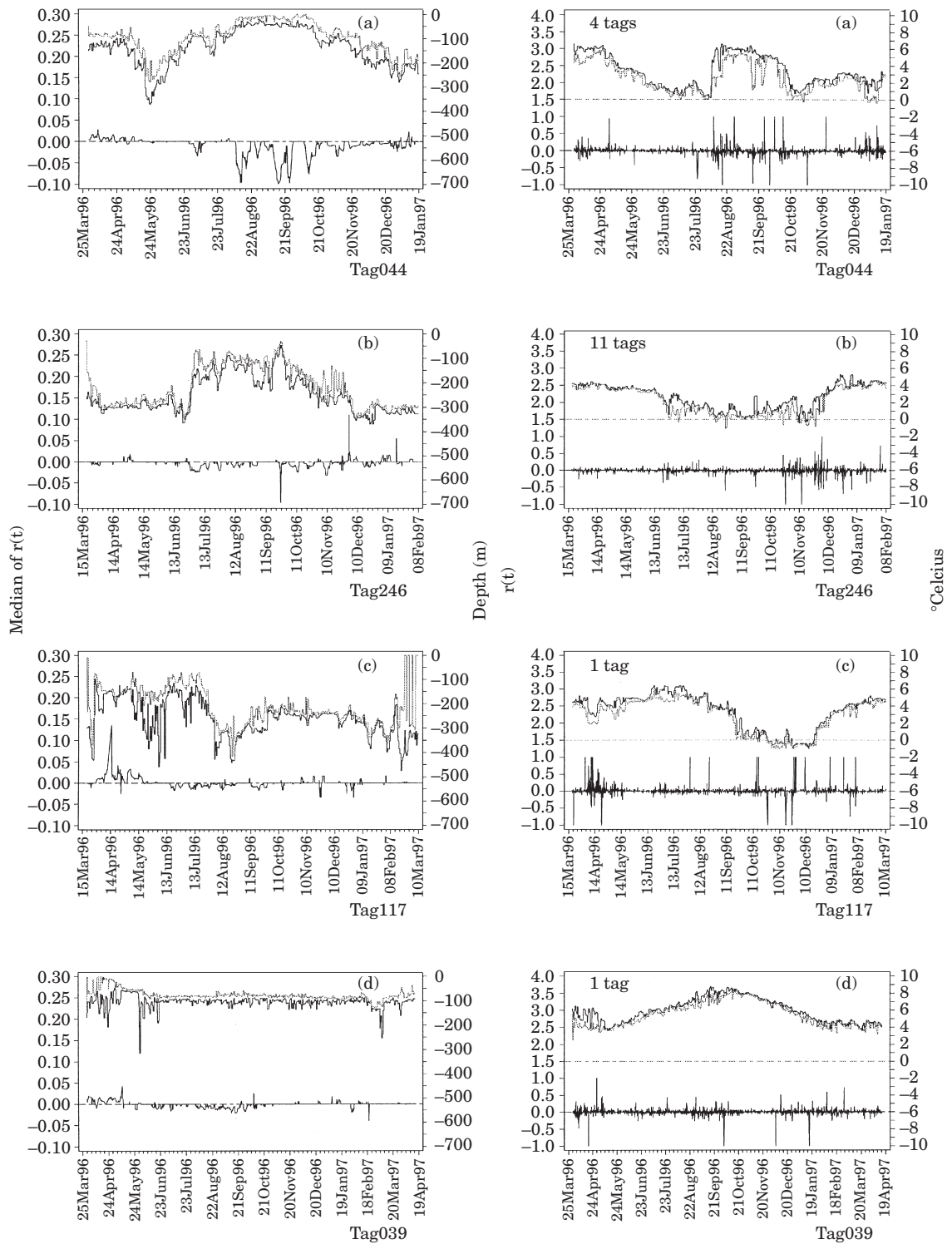


Figure 2. Four patterns of depth and temperature trend with  $r(t)$  and its moving median. Left: daily maximum and minimum of depth (above), and moving median of  $r(t)$  (below). Right: daily maximum and minimum of temperature (above), and  $r(t)$  (below). Reference line at  $0^{\circ}\text{C}$ .  $r(t)$  and its moving median in  $^{\circ}\text{C m}^{-1}$ , and  $r(t)$  cut off at  $\pm 1$ .

Table 1. Diurnal and semi-diurnal cycles are detected in 12 tags. Column 1 gives tag number and release site, L-Lofoten and N-North Cape. Column 2 gives the cycle type. There is one column for each month (April 1996–March 1997) indicating the duration by dates, d, t or d&t indicate the cycles are found in the depth, temperature or both time-series. The — means the series have ended.

Tag no.	Cycle	4	5	6	7	8	9	10	11	12	1	2	3
38 L	24 h 12.5 h	1-30 d 1-30 t	1-31 d		1-15 d		—	—	—	—	—	—	—
39 L	24 h	16-30 d&t				12-31 d&t	1-18 d&t 19-30 d	1-31 d	16-27 d	1-22 d			
	12.5 h 25 h		8-30 d		1-31 t	1-31 t	1-18 t		1-30 t	1-31 t 22-31 d	1-31 d		
44 L	24 h					1-31 d&t	1-30 d&t	1-31 d&t	1-10 d&t	1-21 d&t 22-31 d	1-9 d		
	12.5 h	1-16 d&t				8-23 t							
97 N	24 h 12.5 h 25 h	1-30 t 1-30 t			2-17 d 23-31 d	1-31 d		—	—	—	—	—	—
106 N	24 h 12.5 h		1-31 t			1-31	1-30 d&t	1-30 d&t	1-25 d&t				
110 N	24 h	1-30 d&t		1-30 d	1-31 d	1-11 d 26-31 d	1-30 d	1-31 d	1-17 d				
117 N	12.5 h 24 h 12.5 h		1-16 d&t 20-31 d	1-30 d	1-26 d		10-30 d	1-31 d&t	1-15 d				
131 N	24 h	1-25 d&t						8-31 d&t	1-14 d&t		18-31 d&t	1-12 d&t 25-28 d	1-30 d
	12.5 h	1-25 d&t											
191 N	24 h 12.5 h	1-18 d 5-15 t	13-30 d 3-20 t		16-31 d&t	1-7 d&t	13-30 d&t	1-31 d&t	1-30 d&t				1-31 d
204 N	24 h	1-30 d&t		1-27 d									
206 N	24 h 12.5 h					22-31 d&t 25-31 d&t	1-30 d&t	1-31 d&t	14-25 dw	1-31 d	1-31 d	13-28 d 26-28 d	1-5 d 1-25 d
246 N	24 h 12.5 h		1-30 d			15-31 d	1-9 d	1-31 d	1-30 d		1-31 d&t	1-11 d	

distribution, so the relationship between temperature and depth changes, we expect a relatively low coherency.

Fisher's test (Priestley, 1981; SAS, 1993) is used for testing if the peak of a periodogram ordinate is significantly large. Approximate confidence intervals for spectral ordinates, coherencies and phase spectra can be found in Priestley (1981) and Diggle (1990).

#### *r(t) an indicator of temperature distribution*

Stensholt and Stensholt (1999) introduced the analysis of the  $r(t)$  time-series to obtain some information about the temperature gradient, its value and angle, in an environment where the fish migrate for a certain duration (the gradient vector points in the direction of fastest temperature increase). The  $r(t)$  time-series can be derived from the DST records. The ratio  $r(t) = dc(t) \cdot dd(t)^{-1}$  is defined when  $dd(t) \neq 0$ .

The movement of the fish in the time interval  $[t-1, t]$  is described as a vector  $\vec{F}$  of length  $F$ . Let  $\phi$  be the angle from the downwards oriented vertical depth axis  $D$  to  $\vec{F}$ , and let  $\beta$  be the angle from  $\vec{F}$  to the temperature gradient  $\nabla T$ . Then  $dc(t) = |\nabla T| \cdot F \cos \beta$  and  $dd(t) = F \cos \phi$ , so  $r(t) = |\nabla T| \cdot (\cos \beta) \cdot (\cos \phi)^{-1}$ . If  $\nabla T$  is exactly vertical, then  $\cos \phi = \pm \cos \beta$ , and  $r(t)$  tells the size and direction (upwards or downwards) of  $\nabla T$ . An essential fact to keep in mind when one interprets the  $r(t)$  plot is that in the time interval  $[t-1, t]$ , the cod made a movement vector with known vertical component  $dd(t)$  but unknown horizontal component.

Now let  $P$  be a vertical plane containing  $\nabla T$  and decompose the fish movement vector as the sum of its orthogonal projection into  $P$  and a vector orthogonal to  $P$ . Depth and temperature do not change with a move orthogonal to  $P$ . Hence  $(\cos \beta)(\cos \phi)^{-1} = (\cos \beta')(\cos \phi')^{-1}$  where  $\beta'[\phi']$  is the angle between the projected move vector and  $\nabla T$  [ $D$ ]. Now  $\nu = \phi' + \beta'$  is the angle from  $D$  to  $\nabla T$ , and  $\cos \beta' = \cos(\nu - \phi') = \cos \nu \cos \phi' + \sin \nu \sin \phi'$ . Thus, with  $q = \tan \phi'$ ,

$$r(t) = |\nabla T| (\cos \nu + q \sin \nu)$$

This formula shows how  $r(t)$  is determined by the size of the temperature gradient  $\nabla T$ , its deviation from the vertical line, and the fish move, i.e.  $q$ . The parameter  $q$  is the ratio between the length of the fish move vector along the horizontal component of  $\nabla T$  and  $dd(t)$ . This shorter proof is due to E. Stensholt. Mainly  $\nu$  is close to  $\pi$  or 0 and  $|\sin \nu|$  is small. With increased  $|\sin \nu|$  the moves with large  $|q|$  may have significant influence on  $r(t)$ .

The spatial continuity of temperature makes it reasonable to assume  $\nabla T$  is approximately constant within the neighbourhood where the fish migrate for a certain duration. That makes it possible to apply the analysis of a single move to the analysis of a time-series over stationary periods, i.e. periods when the series do not change their characters.

Consider the situation, as in most of the Barents Sea, where  $\nabla T$  is only approximately vertical. Then generally the moving median of  $r(t)$  is a good estimator of the vertical component of  $\nabla T$  over the recorded depth range. However, for movement in an isotherm plane,  $c(t)$  is constant and  $r(t) = 0$ , and a preference for movement near a given tilted isotherm plane may cause an underestimation. Thus a small median  $r(t)$  may be due to environment (a small gradient) or to a preferential movement pattern as mentioned above.

When  $\nabla T$  deviates more from the vertical the probability of observing large  $r(t)$ -values increases, i.e. the larger is the variance and range of the  $r(t)$ -distribution. Thus periods of time with many unusually large positive and negative  $r(t)$  may indicate a relatively large horizontal component of  $\nabla T$ , which will be the case if the fish migrates close to a front.

Since the gradient  $\nabla T$  points towards warmer waters, a positive (negative) moving median  $r(t)$  indicates, respectively, cold (warm) water on top. Frequent movement near or across the thermocline give a large negative median.

When  $\nabla T$  is almost horizontal (at a front) the isotherm planes are almost vertical. Movements along the planes give small  $|r(t)|$ , but crossing the front gives large  $r(t)$ , e.g. at the Polar Front where these observations occur together with low temperatures,  $-1.5^\circ\text{C}$  to  $3^\circ\text{C}$  (Figure 1). Moreover, in the front area during the thermocline season these patterns are mixed, i.e. the  $r(t)$  distribution has large variance with large negative moving median of  $r(t)$ .

