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Behavioural rhythm of cod during migration in the Barents Sea

by
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ABSTRACT

To assess fish abundance by direct methods and to understand and model species interaction, it is important to have proper knowledge about behavioural patterns. Patterns in vertical distribution might strongly affect accessibility of the fish to survey methods and are of importance for modelling within and between species interaction and competition. Such information can be obtained on individual basis by using data storage tags @ST).

In this paper time series from 19 DSTs attached to adult Northeast Arctic cod are analysed. Depth (pressure) and temperature were recorded with 2-hour intervals. The main purpose is to develop a statistical approach to extract information about rhythmic behaviour (diurnal, semi-diurnal), and to discuss possible ecological impacts of such behaviour of adult cod in the Barents Sea. This includes vertical migration, temperature distribution, and spatial-temporal interrelation caused by fish behaviour. To identify the dynamics in behaviour when fish penetrate stratified water masses, an approach using the rate of change of temperature in relation to change of depth was chosen.

The results show that rhythmic behaviour occurred temporarily in 12 of the tags. Spectral density distributions of depth and temperature time series show that rhythms within 24 hour are most common. In 11 out of 12 tags where diel vertical migration (DVM) was detected, this occurred during summer and autumn. In 7 out of 8 tags where semi-diurnal tidal cycles were detected in the temperature series, this occurred during April-May. In some tags diurnal or semi-diurnal cycles appeared in both depth and temperature series. Diurnal rhythms are periodically important for adult cod, but the results are not consistent for all tags and therefore no firm and general principle for such behaviour can presently be concluded.

Key words:
Data storage tags, diurnal vertical migration, Northeast Arctic cod, semi-diurnal cycle, spectral analysis, temperature gradients, time series analysis.

1. INTRODUCTION

Normally, fish behavioural characteristics are ignored in standardised abundance surveys using acoustic and/or bottom trawl sampling methods under the assumption that such phenomenon will affect the assessment similarly from survey to survey (see e.g. Aglen 1994, Godø 1994). Numerous studies have shown that many fish species in general exhibit diurnal rhythms with respect to distribution, activity etc., and cod (Gadus morhua L.), the species of investigation here, in not an exception. Vertical distribution and catch rates of Northeast Arctic cod vary substantially with day and night as described by Engås and Godø (1986), Engås and Soldal (1992), Michalsen et al. (1996), Korsbrekke and Nakken (1999) and Aglen et al. (1999). Aglen et al. (1999) stresses that the vertical migration is size dependent.

It has, however, never become clear what processes create the observed systematic diurnal variation. To what extent does individual behaviour cause systematic diurnal vertical migration (DVM)? From analysing data storage tag records Stensholt (1998), Steingrund (1999) (for wild Faroe Plateau cod), and Godø and Michalsen (2000) found that some large individuals only occasionally and for short periods exhibit DVM rhythm, but there is no information on what drives this behaviour and where it occurs. Further, inter and intra specific interactions as estimated from survey assessment routines that ignore diel fish behavioural patterns, may lead to ecological misinterpretations and erroneous modelling.

It may improve the survey stock assessment process if one knows when, where and why these occasionally rhythmic vertical migrations of fish occur in general. 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 DVM in cod is a feeding response, the picture gets more complicated, as the cod's activity will be influenced by changes in behaviour and availability of important prey species. The data storage tags (DST) contain information on when rhythmic vertical migration occurs and on what the size and angle of the temperature gradient are then. By incorporating other known information about the behaviour and spatial density distribution of cod and its prey species as well as the general knowledge on physical oceanography and spatial-temporal temperature distribution in the Barents Sea, one may discuss the possible areas where the cod migrate during different seasons and the possible cause of such vertical migration behaviour.

The objectives of this paper are twofold. Firstly, we want to establish statistical techniques that can extract information on rhythmic behaviour patterns from the bivariate time series recorded by DSTs. Secondly, the results will be discussed in relation to the ecological adaptation of cod to the Barents Sea environment to improve this understanding and extract useful information needed in stock assessment.

2. MATERIAL AND METHODS

2.1 Data collection

The data storage tags (DST) were attached to 200 adult Northeast Arctic cod of length 50-100 cm during March 1996. These data originate from an experiment that emphasised on the physiological limitations of cod to maintain neutral buoyancy under pressure changes, and a detailed description of the data is found in Godø and Michalsen (1997), and in Godø and Michalsen (2000). There are two release sites: Lofoten (site L, spawning site) for 42 mature cod and off the northernmost coast of Norway (site N, Finnmark) for 158 non-mature cod. A tag gives no direct information on position in the meantime until it is recaptured. The recapture sites are reported in Godø and Michalsen (2000). In the first year, 31 tags were returned but only 19 tags, with time series longer than 3 months, were selected for the analysis. There are 8 tags that have records longer than 10 months, i.e. tag number 39, 44, 117, 13 1, 19 1, 204, 206, 246. Due to the rough handling of fish during catching and tagging, the data record during the first two weeks were not used in the analysis focusing on fish migration behaviour (Godø and Michalsen 2000), but this has no effect on the analysis of temperature gradient distribution.

The CTD data from the O-group survey 21 August to 9 September 1996 are used for information on the Barents Sea bottom depth and spatial distribution of temperature during autumn (Figure 1). The CTD stations were generally 35 km apart, and at each station data were collected at every 5 m along the depth, while a cod may swim about one fish length per second. In one 2-hour interval between two observations, an 80 cm cod can move up to about 6 km horizontally, and the vertical movement can be up to 200 meters or more.

2.2 Data treatment

Each tag recorded the depth (pressure) and temperature every other hour for 6 days and every twelfth hour on the seventh day. To have values at regular intervals, the 10 unobserved values on the seventh day are replaced by interpolated values. With 2-hour resolution a highest frequency of a 4 hours cycle may be detected (Nyquist frequency, see Priestley 198 1).

Temperature values are recorded in degrees Celcius with one decimal, while the measurement accuracy is 0.2°C. Pressure is recorded stepwise and converted to depth in meters with one decimal, with accuracy of 1 bar (9.9 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 effects 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 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.

2.3 Data Analyses

Time series data analysis (Priestley, 1981) both on discrete time domain and on frequency domain (spectral analysis) are employed for analysing trend, cyclical pattern and correlation in the bivariate time series of depth and temperature. Concepts and techniques in spatial data analysis (Cressie, 1991) include spatial continuity which is 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=l , 2, 3, . . . , and dd(t) and dc(t) be the first difference of depth and temperature e.g. dd(t) = d(t)-d(t-1), and let dmax(a), dmin(a), cmax(a), cmin(a) denote the daily maximum and minimum values of d(t) and c(t) during day a. The 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). It informs about the relative size of the vertical component of the temperature gradient over time. Obviously the sea bottom is deeper than dmax(a).

2.3.1 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 over a long time. If the time series has one dominant frequency it may be clearly visible from the time series plot. When there are mixed frequencies and noise then the spectral analysis becomes an important tool in identifying the frequencies. The methods assume the time series to be stationary over the investigated duration. When it is necessary to remove a trend, it is usually good enough to use the first order difference of the tag data.

2.3.1.a 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 ω . Consider a stationary random sequence { Y_t} with autocovariance function $\gamma_k = \mathrm{cov}\{Y_t\ ,\ Y_{t-k}\}$. We define the spectrum of { Y_t} as the Fourier transform of γ_k :

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

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

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

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(O) of the time series e.g.

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

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

The graph of $\hat{f}(\omega)$ as a function of ω can be use to detect which frequency components that contribute large discrete variations in the time series. The peaks in j‘(w) correspond to the cyclic patterns of variation at that frequency.

2.3.1.b Bivariate time series

Moreover, when we study a pair of time series variables, we can define the cross-spectrum of a bivariate stationary process $(X_t\ ,\ Y_t)$ as the discrete Fourier transform of its cross-covariance function γ_{xy} (k) .

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

This is in general 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 $a,(w) = |h_{xy}\ (\omega)|$, this represents a form of covariance between the aligned frequency components of X_t and Y_t at frequency ω .
Consequently the complex coherency between X_t and Y_t at frequency ω ,

$$b_{xy}(\omega) = h_{xy}(\omega) \Big/ \sqrt{h_{xx}(\omega) \cdot h_{yy}(\omega)}\ ,$$

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 ω 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 ω. Hence

$|b_{xy}(\omega)|$ over all ω 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 ω.

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. A phase equal to $\pm\pi$ [0] means that the temperature decreases [increases] with increasing depth. This gives us an idea about the spatial distribution of temperature in the area where the cod migrate. When the fish moves into waters with a different temperature distribution, so the relationship between temperature and depth changes, we expect a relatively low coherency.

2.3.2 r(t) is an indicator of the temperature distribution and vertical gradient

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 stayed for a certain duration. The r(t) time series can be derived from the DST records.

The ratio $r(t)=\dfrac{dc(t)}{dd(t)}=\dfrac{c(t)-c(t-1)}{d(t)-d(t-1)}$, is defined when $dd(t)\neq 0$.

Here d(t) and c(t) denote, respectively, the depth and temperature at time t, dd(t) and dc(t) denote the differences, i.e. dd(t) = d(t)-d(t-1) and dc(t) = c(t)-c(t-1).

