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Fish migration in oscillating stratified water masses
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Abstract

Time series records from data storage tag (DST) attached on Northeast Arctic cod (*Gadus morhua* L.) and Greenland halibut (*Reinhardtius hippoglossoides*) are investigated in connection with hydrodynamic and hydrographic features at specific locations to obtain spatial and temporal variation on fish migration patterns, which may change the availability of fish to survey gears. From spring to autumn, some Greenland halibut, at 500-800 m depth, were exposed to a persistent diurnal fluctuation of temperature between subzero and 5.5°C. Tidally induced topographic trapped waves with diurnal (K_1) frequency were indicated in some region along the Barents Sea escarpment, where the transition zone between warm Atlantic water (AW) and cold Norwegian Sea Arctic Intermediate Water (NAIW) is at 500-700 m. An asymmetry in the temperature diurnal pattern showed a gradual increase followed by a rapid drop. This event may be related to the displacement mechanism of stratified water masses together with the fish diurnal migration pattern in synchrony with tidal motion. The pattern indicates that fish migrated seawards off the slope and was pelagic part of the day, thus unavailable to bottom trawl. Up to three weeks in April, some tagged cod had low vertical activity at a depth exposed to semidiurnal tidal fluctuations of the transition layer between 100-200 m, where cold coastal waters flow on top of warm Atlantic waters. Along the southern coast of the Barents Sea, strong semidiurnal tides can generate baroclinic coastal Kelvin waves causing vertical motion of the pycnocline, thus semidiurnal fluctuation of temperature was observed.

Keywords: bottom trapped waves, data storage tag, diurnal vertical migration, Kelvin waves, NE Arctic cod, NE Arctic Greenland halibut, spawning activity, temperature gradient.

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Introduction

Fish of many species have a seasonal migration over a long distance to feed and spawn in certain regions (Neilson and Perry, 1990; Bergstad *et al.*, 1987). Within each season the fish adapt their migration patterns according to environmental conditions and their own physiological needs and limitations. To manage commercial fish stocks, one needs to understand the mechanism of how the fish survive, grow and reproduce in their own natural environment. Data storage tag (DST) records provide some information on the dynamic of fish migration and adaptation in the natural

environment in relation to the thermal stratification of the water mass (Stensholt and Stensholt, 1999). Possible locations of the tagged fish can be discussed in connection with known specific characteristics of the thermal stratification of each region (Stensholt, 2001; Stensholt and Høines, 2006; Neat *et al.*, 2005). Then spatial and temporal variation of the fish activity in accordance with depth and temperature distribution can be coupled to the hydrographic, hydrodynamic, and fish stock survey data in order to assess its impact on the vulnerability and detectability to different types of survey gear. The actual vertical profiles of fish distribution obtained from DST have been used to estimate the fraction of large fish, which were lost in the bottom acoustic dead zone (Stensholt and Stensholt, 2004). Parameters on fish activity related to their actual thermal habitat, which are used in bioenergetics models and individual based models, can be estimated from the combined information (Jobling, 1988; Jobling, 1994; Bevelhimer and Adams, 1993; Hansen, *et al.*, 1993). This, so that we can evaluate and understand the mechanism on how individual fish adapt to survive, grow and reproduce in their chosen habitat. Detailed dynamical information obtained from DST records provides supplementary information for assessment and management of fish stock that is based on the environmental impact on each individual fish. But the accuracy and variance of the estimated parameters depends on the amount of DST records.

Here the depth and temperature time series were retrieved from data storage tag (DST), attached on adult Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*) and adult Northeast Arctic cod (*Gadus morhua* L.).

Northeast Arctic Greenland halibut (Gr halibut) is a deepwater flat fish without swim bladder and spends most of the time at depth deeper than 400 m, with occasional large ascents. The highest concentration of adult Gr halibut distribute along the continental slope at the Barents Sea opening (BSO) while there is lower density distribution in the Barents Sea. Their main spawning grounds are around the Bear Island, and the nursery grounds are mainly north and east of Spitsbergen (Thangstad *et al.*, 2005). The assessment of the stock is based on bottom trawl catch.

Northeast Arctic cod (NEA cod or cod) is a demersal fish with closed swim bladder, and mainly distributes on the shelf at the warm side of the Polar front in the Barents Sea. During winter they migrate to spawn along the northern coast of Norway, with main spawning grounds around Lofoten (Bergstad *et al.*, 1987). The assessment of the stock is based on samples from combined hydro-acoustics and bottom trawl survey.

Vertical movement of cod depends on the rate of secretion and resorption of gas and the relative change of pressure (Harden Jones and Scholes, 1985). Their vertical distribution and buoyancy status may affect the accuracy in density estimation based on hydro-acoustic target strength. To assess the environmental effect on the cod vertical distribution, the vertical activity of cod should be measured based on the relative change of pressure, so that the vertical profiles from various bottom depths become normalized and comparable (Stensholt, 2001; Stensholt *et al.*, 2002; and Stensholt and Stensholt, 2004).

Depth and temperature distribution retrieved from DST reflect the hydrodynamic and hydrographic conditions of the area in accordance with fish migration activities (Stensholt and Høines, 2006). Both species migrated to feed in regions with thermally heterogeneous water, e.g. the Polar front, coastal front, or thermocline. Various patterns of seasonal trends, vertical migration and occasional diurnal vertical migration (DVM) indicate that both species modified their behaviour according to environmental conditions (Stensholt, 2001; Stensholt and Stensholt, 2004; Stensholt

and Høines, 2006). Such modifications over different regions and times cause change in vulnerability and detectability to different types of survey gear. This contributes to bias, variance, and uncertainty in the estimation of fish stock. However, the effect of some migration patterns can be estimated, since the fish modify in accordance with predictable systematic or rhythmic change of environmental conditions such as season, daylight, or tidal cycles.

Here, specific characteristics of thermally stratified water obtained from DST records were analysed and used as a basis for linking data from DST, hydrography, hydrodynamics, and fish stock surveys, so that the effect of spatial and temporal variation of fish activity in relation to environmental conditions can be evaluated and used in the fish stock management process.

Materials and Methods

Data collection

DSTs were attached to adult Gr halibut (DST milli from Star Oddi, Iceland) and NEA cod (DST centi from Star Oddi, Iceland). Three hundred tagged Gr halibut were released on the shelf slope at the BSO toward the Norwegian Sea (Figure 1a) during autumn and winter in 2001, 2002 and 2003 (Table 1). Tagged cod were released at the North Cape bank (N) and around Lofoten (L) in 1996 (Figure 1b). DST milli is designed for depths down to 900 m.

At predefined record intervals the tag records pressure which are converted into depth, $d(t)$, in meters and temperature, $c(t)$, in degrees Celsius. The tags did not record the geographical locations; thus the horizontal movement was unknown. Release and recapture sites are known, and information on the depth temperature distribution in the neighbourhood of these sites is obtained from conductivity, temperature, and depth (CTD; SBE 911plus from Seabird Electronics, inc., Washington, USA) samples. Some records from Gr halibut were terminated long before recapture, possibly the tagged fish descended beyond the pressure limit for the tag.

Since the horizontal movement, the geographical location, and the bottom depth are not recorded, the dynamics of fish activity are instead linked to geographical location by coupling the depth and temperature distribution from DST according to characteristic of hydrographic and hydrodynamic features of specific regions (Stensholt and Høines, 2006). This is possible since the consecutive records from DST are considered to come from the same area or adjacent areas, and because of the short record interval relative to the fish swimming speed and the range of spatial continuity of bottom depth and temperature.

A limited number of CTD samples from hydrographic stations along the continental slope (Figure 2) were collected during scientific surveys of Greenland halibut in August 2002, 2003 and 2004 (Thangstad and Halland, 2002; Thangstad, 2004). They inform about the spatial variation of temperature profiles. However, they give no information about the dynamics of temperature distribution.

Data Analysis

Time series analysis (Priestley, 1981), both on discrete time domain and on frequency domain (spectral analysis) is employed for analysing trend and cyclical patterns in the bivariate time series of depth and temperature. Spectral density distribution shows a partition of the total variation in each time series over the frequency domain, with a significant peak indicating a cycle at that frequency.

To obtain some information about the temperature gradient (its value and angle) in an environment where the fish migrate for a certain duration, Stensholt and Stensholt

(1999) suggested the analysis of the time series of ratio, $r(t)$, between change of temperature and change of depth.

$r(t) = [c(t) - c(t-1)] \cdot [d(t) - d(t-1)]^{-1}$ is defined when $[d(t) - d(t-1)] \neq 0$, where $d(t)$ and $c(t)$ be the depth and temperature record at time t , $t=1, 2, 3, \dots$.

In the geometrical analysis, the vector $\vec{F}$ is the projection of the fish move vector in the time interval $[t-1, t]$ into a vertical plane that contains the temperature gradient, ∇T . Let ϕ and θ be the angle from the downwards oriented vertical depth axis D to $\vec{F}$ and ∇T , respectively. Then $r(t) = |\nabla T| \cdot (\cos \theta + \sin \theta \cdot \tan \phi)$. ∇T and θ are determined by depth and temperature distribution of the area. ϕ is determined by the fish move vector. A horizontal move, i.e. $\phi = 90^\circ$, results in no change of depth and the $r(t)$ is undefined.

The spatial continuity of temperature makes it reasonable to apply the analysis of a single move to the analysis of time series, i.e. a certain period of consecutive moves.

If the ∇T is vertical everywhere and the fish changes depth, then the ratio $r(t)$ equals (in absolute value) the average ∇T between depths $d(t-1)$ and $d(t)$. Since the gradient ∇T points in the direction of fastest temperature increase, i.e. towards warmer waters, the pattern of $r(t)$ will be negative when a warm water mass lie on top of a cold water mass and be positive in the reverse situation. Frequent moves near or across a thermocline, where warm water lies above cold water, gives a negative median of $r(t)$ with absolute value equal the average vertical component of ∇T .

Where ∇T deviates from the vertical axis, fish movements along the isotherm planes give small $|r(t)|$, but crossing the planes with a significant component in the direction of ∇T increases the variance of $r(t)$ (Figure 3). Thus time stretches with a mixture of some unusually large positive and negative $r(t)$ may indicate a relatively large horizontal component of ∇T . This will be the case if the fish migrates across isotherms at a front. Here we use the term “front” for an area with a large horizontal component of ∇T .

If the fish preferred to migrate in an isotherm plane, $c(t)$ is constant and $r(t) = 0$. Thus a small median $r(t)$ may be due to environment (a small gradient) or to such preferential movement pattern.

If the fish stays stationary in a region with fluctuating thermally stratified water the pattern of $r(t)$ becomes a mixture of positive and negative with some very large absolute values, together with small changes in depth level. This fluctuation may be periodic or episodic depending on the sources of the force that generate such motion.

When the changes of depth and temperature are very small, large positive values of $r(t)$ may be over-represented due to technicalities of the tag. The values are registered in discrete steps and the pressure sensor depends on the temperature. In the conversion of pressure to depth, there is a compensation for this dependence according to the calibration of each tag. The over-represented values are predetermined by the calibration parameters.

Coupling the information obtained from analysing the time series of $r(t)$, $d(t)$, $c(t)$, and the moving median of $r(t)$, together with general knowledge of physical oceanography in a specific region, e.g. depth and temperature distribution, regions with topographic bottom trapped diurnal waves, distribution and movement of different water masses, formation and passage of eddies, one may discuss what areas the fish may possibly have been in.

Results

NE Arctic Greenland halibut

The recapture rate was very low. Only 14 tagged fish were recaptured, and most of them along the continental slope further south (Figure 1). Among the 9 tags with records that can be recovered, only 5 tags have records longer than 2 months (Table 1). In two tags (406 and 407) with long records, the sensors had very low resolution, so that only the trend can be seen. Thus most of the detail studies were based on tags 302, 403, and 404. Depth and temperature distributions from all tag records (Figure 4) show seasonal variation.

Seasonal trend

Most fish were released in winter, and were recaptured on the slope, with records of just 1-3 months due to early recapture or to higher pressure than the tag could stand (Figure 5), but three tags (403, 404, and 406) had long records (figure 6a and 6b). The depth and temperature trends show that from late autumn to early spring fish migrated in areas of depth between 350 m and 500 m with temperature mostly above 2°C, depending on the fish. They had low vertical activity, and changes in depth trend may indicate that the fish migrated up and down a slope, staying close to the seabed. Occasionally the fish ascended and shortly returned to the same depth level. Generally fish ascended into warmer water. Occasionally the temperature level might change up to 3°C for a few days, and otherwise the temperature had small variance.