Both negative (positive) values of the moving median of  $r(t)$  and the phase values  $\pm \pi$  (0) are indicators that fish are ascending into a warm (cold) water mass (see Materials and methods, bivariate time-series).

In applications of the above analysis of  $r(t)$  to a single or a sequence of fish movements, a stable temperature distribution in the area is assumed. Exceptions to this of practical interest are when the fish moves in waters with turbulence or tidal currents. The temperature distribution may be complicated by turbulence with distorted volumes of one water mass found in another, and the direction of the gradient varies. Also this will contribute to the large range or variance of  $r(t)$ . Another special case is an area along a front where there also happens to be tidal currents. Consider a cod that is stationary where the front is pushed back and forth with the tide. A matching vertical rhythm of the cod, with remarkably small range, may let large positive or negative  $r(t)$  dominate, e.g. positive moving median  $r(t)$  of tag 117 in April (Figures 2 and 3).

Interpreting the information obtained from analysing the time-series of  $r(t)$ ,  $d(t)$ ,  $c(t)$ , and the moving median of  $r(t)$ , together with the general knowledge of the Barents Sea's physical oceanography, e.g. the location of fronts and strong tides, makes it possible to discuss what

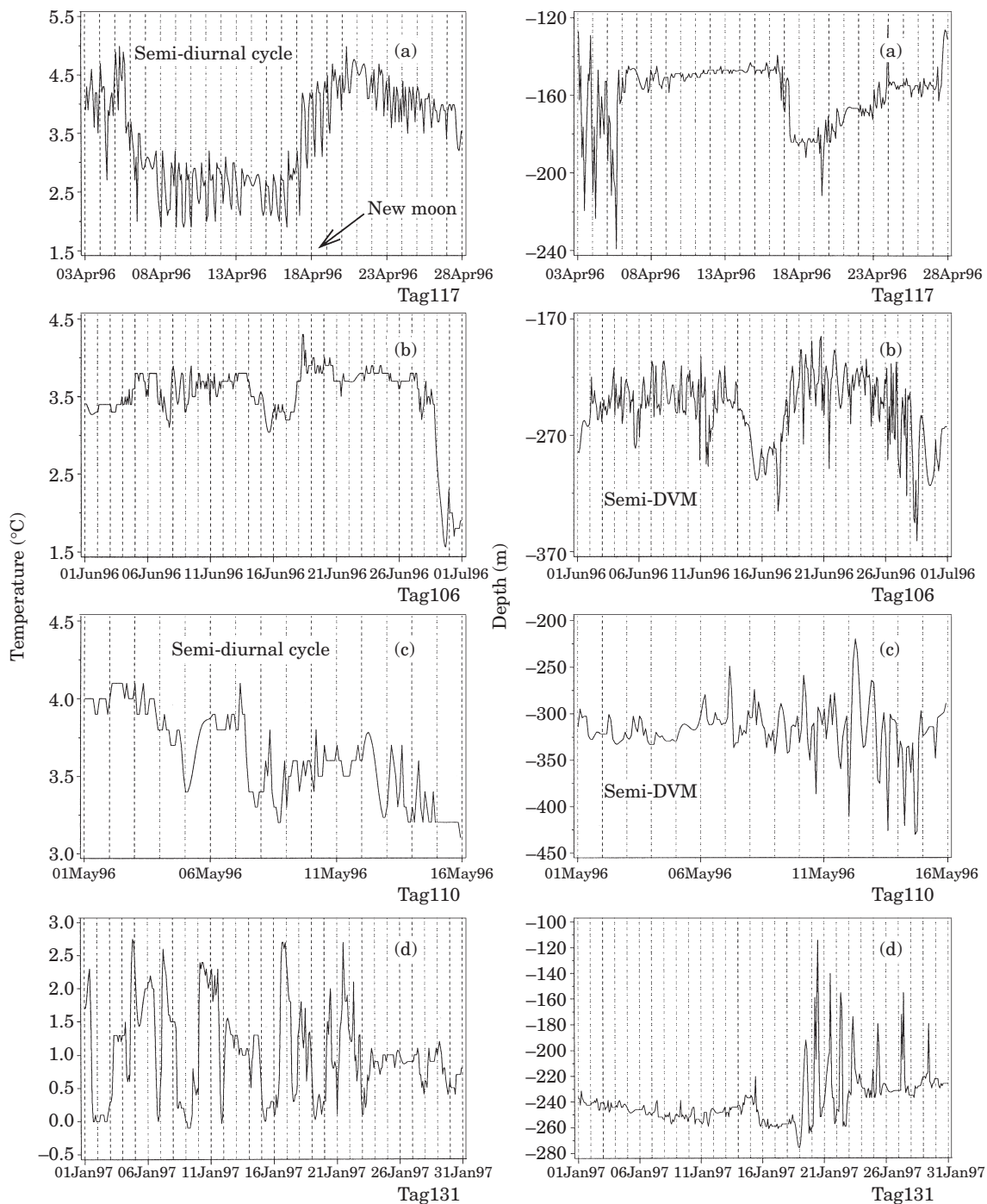


Figure 3. Semi-diurnal patterns occur in temperature alone (a), in depth alone (b), and in both depth and temperature (c). Period of reduced vertical activity without semi-diurnal cycle (d), but with relatively large changes in temperature. Broken lines mark 0 hours (GMT).



areas the cod may possibly have been in (Figures 1 and 2; Table 1).

#### A vertical activity index

The DDR (daily depth range) expressed in “FVR-units” (free vertical range) is used as an index of vertical activity, which takes into account the depth level and physiological limitations to pressure changes. A cod adjusted to neutral buoyancy at depth  $d$  metres has an FVR interval,  $[m, M]$ , where it can move comfortably. Within the FVR the pressure is reduced by 25% ascending from  $d$  to  $m$  and increased by 50% descending from  $d$  to  $M$  (Harden Jones and Scholes, 1981; Arnold and Greer Walker, 1992). Thus  $0 \leq m < d < M$ ,  $0.75(d+10) = m+10$  (for  $3d \geq 10$ ) and  $1.5(d+10) = M+10$ . Then  $M+10 = 2(m+10)$  and  $FVR = M - m = m+10$ . Vertical activity is measured with an index  $act(a)$ , defined by

$$act(a) = \frac{[d_{max}(a) - d_{min}(a)][d_{min}(a) + 10]^{-1}}{-1 + [d_{max}(a) + 10][d_{min}(a) + 10]^{-1}}$$

Thus  $act(a) = 100\%$  means that the DDR interval,  $[d_{min}(a), d_{max}(a)]$ , coincides with an FVR interval for some neutral buoyancy level  $d$  (Figure 7(a)). The actual neutral buoyancy depth throughout the day is not known from the observations but the daily ascent and descent behaviour (see Results) and the significance of the upper limit  $m$  of FVR as a barrier (Harden Jones and Scholes, 1981, 1985; Arnold and Greer Walker, 1992) makes it reasonable to assume that  $d$  is inside the DDR and to choose  $m = d_{min}(a)$ . The main purpose is to measure vertical activity level, so that the same  $act(a)$ -value means roughly the same effort or physiological strain whether the DDR is narrow in shallow or wide in deep water.

## Results

### Depth-temperature interaction as a consequence of cod migration

The Barents Sea bottom topography, release and recapture sites, and temperature distribution in autumn are presented in Figure 1. Figure 2 presents four selected tags that show the main characteristics of each pattern described below. Daily maximum and minimum of depth and temperature indicate their trend and range. Seasonal features of temperature gradient distribution in relation to fish moves are revealed by the plot of  $r(t)$  and its moving median. These patterns indicate the type of depth and spatial temperature distribution in the unknown area where the cod stay during a certain season.

Table 2 presents the tags that have some main character resembling one of the patterns, but the events might not correspond exactly in time to those of Figure 2. Some tags have the characteristics of one

Table 2. Classification of depth and temperature trends together with the  $r(t)$  and moving median of  $r(t)$  as shown in Figure 2. Possible interpretations: (a) migration in thermocline near fronts in summer and autumn, and near fronts in April; (b) migration below and in thermocline near and in Polar Front in summer and autumn; (c) migration in and near the Polar Front, in a deep sea area, in summer and autumn; (d) the cod stays mainly in the same area.

Pattern	Tag number <sup>a</sup>
a	44**, 106**, 191**, 206**
b	38**, 97**, 98, 106**, 110**, 131**, 138, 204*, 228, 238, 246**
c	117**
d	39**

<sup>a</sup>Both diurnal and semi-diurnal cycle are found in tags marked \*\*. The diurnal cycle are found in the tag number marked with \*. The other three tags, 33, 21, 235 are too short to identify the pattern.

pattern for a certain duration and change to another pattern for another duration. Most tags have pattern similar to (a) or (b).

The time-series have distinct characteristics at three separate durations, i.e. April–June, July–November, and December–March. Only eight tags have records longer than ten months, lasting into the December–March period (Figure 2, Table 1 and Materials and Methods, data collection).

### The April–June 1996 and December 1996–March 1997 periods

During April–June and December–March temperatures fluctuate with relatively small variability around a stable level such as 2–4°C, 3–5°C, or 4–6°C, depending on the tag and release site. The depth level is mainly 150–350 m, and the trend and range of vertical migration vary depending on the tag, with the exception of tag 39 [Figure 2(d)]. In most tags there are periods of clearly reduced vertical migration during these seasons.

During April–June the size of  $r(t)$  and its moving median are mainly near zero in most tags, except some tags in April. During April the pattern of  $r(t)$  indicates that some cod, i.e. tags 39, 44, 117 [Figure 2(d), (a) and (c) respectively], 33, 38, 98, 131, 138, 191, 206, 228 migrate near a front, but with different size of  $r(t)$  and its moving median. Often these tags show a relatively large or intermediate positive moving median  $r(t)$  with the exception of tag 131, which has negative values. The changes of depth in tags 117, 131, 191, 206 are small, mainly less than 10 m (Table 3). The semi-diurnal cycle is detected in these temperature time-series [Table 1 and Figure 3(a)].

During December–March the moving median of  $r(t)$  in most tags has mixed positive and negative values of

Table 3. Distributions of depth and temperature, change of depth and temperature (in two-hour intervals) while there are semidiurnal cycles in the temperature time-series.