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

The spatial continuity of temperature makes it reasonable to assume *VT* is approximately constant within the neighbourhood where the fish'stayed for a certain duration. That makes it possible to apply the analysis of a single move to the analysis of 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) that VT is only approximately vertical. Then generally the moving median of r(t) is a good estimator for the vertical component of *VT* over the recorded depth range. However, for moves in an isotherm plane, c(t) is constant and r(t)=0, and a preference for moves near a given tilted isotherm plane may cause an under-estimation. Thus a small median r(t) may be due to environment (a small gradient) or to a preferential movement pattern as mentioned above.

It is also shown that the more VT deviates from the vertical, the larger is the variance and range of the r(t)-distribution. Thus time stretches with many unusually large positive and negative r(t) may indicate a relatively large horizontal component of VT, which will be the case if the fish migrates close to a front.

Since the gradient *VT* points towards warmer waters, a positive (negative) moving median r(t) indicate, respectively, cold (warm) water on top. Frequent moves near or across the thermocline give a large negative median.

When *VT* 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°C to 3°C.

Moreover, in the front area during the thermocline-forming season these patterns are mixed (Figure 1). The temperature distribution may be complicated by turbulence with distorted volumes of one water mass into the other, and the direction of the gradient varies (Sakshaug, 1992 p.24, 58). Some places along a front where there also happens to be tidal currents, the situation is special. 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 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 physical oceanography, e.g. the location of fronts and strong tides, one may discuss what areas the cod may possibly have been in. (Figure 1 and 2, Table 2)

3. RESULTS

3.1 Depth-temperature interaction as a consequence of cod migration

Throughout the migration, each cod experiences a change of temperature level and distribution as a consequence of changing depth level and area. The interaction over time between cod migration behaviour and sea temperature, which is recorded in DST as a bivariate (depth and temperature) time series, can be observed in the pattern of the r(t) time series and its moving median values in relation to the depth and temperature ranges and levels. The dmax(a) series before recapture fit well with the sea bottom depth in the recapture area, which can be found in Godø and Michalsen (2000). Moreover, the DST temperature record also captures the characteristics of the temperature distribution.

Figure 2 presents four selected tags that describe the main characteristics of each pattern. These patterns indicate the type of temperature spatial distribution in the unknown area where the cod stay during a certain season. Table 1 presents the tags that have some main character resembling one of the patterns, but the events might not correspond exactly in time as in figure 2. Some tags have the characteristics of one 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 8 tags have records longer than 10 months, lasting into the December-March period (Table 2 and Section 2.1).

The April - June, 1996 and December, 1996 - March, 1997 periods: During April-June and December-March temperatures are mainly at constant trend with small daily range such as 2°C to 4°C, 3°C to 5°C, or 4°C to 6°C depending on the tag. The depth level in general is deep, mainly 150m to 350m. The depth level and the daily depth range vary depending on the tag.

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

117, 191,206, 33, 39, 44, 138,228, 38, 98, 131, migrate near a front but with different size of r(t) and its moving median.

-- Tag 117, 191, 206 have relatively large positive moving median of r(t) and at the same time relatively large variance of r(t).

-- Tags 33, 39, 44, 138,228 are the same as in 1 but with r(t) of intermediate size.

-- Tags 38, 98, 131 have mixed intermediate and small positive and negative moving median of r(t) and at the same time a relatively large variance of r(t).

Notice that changes of depth in tags 117, 131, 191, 206 are small, mainly less than 10m (Table 3). The semi-diurnal cycle is detected in these temperature time series (Table 2 and Figure 3).

During December-March the moving median of r(t) in most tags has mixed positive and negative values of relatively small or intermediate sizes. The r(t) is a mixture of relatively small and intermediate absolute values (in some tags with a few large absolute values, i.e. tags 117 and 131). The variance of r(t)-values gradually decreases toward February and March. The depth and temperature trends approach the same level as during April-June, i.e. 150m to 350m for depth and 3°C to 5°C for temperature. (Tag 39 with depth level from 100m to 150m (Figure 2) is an exception). DVM is detected in tags 39, 44, 131, 191, 204, 206, 246 (Table 2).

July - November period: During July to November the daily range of vertical migration, the variance of r(t) and it 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 and 4). The cod is demersal, so the daily maximum depth often reflects the sea bottom depth. 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. tag 44, 106, 131, 228, 238, and 246. Only 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 2). The main character of a tag series is similar to one of four patterns (Figure 2).

a.) Increasing/increased temperature trend as a consequence of decreasing/decreased depth trend, the depth range includes the thermocline. The moving median of r(t) has relatively large negative values, up to 0.1°C per meter, at the same time as r(t) has a relatively large variance and range. The pattern indicates that the cod migrates around the thermocline near fronts, in relatively shallow waters. This pattern is observed in tags 44, 106, 191, 206.

b.) Decreasing/decreased trends in both temperature and depth, the depth ranges from 50 to 250m, mainly below the thermocline, the temperature ranges mainly from 0°C to 3°C with occasionally subzero temperature. The moving median of r(t) has intermediate negative values, up to 0.05°C per meter. The r(t) is mainly a mixture of intermediate and small values with a few large values. The pattern indicates that the cod migrates 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. This pattern is observed in tags 38, 97, 98, 106, 110, 117, 131, 204, 206, 228, 238, and 246.

c.) As in (b) but with depth level 200 to 450m and long duration of subzero temperature. The moving median of r(t) has small negative values, up to 0.02°C per meter, the 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. This pattern is observed in tags 117 (November-December), 204 (November), and 98 (August).

d.) Tag number 39 has a record of constant depth trend 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 (up to 0.03°C) in April and negative (up to -0.03°C) during June to 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.

3.2 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 to 150m depth channel) with phase equal to $\pm \pi$. This is due to the thermocline creating a high vertical upwards-oriented temperature gradient. The negative moving median of r(t) also gives the same indication. When there is DVM in both series (Table 2) the coherency is generally high, e.g. the coherency at the frequency of 24 hours 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 the coherency is significantly different from zero, then the phase is estimated to be 0, which indicates a downward pointing temperature gradient. The positive moving median of r(t) also gives the same indication. A special situation with tidal cycles in the temperature series is described in the methods section.

Both negative (positive) values of the moving median of r(t) and the phase values +a (0) are indicators that a warm (cold) water-mass lie on top. In addition, the moving median of r(t) gives the estimated size of the vertical gradient. In all cases both indicators are in agreement with each other i.e. during spring, summer, autumn (winter) a warm (cold) water-mass lies on top.

3.3 Vertical movement

The time series of dd(t), the change of depth within one recording interval (2 hours), has zero mean with seasonally dependent variance (Figure 4). This indicates a seasonal change in vertical migration behaviour as discussed above. In more than 50 % of the days, the delay between the daily maximal ascent and descent is 4 hours (2 periods) or less. This is true for all tags (Table 4). The remaining changes of depth level were small after this major adjustment. During the vertical migration the cod experiences temperature change as a consequence of the depth change. The time series of dc(t) has zero mean with seasonally dependent variance (Figure 4) but its characteristics depend on the temperature distribution in the area where the cod migrates.

Comparison of the daily net changes of depth and temperature with the daily maximal vertical migration range over a 2-hour interval indicates that the cod neutralizes large sudden depth and temperature changes within 24 hours (Figures 4 and 5). Spectral analysis also supports the above statement since estimated spectral density plots show that most of the variation in the bivariate time series come from high frequency components, i.e. from periods less than or equal to 24 hours (Figure 6).

3.4 Diurnal vertical migration (DVM) and Semi-diurnal patterns

Throughout the entire time series of depth and temperature there is a mixture of irregular and regular cyclical patterns with amplitude and frequency depending on the season, The regular patterns may occur only a few days at a time, e.g. tag 235, 238, 098, or it may persist for weeks or months, e.g. tags reported in Table 2. Spectral analysis shows how the total variation in each time series is distributed over the frequencies, with a significant peak indicating a cycle at that frequency (Figure 6). Notice that in some tags there is a peak at the 24 hour period with subsidiary peaks at the harmonics of the main peak, i.e. at 12, 8, and 6 hours period. This is due to the non-sinusoidal shape of the individual cycles in the data. This makes it difficult to distinguish the 12-12.5 hour cycle from the 12-hour harmonic frequency of the daily cycle. Thus the 12-12.5 hour cycles reported in Table 2 are in seasons without diurnal cycle. In this study there are two commonly found regular cyclical patterns, diurnal cycles (24 to 25 hour per cycle) and semi-diurnal cycle (12 to 12.5 hour per cycle). For certain duration a cycle may be detected in depth or in temperature or both.

Table 2 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 10 of them the cycles are found in both depth and temperature series. In 11 out of 12 cod the DVM activity happened during the July-November feeding season with r(t) patterns indicate the fish migrate near fronts. Among those 11 cod, 8 migrated in the depth channel 0-250m (occasionally penetrating through the thermocline), namely tags 39, 44, 97, 106, 110, 191, 206 and 246. Tags 13 1 and 204 migrated in the depth channel 100-250m while tag 117 migrated in the depth channel 170-350m. In tags 13 1, 191, 204,206, and 246 the DVM (24-hour cycle) is detected at depth mainly below 150m for a certain period during January-March. Tag 39 has DVM (25 hour-cycle) in January (Table 2).