During summer and autumn, the fish migrated in water deeper than 500 m with temperature ranging from -0.5°C to 5.5°C. They had large vertical activity. A few days in August and September, Gr halibut 403 had large ascents and descents of more than 400 m in one hour and with deepest depth registration at 1023 m. Gr halibut 406 had records of 23 months (Figure 6a). The seasonal trend of both depth and temperature in the second year replicated those of the first year. A period of increasing vertical activity begins after migration into an area with depths deeper than 500 m and correspondingly increasing range of temperature. Gr halibut 403 with 11 months' records (6b) showed the fish spent 8 months at depth deeper than 500m and had similar depth and temperature distribution as other fish at these depth levels. The depth trends of the other tags, with short records during winter, confirm that winter generally is a time with low vertical activity, but show that descents to depth deeper than 500 m occur also in winter.

Temperature profiles from the CTD-stations from the hydrographic surveys show spatial variation, each region has specific characteristic features due to the distribution of different water masses (Figure 2). The temperature profile from a DST is compared with the collection of profiles from CTD in order to determine the possible locations of the fish. CTD records from stations along the continental slope (Figure 2a and 2b) show that at depth > 300 m, the temperature decreases with increasing depth. Water on the shelf slope at the SW of Bear Island is warmer than water on the shelf slope west and southwest of Spitsbergen. Further south the water can be 5°C at 600 m depth. In two different regions in the vicinity of the shelf edge, temperature profiles from two neighbour CTD stations, one on the shelf and one on the slope, show that at given depth, the temperature increases in a seaward direction (Figure 2c to 2f).

Diurnal pattern

A time series plot from Gr halibut 403 shows various, persisting diurnal patterns in both depth and temperature from April until the beginning of October. Spectral density distributions of both series (Figure 6c and 6d) show significant peak at 24-

hour period with subsidiary peak at 12-hour period, which is due to non-sinusoidal shape of the individual cycle.

May 6(13)-22 (Figure 7a and 7c) show that Gr halibut had diurnal migration in correspondence with temperature, with the fish staying in shallower and colder water around 18:00 hour and in deeper and warmer water at 6:00 hour. However during the diurnal migration the fish also had large ascents to near 500 m depth (change of depth in 1 hour up to 200m) into warmer water and descended back within the next two hours. The fish is pelagic during the large ascent.

Depth-temperature time series during May 25-31 (Figure 7a and 7d) show that the fish migrated with upward trend from 800 m to 550 m while the temperature oscillated between -0.5°C to 4°C with a 24 hours cycle. The peak of the temperature cycle increased as the fish migrated higher up. The trough of the temperature cycle stayed the same at just below sub-zero, -0.5°C . Similar observations are also found toward the end of April.

The diurnal patterns in depth and temperature, and the pattern of $r(t)$ (Figure 7b) indicate that the fish migrated in a “front” area. A cluster of negative $r(t)$ during 8-20 May indicates that the fish ascended into warmer water. From May 21 to 25, the fish migrated in a “front” area where the temperature decreased as the fish ascended from 800 m to 350 m. Changes of the $r(t)$ pattern indicate that the fish may have migrated into new levels of depth or into a new area with a different composition of water masses.

Depth-temperature time series during 15-30 June give the appearance as if the fish had ascended into cold water to be pelagic during nighttime, with asymmetric rise and fall of the temperature level (Figure 8a). However, the depth-temperature distribution in correspondence with the $r(t)$ time series (Figure 8b and 7c) show that the fish spent half a day (from around 18:00 hours to 6:00 hours) at the same depth level while the temperature increased, from 0°C to nearly 5°C and the $r(t)$ was a combination of very large positive and negative values. This indicates that a thermally stratified water mass fluctuated across the area. Then just before 6:00 hours the fish descended into warmer water (5°C) and after 12:00 hours it ascended and migrated across thermally stratified water to be back at depth around 550 m with colder water of near 0°C at 18:00 hours. Then again it spent the night until morning with very small change of depth, while the temperature continued to increase. Then it descended into warmer water. The rise of temperature during descent caused asymmetry in the temperature cycle. This cycle repeated for several days with variable maximum depth of the day.

During the ascent and descent the $r(t)$ -values were mainly clustered around small positive, indicating fish ascended into cold water, but the mixture of positive and some negative values, indicates that the fish migrated in a “front” area, where the temperature gradient was significantly tilted away from the vertical axis. Once the fish was in cold or warm water, the vertical temperature gradient was low. While the fish remained at the same depth, the $r(t)$ had very large positive and negative values which indicates passing of thermally stratified water across this depth level.

During Aug 1-22 the fish had a daily migration pattern in synchrony with the temperature cycle while the depth trend oscillated over a period of one week (Figure 9a). On the 25th from 17:00 to 0:00 the fish had two large ascents and descents up to 422 m. On the 26th at 7:00 the fish descended to the record depth of 1023.33 m. A depth change of 600 m occurred within 12 hours and the fish ascended into warmer water. At depth deeper than 800 m the diurnal oscillation of temperature ceased. These were repeated again in September (Figure 9c) for a few days. The pattern of $r(t)$ (Figure 9b) indicates that the fish migrated in a “front” area. Changes of average level

of $r(t)$ over a certain period indicates a change in the composition of the water masses where the fish had its DVM, as the change of the depth level and range caused change in the depth and temperature distribution. During August 1-6 the $r(t)$ clustered at a small negative level, during August 7-21 at a small positive level and during August 22-31 at small negative level.

During September to November (Figure 9c and 9d) Gr halibut 403 had DVM occasionally, but the diurnal oscillation in temperature persisted through September and faded out from October to November.

Gr halibut 404 had DVM and was often in shallower depth at night (Figure 10a to 10c) from the time it was released in August but the pattern was different from tag 403. In tag 404, the fish mainly ascended into warmer water and the diurnal patterns of temperature were mostly in correspondence with the DVM. Spectral density distributions of the depth series show a significant peak at 24-hour period with subsidiary peak at 12-hour period.

During November, Gr halibut 404 had low vertical activity, with change of depth trend over several days, a typical observation in winter (Figure 10d). Occasionally the fish ascended (approx. 20 m) and shortly returned to the same depth level. Generally decrease in depth was accompanied by increase in temperature, but during 19 to 25 November, with a gradual reduction in depth trend by 30 m, the temperature dropped temporarily from 3.5°C to 1°C. The $r(t)$ indicates that the fish was in a “front” region and with warmer water on top (Figure 10e and 10f).

Spawning Pattern

A spawning pattern was observed in tags coded 302 (Figure 11a and 11c) and 404. During the peak of spawning season in December, in the midst of low vertical activity, a sudden burst of vertical activity was observed in the two Gr halibut 302 and 404. They had large vertical migration of range up to 150 m in one hour, with high frequency that lasted for one week. They ascended into warm water of temperature up to 5°C, from a bottom depth between 400 m and 650 m, with temperature at seabed between 1.5°C and 3.2°C, depending on depth. Temperature at seabed increased as the fish descended down the slope. This vertical migration went on for three days, then it paused for one day and then it repeated for another three days. During the one day pause the fish may have changed depth and temperature levels. Both tag records show that the events took place near the shelf edge.

Soon after this event Gr halibut 302 was caught on the steep continental slope at 68°50'N (Figure 1 and Table 1) far from the main spawning ground around the Bear Island of most Gr halibut. For the first three days, the fish ascended from 480 m to 330 m with temperature from 2.5°C to nearly 4°C. It paused for one day and changed location. For the next three day the fish descended down to between 550m and 650 m with warmer water, around 3.2°C. From these depths, it ascended up to depths of nearly 380 m with temperature up to 5°C. In the second location the sea bottom was nearly 150 m deeper, the bottom temperature 0.8°C higher, and the temperature at 400 m nearly 1.5°C higher than in the first location.

The pattern of $r(t)$ indicates that the fish spawned in an area with warm water on top (Figure 11b). An average vertical gradient of -0.9°C per 100 m was estimated from the $r(t)$ series. During the period with small change of depth, while the temperature fluctuated around 0.5°C, the $r(t)$ was a mixture with positive and negative values larger than the average vertical temperature gradient. The pattern indicates this fish stayed in an area with fluctuating thermally stratified water.

NE Arctic Cod

The first week of April the immature tagged cod 117 (Figure 12a) had vertical migration between 120 m and 220 m with temperature between 3°C and 5°C. It ascended into colder water. Semidiurnal oscillation of temperature with amplitude of 1°C was observed in April at depth around 150 m. From 7 to 17 April, the depth series oscillated with semidiurnal frequency and low amplitude around a stable depth trend. On 17 April, the cod descended by 30 m into warmer water between 3°C and 5°C. For the rest of the month it slowly ascended back while the temperature gradually decreased. The $r(t)$ series indicates that the cod stayed in an area where cold water was on top and in the vicinity of a thermal front (Figure 12b). Temperature, salinity and density profiles from CTD stations (Figure 13a and 13b) along the Norwegian coast show the presence of a thermocline, halocline, and pycnocline at depth around 150 m, at the interface between CW and AW.

Large fluctuation of temperature between 0°C and 3°C, while the cod stayed at stable depth around 240 m, was observed in immature tagged cod 131 until 19 January (Figure 12c and 12d). Then it had DVM for five days. After that it migrated to 30 m shallower bottom depth where the temperature fluctuated between 0.4°C and 1.2°C. Occasionally it made large ascents. The $r(t)$ series indicates that the cod stayed in an area with fluctuating thermally stratified water (Figure 12d).

Discussion

From spring to autumn, cod generally migrated into regions of shallower depth, but the range of temperature may vary depending on each cod. In general cod had DVM with nighttime ascents in autumn and daytime ascents in winter (Stensholt, 2001). On the contrary the Gr halibut migrated to depths deeper than 500 m with temperatures between -0.5°C and 5.5°C. Also Gr halibut had DVM, but some DVM patterns indicate that the fish migrated in synchrony with diurnal tidal oscillations of thermally stratified water (Stensholt and Høines, 2006).

During winter to spring, both species had low vertical activity with some change in depth and temperature trend, at levels depending on each individual. For most tagged cod, they migrated along stable thermal paths to deeper water, of depth between 200 m and 400 m with temperature from 2°C to 5°C, depending on each individual (Stensholt, 2001). Some immature cod occasionally had DVM with daytime ascent up to 150 m. Hydro-acoustic records shows that cod distributed high in the water column along the Polar front at the warm side with bottom depth deeper than 200 m and where the distributions of cod and capelin overlapped (Stensholt and Stensholt, 2004). Probably they were feeding on prey with DVM, e.g. capelin. Some tag records had stable temperature around 3°C and some had large fluctuation between subzero and 3°C (Stensholt and Høines, 2006). But the tagged Gr halibut migrated along the depth between 350 m and 500 m, and temperature fluctuated with low frequency mainly between 2°C and 4°C. However, during the peak of spawning season in December, two Gr halibut had large vertical migration with high frequency that lasted for one week. Such vertical movement related to spawning has also been described in Pacific halibut and other flat fish (Seitz *et al.* 2003), thus we interpret such activity to be spawning event (Stensholt and Høines, 2006). Both tag records show that the events took place in the region around the shelf edge.

The depth and temperature distribution from tag 302 confirms that in the region around the continental shelf slope the fish could descend into warmer water as well as having large ascents up to even warmer water, while the seabed temperature is colder on the shelf near the edge than on the slope. The temperature profiles from CTD

stations from two regions further north in the vicinity of the upper continental slope also confirm similar characteristics of depth and temperature distribution (Figure 2d to 2f). Thus along the upper shelf slope, a fish swimming seaward from the shelf across the slope could descend into warmer water or ascend into even warmer water. Such conditions exist along the shelf break front (Tomczak, 1998). Such characteristics of depth and temperature distribution are also observed in tag 403 in connection with DVM during summer feeding. This is due to the influence of Norwegian Atlantic Current (NAC) (Figure 14) which flows northward along the 500 m bathymetry.

The Barents Sea is a shelf sea of depth mainly shallower than 500 m (average depth 300 m) with water temperature influenced by inflow of cold Arctic water from the north and northeast and by inflow of warm Atlantic water (AW) along the southern slope of the Bear Island Trough (Loeng *et al.*, 1992, Ingvaldsen *et al.*, 2004) as well as colder and fresher coastal water (CW) flow eastward above AW as a Norwegian Coastal Current (NCC) along the Norwegian coast (Björk *et al.*, 2001) (Figure 14). Thus a large part of the southwest Barents Sea is occupied by warm water of Atlantic origin (Figure 2a to 2d). Cold dense bottom water flows out as gravity current along the Bear Island Trough (Ingvaldsen *et al.*, 2002) and along the deep channel south of Spitsbergen toward the shelf edge, and cascades down the shelf slope (Blindheim, 2004; Fer *et al.*, 2003). In comparison with other seasons, during winter the Atlantic inflow into the Barents Sea is generally higher and the Atlantic domain is displaced northwards, the NCC is narrower and deeper and the water level along the Norwegian coast rises higher (Ingvaldsen *et al.*, 2004). “The water mass distribution and characteristics greatly influence the production processes and the current pattern largely determines the zoogeographical boundaries in the area” (Bergstad *et al.*, 1987).