Tag (month)		Max	Min	Mean	5%	10%	25%	Median	75%	90%	95%
38 (4)	Depth	273	57	109	81	86	94	104	119	138	155
	Ddepth	155	-155	0	-38	-27	-6	0	6	25	39
	Temp	6.6	4.2	5.9	4.8	5.4	5.7	6	6.3	6.4	6.4
	Dtemp	1.6	-1.7	0	-0.6	-0.3	-0.1	0	0.1	0.3	0.6
44 (4)	Depth	152	56	102	83	87	93	101	109	121	129
	Ddepth	67	-48	0	-24	-20	-8	-1	8	20	32
	Temp	6.3	3.5	5.3	4.3	4.6	4.9	5.4	5.8	5.9	6.0
	Dtemp	1.6	-1.5	0	-0.8	-0.5	-0.2	0	0.2	0.6	0.8
97 (4)	Depth	258	94	176	141	148	155	174	190	210	221
	Ddepth	65	-47	0.3	-21	-14	-4	0	4	13	22
	Temp	4.9	3.5	4.2	3.6	3.7	3.9	4.2	4.4	4.6	4.7
	Dtemp	0.6	-0.5	0	-0.2	-0.2	-0.1	0	0.1	0.1	0.2
117 (4)	Depth	212	123	157	141	145	147	153	166	182	184
	Ddepth	32	-32	0	-10	-4	-2	0	2	4	8
	Temp	5	1.9	3.4	2.1	2.2	2.7	3.4	4.1	4.4	4.6
	Dtemp	1.3	-1.3	0	-0.6	-0.4	-0.2	0	0.1	0.6	0.8
131 (4)	Depth	135	88	94	90	90	92	92	94	99	103
	Ddepth	28	-43	0	-7	-2	-2	0	2	4	6
	Temp	5.1	2.8	3.7	3.3	3.3	3.5	3.7	3.9	4.2	4.5
	Dtemp	0.9	-1	0	-0.4	-0.3	-0.1	0	0.1	0.3	0.4
191 (4)	Depth	275	197	225	205	209	219	222	228	242	268
	Ddepth	26	-30	0.5	-7	-5	-2	0	2	7	14
	Temp	4.5	1.3	2.8	1.5	1.6	2.3	2.7	3.5	4	4.1
	Dtemp	2	-1.8	0	-1	-0.9	-0.4	0	0.3	1	1.2
206 (4)	Depth	158	120	134	127	129	132	134	135	135	144
	Ddepth	23	-23	0	-7	-5	-2	0	2	5	7
	Temp	4.7	3.1	4	3.4	3.4	3.6	4	4.3	4.5	4.6
	Dtemp	1.3	-0.9	0	-0.5	-0.3	-0.2	0	0.1	0.4	0.6
39 (7, 8, 9)	Depth	133	61	89	78	82	85	89	93	99	104
	Ddepth	61	-38	0.02	-15	-11	-4	0	6	10	15
	Temp	9.5	5.2	6.6	5.6	5.8	6	6.4	7	7.7	7.9
	Dtemp	0.9	-0.9	0	-0.3	-0.2	-0.1	0	0.1	0.2	0.3
39 (11, 12)	Depth	144	64	93	82	85	89	93	97	100	108
	Ddepth	51	-55	0.02	-15	-11	-4	0	4	11	15
	Temp	8.1	5.4	6.9	5.7	5.9	6.4	6.8	7.3	7.8	7.9
	Dtemp	0.5	-0.5	0	-0.1	-0.1	-0.02	0	0	0.1	0.1
110 (5)	Depth	430	220	315	277	289	302	314	327	337	360
	Ddepth	109	-126	0	-44	-25	-8	0	8	29	42
	Temp	4.1	3.1	3.6	3.2	3.2	3.3	3.6	3.8	4	4.1
	Dtemp	0.4	-0.4	0	-0.2	-0.1	0.1	0	0	0.1	0.2

relatively small or intermediate sizes. The  $r(t)$  distribution is a mixture of relatively small and intermediate absolute values, but some tags have a few large absolute values, i.e. tags 117 and 131. The variance of  $r(t)$  gradually decreases toward February and March. The depth and temperature trends approach the same level as during April–June, i.e. mainly 150–350 m for depth and 3–5°C for temperature. Tag 39 with depth level from 100–150 m (Figure 2) is an exception. DVM is detected in tags 39, 44, 131, 191, 204, 206, 246 (Table 1). During 1–18 January 1997, before a transition to DVM with large depth range and temperature range from 0–1°C) in tag 131, the vertical migration is very small at depths around 250 m with temperature range from 0–3°C [Figure 3(d)]. The  $r(t)$  series has a relatively large range and

variance, and its moving median has a mixture of positive and negative values, indicating migration near the Polar Front.

#### July–November period

During July–November the daily range of vertical migration, the variance of  $r(t)$  and its moving median are relatively large in comparison with other seasons for most fish. The depth and temperature levels and daily ranges are different for different fish (Figure 2). In all tags the temperature is above zero most of the time. Some tags have occasional records ranging from -1.5°C to 4°C, e.g. tags 44, 106, 131, 228, 238, and 246. Only a few tags have long duration of subzero

temperatures: tag 98 (August), 117 (November and December), and 204 (November). A clear and long duration of DVM is detected in 11 tags (Table 1). The main character of a tag series is similar to one of four patterns (Figure 2):

(a) Increasing/increased temperature trend and decreasing/decreased depth trend, the depth range includes the thermocline. The moving median of  $r(t)$  has relatively large negative values ( $> -0.1^\circ\text{C m}^{-1}$ ), at the same time as  $r(t)$  has a relatively large variance and range. Within two hours in September, tag 191 has large temperature changes, e.g. from  $9.1^\circ\text{C}$  to  $3.6^\circ\text{C}$  with depth change from 21–100 m, and from  $9.1^\circ\text{C}$  to  $5.6^\circ\text{C}$  with depth change from 14–37 m. The pattern indicates that the cod may migrate toward warmer water around the thermocline near fronts (e.g. coastal fronts), in relatively shallow waters. Pattern (a) is found in tags 44, 106, 191, 206.

(b) Decreasing/decreased trends in both temperature and depth, the depth ranges from 50–250 m, mainly below the thermocline, the temperature ranges mainly from  $0\text{--}3^\circ\text{C}$  with occasionally subzero temperature. The moving median of  $r(t)$  has intermediate negative values ( $> -0.05^\circ\text{C m}^{-1}$ ), and  $r(t)$  is mainly a mixture of intermediate and small values with a few large values. The pattern indicates that cod migrates toward colder water below and around the thermocline near and at the Polar Front, but mainly stays on the warm side and occasionally migrates across the front to the cold side. Pattern (b) is found in tags 38, 97, 98, 106, 110, 117, 131, 204, 206, 228, 238, and 246.

(c) As in (b) but with depth level 200–450 m and long duration of subzero temperatures. The moving median of  $r(t)$  has small negative values ( $> -0.02^\circ\text{C m}^{-1}$ ),  $r(t)$  is mainly a mixture of small values with a few large values. The pattern indicates that the cod migrates in a deep sea area, near and at the cold side of the Polar Front. Pattern (c) is found in tags 117 (November–December), 204 (November), and 98 (August).

(d) In the series of tag 39 depth fluctuates about the same level with temperature trend changing according to season, the distribution of  $r(t)$  remains unchanged with intermediate range. The moving median of  $r(t)$  is positive ( $< 0.03^\circ\text{C m}^{-1}$ ) in April and negative ( $> -0.03^\circ\text{C m}^{-1}$ ) during June–October and has a mixture of small positive and negative values in winter. The patterns indicate that the cod mainly stays in the same area.

### Coherency and phase between depth and temperature time-series

In general during summer and autumn the estimated coherency is relatively high (especially for cod that migrate in the 0–150 m depth channel) and out of phase by half a cycle (temperature increases as

depth decreases). This is due to the thermocline or coastal front creating a high vertical upwards-oriented temperature gradient. The negative moving median of  $r(t)$  also gives the same indication. When the spectral analysis detects DVM in both series (Table 1) the coherency is generally high, e.g. the coherency at the frequency of 24 h per cycle is 0.76 for tags 204, 106; 0.8 for tags 191, 246; 0.5 for tags 44, 110; 0.4 for tags 39, 131. All standard deviations are less than 0.1.

During April the coherency is mainly not significantly different from zero, but when it is, the phase is estimated to be 0, i.e. temperature increases with depth. Similarly, positive moving median  $r(t)$  indicates the fish ascends into cold water.

### Vertical movement

Cod mainly migrate at depth 100–300 m with variable temperature range, depending on release site and season, but mainly within  $1\text{--}6^\circ\text{C}$  [Figure 4(a) and (b)]. Both the  $d(t)$  and  $c(t)$  time-series appear to have non-linear trend, but the first-order difference series  $dd(t)$  and  $dc(t)$  appear to be without trend. Thus the apparent trend may be a stochastic trend (drift) in a process described by a model with a component of random walk (Diggle, 1990), confined within certain boundaries.

The time-series of  $dd(t)$  has zero mean and seasonally dependent variance [Figure 5(a)]. This indicates a seasonal change in vertical migration behaviour. A large vertical move is often followed by an opposite large move within one or two intervals. In more than 50% of the days, the delay between the daily maximal ascent and descent is four hours (two periods) or less (Table 4). The remaining changes of depth level were small after this major adjustment. The time-series of  $dc(t)$  also has zero mean with seasonally dependent variance [Figure 5(b)]. Its characteristics depend on the temperature distribution in the area where the cod migrates. The cod neutralizes large short-term changes within 24 h, compare e.g. the two-h and 24-h changes of depth and temperature [Figure 4(c)–(f)] and the daily ranges (Figure 2). This is in agreement with spectral analysis which shows that most of the variation comes from high frequency components less than or equal to 24 h (Figure 6).

The  $act(a)$  measures the cod's vertical activity in a way that, in contrast to the differences  $dd(t)$ , compensates for change of pressure level. Mostly  $act(a)$  is below 100%, so the DDR is contained in an FVR of some possible neutral buoyancy depth [Figure 7(b), (c) and (d)]. Ratios close to 100% or, occasionally, above 100% are observed in all tags just after release, at the transition to a new depth level [Figure 7(c)], in most tags during mid-June–November [Table 1, Figure 7(b) and (c)], and February–March (for tags with record into 1997). In tag 117 large  $act(a)$  occurs during mid-May to mid-June, but it mainly