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 to November the cod usually migrates in the 0 to 150 m depth channel (with thermocline) with a large negative moving median r(t).

The semi-diurnal cycle is found in the temperature time series of 9 tags. In 4 of them the cycle is also found in the depth series. In 9 of them the cycle occurred during April-May and only 2 tags have semi-diurnal cycles during July-September and/or November-December (Table 2). In tags 44, 117 (Figure 3), 13 1, 19 1,206 a semi-diurnal cycle was detected in April together with increased variance or range of the r(t) series (indication that the cod migrates near fronts), the moving median of r(t) having large positive values, except tag 131 that is dominated by large negative values, and relatively small changes of depth. It occurs at depths from 150m to 300m with temperatures from 3°C to 5°C. (Figure 2 and Table 3) In some tags (number 33, 39) with large r(t) variance but without semi-diurnal cycle, the depth change is larger than in the tags with the cycle (Figure 2).

3.5 Time spent in the upper/lower level during DVM

There are at least 4 patterns of DVM according to the time the cod stay in the upper, middle, and lower part of the daily depth range (Figure 7). 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 single 2-hour moves. The delay time between the largest ascent and descent depends on the pattern of DVM (Figure 8). The largest ascent (descent) takes place at approximately the same hour each day, which depends on the tag (Table 5).

Cod 204 spends about equal time in top and bottom layers (pattern 1, Figure 7); cod 191 is mainly in the middle layer with short visits to 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). Taking into account the rates of swimbladder adjustment (Harden Jones and Scholes 1985), the figures tell how far from the neutral buoyancy level a cod will migrate, and for how long.

All cod with detected DVM in winter ascend and stay on the relative upper depth level during daytime. During summer and autumn the ascent hours can vary from very early in the morning, afternoon or evening (Table 5 and Figure 8). The distribution of these upward hours and 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. Arnold and Cook (1984) use the ratio of time spent in mid-water to time spent near the sea bottom in the computer simulation model for studying cod migration by selective tidal stream transport.

4. DISCUSSION

The bivariate time series of depth and temperature obtained from DST are results of individual cod behaviour in the Barents Sea ecological system. Such data contain detailed information on seasonal short-term and long-term migration patterns in relation to the temperature distribution. On the other hand, for different seasons, annual scientific surveys provide large-scale observations. Combining tag information with information on the spatial and temporal distribution and behaviour of cod and its prey species and on the physical oceanography of the Barents Sea, one can discuss the possible influences on the behaviour and possible location. Such results may help to understand how the composition of individual fish behaviour patterns contribute to the large scales observations. An example of such work is the reconstruction of the migration routes for demersal fish in the North Sea/English Channel, making use of the tidal current patterns (Arnold and Holford, 1995).

The Barents Sea has high temperature gradients due to summer heating and cold-water outflow. The thermocline layer, with a very high vertical temperature gradient pointing upwards, builds up from spring and breaks down in autumn. In front areas a cold water mass faces a warm water mass, and the temperature gradient has a large horizontal component. The fronts move according to seasons and other conditions. At the Polar front cold Arctic water meets warm Atlantic water, and the temperatures are in the range -1.5°C to 3°C. The bottom depth along the polar front area ranges from 100 - 400 meters (Figure 1). The polar front is outlined by Bear Island, Svalbard Bank, Great Bank, Central Bank, Southeast Basin, Goose Bank, and Skolpen Bank. Similar conditions may be found outside river estuaries. In the front area during the thermocline season these patterns are mixed (Figure 1). Temperature distribution may be complicated by turbulence with distorted volumes of one water mass into the other, and the direction of the gradient varies (Sakshaug et al, 1992 p.24, 58).

Tidal forces also generate movement in the water masses that influence temperature distribution and fish behaviour. The atlas of tides (Gjevik, et al, 1990) shows that strong diurnal and semi-diurnal tides occur at the following locations: Lofoten and Vesterålen area (inside 67°N-69°N and 10°E-16°E), the area north of Troms (inside 70°N-74°N and 15°E-21°E), Svalbard Bank and the stretch along northern coast of Norway and Russia, including the Skolpen Bank. Quite special conditions, strong currents, and Arctic waters on top of warmer Atlantic waters of higher salinity are found in the bank areas, e.g. at the Svalbard Bank, inside a huge bulge of the polar front. The area southwest of Novaya Zemlya is shallow (less than 200m) with high surface temperature and strong vertical gradient in summer and autumn, and with fronts from outflow of cold arctic water and big rivers. For each location in the Barents Sea, during a certain season, all these conditions create special characteristics of depth and temperature distribution, which are recorded in the DST as the cod migrates. They can be analysed and used in a discussion of the possible area where the cod migrates.

The North-East Arctic cod is mainly found in the southern part of the Barents Sea, sometimes as far east as Novaja Zemlja, around Bjørnøya and Hopen, and along the western coast of Spitsbergen. Immature cod feed both at the bottom and in midwater layers and make seasonal east-west and north-south migration within the Barents Sea and along the western coast of Spitsbergen (Nakken 1994). Mature cod migrate between the feeding areas and the spawning areas. Spawning takes place all the way along the Norwegian coast from Møre to western Finnmark. The most important spawning grounds are around Lofoten and Vesterålen. The spawning period lasts from February to May with the main spawning in March and April, with a peak at April 1 (Pedersen 1984). After spawning it migrates to be in the feeding area, stretching from the west coast of Norway into the Barents Sea, in summer and autumn (June-November) (Sakshaug et al, 1992). Aglen (1999) reports that during summer and autumn of 1996 and 1997, cod larger than 19cm was distributed south of the polar front with higher density distribution along the polar front. During January to March there are high concentrations of immature cod preying on mature capelin that migrate to spawn along the northern Norwegian and Russian coast, including the Skolpen Bank (Bogstad and Gjøsæter 1994, Gjøsæter 1998). The cod's spatial distributions during the winters 1996 and 1997 are reported in Mehl and Nakken (1996) and Mehl(1997).

If the cod's migration behaviour is a feeding response, it will be influenced by the prey's migration behaviour and spatial distribution. The type of temperature spatial distribution from DST should be in agreement with the type of temperature spatial distribution where the prey is distributed. Bogstad and Mehl (1997) report that the cod's consumption of the important prey species in 1996 is krill (1099), cod (540), capelin (517), amphipods (472), shrimp (384), redfish (15 1), haddock (78), polar cod (67), herring (59), and others (908); the numbers are in 1000 tons. In years with high capelin stock the species composition in the cod's stomach content is dominated by capelin in the season when it is available. Krill become particularly important for the cod in years with a low capelin stock. This was the situation in 1996. In spring, summer and autumn a high density of plankton and small fish can be found around the thermocline layer and the polar front, at which side of the polar front depends on the species. Zooplankton and capelin have DVM that is more pronounced during the spring and autumn when the day and night are clearly distinguishable. DVM behaviour of O-aged cod during August-September is also reported (Stensholt and Nakken, in press). They distribute in the upper layers during night and deeper during day. During winter krill and capelin stay in deep layers below 100m, while capelin have no vertical migration. (Sakshaug et al, 1992, pp123, 185, Luka, G.I., 1984).

Gjøsæter (1998, 1999) reports that mature capelin migrates from polar front wintering area to spawn in the warm water along the coastal area north of Norway and Russia. There are high concentrations of spring larvae along the coastal area. During July-August the capelin migrate to the feeding area in cold waters beyond the polar front and concentrate there in September. During October the capelin migrate back from the feeding area toward the polar front and have high concentration around and south of the polar front in November-December.

4.1 Agreement of tag analysis with large-scale observations

In general the patterns of dd(t), dc(t), r(t) and its moving median have seasonally dependent variance (Figure 2 and 4). The change of these patterns over time indicates a change of temperature distribution that may be due to change of season or to change of area. Characteristics of the spatial and temporal temperature distribution in the Barents Sea and adjacent waters are observed in the time series of DST, e.g. polar front or fronts, thermocline, tidal cycles. These are in agreement with the general knowledge of the cod's seasonal migration. A cod migrating in the Barents Sea may show patterns a, b or c. A cod staying in the coastal area may have pattern d, as in tag 39 which may be a coastal cod (Godø, 1995).

During May to June and December to February the pattern of depth and temperature trend, the small variance of dd(t), dc(t), and r(t), the near zero values of coherency, all indicate that the cod has a long distance migration through different areas and that it moves in a water-mass with low vertical stratification, i.e. with a low temperature gradient, or that it has preferential migration along the isotherm. Figure 2 shows that during these two periods the temperature level of most tags range from 3°C to 5°C at depth levels varying from 100 to 400m depending on the cod. The Atlantic waters have temperature around 3°C where they face Arctic waters. Such migration roughly following the isotherm brings the fish sufficiently close to areas near the polar front, when it changes behaviour and moves towards colder waters to forage at the front during July to November (Figure 2). Most cod have pattern a, b, and c of Table 1. This indicates that the cod's summer and autumn distribution is in the vicinity of the polar front or other fronts, at different depth levels i.e. around the thermocline layer, mainly below it, and near the sea bottom.