Narrow regions of high gradient are developed along the boundaries between the different water masses, namely the Polar front region where the AW confronts the Arctic water, and the coastal front region where the AW confronts and flows under the CW. They form a natural boundary for fish distribution depending on sizes and species (Bergstad *et al.*, 1987; Stensholt and Nakken, 2001). The majority of NE Arctic cod distribute in the shelf sea at the warm side of the Polar front. Some stretches of the fronts may be displaced over season and year (Loeng *et al.*, 1992, Ingvaldsen *et al.*, 2004) or may oscillate due to various forces. Within a front region, instabilities due to geotrophic unbalance may cause irregularity of the isotherms and produce eddies.

The fluctuation of temperature between 0°C and 3°C with stable depth at 240 m observed in cod 131, may be due to the cod staying at depth exposed to instability or displacement of the Polar front. The northward displacement of the Atlantic domain during winter at the BSO, occurring due to variation of local or remote wind fields, may cause episodic fluctuation of temperature (Ingvaldsen *et al.*, 2004). In the vicinity of the fluctuating Polar front, the cod could stay close to sea bed with high probability to be within the bottom acoustic dead zone. But it could also change to have DVM and ascend high during daytime and not be vulnerable to bottom trawl.

The phase of M_2 tide propagates eastward along the northern Norwegian coast on the right hand side and with the amplitude increasing toward the coast (Gjevik, 1990; Kowalik and Proshutinsky, 1995), indicating the presence of a coastal Kelvin wave. This generates the semidiurnal vertical motion and causes vertical displacement of the transition layer between CW and AW.

The semidiurnal oscillation of temperature and of depth with low amplitude and stable trend at depth around 150 m was observed in tagged cod 117 and other tagged cod during April. This may be due to the cod staying on a slope at depth exposed to semidiurnal oscillation of the thermocline, created by the transition layer between CW and AW. The depth and temperature records indicate warm water underneath. At depth below the thermocline, around 150 m, the temperature between 3°C and 5°C is typical of Atlantic water. Vertical motion of a thermocline, up and down across the slope, due to variation of water level along the coast, has been observed from fixed hydrographic stations further south along the Norwegian coast (Yttervik and Furnes, 2005). The events of this report were generated by a passing storm, so they only lasted for some days. But in the case of generation by tidal forces, such events will be persistent. In the case of this cod, gradually decreased temperature could be associated with a down-slope flow. As fish stayed at seabed the DST registered the increase and decrease of pressure due to tidal oscillation of the water level at the coast, thus the records of pressure from DST show semidiurnal oscillation with low amplitude. Cod with this pattern, in this kind of environment, may have high probability to be within the bottom acoustic dead-zone.

Toward the Norwegian Sea at the BSO, the shelf break is at depths around 500 m, and the majority of adult Gr halibut distribute along the slope. Here the water of Atlantic origin with temperature between 2°C and 8°C occupies the upper part of the water column down to depth of 500m to 800m, depending on location. Along the shelf slope, the NAC flows over the Norwegian Arctic Intermediate water (NAIW) with intermediate layer from 700 m to 1000 m and temperature from -0.5°C to 0.5°C. Below this is the cold and dense bottom water at depth greater than 1000m (Blindheim, 2004).

Topographic features at the shelf slope can be important in the dynamical mechanisms for generating shelf waves of various frequencies or eddies. This may also determine specific locations along the shelf break where the outflow of cold dense shelf water is large. On the slope at the BSO, continental shelf waves with different frequencies can be present. The driving force of the continental shelf waves is the vorticity gradient across the slope, and the oscillation period depends on the steepness of the slope. Since the steepness of the bottom slope varies along the BSO, the presence of vorticity waves with different frequencies may be expected if the proper forcing is given. Tidal forcing may induce and enhance a vorticity wave with its own frequency when the tidal frequency is close to the natural frequency of vorticity waves. But the decay distance of the current amplification from the slope limits the region of influence. Kowalik and Proshutinsky (1995) and Kasajima *et al.*, (2001) identified the presence of diurnal (K_1 of 23.93 hours period) tidally-induced continental shelf waves on the BSO, that is, on the slope north of the Norwegian mainland around 71°30'N, and south of Bear Island and southwest of Spitsbergen around 75°40'N.

Under the stratified ocean, the vorticity wave will be depth-dependent (baroclinic) and take the form of a bottom trapped wave (Wang and Mooers, 1976). The energy of a bottom trapped wave is confined near the shelf break and the effects are significant on the benthic zone. Topographically trapped vorticity waves with a longer period could also be possible on the gentle slope, but the continuation of the phenomenon only occurs in the case of persistent forces such as the tidal force. When the scale of undulation of the shelf topography is close to the wavelength of a tidal wave component, this may generate and enhance waves with tidal frequency. Wave with K_1

tidal frequency is suggested along the northern part of BSO (Kasajima and Marchenko, 2001).

Fluctuation of temperature in the DST record in the vicinity of the shelf slope may have several explanations.

1. The fluctuation of temperature corresponds to vertical migration of fish, ascending into warmer AW.

2. Low frequency waves that cause episodic fluctuations of the thermally stratified water may occur along the stretch of gentle slope at the release site. The flow of NAC over rough terrain or along the irregular shelf edge and slope may produce eddies (Gascard *et al.*, 2003). The passing of an eddy squeezing against the shelf may lift the permanent thermocline up, bringing cold water onto the shelf, and causing episodic fluctuations of the temperature level (Tomczak, 1998).

3. Variation of the Atlantic inflow through the BSO (Ingvaldsen *et al.*, 2002 and Ingvaldsen *et al.*, 2004) may episodically raise the temperature level on the shelf and the upper shelf slope.

4. Moreover, at depths around 500 m, the drop in temperature to 1°C might be due to the fish approaching a location where cold dense shelf water flows seaward across the shelf break and cascades down the slope. Along the slope at BSO out-flow of dense water mainly occurs west of the Bear Island and Storfjord trough.

5. Bottom trapped waves can be generated by various forces, e.g. tidal as described above. Such forces may lift the permanent thermocline up, bringing cold water onto the shelf, and causing periodic or episodic fluctuations of the temperature level.

All fish were released and recaptured on the shelf slope. The depth and temperature distribution from DST shows that it is in agreement with the hydrographic (Figure 2 and Edvardsen *et al.*, 2006) and hydrodynamic features of the region. Change in trend and variance of depth and temperature over seasons were observed in tag 403 and 406 with long records indicating that over the year Gr halibut migrated to different locations and modified their vertical activities according to environmental conditions. Depth and temperature distributions from Gr halibut 406 indicate that it migrated into and stayed in the western Barents Sea during the winter, spring and early summer. Late summer and autumn, it migrated and stayed at the shelf slope. It repeated the same migration pattern in the second year. This fish migrated in an east-west direction. When Gr halibut 301 and 406 migrated in an area with shallower depth, between 350 m and 480 m, the temperature was mostly between 1.5°C and 4.5°C, a typical temperature on the warm side of the Polar front in the Barents Sea. Similar patterns are observed in tagged cod during winter (Stensholt, 2001). This shows that DST data in general reflect environmental characteristics of the regions. Depth and temperature distributions indicates that during winter Gr halibut preferred to be in warm water and might migrate on the shelf near the shelf edge or in the deep basin in the Barents Sea, mostly on the warm side of the Polar front. Some episodic fluctuation of temperature as described above was observed in DSTs during winter, and during 19-25 November of tagged Gr halibut 404.

From spring to autumn Gr halibut migrated into depth deeper than 500 m and temperature oscillating from -0.5°C to 5.5°C at the depth level between 500 m to 800 m. CTD samples from hydrographic stations in the Lofoten basin south of 72°N indicate that a sharp thermocline between AW and NAIW occurs at these depths, and temperature varied between -0.5°C and 7°C (Edvardsen *et al.*, 2006). The fish had high vertical activity and some fish performed daily migration with different patterns.

Gr halibut 403 may have migrated southward experiencing low frequency fluctuation of the thermally stratified water. By the end of February and in March it

had reached the region where the stratified water oscillates with higher frequencies and near diurnal frequency. In April it entered the region where the topographic bottom trapped diurnal waves are generated (Kowalik and Proshutinsky, 1995) and cause persistent diurnal oscillation of the thermally stratified water, likely to be the transition layer between AW and NAIW. It stayed in the area until the beginning of October, when it departed and migrated into shallower water and experienced a similar low frequency fluctuation of temperature during December to February. It was recaptured on 8 November 2003, 56 km from the release site (Figure 1a). Thus this fish migrated in a north-south direction.

The diurnal pattern, observed in Gr halibut 403 from April to August, is interpreted as a daily migration in synchrony with a diurnal oscillation of thermally stratified water. The depth and temperature distribution from DST agree with the depth and temperature distribution from CTD stations located south of 72°N (Figure 2). During night in the last half of June, the fish stayed stationary in cold water while the descending thermally stratified water passed. Next morning (10-12 hours later) the warm water mass had reached and occupied the location. Then the fish descended into even warmer waters and reached the maximum temperature of about 5°C, which is characteristic of the AW, at the maximal depth of the day. However, there is relatively large variation in the maximal depth together with small increase of temperature during the descent in warm water. We therefore interpret that the fish migrated off the slope and descended to be pelagic in the AW mass and it will not be vulnerable to bottom trawl for half a day. Such situation can occur near the shelf edge and this is demonstrated with temperature profiles from two neighbouring CTD stations near the shelf edge in Figure 2c to 2f. The seaward station registered warmer water at deeper depth. As well as the records from tag 302 confirms such feature exist in the vicinity of the shelf edge. By the time it returned the transition layer might have been lifted up and formed a front, which the fish must swim across and ascended to the same depth, by now occupied by cold water.

We interpret the pattern observed during May from Gr halibut 403 as the fish entering the region where motion of transition layer between AW and NAIW is influenced significantly by the diurnal bottom trapped waves at 550 to 800 m depth. Diurnal oscillation of temperature between -0.5°C and 4°C, during May 1-4 and 25 - 31, is observed in the absence of DVM in the fish activity confirms diurnal motion of thermally stratified water unrelated to diurnal vertical migration of fish. During May 1-4 it migrated down the slope to feed during May 5-24 and during May 25-31 it went back up the slope, and the peak of temperature rise from 3°C to 4°C as fish ascent to shallower depth. The diurnal pattern observed during 13-22 May indicates diurnal migration and being pelagic in connection with feeding activity. Possible explanation is that the fish migrated up and down the slope in synchrony with diurnal fluctuation of the transition layer. A concentration of prey distributed about 100 m higher in the warm AW. Occasionally the fish ascended to reach the prey concentration in warm AW at depth deeper than 500 m.

The diurnal oscillation of thermally stratified water mass is also evident throughout August except for a few days when the fish stayed at depth between 800 m and 1023 m, where the diurnal oscillation of temperature ceased to exist. However, the fish had a few very large ascents into warmer water (Figure 9a). Similar incidents are also observed in mid September. This is further evidence that the diurnal oscillation, observed in the temperature series of tag 403, is caused by bottom trapped diurnal waves, generated and enhanced at the steep slope with stratified water. The energy of a bottom trapped wave is confined near the shelf slope between 500 m and 800 m.

The diurnal pattern observed in Gr halibut 404 seems to be a daily migration up and down the slope with occasional large ascents off the slope into water column. The diurnal fluctuation of temperature is in correspondence with DVM activity, and that the fish ascended into warmer water. Similar DVM pattern was observed in tag 403 during May.

Conclusions

The fish spends much of its time in thermally stratified waters, and patterns in the time series of $r(t)$, which expresses a connection between DST data and the temperature gradient, indicate specific features of the thermally stratified waters. These features form a basis for linking data from DST, hydrography, hydrodynamics, and fish stock surveys, so that the effects of spatial and temporal variation of fish activity in relation to environmental conditions can be evaluated and used in the fish stock management process. However, a reliable representation of fish behaviour in a region depends on the number of DST records.