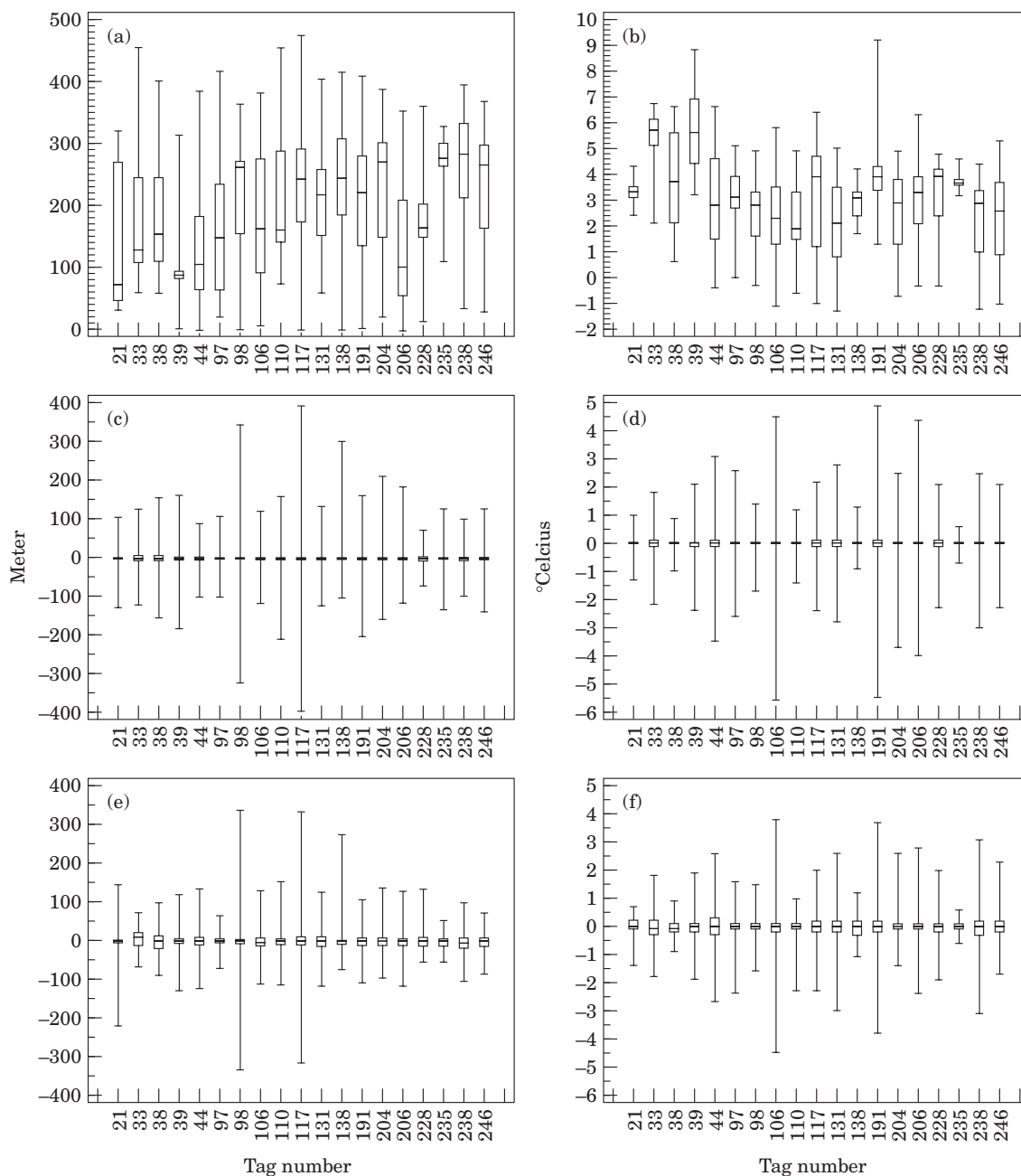


Figure 4. The distribution, for each tag, of depth (a) and temperature (b); changes of depth (c) and temperature (d) in two hours; and change of depth (e) and temperature (f) in a day. Boxes mark 25- and 75-percentiles; lines mark the range. Length of the time-series is different from tag to tag.

has low vertical activity afterwards [Figure 7(d)]. The depth record just before recapture indicates a malfunction in tag 117, perhaps caused by a dive deeper than 480 m, beyond the tag’s pressure limit (Godø and Michalsen, 2000). Long periods with act(a) above 100% on most days are observed in tag 39 during April–May,

and in tags 44, 191 [Figure 7(b)], and 206 during August–October.

### Diurnal vertical migration (DVM)

Throughout the entire time-series of depth and temperature there is a mixture of irregular and regular cyclical

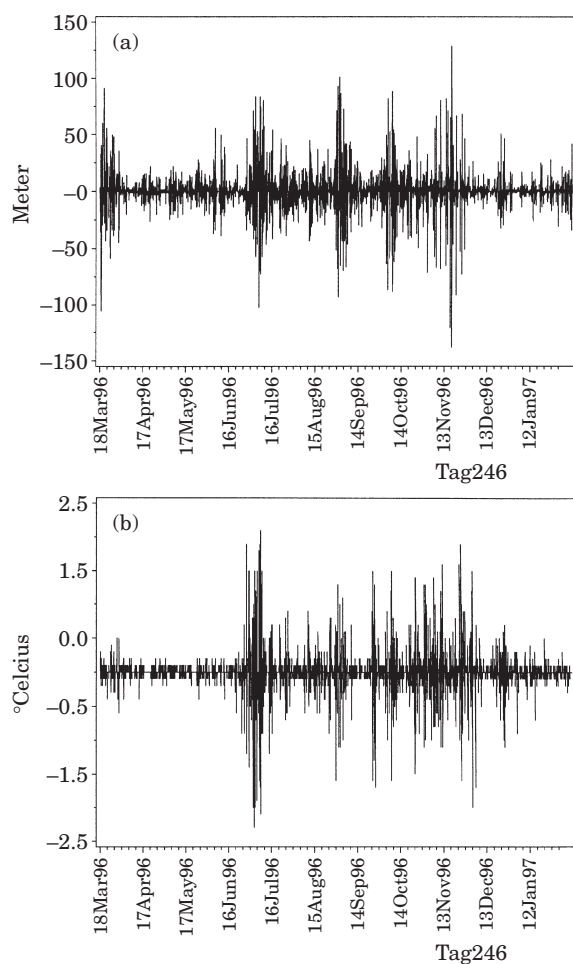


Figure 5. (a) Change of depth ( $dd(t)$ ); (b) change of temperature ( $dc(t)$ ) at each two-h period.

patterns with amplitude and frequency depending on the season. The regular patterns may occur only for a few days at a time, e.g. tag 235, 238, 098, or they may persist for weeks or months (Table 1). Spectral density distribution shows how the total variation in each time-series is distributed over the frequencies, with a significant peak (5% level) indicating a cycle at that frequency (Figure 6). In some tags there is a peak at the 24 h period with subsidiary peaks at the harmonics of the main peak, i.e. at 12, eight, and six h period. This is due to the non-sinusoidal shape of the individual cycles in the data and makes it difficult to distinguish the 12–12.5 h cycle from the 12-h harmonic frequency of the daily cycle.

In this study there are two commonly found, regular cyclical patterns, diurnal cycles (24–25 h per cycle) and semi-diurnal cycle (12–12.5 h per cycle). Table 1 reports for each tag the duration (over one week) when diurnal and semi-diurnal cycles are detected. The diurnal cycles

are mainly found in the depth series of 12 tags, in ten of them the cycles are found in both the depth and temperature series. In 11 out of 12 cod the DVM activity happened during the July–November feeding season with  $r(t)$  patterns indicating that the fish migrate near fronts (Figure 2) and  $act(a)$  mainly indicating relatively high vertical activity (Figure 7). Among those 11 cod, eight migrated in the depth channel 0–250 m (occasionally penetrating through the thermocline), namely tags 39, 44, 97, 106, 110, 191, 206 and 246. Tags 131 and 204 migrated in the depth channel 100–250 m while tag 117 migrated in the depth channel 170–350 m. In tags 131 [see also Figure 3(d)], 191, 204, 206, and 246 the DVM (24-h cycle) is detected mainly deeper than 150 m for a certain period during January–March. Tag 39 has DVM (25 h-cycle) in May, December–January (Table 1).

When a cycle is detected in both series at the same time it is usually accompanied by high coherency values. Moreover when this occurs during July–November the cod usually migrates in the 0–150 m depth channel (possibly with thermocline or a coastal front) with a large negative moving median  $r(t)$ .

### Semi-diurnal cycle

Semi-diurnal cycles are detected (Figure 6) occasionally, and they may be found only in the temperature series, only in the depth series, or in both (Table 1). There are seven tags with a semi-diurnal cycle in the temperature while the cod has DVM (Table 1). Time-series plots of semi-diurnal patterns from selected tags are presented in Figure 3. A semi-diurnal cycle in the temperature series is often accompanied by clearly reduced vertical migration, e.g. during April in tags 117 [Figure 3(a)], 131, 191, and 206 (Tables 1 and 3). This occurred together with increased variance or range and large positive moving median of  $r(t)$  in tags 117 [Figure 2(c)], 191, and 206, but large negative values in tag 131. Tags 131 and 206 are at approximately constant depth level, which last for 24 d. Tag 117 has small upward depth trend with a sudden decrease of depth level (Figure 3). Tag 191 has small downward depth trend.

### Patterns of DVM

There are at least four patterns of DVM according to the time the cod stay in the upper, middle, and lower part of the daily depth range (Figure 8). During the period with DVM a fish may maintain one pattern for some days and then switch to another pattern. All patterns involve one relatively large ascent (descent), which usually consists of one or two large two-h moves. The delay-time between the largest ascent and descent depends on the pattern of DVM (Figure 9). The largest ascent (descent) takes place at approximately the same hour each day, which depends on the tag (Table 5). Cod 204 spends

Table 4. Distribution of the time difference between the daily maximum upward migration hour and the daily maximum downward migration hour. Difference is positive (negative) if ascent comes before (after) descent. Recapture time in parentheses.<sup>a</sup>

Tag (month/year)	Difference in recorded hours							
	< -6	-6	-4	-2	2	4	6	>6
021 (5/96)	10	5	10	35	35	0	0	5
033 (5/96)	11.9	4.1	4.0	7.9	36.5	9.9	5.9	19.8
038 (8/96)	16.1	9.6	8.8	16.6	22.5	4.8	6.5	15.0
039 (9/96)	15.7	3.8	7.0	16.6	32.5	9.0	4.4	10.8
044 (2/97)	24.6	10.3	11.2	18.3	13.0	7.8	3.1	11.6
097 (9/96)	20.0	4.9	8.5	26.7	7.6	4.8	2.9	24.7
098 (10/96)	9.9	14.6	3.8	32.8	0.0	16.3	3.8	18.9
106 (11/96)	14.1	6.1	12.7	28.8	12.2	3.0	3.5	19.6
110 (11/96)	20.5	3.0	14.2	23.4	10.3	5.4	5.4	18.0
117 (3/97)	12.7	6.4	10.5	22.2	16.0	6.3	7.6	18.3
131 (4/97)	14.9	7.4	15.8	26.9	12.9	4.8	2.3	15.1
138 (6/96)	17.5	2.2	19.7	25.1	6.6	6.6	4.4	17.5
191 (3/97)	14.7	5.1	7.2	18.2	18.2	6.1	4.1	26.3
204 (3/97)	22.6	6.0	6.9	29.0	7.6	5.0	5.0	17.7
206 (3/97)	18.4	6.0	9.5	25.3	11.6	4.1	3.6	21.5
228 (7/96)	23.1	2.0	6.0	16.5	25.3	5.0	7.0	15.0
235 (6/96)	16.1	6.7	6.7	31.9	3.4	6.7	3.4	20.1
238 (7/96)	15.1	5.3	10.0	31.4	10.8	5.4	4.4	17.8
246 (2/97)	16.7	8.7	12.7	31.4	9.2	3.0	2.6	15.6

<sup>a</sup>All tags released in middle of March 1996.

about equal time in the upper and lower layers of the daily vertical migration range (pattern 1, Figure 8); cod 191 is mainly in the middle layer with short visits to the top or bottom (pattern 2); cods 44 and 206, respectively in December and March, are mainly in the lower level with short visits to the top (pattern 3); cod 39 is mainly in the top level with short visits to the bottom (pattern 4).

All cod with detected DVM in January–March ascend and stay on the relative upper depth level during daytime (Tables 1 and 5; Figures 8 and 9 of tag 206). During summer–autumn the ascent hours can vary from very early in the morning, afternoon or evening (Table 5 and Figure 9).

The distribution of these upward/downward hours over different fish can be useful in understanding how the large-scale DVM is composed of individual DVM as well as the correspondence in ascent/descent time to the prey species DVM patterns. The ratio of time spent in mid-water to time spent near the sea bottom may relate to cod migration by selective tidal stream transport (Arnold and Cook, 1984).