The analysis of the depth and temperature from DST records indicates agreement with the depth and temperature distribution in the habitat of the prey species. The DVM behaviour detected in some cod during July-November, and February-April (Figure 1 and 2, Table 1 and 2) also fit with known DVM of prey species. The findings also agree with the large-scale observations by Aglen (1999) and Mehl and Nakken (1996) and Mehl(1997).

4.2 Cyclical vertical migration bebaviour

Natural cyclical phenomena such as the sun light (24 hour per cycle), the semi-diurnal tidal cycle (M2 with 12.42 hour per cycle or S2 with 12 hour per cycle) and the diurnal tidal cycle (K1 with **24.8** hour per cycle) 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 DVM behaviour. Evidence of DVM based on repeated trawl hauls or combined trawl and acoustic sampling at the North Cape Bank during March to April are reported in Engås and Soldal (1992), Michalsen et al (1996), and Aglen et al (1999). Aglen et al (1999) report that large (small) cod ascend (descend) during daytime. Korsbrekke and Nakken (1999) report, based on the series of annual bottom-trawl surveys for demersal fish in the Barents Sea during **January** to March, that catch rates increase during daylight for all sizes of most species. For cod the day/night ratio peaked at a length interval 23-3 1 cm with a substantial reduction for larger fish, but not significantly below 1. They explain that this difference from the report of Aglen et al (1999) may be caused by adult cod in mid-water that dive down by as much as 100m because of vessel noise and get caught in the bottom trawl. Avoidance reaction to noise in several species has long been a research topic. Ona (1988) studied the case of cod.

The DST record has the advantage that it is not systematically distorted by vessel noise, but it limits the study to only small number of fish, and DST cannot replace bottom trawl. However, DST studies may help to interpret the trawl results. During February-March 1997 the tags 13 1, 191, 204, and 206 show DVM at depth deeper than 150m and with daily range 50 to 100m, and the cod swam higher during day than during night (Tables 2 and 5, Figure 7 and 8 of tag 206). Shortly afterwards these cod were recaptured in the bottom trawl survey area mentioned above. All the cod were immature at release time but it is not known if they were still immature at recapture time, however the recapture date and site (Godø and Michalsen, 2000) may indicate if they were migrating towards or away from the spawning grounds.

A clear DVM behaviour occurs during August to November with varying ascending/descending hour (GMT) and at varying depth level near fronts (Table 2 and 5, Figure 2). These variations may blur off in the aggregate composition of the DVM pattern in large-scale observations. 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 (Figure 7, 8 and Table 5) and irregular cycles. The Barents Sea stretches over 2 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, one may obtain a better understanding of how the large scale DVM should be decomposed.

Hjellvik et al (1999) investigates a diurnal variation in bottom trawl catch during winter and autumn from 1985 to 1999. In winter the catches of cod have diurnal variation with higher catches at daytime, while in autumn the difference is much less distinct. In both seasons the effect tends to increase with depth.

4.3 Diel behaviour as a feeding response

The DVM is not the common behaviour in every tag and its duration varies. The patterns of DVM also vary depending on tags and depth level, but all patterns have a single large ascent and descent (Figure 7). An explanation may be that the cod moves temporarily out of the preferred depth channel in search for prey (Stensholt, 1998, Godø and Michalsen, 2000). The moves may depend on the cod's demand for food and its adaptation to the availability and behaviour of different prey species in the area. The diversity of prey species and cod 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 change in availability of capelin stock (capelin seasonal migration patterns are mentioned above). The cod's diel behaviour while searching for food was observed by Løkkeborg and Fernö (1999).

DVM activity occurs during July to November and the r(t)-series supports the hypothesis that it happens in or near the front areas, in or below the thermocline layer, where prey species with DVM are abundant. This seems to support the conclusion that the cod's DVM is a feeding response. However, how accurately the vertical migration hours for cod and its prey correspond has not been established, and the composition of prey species in the tagged cod's diet is not known. That the tags lack records of location (or local time) may also be a factor that reduces the accuracy.

The semi-diurnal cycle observed in temperature time series during April together with small depth change and large variance of r(t) may be connected to the cod feeding in an area characterized by strong tidal currents and the presence of a front. Strong tides in shallow areas of depth less than 100m break down the stratification in the water mass. However, the influence of a front may maintain a strong stratification in a water mass that is periodically moved by tidal forces. To explain how the tag records the semi-diurnal cycle of temperature, we believe that the cod stayed in a front area where the front moves horizontally with strong tidal currents. Moreover, the cod either migrate against the tidal current stream or stay approximately in the same location i.e. at sea bottom and migrate up to a certain depth level above the sea bottom where it can get effect of the tide, and DST record the rhythmic change of temperature. There may well be many other occasions when strong tidal currents cause reduced vertical activity, but without the stratification the tidal cycle cannot be detected in the temperature series.

Areas with strong tides exist along the migration routes, e.g. along the coastal area east of the release site N (for immature cod) where there are main winter cod fishing grounds with an environment that may give the characteristic temperature distribution as described above. During winter the area northeast of the Skolpen Bank (33°E and 71.5°N) is part of the polar front with relatively high gradient. The area southwest of the bank has the depth 200-300m with bottom temperature 2°C to 3°C and with a strong M2 tidal current in the direction along the coast. (Mehl and Nakken, 1996, p.19, Gjevik, 1990). Other areas with strong front and strong tide are around Bear Island and the Svalbard bank (Gjevik, 1990).

Løkkeborg (1994) observes that cod in natural environment responding to a baited hook more often swam upstream than non-responding fish. But the response of fish to a baited hook has been shown to decrease when current is strong. He also reports that with a current below 18cm/sec, the swimming activity of cod was two or three times as high as in periods with stronger current. He explains this behaviour as due to energy optimisation for fish: it swims upstream to the source of odour during periods of moderate or low current velocity and stays in shelter when the current is strong. The feeding behaviour related to current and prey was studied by Arnold, G.P. et al., 1994, Løkkeborg and Fernö 1999.

4.4 Vertical migration as an adaptation

During long distance migration the cod has varying depth level and range of vertical migration. It remains in the deepwater channel with approximately constant temperature trend (3°C-5°C) and about 2°C range as if the cod has its preferential migration route along the isotherm plane, avoiding or neutralizing abrupt change in depth and temperature (Figure 2 b). But when it reaches the destination it can change patterns of vertical migration, the level and range of temperature and depth.

During the July to November feeding season, and occasionally December to March, the cod often makes an ascent or descent consisting of a few large vertical 2-hour moves followed by a similar opposite migration. This behaviour may or may not be connected to DVM. The time delay between these two major moves depends on the tag but is mainly not more than 2 recorded periods (Table 4). The cod gets exposed to abrupt changes in temperature especially when it migrates through the thermocline layer or migrates in the vicinity of a front (Figure 2). But it always neutralise abrupt changes in depth and temperature so that the short-term (daily) net changes will be small (Figure 5). Neutralization of depth change may be linked to the buoyancy adaptation (Harden Jones and Scholes, 1985). The cod's adaptation to neutral buoyancy is very slow compared to many of its swift vertical moves (See also Godø and Michalsen, 1997 and 2000). Harden Jones and Scholes (1985) experiment with the cod in capture under continuous observation shows that there are bounds to how long and how far the cod can deviate from the level of neutral buoyancy. Feeding activity must be a major reason for accepting the energy loss, which increases with the size and duration of a deviation. Moreover most of the records show they prefer to stay in areas with temperature above zero, and some cod have occasionally sub-zero records. Thus it seems that the cod will move out of the preferred zone into sub-zero waters only when it is necessary to follow the prey.

4.5 Selective tidal stream transport

Arnold et al (1994) give a detailed discussion on the North Sea cod's migration by selective tidal stream transport. They describe "The behaviour, which we have called selective tidal stream transport, is a consistent pattern of semidiumal vertical migration, in which the vertical movements of the fish from the bottom up into mid-water are linked to the tidal streams." Both release sites are in areas with strong tidal currents, and there are other strong tide areas along the migration route and feeding area as described above. But the semi-diurnal vertical migration is detected occasionally in 8 tags, e.g. 38, 44, 97, 106, 110, 13 1, 191, and 246 (Table 2). However, when there is a cycle in the temperature series as well, it is not likely that the fish uses the tidal stream for transport, as it might soon be taken out of the special area where temperature cycles exist.

Tag 39, with 25-hour cycles during December-January, and with several months with semidiumal 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, both semidiumal and diurnal (M2 and K1) (Gjevik et al, 1990).