Greenland Halibut: From spring to autumn, they migrated along the shelf slope at depth between 500 m and 800 m. It increased the vertical activity, occasionally had large ascent and sometime performed DVM. Then part of the day, it would not be vulnerable to the bottom trawl. One tagged Gr halibut performed DVM in synchrony with diurnal oscillations of the transition layer between AW and NAIW, possibly caused by bottom trapped diurnal waves, which are generated in two regions at the BSO. During winter they migrated at depths between 350 m and 500 m with temperature mostly above 2°C. They reduced their vertical activity and occasionally experienced low frequency fluctuations of temperature between 1°C and 4°C. During mid December, possible spawning activity lasting for one week was observed in two tag records at depth around 430 m to 650 m. The fish then had large vertical migration with high frequency and ascended more than 100 m into warm AW.

NE Arctic cod: Tagged cod 117 had very low vertical activity. It may have stayed on a slope along the northern Norwegian coast at the thermocline depth level between 150 m and 180 m, being exposed to semidiurnal oscillation of the transition layer between CW and AW. Tagged cod 131 stayed close to the seabed in vicinity of the fluctuating Polar front, and later it had large ascents during day. During low vertical activity, the cod had high probability to be in the bottom acoustic dead zone.

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Table 1 Release and recapture sites and dates, record interval, months with diurnal pattern

Date of Record start Record end	Tag no	Code	Record interval	Release		Recapture		Distance between (km)	Days at Sea	Age	Sex	Spawning	Diurnal Depth	Diurnal Temperature
				Latitude	Longitude	Latitude	Longitude							
12.08.2003 10.01.2004	3760	404	10 min	7250	1444	7240	1446	18.5	263			Dec	Aug-Oct	Aug-Oct Correspondence to depth
08.12.2002 07.11.2003	3796	403	1hr	7300	1500	7330	1516	56.2	334	11	F		Apr-Aug, part of Oct	Apr- 8 Oct clear
08.12.2002 01.01.2003	3797	402	1hr	7300	1500	6849	1250	471.4	184					
12.12.2002 30.12.2002	3905	401	1hr	7250	1500	6903	1339	423.2	178	10	F			
08.12.2002 20.12.2002	3956	302	1hr	7300	1500	6850	1252	469.3	198	7	M	Dec		
13.12.2002 29.12.2002	4219	405	1hr	7300	1530	6723	859	669.7	198	11	F			
13.12.2002 21.02.2003	4227	301	1hr	7300	1530	7125	1632	179.4	185		F			
30.11.2002 17.10.2004	1M39 51	406	1 hr	7330	1520	7355	1545	48.1					Occasionally Jul-Sept	Correspondence to depth
12.08.2003 10.01.2004	3M37 76	407	10 min	7250	1444	7211	1544	79.6					Sept-Nov	
03.12.2002	4245			7350	1530	6842	1228	580.4	564	17	F	unrecover		
11.12.2002	4268			7255	1500	6922	1443	394.6	561	13		unrecover		
11.12.2002	4283			7255	1500	7030	1830	294.8	541			unrecover		
12.12.2002	3911	0		7250	1500	6959	1644	322.5	546			unrecover		
22.09.2001	445	1		7245	1452	7355	1515	130	414		F	unrecover		

Figure description

Figure 1 (a) Greenland halibut: release sites marked with red plus and recapture sites marked with blue dot on bathymetry map of the continental slope at the BSO. (b) NE Arctic cod: release sites marked with red N (L) and recapture sites marked with red (blue) dot on bathymetry map of the Barents Sea.

Figure 2: (a), (c), and (e) Location of CTD stations on bathymetry map together with (b), (d), and (f) their corresponding vertical profiles of temperature. Both are grouped in corresponding colors. Data are from scientific surveys in August 2002, 2003 and 2004. Two red stations in (c) 34 km apart and in (e) 27 km apart. The seaward station registered warmer water.

Figure 3 Pattern of simulated $r(t)$ time series. The simulation used random positions for a fish migrating through areas where the temperature gradient gradually deviates away from the vertical axis as indicated in five colours. Left hand side shows situation when warm water mass lies on top of cold water mass. The right hand side shows the reverse situation.

Figure 4 Greenland Halibut depth and temperature distribution over different seasons, derived from tag records attached on nine Greenland Halibut. Colours indicate the months.

Figure 5 Depth (black) and temperature (red) time series from Gr halibut 301, 401, 402, and 405 during winter.

Figure 6 Time series of depth (black) and temperature (red) from Gr halibut (a) tag 406. The second year replicated the seasonal trends and seasonal variation. (b) tag 403. Spectral density distribution of time series from tag 403 from April to 8 October (c) change of depth and (d) change of temperature.

Figure 7 (a) Time series of depth (black) and temperature (red) from Gr halibut 403 in May. (b) Time series of $r(t)$ (black dot) and change of depth over a record interval (red line). (c) and (d) Depth and temperature plot with consecutive records connected by line, clockwise progression. Large dots mark six hour; Black at 0:00; Green at 6:00; Red at 12:00; and Blue at 18:00. Green line mark midnight local time.

Figure 8 (a) Time series of depth (black) and temperature (red) from Gr halibut 403 in June. (b) Time series of $r(t)$ (black dot) and change of depth over a record interval (red line). (c) Depth and temperature plot with consecutive records connected by line, clockwise progression. Large dots mark six hour; Black at 0:00; Green at 6:00; Red at 12:00; and Blue at 18:00. Green line mark midnight local time.

Figure 9 Time series of depth (black) and temperature (red) from Gr halibut 403 in (a) August, (c) September, (d) October and (b) Time series of $r(t)$ (black dot) and change of depth over a record interval (red line). Green line mark midnight local time.

Figure 10 Time series of depth (black) and temperature (red) from Gr halibut 404 in (a) August, (b) September, (c) October, (d) November. (e) And (f) Time series of $r(t)$ (black dot, with blue plus for some large positive $r(t)$ due to predetermined calibration

parameters of the tag) and change of depth over a record interval (red line). Green line mark midnight local time.

Figure 11 Spawning activity in December (a) Time series of depth (black) and temperature (red) from Gr halibut 302. (b) Time series of $r(t)$ (black dot) and change of depth over a record interval (red line) (c) Depth and temperature plot with consecutive records connected by line. Large dots mark six hour; Black at 0:00; Green at 6:00; Red at 12:00; and Blue at 18:00. Green line mark midnight local time.

Figure 12 (a) and (c) Time series of depth (black) and temperature (red) from NE Arctic cod 117 and 131 (b) and (d) Time series of $r(t)$ (black dot) and change of depth over a record interval (red line) from cod 117 and cod 131. Green line mark 0:00 GMT.

Figure 13: (a) Location of CTD stations on bathymetry map together with their corresponding (b) temperature profiles; (c) salinity profiles; and (d) density profiles. The CTD stations and profiles are grouped in corresponding colors. Data are from scientific surveys in February-March, 1996.

Figure 14 Bathymetry map of the Nordic Seas with the schematic movement of the warm AW in red, the cold Arctic water in blue, and the cold CW in green.