## Discussion

In the Barents Sea there are areas with highly stratified water mass characteristics due to temperature, salinity or density differentiation, e.g. the thermocline, coastal fronts (5–9°C), and the Polar Front, where

Arctic and Atlantic waters meet, with temperatures from –1.5°C to 3°C, and outlined by Bear Island, banks and basins (Figure 1). These stratified areas develop and move according to seasons and other conditions. Such areas have significant influence on the species distribution in the marine ecosystem. At the thermocline layer the temperature gradient has a very large upward pointing vertical component. In frontal areas the horizontal component is much larger than elsewhere (Figure 1). Temperature distribution may be complicated by turbulence with distorted volumes of one water mass into another, and the direction of the gradient varies. The size of the gradient and its direction can be extracted from the tag data by means of the r(t)-series.

Tides are composed of different astronomical constituents. The relative strengths depend on local conditions of topography, physical oceanography, and meteorology (Neumann and Pierson, 1966). Tides along the European continental shelf are dominated by the semi-diurnal component (Garrison, 1999). Tidal forces generate local movement in the water masses that influence fish behaviour (Arnold *et al.*, 1994; Løkkeborg, 1994).

Northeast Arctic cod is mainly found in the southern Barents Sea, sometimes as far east as Novaya Zemlya, around Bear Island and Hopen Island, and along the western coast of Spitsbergen. Immature cod feed both at the bottom and in mid-water and make seasonal east-west and north-south migrations within the Barents Sea and along the western coast of Spitsbergen (Nakken, 1994). The most important spawning grounds are

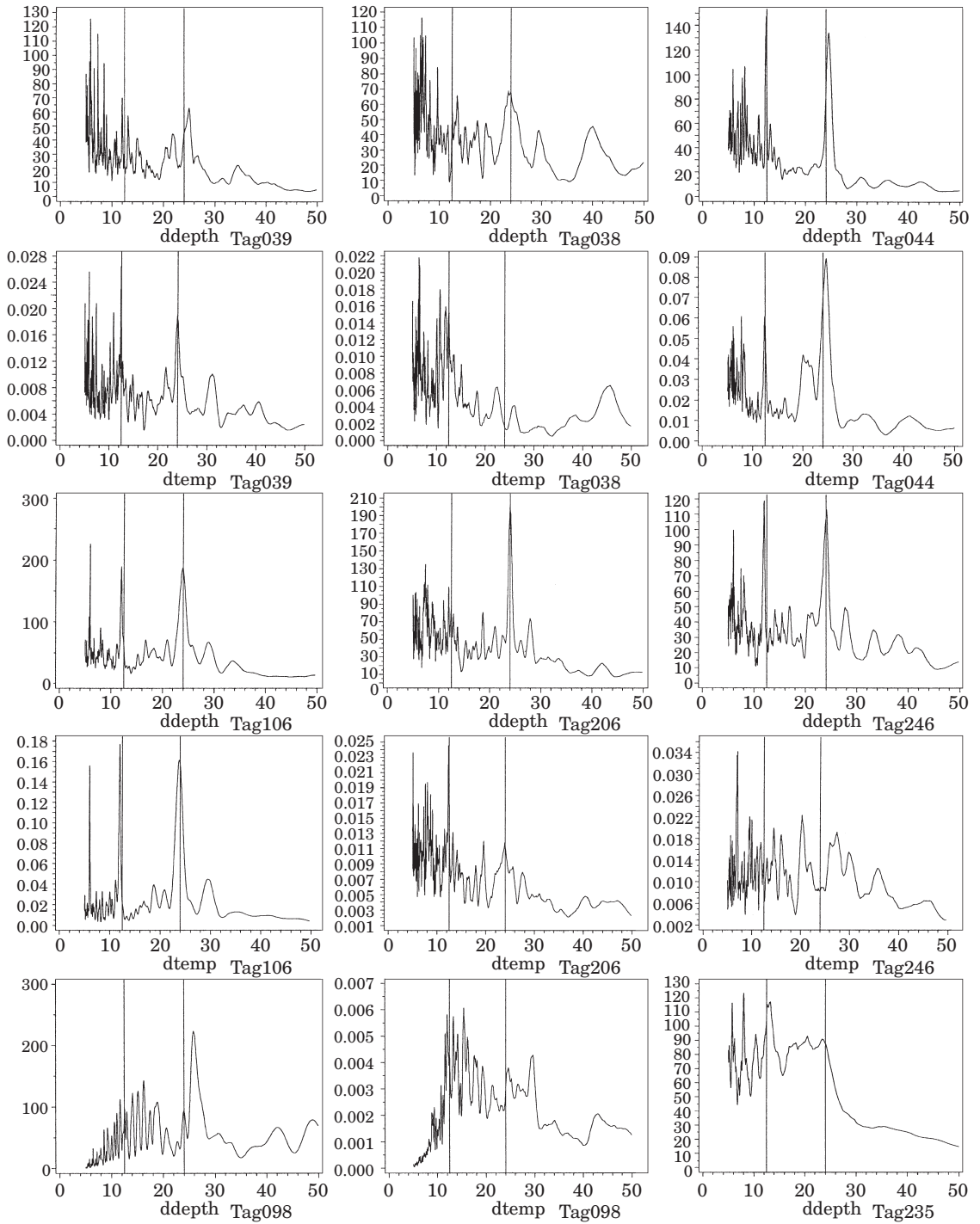


Figure 6. Estimated spectral density distribution for the entire time-series of depth and temperature changes (two-hour periods). Reference lines at 24-h and 12.5-h periods.

around Lofoten and Vesterålen with the main spawning in March and April (Pedersen, 1984). The cod migrates with the Atlantic current from spawning to feeding

grounds (Trout, 1957; Cushing, 1981) that stretch from the west coast of Norway into the Barents Sea (Gjøsaeter et al., 1992).

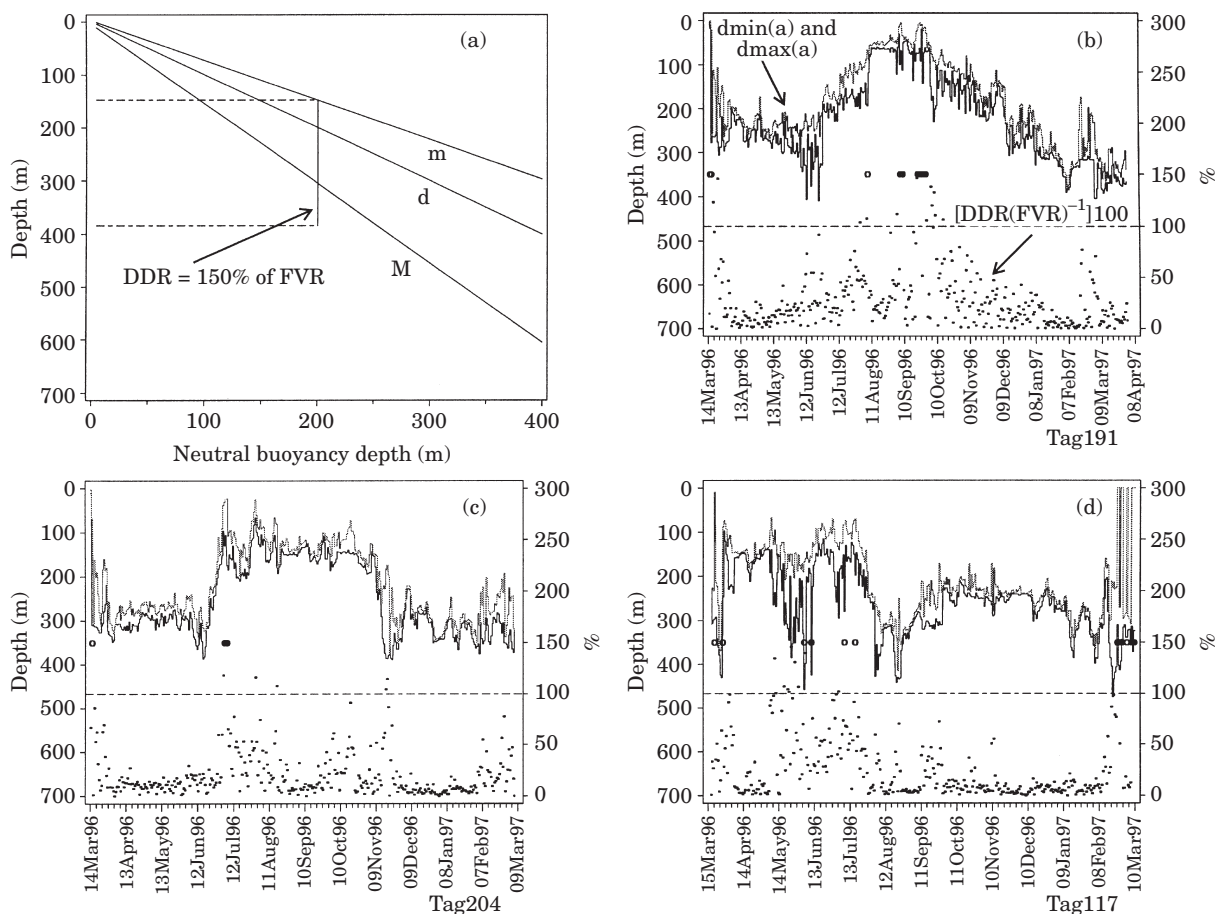


Figure 7. (a) Free vertical range (FVR) for a cod neutrally buoyant at depth  $d$  metres, lines  $m$ ,  $M$ , and  $d$  for minimum and maximum depth of FVR, and neutral buoyancy depth, with a daily depth range (DDR) giving  $\text{act}(a)=150\%$  and  $d=200$  m; (b)–(d) daily maximum and minimum depth ( $d_{\text{max}}(a)$  and  $d_{\text{min}}(a)$ ),  $\text{act}(a)$  in percent marked with dot (●), but with circle (○) at 150% when  $\text{act}(a)$  is larger than 150%. Reference line at 100%.

Several studies conclude that light, temperature and prey density distribution influence the foraging migration pattern of cod (Lee, 1956; Trout, 1957; Woodhead and Woodhead, 1959; Beverton and Lee, 1965; Konstantinov, 1965; Midttun, 1965; Brunel, 1972; Rose and Leggett, 1989, 1990). Because of the release time and the record length the DST mainly records the feeding migration and may reflect interplay between the cod's physiological limitations, its own and its prey's migration behaviour and environmental conditions.

The cod's consumption of important prey species in the release year 1996, ranked by weight, are krill, cod, capelin, amphipods, shrimp, redfish, haddock, polar cod, herring, and others (Bogstad and Mehl, 1997). Krill became an important prey because of the low capelin stock. Capelin is the cod's preferred prey species, and capelin migration (Gjøsaeter, 1998) is an important factor in the cod's migration pattern (Konstantinov, 1965; Gjøsaeter *et al.*, 1992; Gjøsaeter,

1998). Aglen (1999) reports that during summer and autumn 1996 and 1997 cod larger than 19 cm was distributed south of the Polar Front with higher density distribution along the Polar Front. During January–March there are high concentrations of immature adult cod preying on mature capelin that migrate to spawn along the northern Norwegian and Russian coast, including the Skolpen Bank (Mehl, 1997; Gjøsaeter, 1998).