4.6 Conclusion

Using the bivariate time series of depth and temperature from DST, we investigate the cod migration patterns in relation to the sea temperature over time. Spectral analysis offers a method for identifying the frequency of regular cycles as well as their correlation. The analysis of DST data confirms the existence of occasional diurnal and semi-diurnal cycles in depth and temperature. The pattern of r(t)-values and its moving median are used as indicators of the temperature gradient angle and size in the area where the cod migrates. During winter the DVM occurs at depths below 150m and the fish stay on the upper vertical migration range during the day. During July to November some cod have a clear DVM that occurs at various depth levels (most likely, in areas with different sea bottom depth) with indication that the cod migrate near or in polar or other fronts and the thermocline. Because the cod is a demersal fish some recorded depths may indicate the bottom topography. In April some cod migrate in areas with strong tides near fronts and the cod have small vertical migration.

The vertical migration of fish can cause bias in bottom trawl and acoustic stock estimates. The understanding of factors that induce systematic rhythmic movement can be useful in correcting such bias.

Different patterns of vertical migration are observed, and thus knowledge of where, when, and why these types of individual behaviour occur is important to assess how they cause DVM on a large scale which influences the survey observations, and thereby also the stock estimates.

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Table 1: 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[a]
a	44^{**}, 106^{**}, 191^{**}, 206^{**}
b	38^{**}, 97^{**}, 98, 106^{**}, 110^{**}, 131^{**}, 138, 204^{*}, 228, 238, 246^{**}
c	117^{**}
d	39^{**}

a. 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.

Table 2: Diurnal and semi-diurnal cycles are detected in 12 tags. Columns 1 gives tag number and release site, L-Lofoten and N-Finnmark. Column 2 gives the cycle type. There is one column for each month (April 96 – March 97) 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**	**1-30 d**	**1-31 d**				-	-	-	-	-	-	-
	12.5 h	**1-31 t**			**1-15d**		-	-	-	-	-	-	-
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				**1-31 t**	**1-31 t**	**1-18 t**		**1-30 t**	**1-31 t**			
	25 h									**22-31 d**	**1-31 d**		
44L	**24h**					**1-31 d&t**	**1-30d&t**	**1-31d&t**	**1-10 d&t**	**1-21d&t** **22-31d**	**1-9 d**		-
	12.5 h	**1-16 d&t**				**8-23t**							-
97N	**24 h**				**2-17d**			-	-	-	-	-	-
	12.5 h	**1-31 d&t**			**23-31 d**	**1-31 d**		-	-	-	-	-	-
	25 h	**1-31t**	**1-31t**										
106N	**24 h**				**1-31**	**19-31 d&t**	**1-30 d&t**	**1-25 d&t**		-	-	-	-
	12.5 h			**1-30 d**									
110 N	**24 h**	**1-30 d&t**	**1-16 d&t**	**1-30 d&t**	**1-31 d**	**1-11 d** **26-31 d**	**1-30 d**	**1-31 d**	**1-17 d**	-	-	-	-
	12.5 h		**1-16 d&t** **17-31 t**							-	-	-	-
117N	**24 h**	**1-31 d**	**20-31 d**	**1-30 d**	**1-26 d**		**10-30 d**	**1-31 d&t**	**1-15 d**				
	12.5 h	**7-28 t**											
131N	**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**											
191N	**24 h**	**1-18d**	**13-30d**		**16-31** **d&t**	**1-7 d&t**	**13-30** **d&t**	**1-31 d&t**	**1-30 d&t**				**1-31 d**
	12.5 h	**5-15 t**	**3-20 t**	**1-27 d**									
204N	**24 h**	**1-30 d&t**				**22-31 d&t**	**1-30 d&t**	**1-31 d&t**	**14-25 dw**			**13-28 d**	**1-5 d**
206N	**24 h**					**25-31 d&t**	**1-30 d&t**	**1-10 d&t**				**26-28 d**	**1-25 d**
	12.5 h	**1-26 t**											
246N	**24 h**					**15-31 d**	**1-9 d**	**1-31d**	**1-30 d**		**1-31d&t**	**1-11d**	-
	12.5 h		**1-30d**										

Table 3: Distributions of depth and temperature, change of depth and temperature (in 2-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	168	29	102	82	87	93	103	109	121	129
	ddepth	67	-69	0	-24	-18	-8	0	8	17	27
	temp	6.5	3.5	5.5	4.3	4.6	5.1	5.7	5.9	6.1	6.2
	dtemp	1.6	-1.5	0	-0.6	-0.4	-0.14	0	0.17	0.4	0.6
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	403
	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	296	121	151	128	130	132	134	150	201	250
	ddepth	85	-75	0.3	-14	-7	-2	0	2	8	15
	temp	4.7	3.1	4	3.4	3.5	3.7	4	4.3	4.4	4.5
	dtemp	1.3	-0.9	0	-0.5	-0.3	-0.2	0	0.1	0.4	0.5
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	455	220	331	284	299	312	331	345	363	382
	ddepth	111	-126	0.2	-34	-25	-7	0	6	25	40
	temp	4.1	3.1	3.5	3.2	3.2	3.3	3.4	3.6	3.9	4
	dtemp	0.4	-0.4	0	-0.1	-0.1	0	0	0	0.1	0.1

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 parenthesis[a].

	difference in recorded hours							
tag (month/year)	<-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

a. All tags released in middle of march 96.

Table 5: Distribution of time interval[a] (in GMT) for daily maximal[b] 2-hour descent (plain) and ascent (**bold**) during DVM activity, in the months indicated.

	hour (GMT) -->	24-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20	20-22	22-24
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**	5.6	6.8	6.2	5.0	0.6	3.7	6.2	1.9	5.6	1.9	5.0	3.1
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**	4.4	1.1	1.1	0	9.8	11.5	8.7	5.5	2.7	2.2	1.1	1.1
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**	0.8	2.2	3.7	0	9.0	3.7	2.2	7.5	9.0	10.4	1.5	0.8
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**	1.1	1.1	0	1.1	7.6	2.2	2.2	26.1	7.6	3.3	1.1	0
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**	2.0	0	0	2.0	2.0	2.0	0	6.1	16.3	16.3	0	2.0
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**	2.3	3.5	5.8	3.5	8.1	11.6	4.7	8.1	1.2	0	0	1.2
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**	6.9	6.9	7.8	2.0	4.9	2.9	2.0	8.8	4.9	2.0	0	1.0
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**	3.3	0	5.6	7.8	2.2	1.1	14.4	10.0	1.1	3.3	2.2	0
tag 204	down	10.0	22.5	0	2.5	0	0	0	5.0	0	5.0	0	5.0
month 10	**up**	5.0	0	2.5	0	0	0	27.5	0	7.5	2.5	2.5	2.5
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**	0	12.5	12.5	15.3	4.2	1.4	0	2.8	0	0	0	0
tag 44	down	2.5	0	0	7.7	20.5	12.8	0	0	0	0	5.1	0
month 12	**up**	15.4	20.2	5.1	2.6	0	0	0	0	0	0	0	0
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**	3.9	5.3	6.6	9.2	2.6	5.3	3.9	1.3	5.3	5.3	1.3	2.6
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**	5.3	5.3	2.6	5.3	5.3	7.9	0	18.4	0	0	0	0
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**	0	0	7.3	14.5	5.5	1.8	0	14.6	1.8	0	1.8	0
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**	2.5	5.1	16.1	9.3	7.6	1.7	0.9	1.7	0.9	0	1.7	0
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**	1.9	1.9	9.2	18.5	3.7	1.9	5.5	0	3.7	1.9	0	0

a. Percentages may not add up to 100 due to rounding.

b. Maximal values less than 10m are removed from the material.