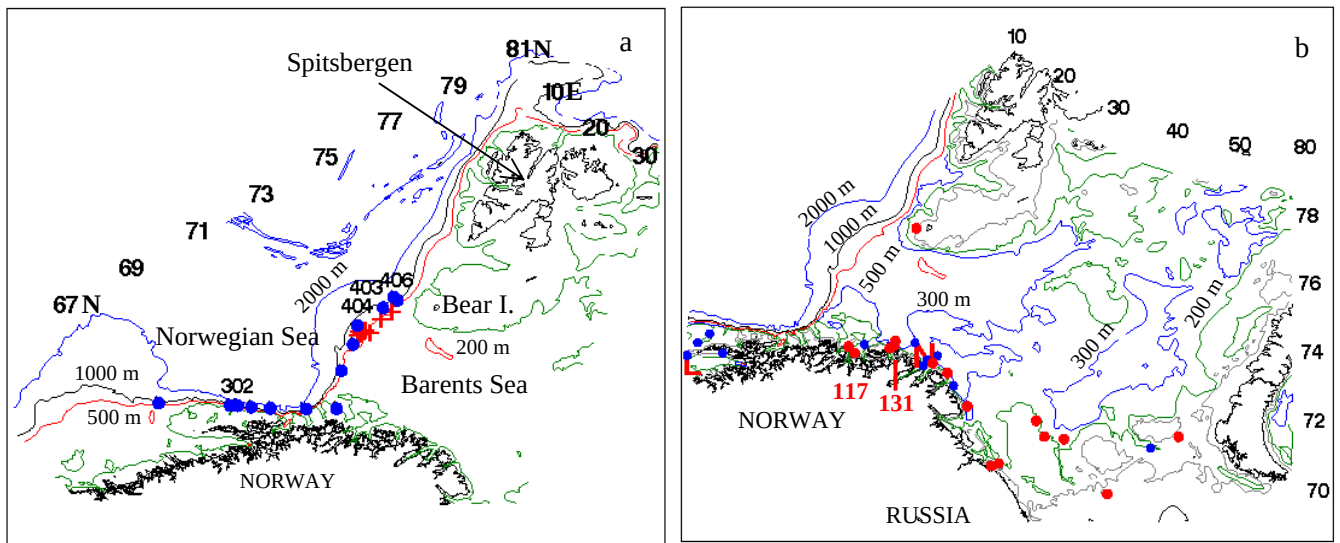


Figure 1

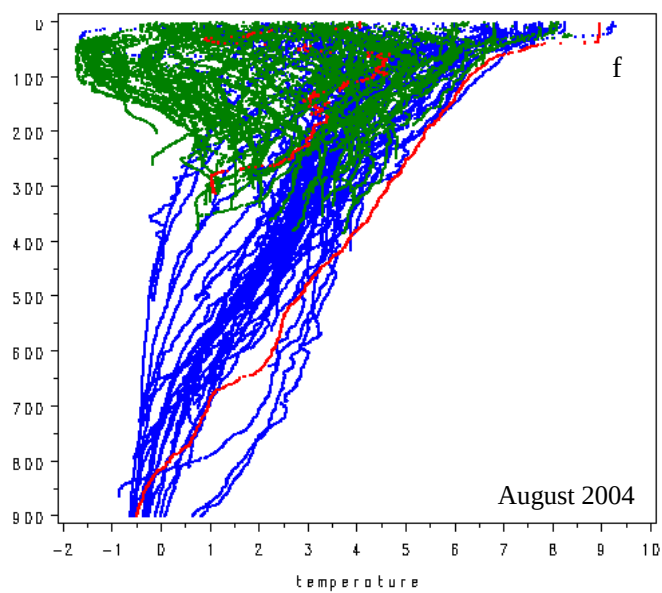
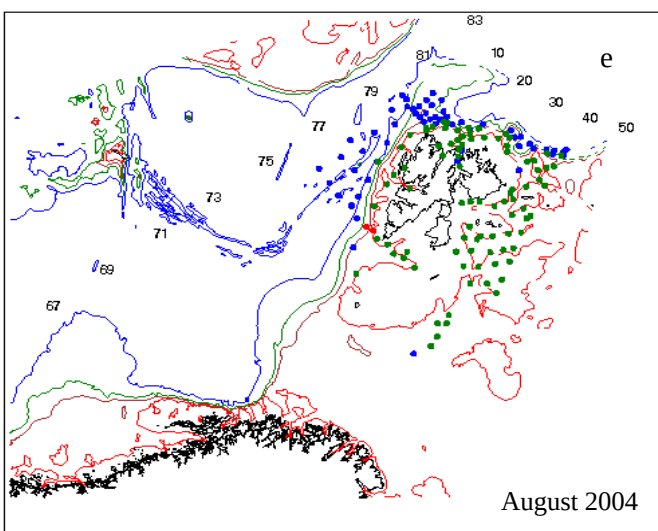
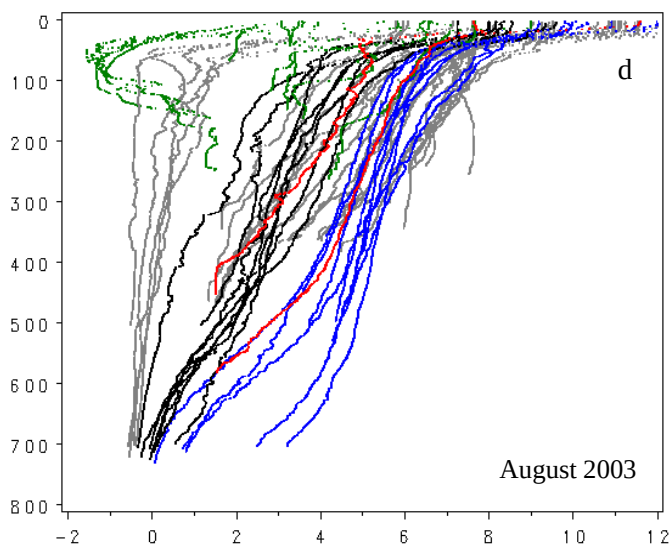
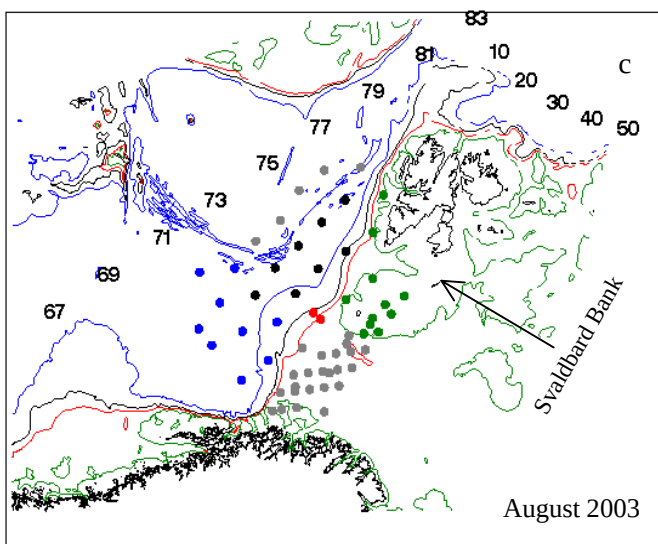
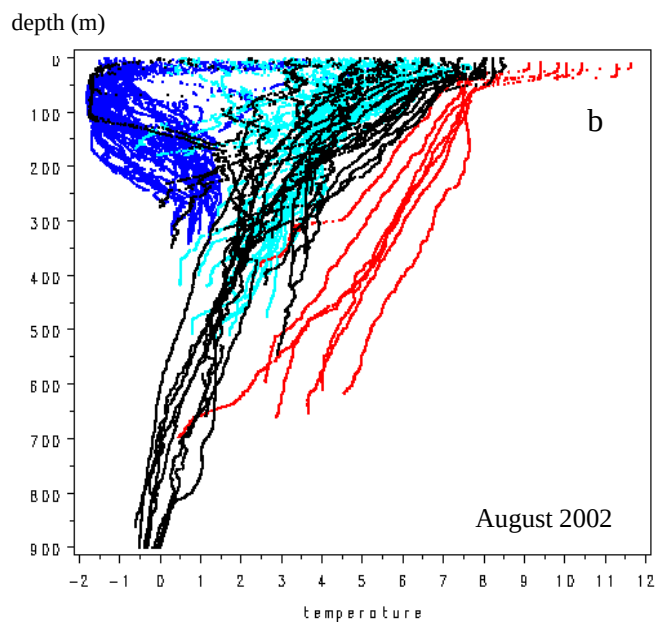
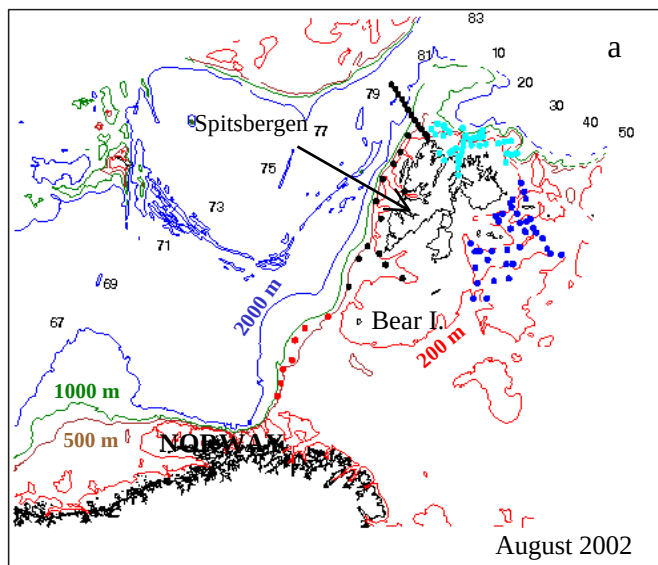