Neilson and Perry (1990) discuss several reasons for DVM in marine fishes. Sunlight and DVM of the cod's potential prey species may induce DVM of cod. In spring, summer and autumn a high density of plankton and small fish can be found around the thermocline layer and the Polar Front, which side of the Polar Front depending on the species. Zooplankton and capelin exhibit DVM that is more pronounced during the spring and autumn when the day and night are clearly distinguishable, but during winter krill and capelin stay in



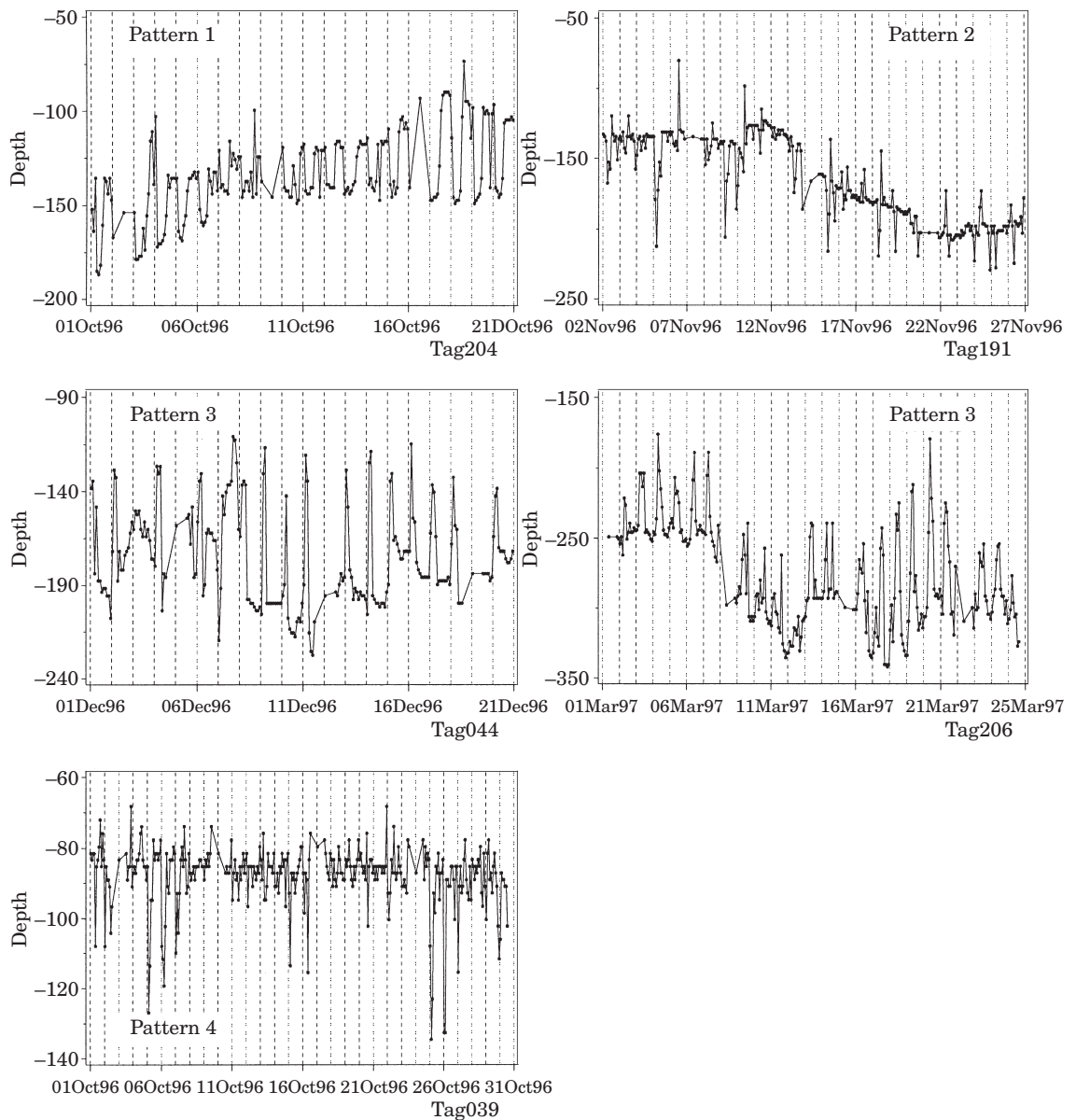


Figure 8. Different patterns of diurnal vertical migration from five selected tags. Broken lines at 0000 h GMT. Dot (●) marks the recorded depth at two-hour intervals.

deep layers below 100 m (Tande *et al.*, 1992; Gjosæter, 1998). In August–September 0-group cod are distributed deeper during the day than at night but very few are below the thermocline (Stensholt and Nakken, *in press*).

#### Individual behaviour and large-scale observations

The DST depth-temperature time-series are the results of individual cod behaviour interacting with the Barents Sea environment. They contain details of seasonal

Figure 9. Distribution of hours GMT during DVM with pattern as shown in Figure 8. Left: when the cod stays in the top, middle 10 m, or bottom part of the daily depth range. Filled, bottom; hatched, middle; open, top. Right: when the cod makes the daily maximum two-hour ascent (white) and two-hour descent (black).

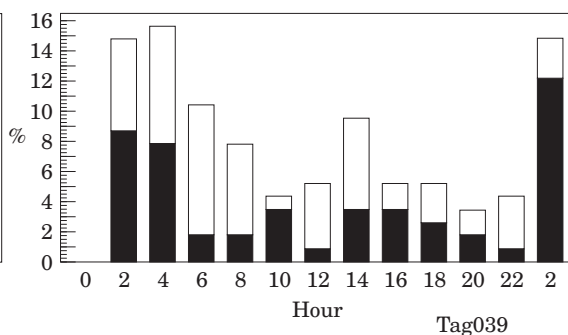
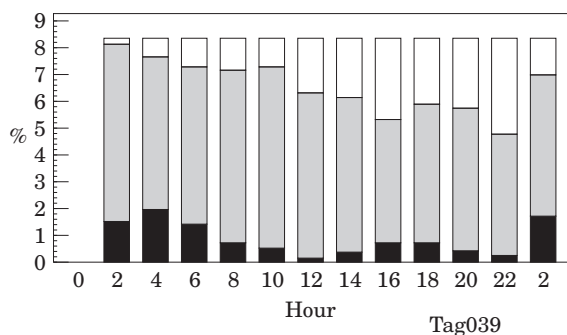
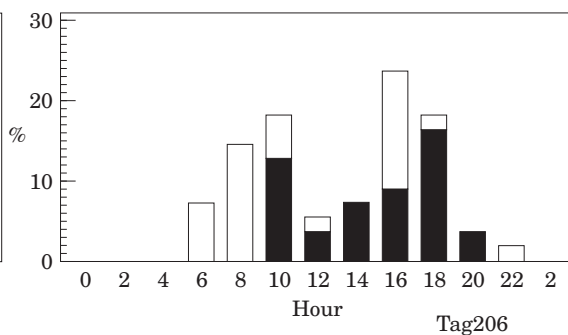
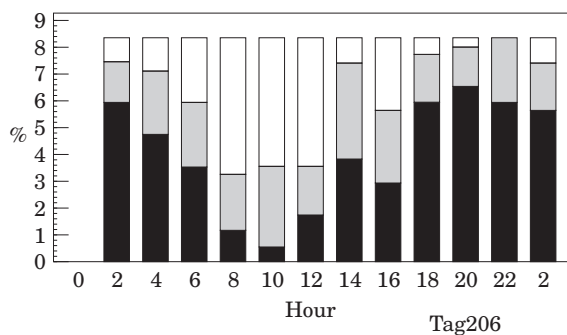
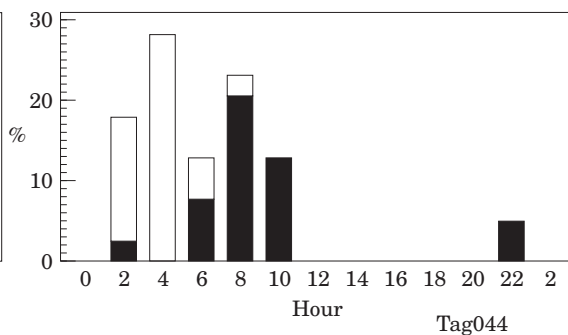
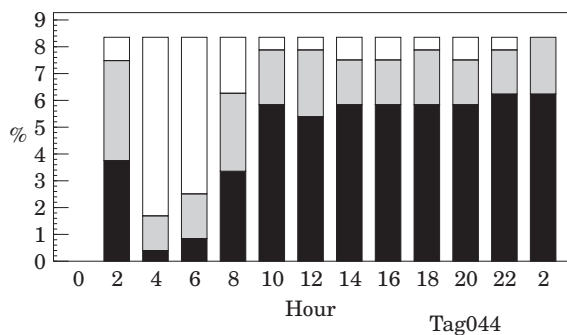
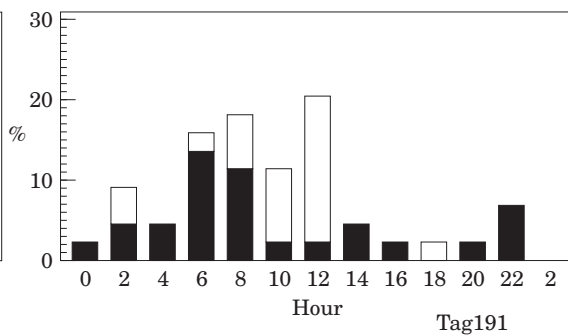
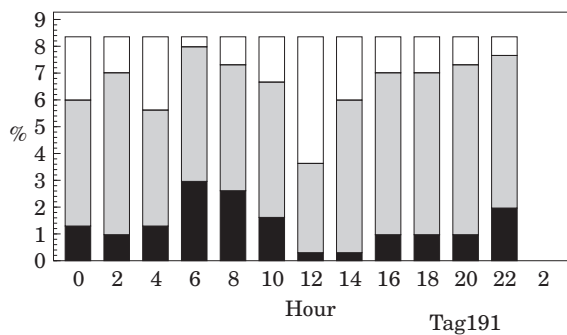
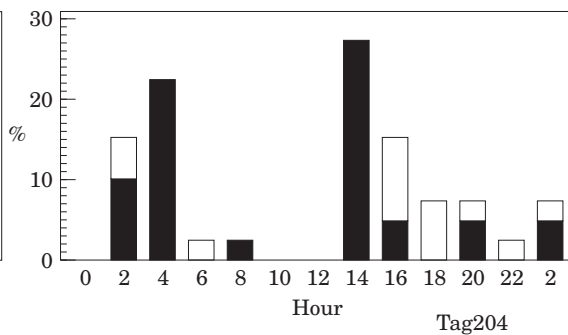
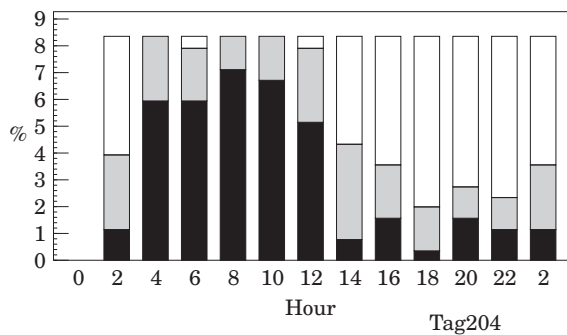


Table 5. Distribution of time interval<sup>a</sup> (in GMT) for daily maximal<sup>b</sup> two-hour descent (plain) and ascent (bold) during DVM activity, in the months indicated.