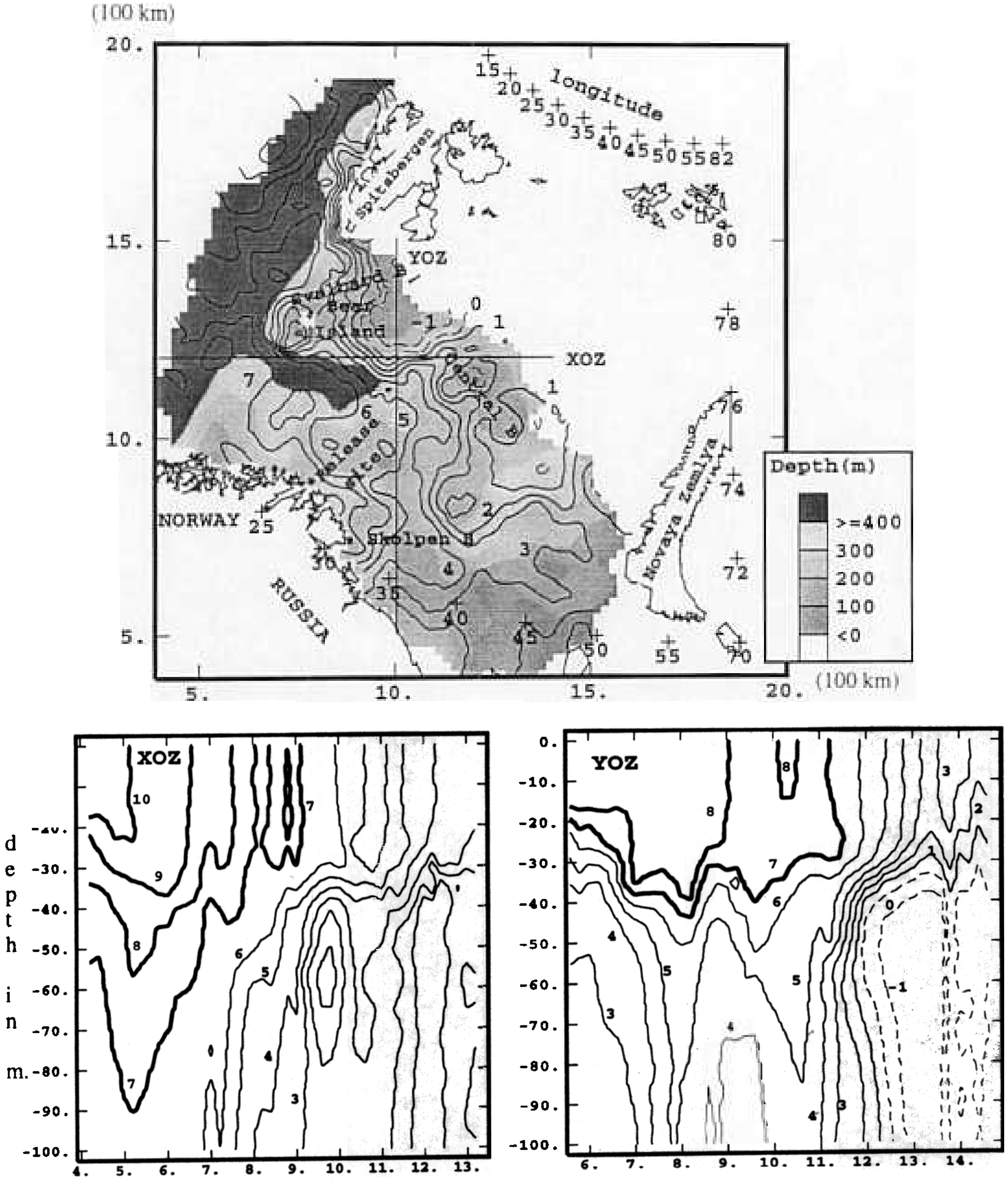


Figure 1: Bottom topography of the Barents Sea with release site N, horizontal (at 50m) and vertical distribution of temperature showing polar front and thermocline (from CTD-data sampled August 22 to September 17, 1996).

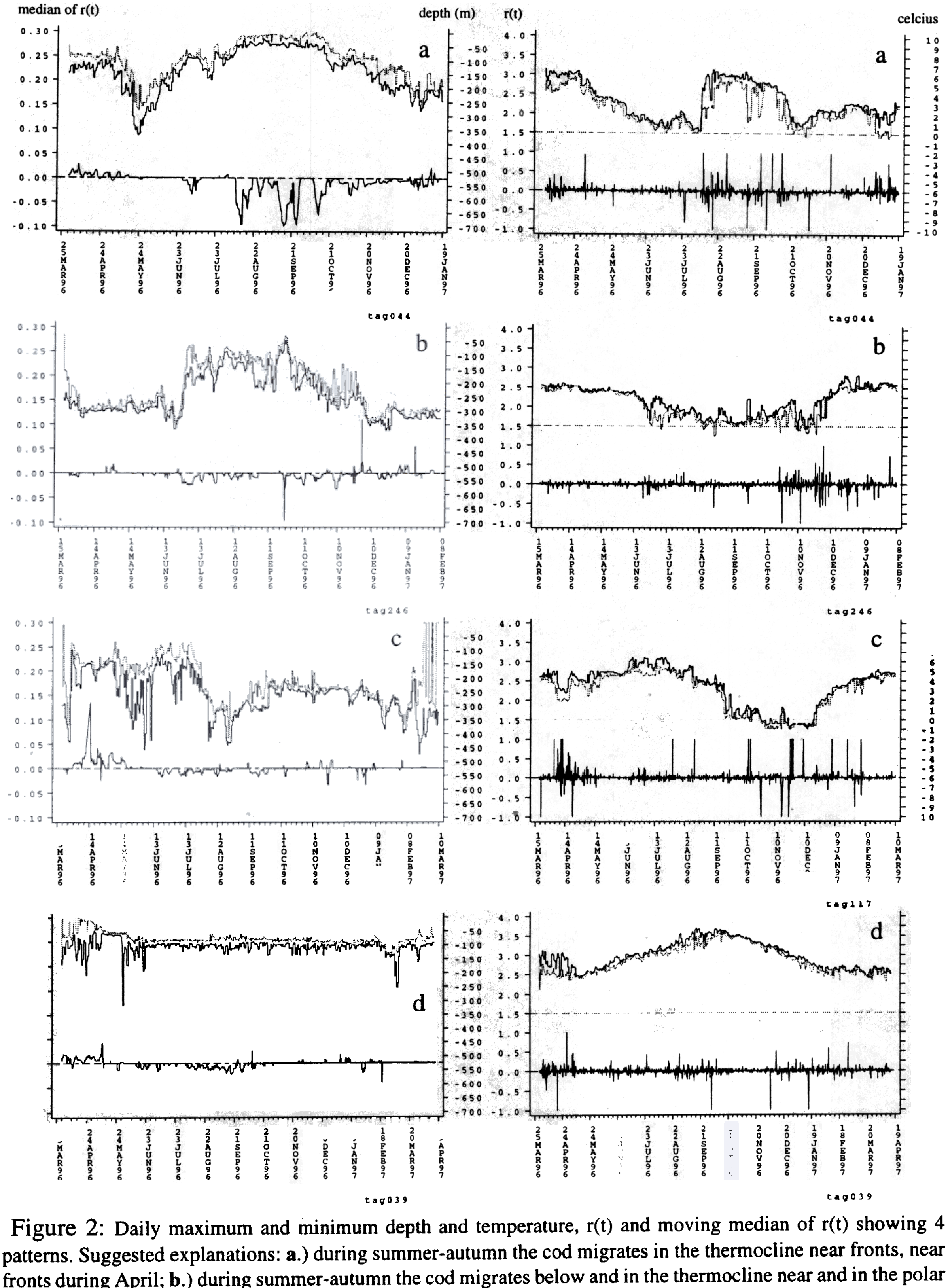
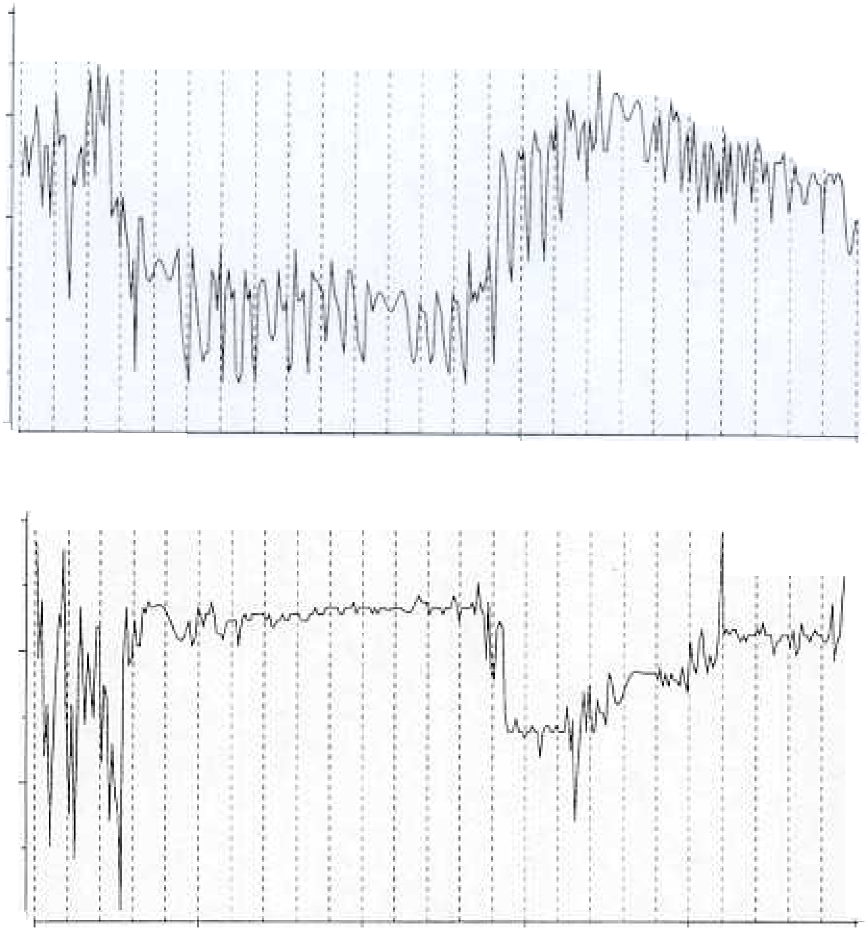


Figure 2: Daily maximum and minimum depth and temperature, r(t) and moving median of r(t) showing 4 patterns. Suggested explanations: **a.**) during summer-autumn the cod migrates in the thermocline near fronts, near fronts during April; **b.**) during summer-autumn the cod migrates below and in the thermocline near and in the polar fronts, occasionally with subzero temperature; **c.**) during summer-autumn the cod migrates in relatively deep waters near and in the polar front, with long period of sub-zero temperature, near fronts during April; **d.**) the cod stays mainly in the same area. The daily maximum depth may indicate the sea bottom depth.