Figure 2

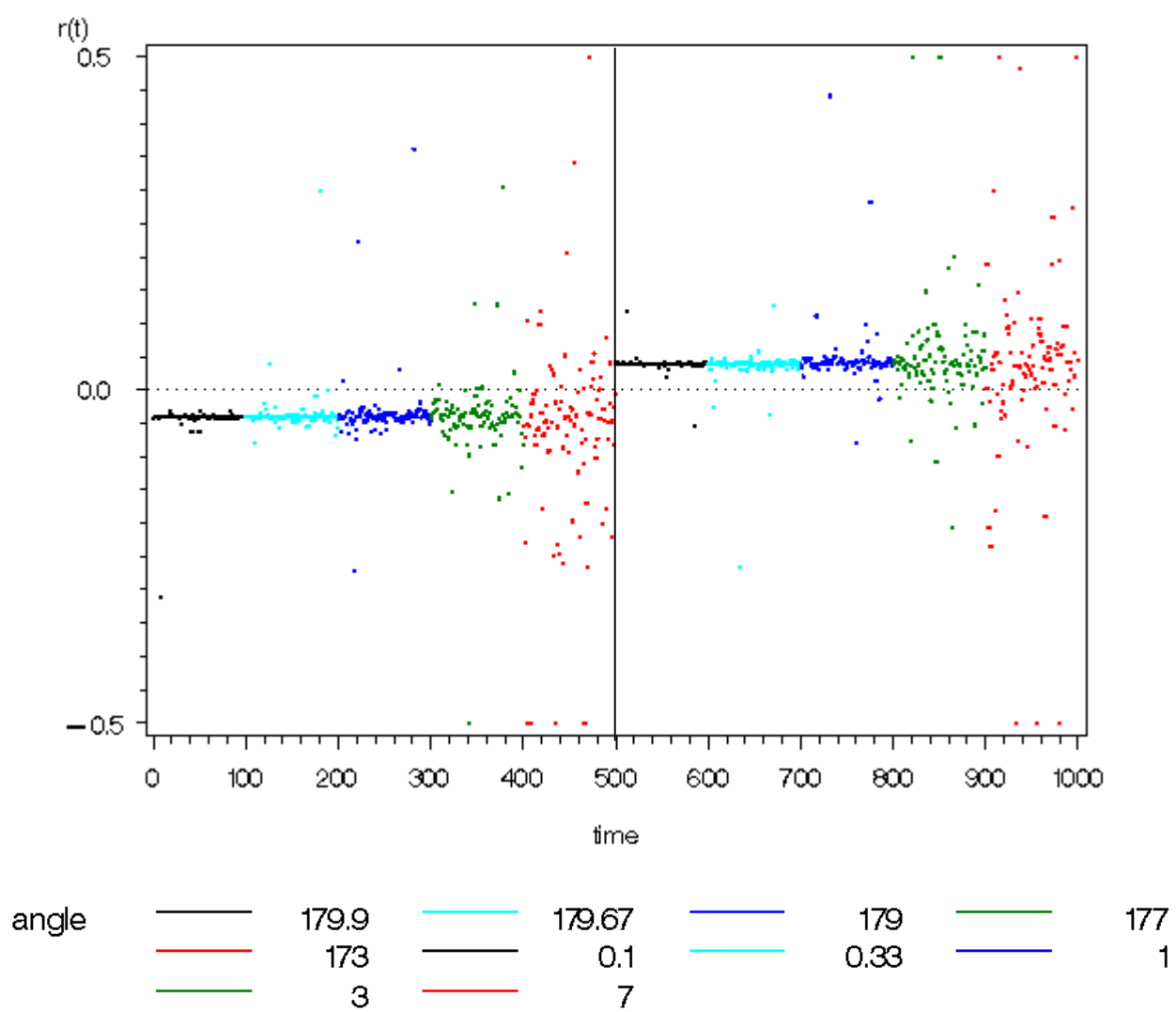


Figure 3

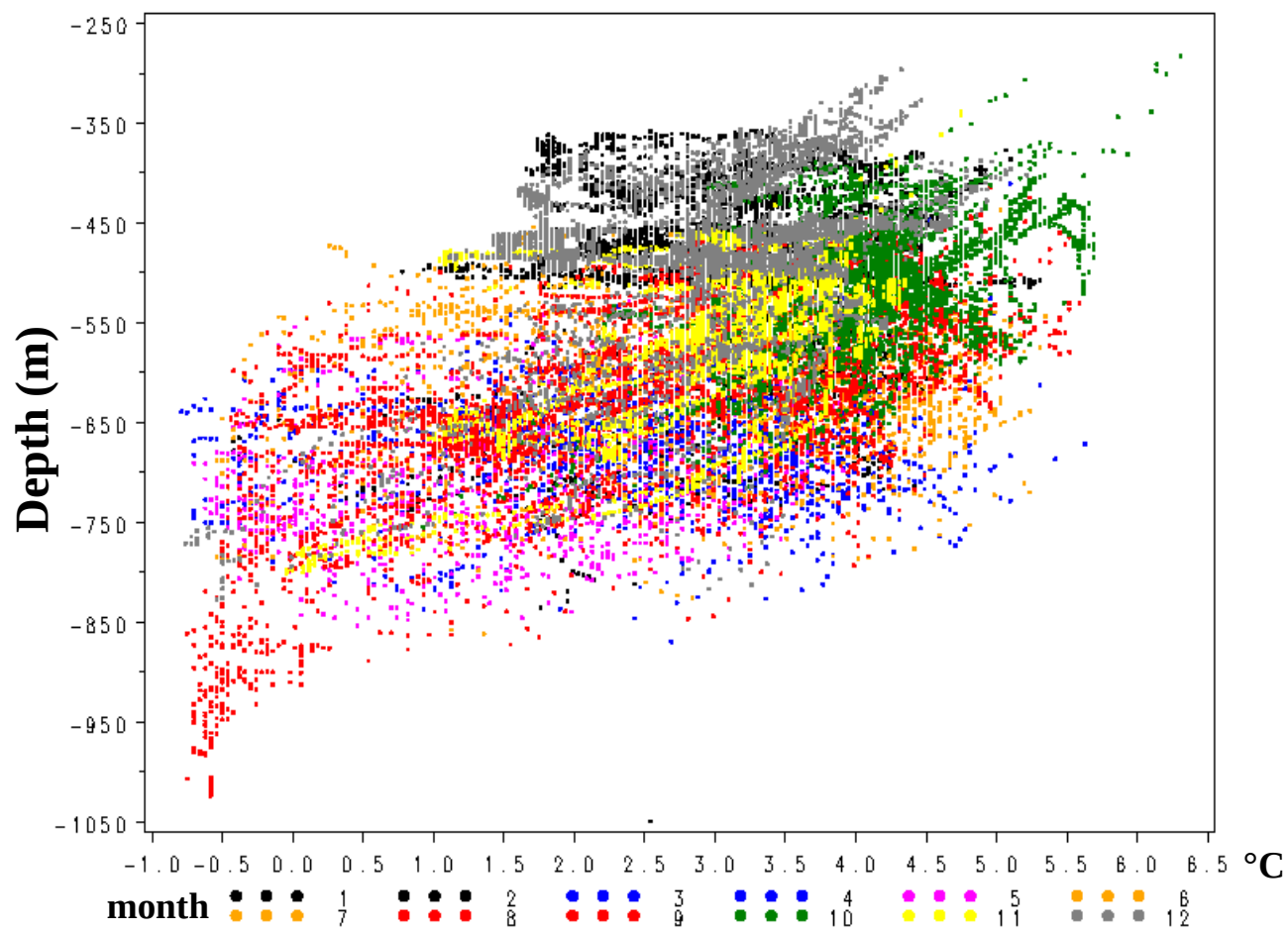


Figure 4

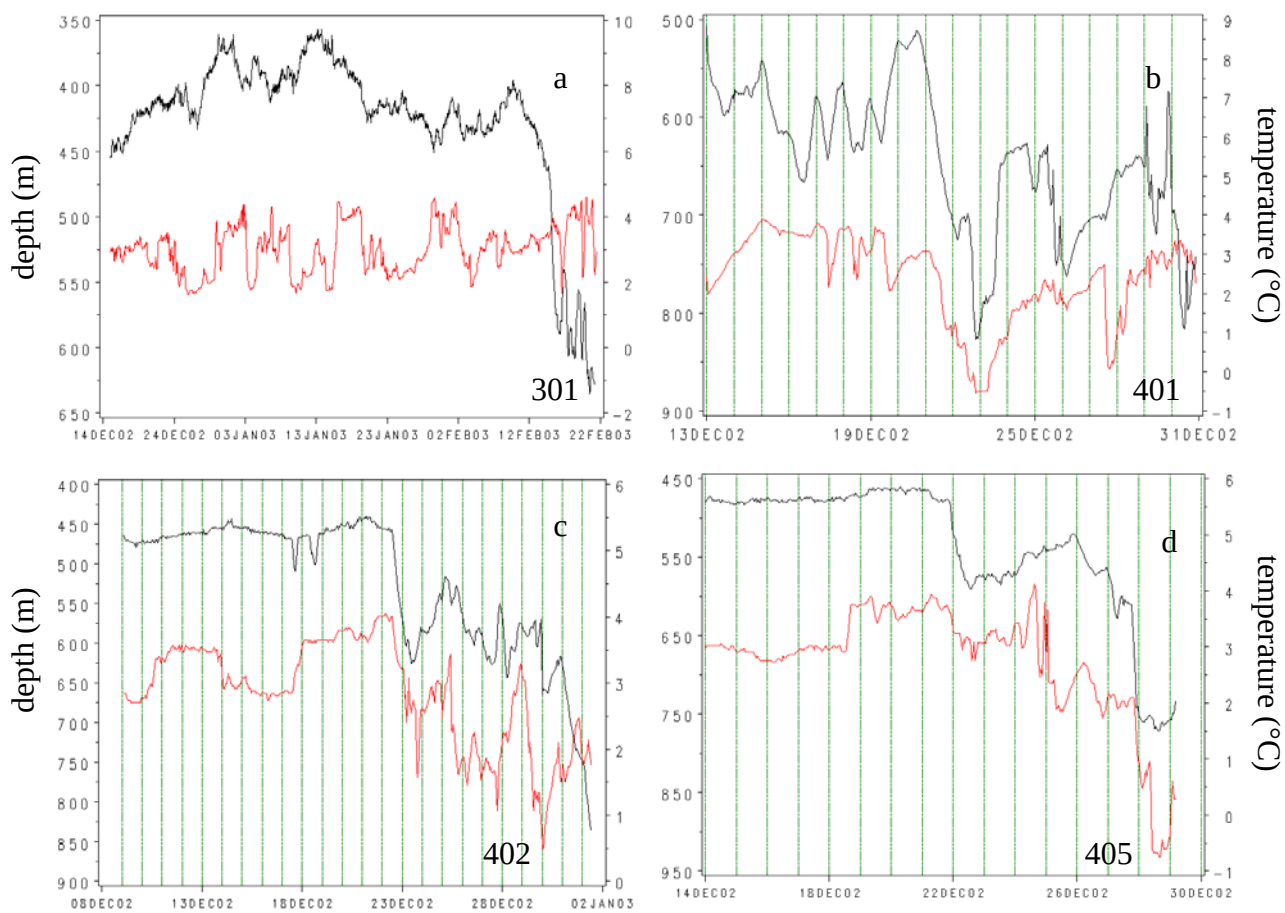


Figure 5

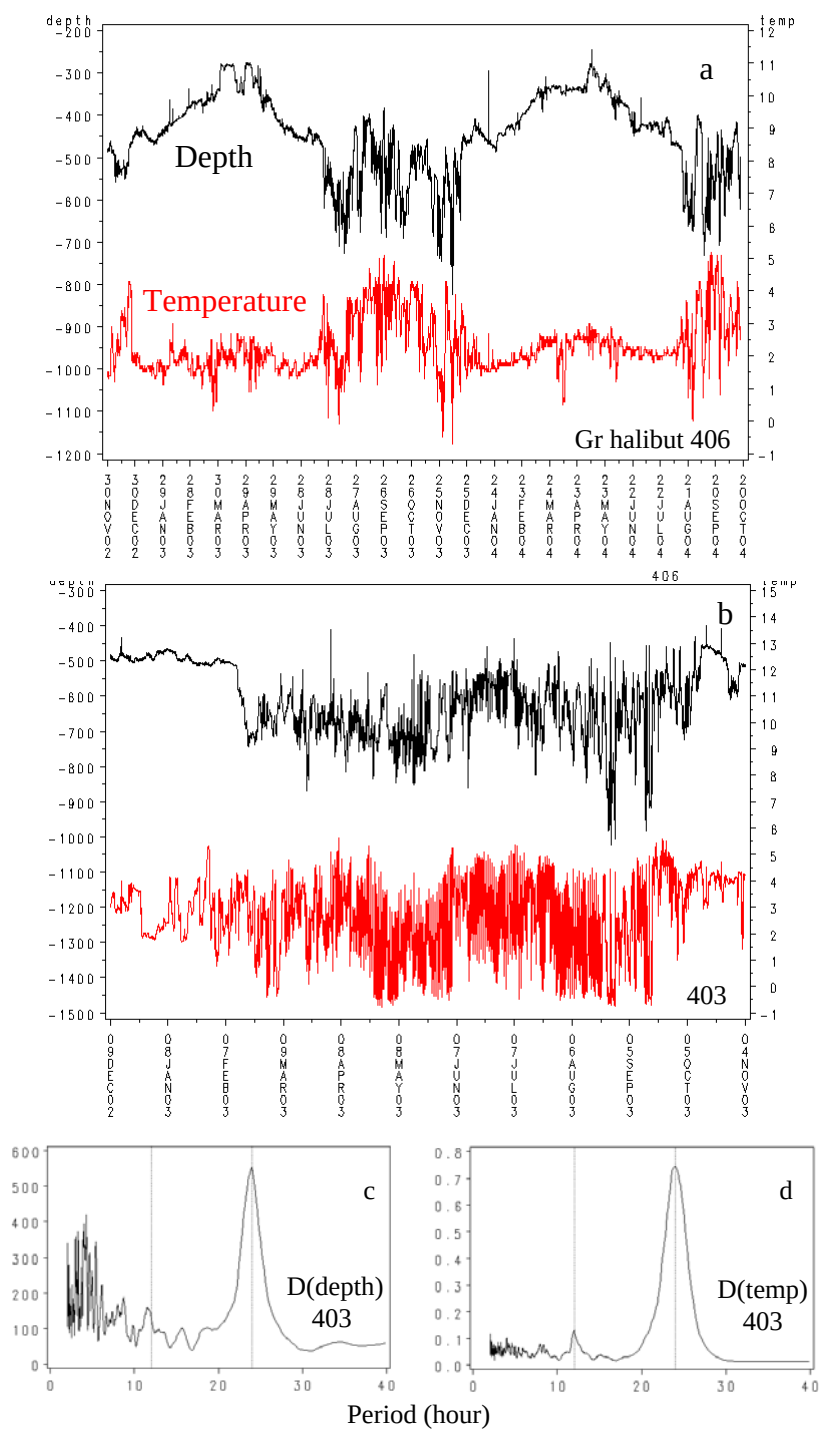


Figure 6

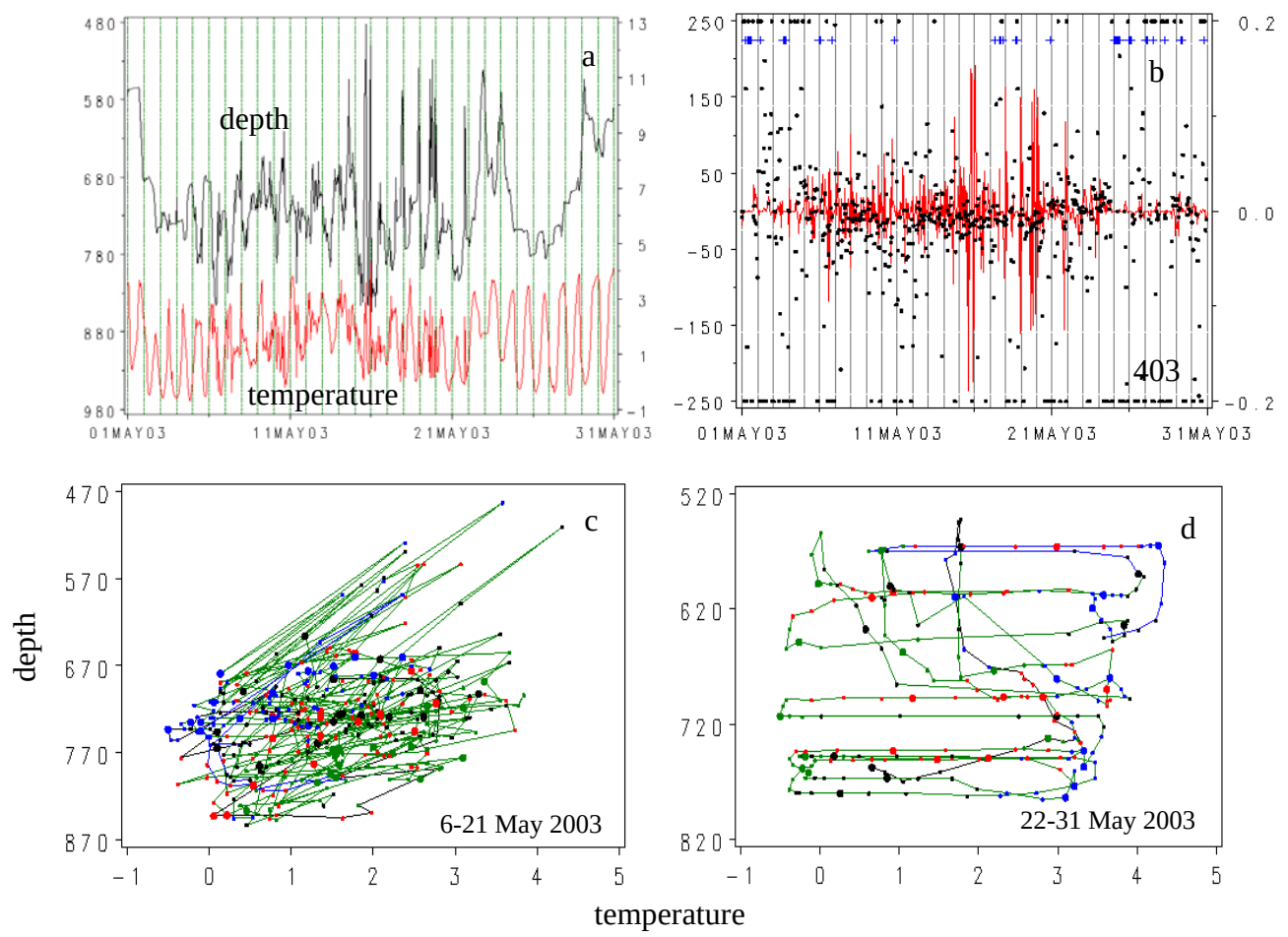