Hour (GMT)→		00–2	2–4	4–6	6–8	8–10	10–12	12–14	14–16	16–18	18–20	20–22	22–00
Tag 39	Down	8.7	6.2	2.5	1.2	2.5	1.9	3.7	3.1	2.5	3.7	2.5	9.9
Month 8–10	Up	<b>5.6</b>	<b>6.8</b>	<b>6.2</b>	<b>5.0</b>	<b>0.6</b>	<b>3.7</b>	<b>6.2</b>	<b>1.9</b>	<b>5.6</b>	<b>1.9</b>	<b>5.0</b>	<b>3.1</b>
Tag 44	Down	2.9	1.6	0	1.6	0.6	3.8	8.2	3.8	3.3	8.7	12.0	4.9
Month 8–10	Up	<b>4.4</b>	<b>1.1</b>	<b>1.1</b>	<b>0</b>	<b>9.8</b>	<b>11.5</b>	<b>8.7</b>	<b>5.5</b>	<b>2.7</b>	<b>2.2</b>	<b>1.1</b>	<b>1.1</b>
Tag 106	Down	10.5	1.5	0	3.0	3.7	0.8	2.2	5.2	2.2	2.2	9.0	9.0
Month 8–10	Up	<b>0.8</b>	<b>2.2</b>	<b>3.7</b>	<b>0</b>	<b>9.0</b>	<b>3.7</b>	<b>2.2</b>	<b>7.5</b>	<b>9.0</b>	<b>10.4</b>	<b>1.5</b>	<b>0.8</b>
Tag 206	Down	16.3	7.6	0	0	0	0	0	0	1.1	1.1	7.6	13.0
Month 8–10	Up	<b>1.1</b>	<b>1.1</b>	<b>0</b>	<b>1.1</b>	<b>7.6</b>	<b>2.2</b>	<b>2.2</b>	<b>26.1</b>	<b>7.6</b>	<b>3.3</b>	<b>1.1</b>	<b>0</b>
Tag 246	Down	2.0	2.0	4.1	0	0	4.1	0	0	2.0	4.1	14.3	18.4
Month 8–9	Up	<b>2.0</b>	<b>0</b>	<b>0</b>	<b>2.0</b>	<b>2.0</b>	<b>2.0</b>	<b>0</b>	<b>6.1</b>	<b>16.3</b>	<b>16.3</b>	<b>0</b>	<b>2.0</b>
Tag 110	Down	0	5.8	1.2	7.0	5.8	7.0	11.6	3.5	2.3	4.7	0	1.2
Month 9–10	Up	<b>2.3</b>	<b>3.5</b>	<b>5.8</b>	<b>3.5</b>	<b>8.1</b>	<b>11.6</b>	<b>4.7</b>	<b>8.1</b>	<b>1.2</b>	<b>0</b>	<b>0</b>	<b>1.2</b>
Tag 117	Down	2.9	7.8	2.9	1.0	3.9	5.9	6.9	4.9	6.9	3.9	1.0	2.0
Month 9–10	Up	<b>6.9</b>	<b>6.9</b>	<b>7.8</b>	<b>2.0</b>	<b>4.9</b>	<b>2.9</b>	<b>2.0</b>	<b>8.8</b>	<b>4.9</b>	<b>2.0</b>	<b>0</b>	<b>1.0</b>
Tag 191	Down	8.9	15.6	2.2	4.4	0	2.2	1.1	2.2	0	7.8	2.2	2.2
Month 9–10	Up	<b>3.3</b>	<b>0</b>	<b>5.6</b>	<b>7.8</b>	<b>2.2</b>	<b>1.1</b>	<b>14.4</b>	<b>10.0</b>	<b>1.1</b>	<b>3.3</b>	<b>2.2</b>	<b>0</b>
Tag 204	Down	10.0	22.5	0	2.5	0	0	0	5.0	0	5.0	0	5.0
Month 10	Up	<b>5.0</b>	<b>0</b>	<b>2.5</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>27.5</b>	<b>0</b>	<b>7.5</b>	<b>2.5</b>	<b>2.5</b>	<b>2.5</b>
Tag 131	Down	0	6.9	2.8	4.2	19.4	13.9	2.8	1.4	0	0	0	0
Month 10–11	Up	<b>0</b>	<b>12.5</b>	<b>12.5</b>	<b>15.3</b>	<b>4.2</b>	<b>1.4</b>	<b>0</b>	<b>2.8</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
Tag 44	Down	2.5	0	0	7.7	20.5	12.8	0	0	0	0	5.1	0
Month 12	Up	<b>15.4</b>	<b>20.2</b>	<b>5.1</b>	<b>2.6</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
Tag 39	Down	2.6	10.5	5.3	5.3	5.3	2.6	1.3	3.9	3.9	2.6	0	0
Month 12–1	Up	<b>3.9</b>	<b>5.3</b>	<b>6.6</b>	<b>9.2</b>	<b>2.6</b>	<b>5.3</b>	<b>3.9</b>	<b>1.3</b>	<b>5.3</b>	<b>5.3</b>	<b>1.3</b>	<b>2.6</b>
Tag 204	Down	0	0	0	0	5.3	2.6	7.9	7.9	23.7	2.6	0	0
Month 2–3	Up	<b>5.3</b>	<b>5.3</b>	<b>2.6</b>	<b>5.3</b>	<b>5.3</b>	<b>7.9</b>	<b>0</b>	<b>18.4</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
Tag 206	Down	0	0	0	0	12.7	3.6	7.3	9.1	16.4	3.6	0	0
Month 2–3	Up	<b>0</b>	<b>0</b>	<b>7.3</b>	<b>14.5</b>	<b>5.5</b>	<b>1.8</b>	<b>0</b>	<b>14.6</b>	<b>1.8</b>	<b>0</b>	<b>1.8</b>	<b>0</b>
Tag 131	Down	0.9	4.2	1.7	3.4	9.3	16.9	6.8	5.9	3.4	0	0	0
Month 1–3	Up	<b>2.5</b>	<b>5.1</b>	<b>16.1</b>	<b>9.3</b>	<b>7.6</b>	<b>1.7</b>	<b>0.9</b>	<b>1.7</b>	<b>0.9</b>	<b>0</b>	<b>1.7</b>	<b>0</b>
Tag 191	Down	0	1.9	7.4	7.4	1.9	9.2	9.2	11.1	0	3.7	0	0
Month 3	Up	<b>1.9</b>	<b>1.9</b>	<b>9.2</b>	<b>18.5</b>	<b>3.7</b>	<b>1.9</b>	<b>5.5</b>	<b>0</b>	<b>3.7</b>	<b>1.9</b>	<b>0</b>	<b>0</b>

<sup>a</sup>Percentages may not add up to 100 due to rounding.

<sup>b</sup>Maximal values less than 10 m are removed from the material.

short-term and long-term migration patterns in relation to the temperature distribution and indicate the presence of e.g. Polar or other fronts, the thermocline, and tidal cycles. On the other hand, scientific surveys provide large-scale observations. Combining information from tags and surveys allows the discussion of the possible influences on the individual fish behaviour and possible locations and also how the composition of the individual behaviour patterns contributes to the large-scale observations. Arnold and Holford (1995) reconstructed migration routes for demersal fish in the North Sea/English Channel by combining similar sources.

In general the patterns of  $dd(t)$ ,  $dc(t)$ ,  $r(t)$  and its moving median have seasonally-dependent variance (Figures 2 and 5). The change of these patterns over time indicates a change of temperature distribution that may be due to change of season, to change of area or to seasonal changes of the cod's migration behaviour. These are in agreement with the general knowledge of the cod's seasonal migration patterns (Lee, 1956; Trout, 1957; Woodhead and Woodhead, 1959; Konstantinov,

1965; Midttun, 1965; Brunel, 1972; Cushing, 1981; Rose and Leggett, 1989; Rose, 1993; Rose *et al.*, 1995). A cod migrating in the Barents Sea may show patterns (a), (b) or (c) (Trout, 1957). A cod staying in the coastal area may have pattern (d), as in tag 39 which may have been attached to a coastal cod (Godø, 1995).

Most cod have pattern (a), (b), or (c) of Figure 2. During May–June and December–February the pattern of depth and temperature trend, the small variance of  $dd(t)$ ,  $dc(t)$ , and  $r(t)$ , low act(a), and the coherency values near zero, all indicate that the cod undertake a long distance migration through different areas and move in a water mass with low temperature gradient, or have preferential migration along a stable thermal path (isotherm). During these two periods the temperature levels of tags with pattern of Figure 2(b) range from 3–5°C and depth levels vary from 200–400 m. The Atlantic waters have temperature around 3°C where they face Arctic waters. This migration roughly following the isotherm (e.g. along Atlantic current) brings the fish sufficiently close to the Polar Front, where it

changes behaviour and moves towards colder waters, possibly to forage at the Front during July–November. Such migration behaviour is also observed in large-scale studies (Lee, 1956; Trout, 1957; Woodhead and Woodhead, 1959; Konstantinov, 1965; Midttun, 1965; Rose and Leggett, 1989; Rose, 1993; Rose *et al.*, 1995). Konstantinov (1965) wrote “In a great number of cases water temperature is a guiding factor for fish. The choice of a particular temperature helps a fish to reach the area with the optimum biotic conditions in due time.”

During summer to autumn the cod migrate near fronts, e.g. the Polar Front or a coastal front, and are mainly closer to surface than during winter, e.g. around the thermocline depth or mainly below it. Different daily maximal depths may indicate different areas of varying bottom depth. The near- and subzero temperatures in July–August and October–November suggest that the cod stayed near or at the Polar Front, probably following krill and capelin (Lee, 1956; Gjørseter, 1998).

The analysis of depth and temperature from DST records indicates agreement with the depth and temperature distribution in the habitat of the prey species. The DVM in some cod during July–November near a front, and during February–April (Figures 1 and 2; Tables 1 and 2) also fit with the known DVM of prey species, as mentioned above. The seasonal depth and temperature distributions also agree with the large-scale observations (Lee, 1956; Trout, 1957; Konstantinov, 1958, 1965; Woodhead and Woodhead, 1959; Midttun, 1965; Mehl, 1997; Aglen, 1999).

Cod is a demersal fish, so the daily maximum depth,  $d_{\max}(a)$  often reflects the sea bottom depth. The  $d_{\max}(a)$  series before recapture fit well with the sea bottom depth in the recapture area (Figures 1 and 2; Table 1). At some seasons however, cod may have pelagic behaviour (Trout, 1957; Brunel, 1972). Using acoustic echo-sounders Rose *et al.* (1995) observed that cod mainly distributed in the bottom 25–50 m when less mobile but moved upwards in the water to 150–200 m off the bottom during migration. Moreover, the DST temperature record also captures the characteristics of the temperature distribution in the area.

Evidence of DVM based on repeated trawl hauls or combined trawl and acoustic sampling at the North Cape Bank during March–April have been reported (Engås and Soldal, 1992; Michalsen *et al.*, 1996; Aglen *et al.*, 1999). Large (small) cod ascend (descend) during daytime (Aglen *et al.*, 1999). Korsbrekke and Nakken (1999) report, based on the series of annual bottom-trawl surveys 1985–1996 for demersal fish in the Barents Sea during January–March, that catch rates increase during daylight for all sizes of most species. For cod the day/night ratio peaked at a length interval 23–31 cm with a substantial reduction for larger fish, but not significantly below 1. They explain that the difference from Aglen *et al.* (1999) may be caused by an avoidance

reaction to vessel noise (Ona, 1988). Hjellvik *et al.* (1999) investigate diurnal variation in bottom trawl catch during winter and autumn from 1985–1999. In winter, January–March, the catches of cod have diurnal variation with higher catches at daytime, while in the autumn the difference is much less distinct. In both seasons the effect tends to increase with depth.