Reference line $0°C$, r(t) and its moving median in degree Celcius per meter, $°C$/m. r(t) is cut off at -1 and 1.



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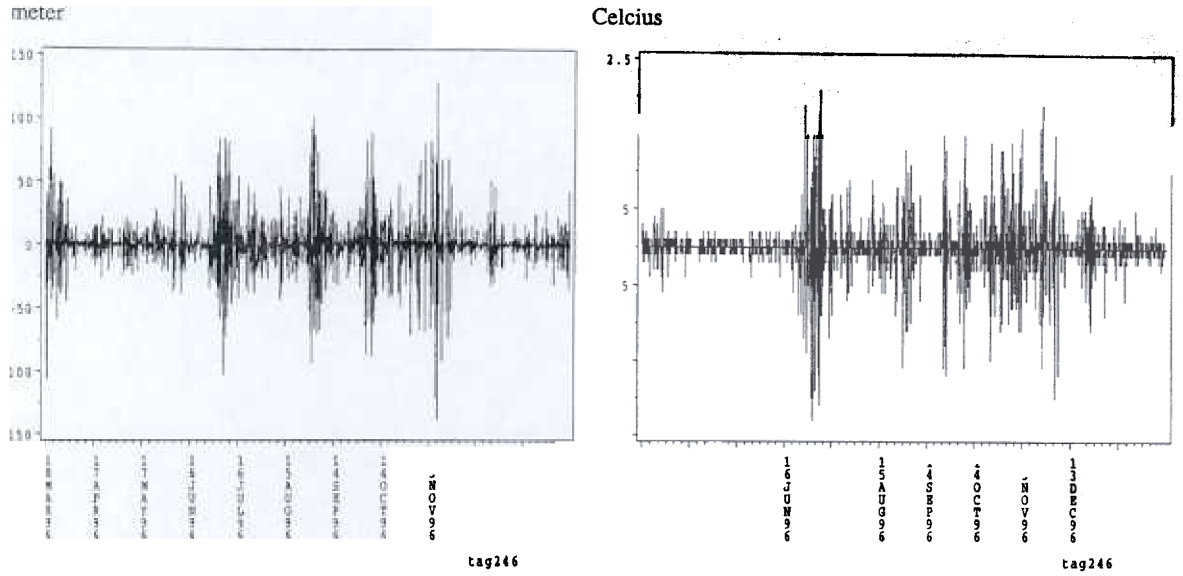
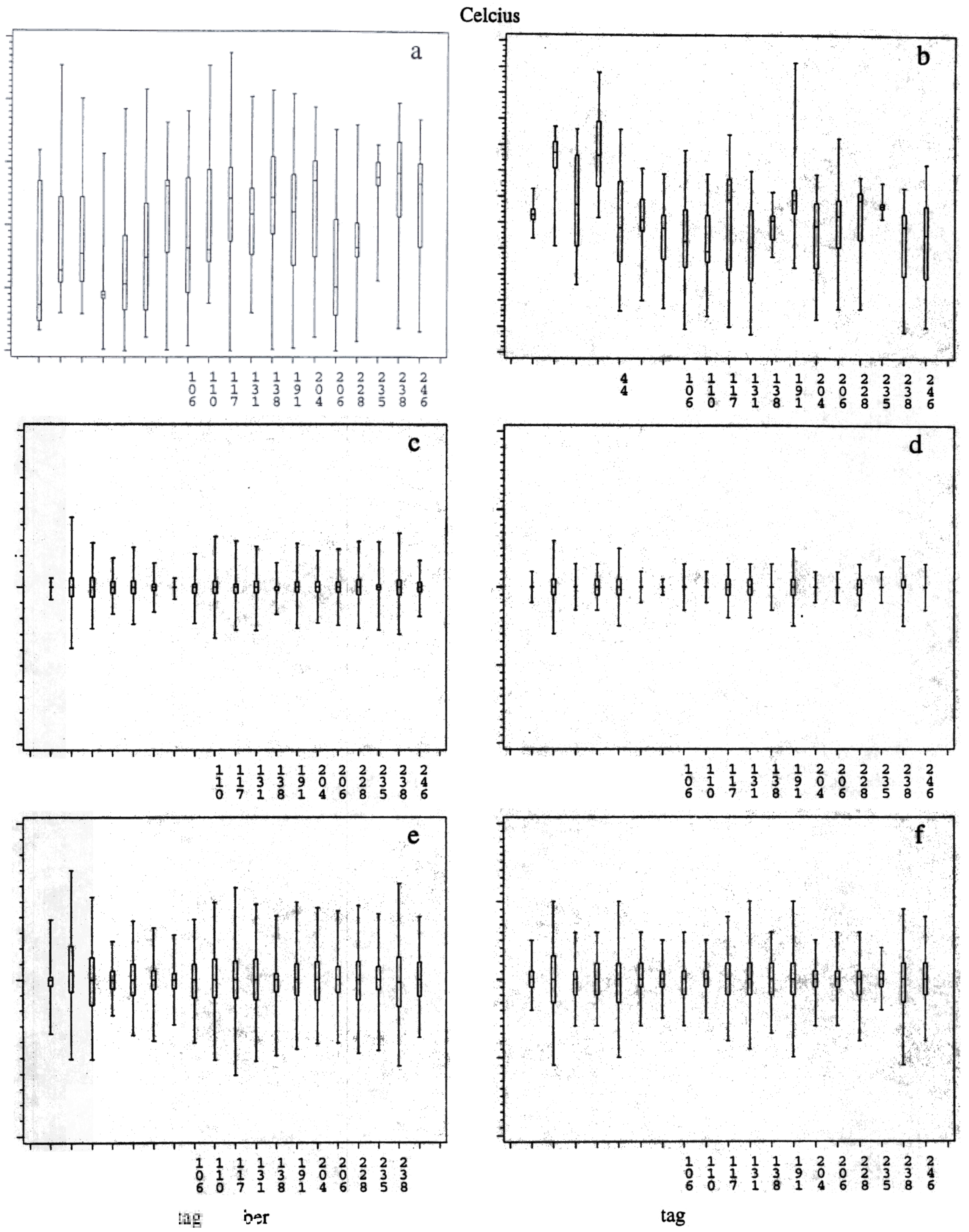


Figure 4: The change of depth (dd(t), left) and temperature (dc(t), right) at each 2-hour period showing time dependent variances and ranges.