Figure 7

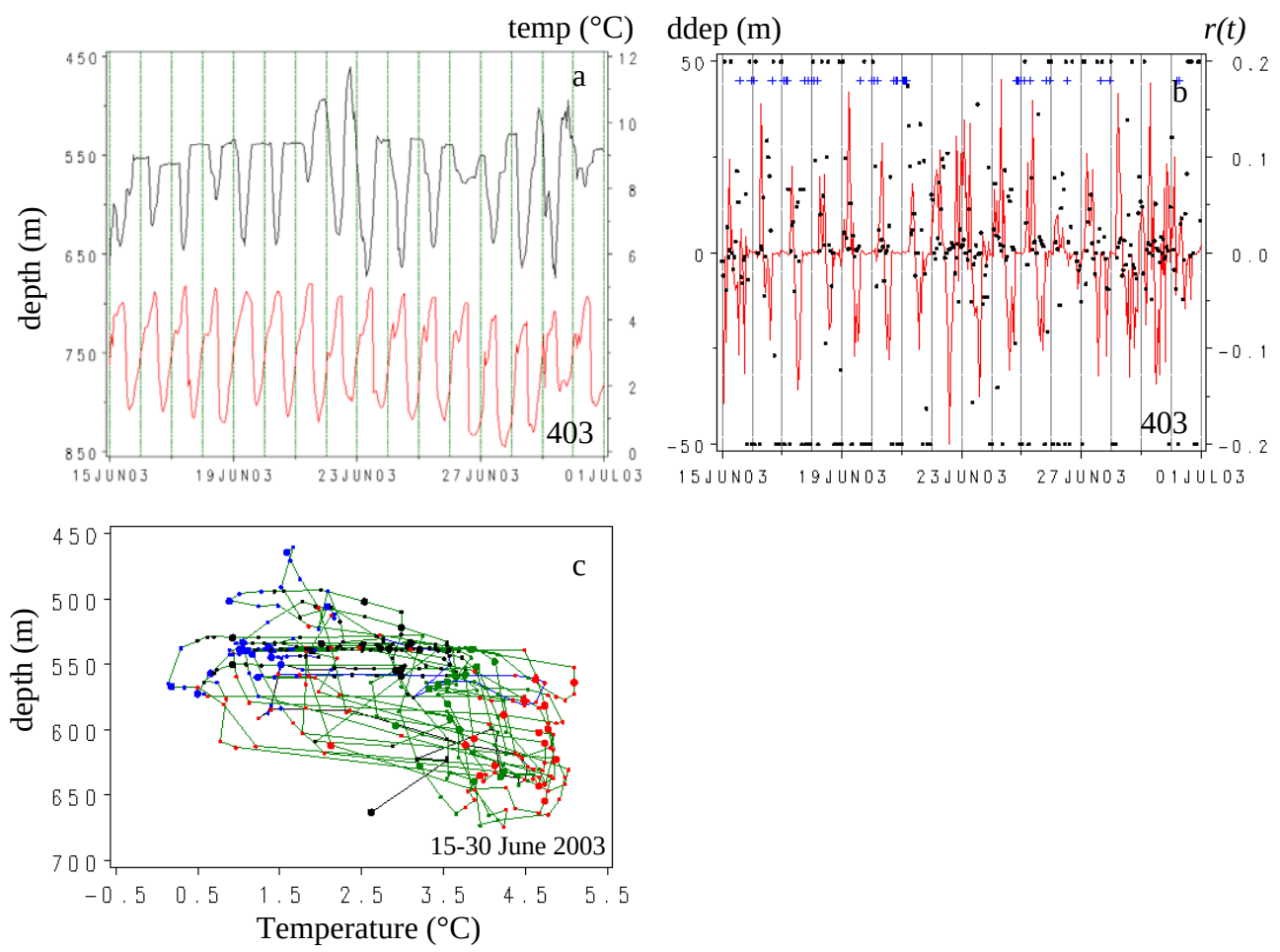


Figure 8

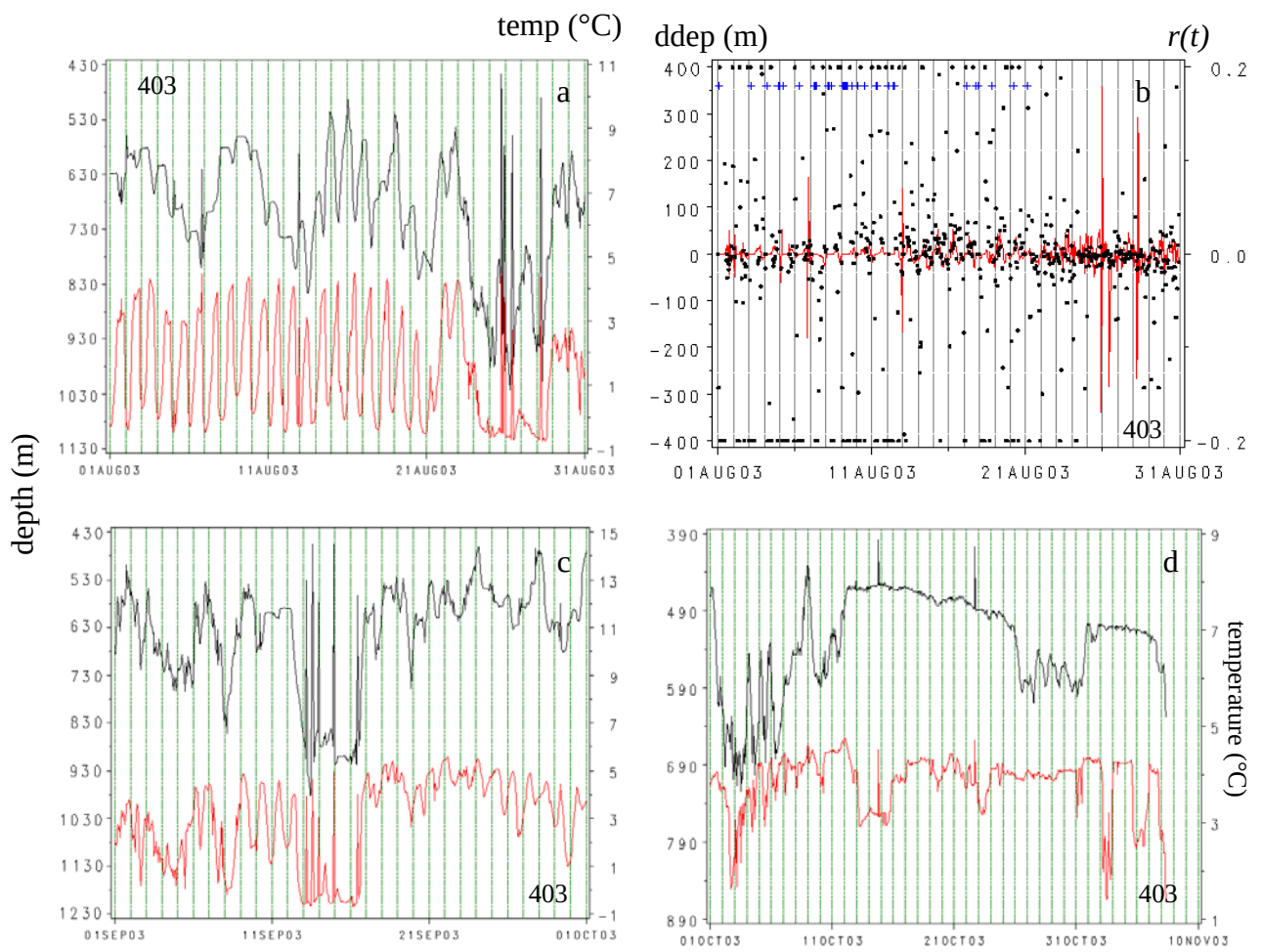


Figure 9

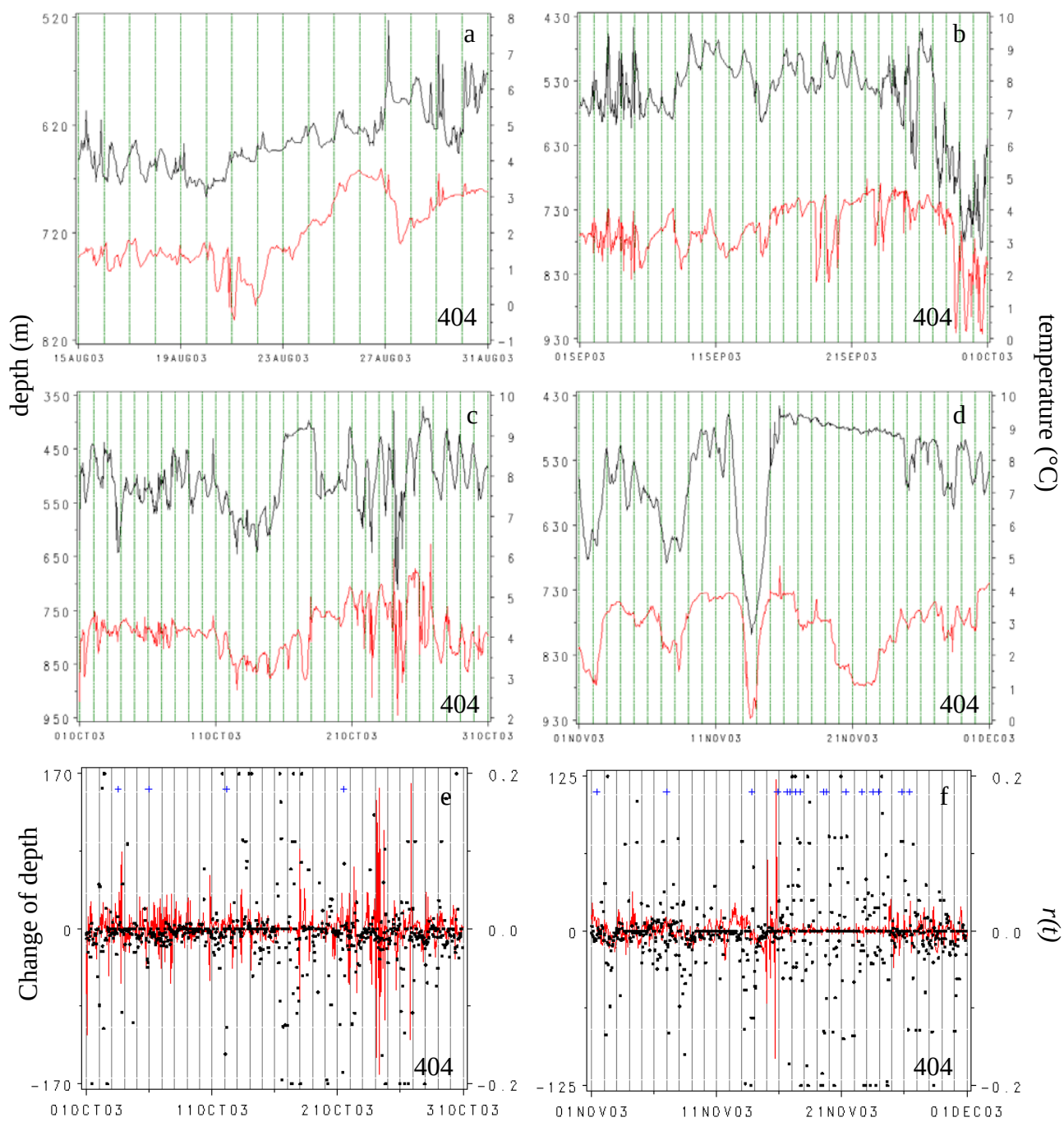


Figure 10

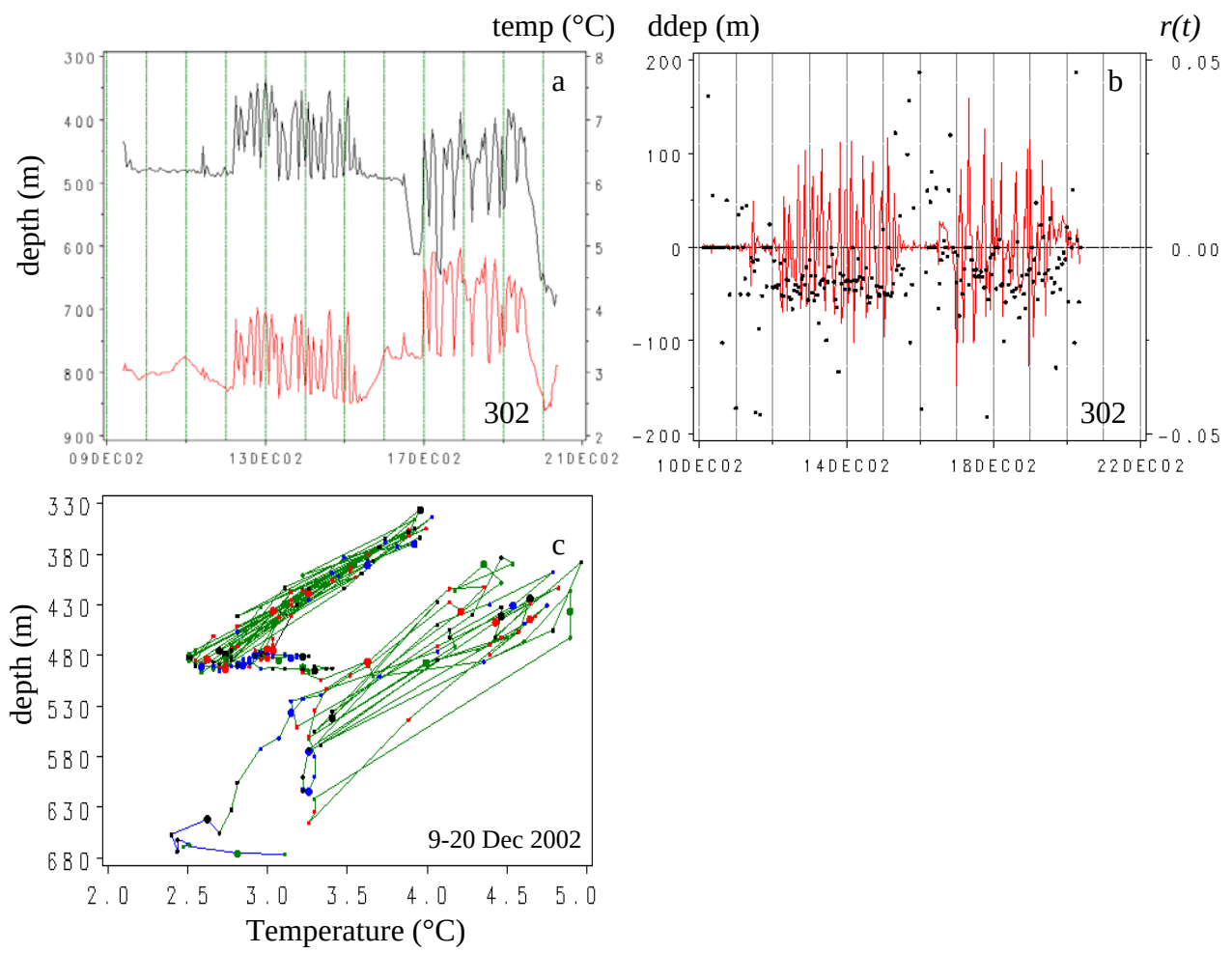


Figure 11

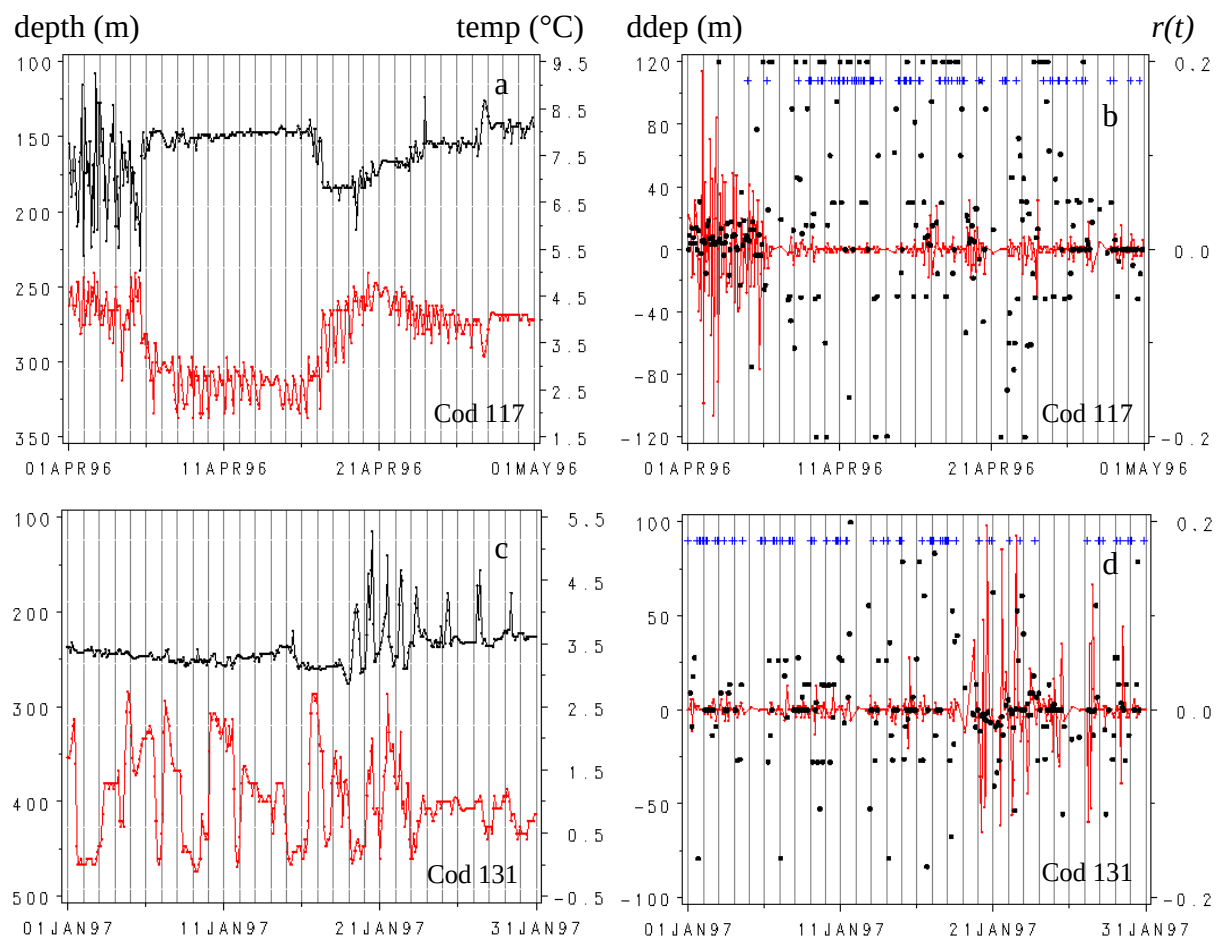