DST studies may help to interpret the trawl results. During February–March 1997 the tags 131, 191, 204, and 206 show DVM at depth deeper than 150 m and with daily range from 50–100 m, and the cod swam higher during day than during night (Tables 1 and 5; Figures 8 and 9 of tag 206). Shortly afterwards these cod were recaptured in the area of the bottom trawl survey mentioned above (Figure 1; Table 2).

Clear DVM behaviour occurs during August–November with season- and tag-dependent hours of ascent and descent, and at varying depth level (implying different areas) near fronts (Tables 1 and 5; Figure 2). These variations may cause the aggregate DVM pattern in large-scale observations to be smoother or less distinct than the individual patterns (Hjellvik *et al.*, 1999). A large-scale pattern may of course come from a sufficient number of individuals having synchronized activity patterns, but it is more likely a combination of different individual DVM-patterns (Figures 8 and 9; Table 5) and irregular cycles. The Barents Sea stretches over two full time zones, and therefore the uncertainty in location must be taken into account in any attempt to determine the degree of synchronization from a comparison of several tags. With an increased number of analysed tag series available will come a better understanding of how the large-scale DVM should be decomposed.

#### Diurnal and semi-diurnal cycles and the feeding behaviour

Natural cyclical phenomena such as the sun light, the semi-diurnal and diurnal tidal cycle, which are the combined effect of different tidal constituents, e.g.  $M_2$ ,  $S_2$ ,  $K_1$  with 12.42, 12, and 23.93 h per cycle, respectively (Neumann and Pierson, 1966), may have direct and indirect effect on the cod's diurnal or semi-diurnal vertical migration behaviour, e.g. as the cod's response to prey with DVM behaviour (Neilson and Perry, 1990).

DVM is not the common behaviour in every set of tag data and its duration varies, which is evidence that it is driven by external factors. The pattern of DVM also varies depending on tag and depth level, but all patterns have a single large ascent and descent (Figure 8). Mainly it occurs during late summer and autumn (Table 1) near the frontal areas, in or below the thermocline layer (Figure 2), where prey species with DVM are abundant. An explanation may be that the cod moves temporarily out of the preferred temperature and depth level in search and pursuit of prey (Beamish, 1966; Zatsepin and

Petrova, 1939). The moves may depend on the cod's appetite and its adaptation to the availability and behaviour of different prey species in the area (Trout, 1957; Brunel, 1965; Turuk, 1973), but must be within the cod's physiological limitations, e.g. its ability to adapt to low temperature (Woodhead and Woodhead, 1959), or to pressure change (Tytler and Blaxter, 1973; Harden Jones and Scholes, 1985).

The diversity of prey species and the cod's preference for capelin may contribute to the variation of cod migration patterns over areas, seasons and years. The more varied migration patterns observed in summer and autumn than in winter may be due to the dominance of capelin in the cod's winter diet and the greater diversity of species in the summer diet. Different prey species will cause different feeding behaviour, and the combined effect may be that there is no clear large-scale pattern of DVM (Hjellvik *et al.*, 1999). However, how accurately the vertical migration hours for cod and its prey correspond has not been established. Moreover, the tags lack record of location and the composition of prey species in the tagged cod's diet is not known.

During April semi-diurnal cycles are observed in the temperature series of tags 117, 131, 206 while the fish stays mainly at the same depth level with large variance of  $r(t)$ . The cod may be feeding in a coastal area where a front moves with the tide and where zooplankton and small fishes accumulate (Shanks, 1983).

### Vertical migration and adaptation

During the long-distance migration season cod often have relatively small vertical migration fluctuating around stable or varying depth trends with a stable temperature level. In the July–November feeding season, and occasionally December–March, the cod change behaviour and often make a major ascent or descent consisting of a few large, vertical, two-hour moves followed by a similar opposite migration. The time delay between these two major movements varies with individual fish but is mainly not more than two record periods. This behaviour may or may not be connected to DVM, but in cases of DVM the time delay depends on the DVM pattern. As a consequence the cod is exposed to abrupt changes in temperature especially when it migrates through the thermocline layer or migrates in the vicinity of a front [Figure 2(a)]. However, it always neutralizes large, abrupt changes in depth and temperature so that the daily net changes are relatively small.

Neutralization of depth change may be linked to the buoyancy adaptation, physiological limitations of the swimbladder (Harden Jones and Scholes, 1985; Tytler and Blaxter, 1973; Arnold and Greer Walker 1992), energy saving and staying in a safe or preferred environment. The cod's adaptation to neutral buoyancy is very slow compared to many of its swift vertical moves and

mainly it is under-buoyant (Harden Jones and Scholes, 1985; Godø and Michalsen, 1997, 2000). Most of the DDR is the result of a few large moves, so the time for swimbladder adjustment is short, and it seems natural to use act(a), i.e. to compare DDR with the FVR for a fixed neutral buoyancy level. According to the act(a) definition the DDR generally is well inside the FVR, but during the feeding season most cod often extend their DDR to the full FVR and occasionally beyond the FVR. However, cod 117 stayed near the bottom with low vertical activity during August and October–January. There are much wider bounds than FVR, which define the zone of danger for swimbladder rupture (Tytler and Blaxter, 1973).

Feeding activity must be a major reason for accepting the energy loss, which increases with the size and duration of a deviation from the adaptation level. Cod mainly prefer to stay in areas with temperature above 2–3°C [Figure 4(b)], but some cod have occasional subzero records during summer and autumn. Thus it seems that the cod occasionally move out of the preferred zones of depth (FVR) or temperature, into near- and subzero waters, but only when it is necessary to follow prey. Woodhead and Woodhead (1959) found that cod had a physiological limiting temperature at 2°C from October–June that falls to below 0°C during summer when the cod feed on capelin and krill in cold water (Lee, 1956). In the present study the temperature records mainly support the above observations, but several DST occasionally have subzero temperature records during November–January. Time spent at each depth in the range of vertical migration is connected to the buoyancy state, which has implications for the acoustic target strength (Harden Jones and Scholes, 1981).

### Cod migration in relation to tides

Using acoustic tag records, Arnold *et al.* (1994) give a detailed discussion on the North Sea cod's migration by selective tidal stream transport where vertical migration (DVM and semi-DVM) interacts with oscillatory tidal flows to produce horizontal transport (Hill 1995, 1998). However, whilst the analysis of DST data shows when semi-DVM, DVM and change in depth levels occur it cannot be used to see whether there is a net horizontal tidal transport, and whether the ascent and descent times are synchronized with the tide. Both release sites are in areas with strong tidal currents, and there are other areas of strong tides along the migration route and feeding area (Gjævik *et al.*, 1990). Only seven tags, i.e. 38, 44, 97, 106, 110, 191, and 246, occasionally have semi-DVM [Table 1; Figure 3(b) and (c)], all during migration in April–August, which is generally towards east and north. In the west- and south-bound migration of cod in November–February, there is only evidence of DVM.

Tag 39, which has 25-h cycles during May and December–January, and several months with semi-diurnal cycles in the temperature series, was released at Lofoten, and appears to have stayed in the same area. The area of Lofoten and Vesterålen has strong tides, with semi-diurnal and diurnal ( $M_2$ , and  $K_1$ ) constituents (Gjevik *et al.*, 1990).

During April, tags 117, 131, 206 record semi-diurnal cycles in the temperature time-series together with small variability in depth, with  $r(t)$  indicating that the cod migrates near a front, and with the median  $r(t)$  showing that the fish ascend into colder water. As suggested by O. Nakken (pers. comm.) the cod may feed in the transition layer where cold low saline water flows over warm saline water, which is periodically moved by tidal forces. The cod may swim against the tidal current pursuing prey and stay in shelter when the current is strong (Løkkeborg, 1994) so that the DST records the tidal rhythmic change of temperature. Løkkeborg and Fernö (1999) observed area-restricted search in cod after encountering prey. It is likely that a better description of the water masses surrounding the fish at any given time will come with more advanced tags that also record salinity.

Strong tidal currents occur along the coast and east of release site N (Gjevik *et al.*, 1990). This is the main winter cod fishing ground where immature cod feed on spawning capelin during March–April (Konstantinov, 1965). During winter the area northeast of the Skolpen Bank is part of the Polar Front with relatively high gradient. The area southwest of the bank has a depth of 200–300 m (Figure 1) with bottom temperatures of 2–3°C. (Mehl, 1997). Other parts of the Polar Front with strong tide are around Bear Island and the Svalbard bank (Gjevik *et al.*, 1990), where high concentrations of cod are found in winter (Trout, 1957).

Low vertical activity and a large temperature range may occur in an area with strong tides without semi-diurnal cycles in the series, e.g. if the cod's migration is not synchronized with the tide. In tag 131, during January [Figure 3(d)], the depth and temperature level and range and  $r(t)$  indicate that the cod migrates near the Polar Front with strong tide, which fits within the area south of Bear Island.

If reduced vertical activity is common because of strong tidal currents (Table 3), there will be a high proportion of cod near the bottom and this may cause error in acoustic estimation because the fish are hidden in the acoustic bottom-dead-zone (Aglen, 1994; Aglen *et al.*, 1999).

## Conclusion

Analysing the bivariate time-series of depth and temperature from DST provides information on the

interplay between the cod's migration behaviour, its physiological limitation and environmental conditions over different seasons. The cod's vertical migration activity in relation to depth, and physiological limitations to pressure change, is measured with  $act(a)$ , the daily depth range in free vertical range (FVR)-units. Patterns of  $r(t)$ -values, the ratio of temperature change to depth change over the two-hour interval, and its moving median are used as indicators of the temperature gradient (angle and size) in the area where the cod migrates. Spectral analysis is used to identify the frequency of regular cycles and their cross-correlation.

The depth and temperature trends, together with the  $r(t)$  and  $act(a)$  patterns in most tags, show that during long-distance migration cod swim along a stable thermal route of temperature above 2°C but below 6°C and mostly in the depth layer 150–400 m with relatively low vertical migration activity. In summer-autumn most cod change to a new depth level that is, in the main, closer to surface, increase vertical migration activity, and occasionally have temperature records down to -1°C and up to 9°C. Together with the  $r(t)$ -pattern this suggests that the cod is near a front, or has penetrated a thermocline. Some cod have a clear DVM that occurs at various depth levels. During February–March most cod have relatively high vertical migration activity, with small variability in temperature (above 2°C but below 5°C), depending on the individual fish. DVM is detected in some cod at depth 150–400 m and the fish stay in the upper vertical migration range during the day. Otherwise the vertical activity is mainly much smaller than one FVR unit. In April some cod have a very small vertical migration with a semi-diurnal cycle in the temperature series with  $r(t)$  indicating that the cod are moving around a front periodically shifting with tidal current.

The (semi-) DVM or reduced vertical migration can cause bias in stock estimates based on bottom trawl and acoustic surveys. Analysis of DST time-series data gives information on the conditions when such behaviour occurs.

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