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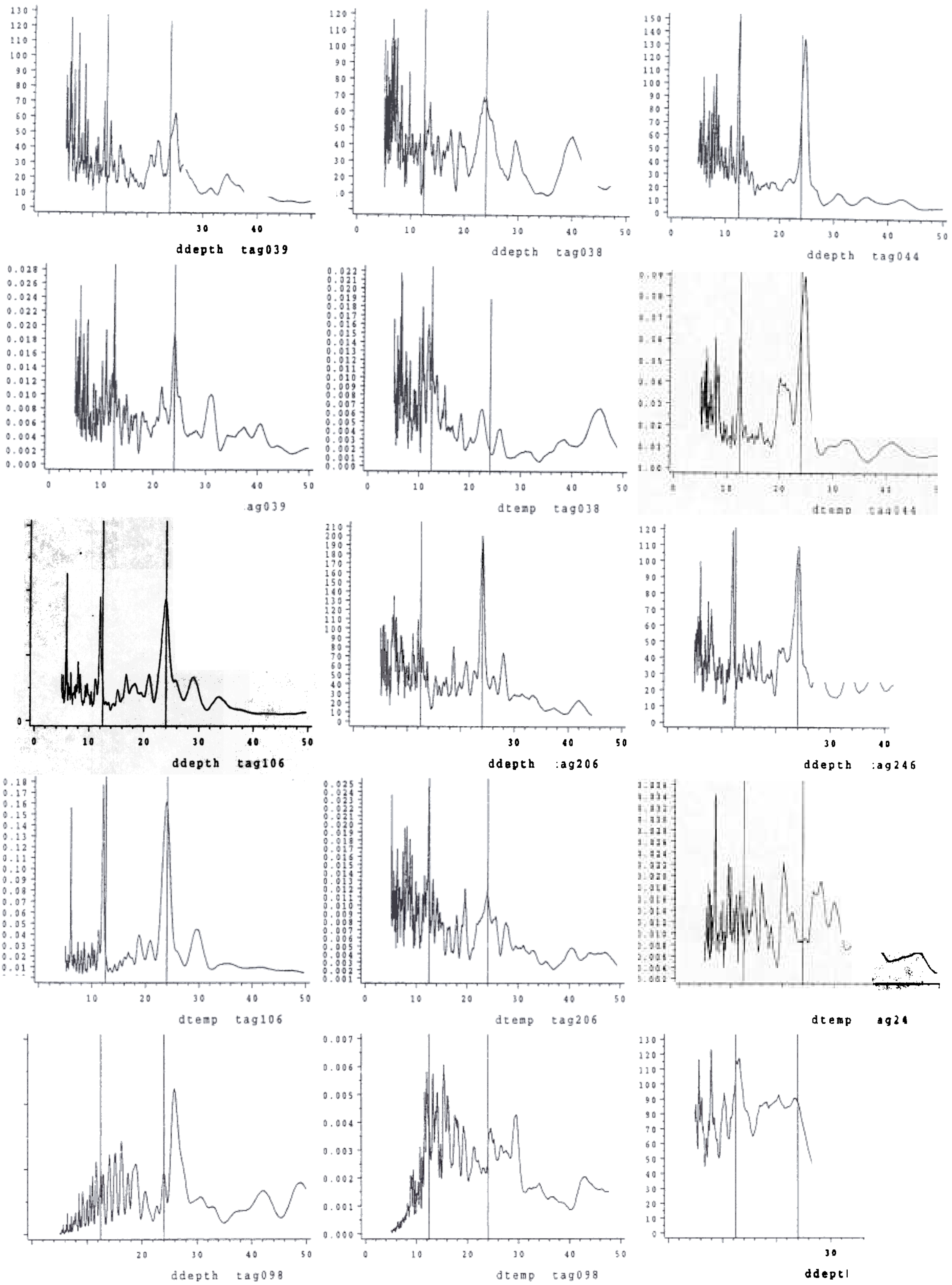
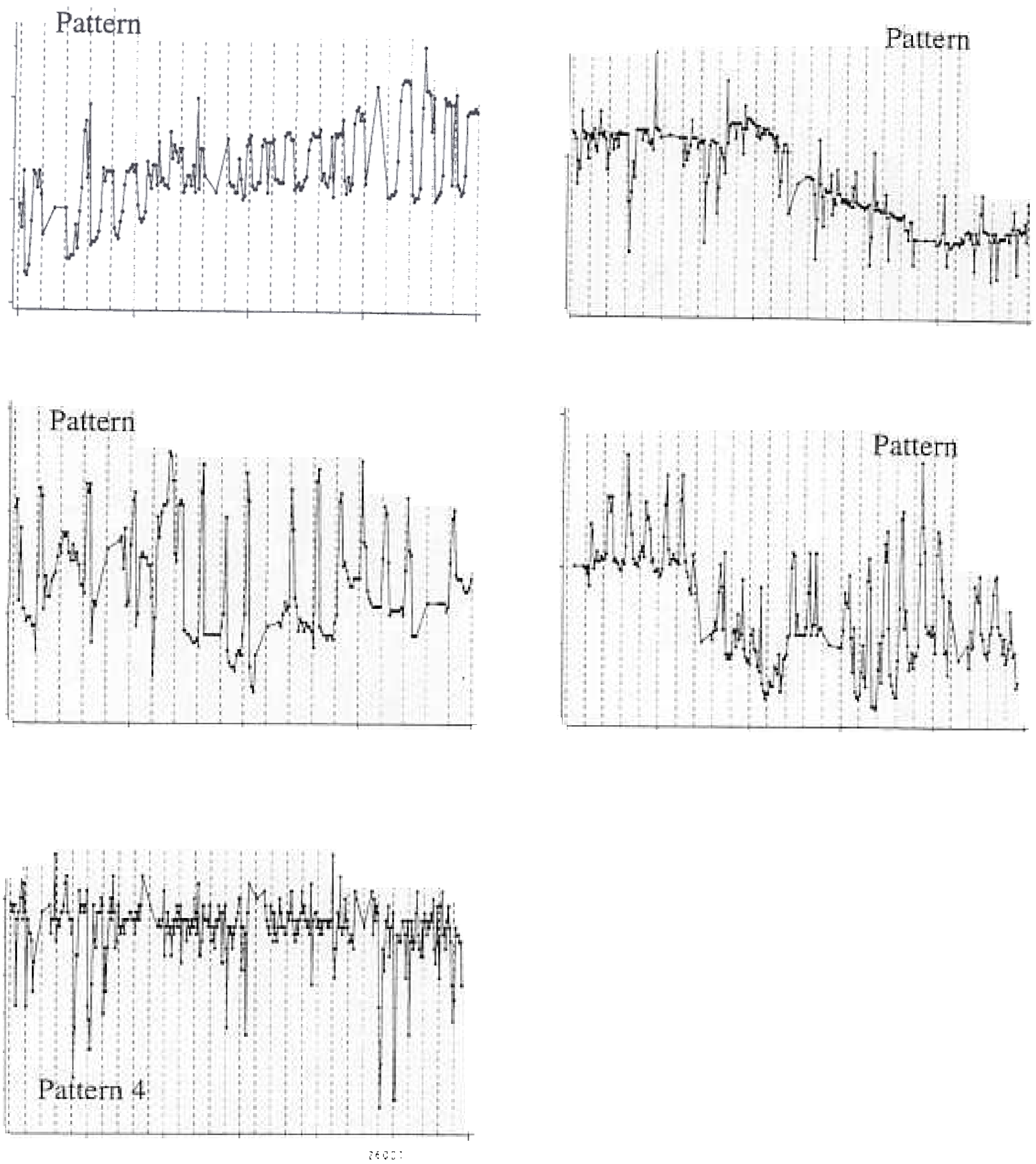


Figure 6: Estimated spectral density distribution in the time series of depth and temperature changes (2-hour periods). Reference lines for 24-hour and 12.5-hour periods.



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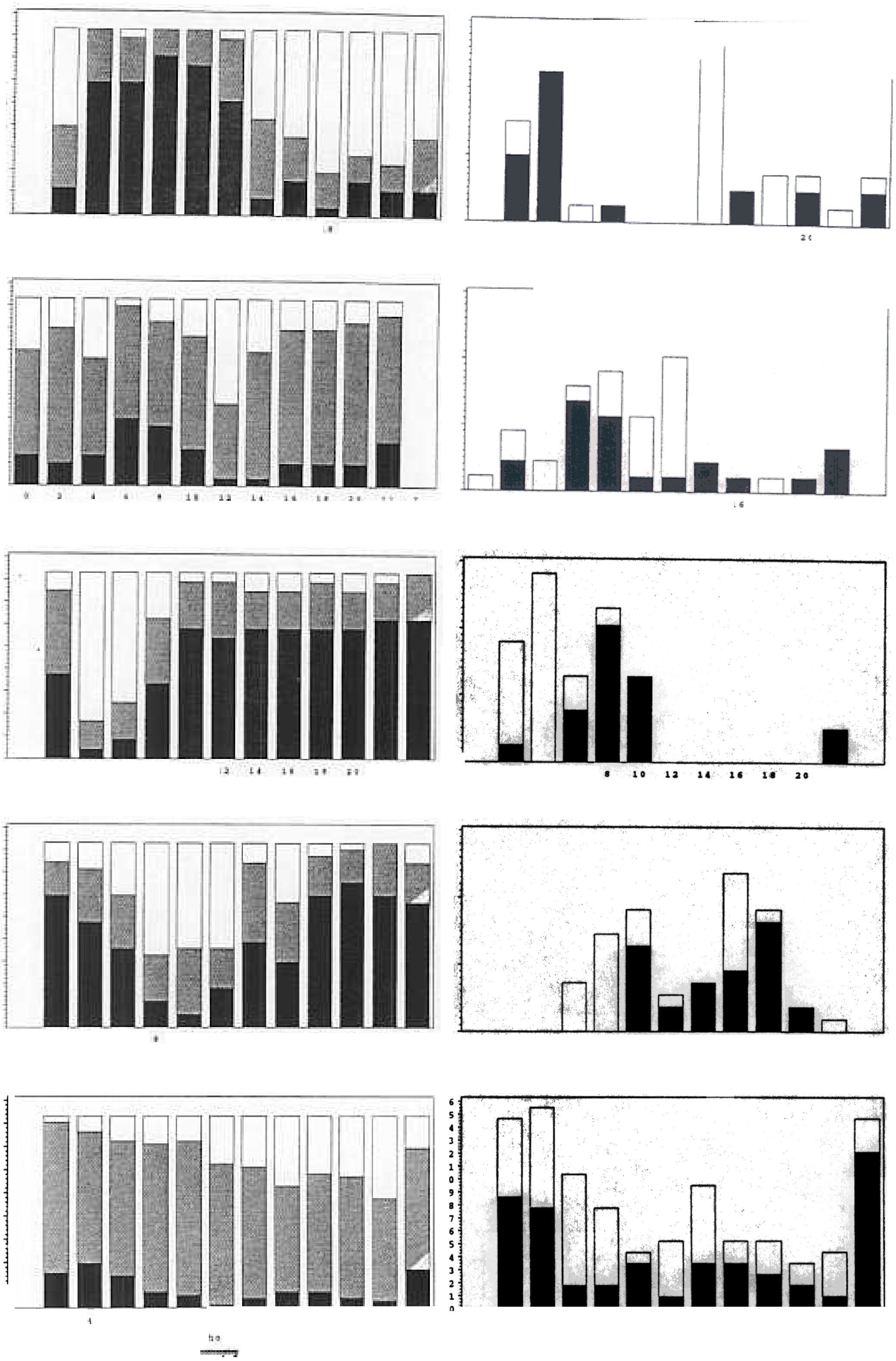

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