Figure 12

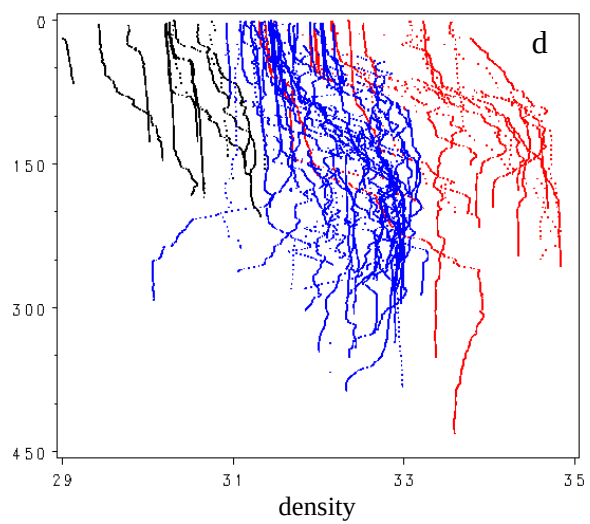
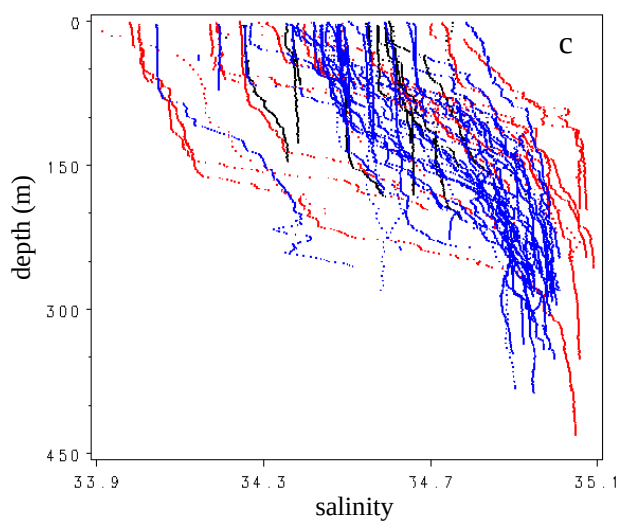
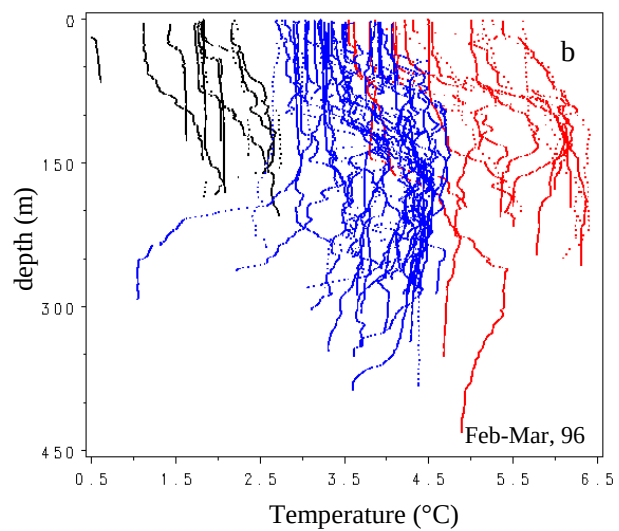
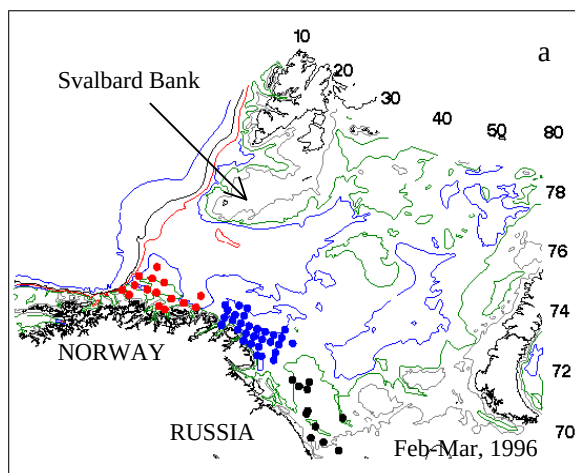


Figure 13

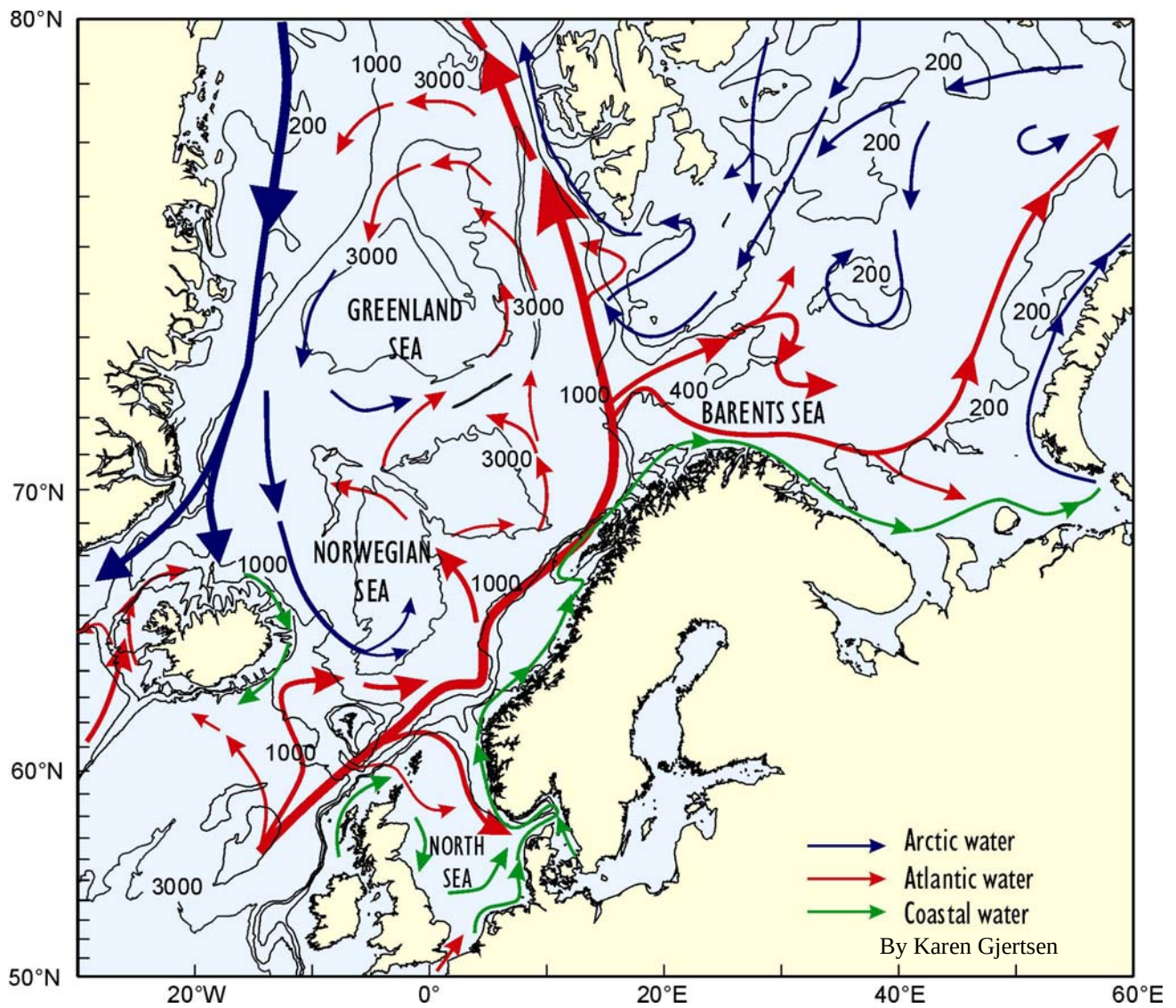


Figure 14