

# Migratory behaviour of north-east Arctic cod, studied by use of data storage tags

Olav Rune Godø\*, Kathrine Michalsen

*Institute of Marine Research, PO Box 1870 Nordnes, N-5024 Bergen, Norway*

Received 1 September 1999; received in revised form 7 December 1999; accepted 3 February 2000

## Abstract

To understand the variation in availability of demersal fish to bottom trawls and to evaluate the reliability of the target strength used in acoustic surveys, more knowledge about individual fish behaviour, such as the range, speed and repeatability of the vertical movements, is required. In this paper, data storage tags have been used to study vertical movements of individually tagged cod (*Gadus morhua* L.). In general, the short term vertical movements were less than 10 m. Rapid movements of up to 250 m within 2 h interval were recorded sporadically. During restricted periods some of the fish did move vertically with a distinct diel rhythm. Calculations of the time needed to equalise the pressure to remain at a constant buoyant state indicated that the fish probably were negatively buoyant most of the time. However, the direct effect of the vertical movements on the acoustical target strength could not be quantified. Seasonal differences in mean depth and ambient temperature were observed. As a result of horizontal and vertical migrations, north-east Arctic cod experience higher temperatures in winter and spring than in summer and autumn. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Data storage tags; Environmental factors; Fish behaviour; Vertical movements; Abundance surveys; Ambient temperature; North-east Arctic cod; *Gadus morhua*

## 1. Introduction

The standard estimation procedure used in most demersal fish surveys does not take into account the impact of changes in vertical distribution. The reliability of these survey indices thus depends on the stability of the bias caused by the vertical distribution of the fishes. For north-east Arctic cod the vertical distribution may vary with time of day, as well as between years. Among the factors affecting the distribution is light, current (Michalsen et al.,

1996; Aglen et al., 1999), bottom depth and fish abundance (Godø, 1994), so diel differences in catch rates and acoustical recordings do occur (Engås and Soldal, 1992; Michalsen et al., 1996; Aglen et al., 1999).

When echo energy is converted to fish densities, mean target strength is used. This method is based on the assumption that fish are always neutrally buoyant and that the swimbladder acts as a buoyancy organ with volume and shape independent of depth changes (Foote, 1980). However, the process of gas secretion and resorption is slow (Harden Jones and Scholes, 1985), and compensation for rapid depth changes is likely to lag behind the ascents and descents. The classical theory concerning neutral buoyancy at all depths was tested and disproved by Arnold and Greer

\* Corresponding author. Tel.: +47-55-23-8500;  
fax: +47-55-23-8687.

E-mail addresses: olavrune.godoe@imr.no (O.R. Godø),  
kathrine.michalsen@imr.no (K. Michalsen)

Walker (1992), who concluded that fish were neutrally buoyant at the top of their vertical range.

The greatest potential source of variation in target strength is the orientation of the fish relative to the horizontal plane (the tilt angle, Aglen, 1994). Compensation for negative buoyancy by altering the angle of attack of the body can have a marked effect on the acoustic measurements. Systematic tilt angle differences between day and night have been observed in herring (Beltestad, 1974; Huse and Ona, 1996). The observed variation in vertical distribution recorded by Michalsen et al. (1996) and Aglen et al. (1999) indicate that a diel change in tilt angle may occur for cod and haddock. Such systematic changes in vertical movement of fishes could have serious consequences for the bottom trawl indices. Changes in the vertical distribution of fish will thus generate a large and variable bias for both acoustic recordings and bottom trawl catches. To improve the reliability of both these methods, more knowledge about vertical movements of individual fish is needed.

In recent years, individual fish behaviour patterns have been reported for cod tagged with acoustic tags (e.g. Arnold and Greer Walker, 1992; Arnold et al., 1994; Godø, 1995). The applicability of these experiments has been restricted by the low number of fish tagged and the short observation period. By using data storage tags (electronic tags) it is possible to tag a much higher number of fish and to get long term, high resolution data on migration dynamics. These tags have been used on several free-ranging fish species in the open sea, including cod (Arnold et al., 1994), plaice (Metcalf and Arnold, 1997), tuna (Gunn et al., 1994), and salmon (Karlsson et al., 1996). Thorsteinsson (1995) using data storage tags observed the vertical distribution of cod off Iceland, but the time between recordings (8–9 h) was too long to identify any diel rhythm.

We studied the individual migratory behaviour of north-east Arctic cod (*Gadus morhua* L.) using data storage tags. The dynamics of the vertical movements have been analysed with emphasis on the physiological limitation of cod to maintain neutral buoyancy under pressure changes. This study gives an overview of the data available from data storage tags and emphasises the problems and potentials of using this methodology as a tool for studying fish behaviour and its effect on survey results.

## 2. Material and methods

### 2.1. Data storage tags

The electronic data storage tags (DST 100), produced by Star Oddi, Iceland, are slightly positively buoyant. These tags are 56 mm in length, 17 mm in diameter, and have a storage capacity of 3900 recordings. An experiment with transponding acoustic tags showed that although the tags were attached externally, they did not significantly affect the swimming performance of fishes (Arnold and Holford, 1978). The data storage tags are half the size of the acoustic tags, consequently the drag will be reduced and the effects on swimming speed will be neglected.

During the first 6 days, temperature and depth were recorded every 2 h. On the seventh day only two recordings, one every 12 h, were stored. This 7 day pattern was repeated during the time the fish spent in the sea. According to a calibration test by the tag manufacturer, the precision of the temperature and depth recordings were  $\pm 0.2^\circ\text{C}$  and  $\pm 1$  atmospheres (1 ATA), respectively.

### 2.2. Fish and tagging

In March–April 1996, 158 tagged cod were released off the Finnmark coast ( $71^\circ\text{N}$ ,  $25^\circ\text{E}$ ), while 42 cod were tagged and released at the Lofoten spawning grounds (Fig. 1). According to the trawl catches, cod from the spawning ground in Lofoten were mature, while the bulk of the fish caught off the Finnmark coast were immature. The cod were captured at 50–200 m depth using bottom and pelagic trawls, which were hauled slowly to the surface. To secure optimal survival after release, all specimens were kept in tanks for 4–5 h before and after tagging. The individuals in best condition were tagged and released. The tags were attached through the muscles anterior to the first dorsal fin using a mono filament line similar to conventional tagging (Anon., 1953; Godø, 1989). All fish were measured to the nearest centimetre below before tagging. The length compositions of the tagged and recaptured fish from the two release sites are shown in Fig. 2. As with conventional experimental tagging methods, recovery of these tags was through the commercial fishery.

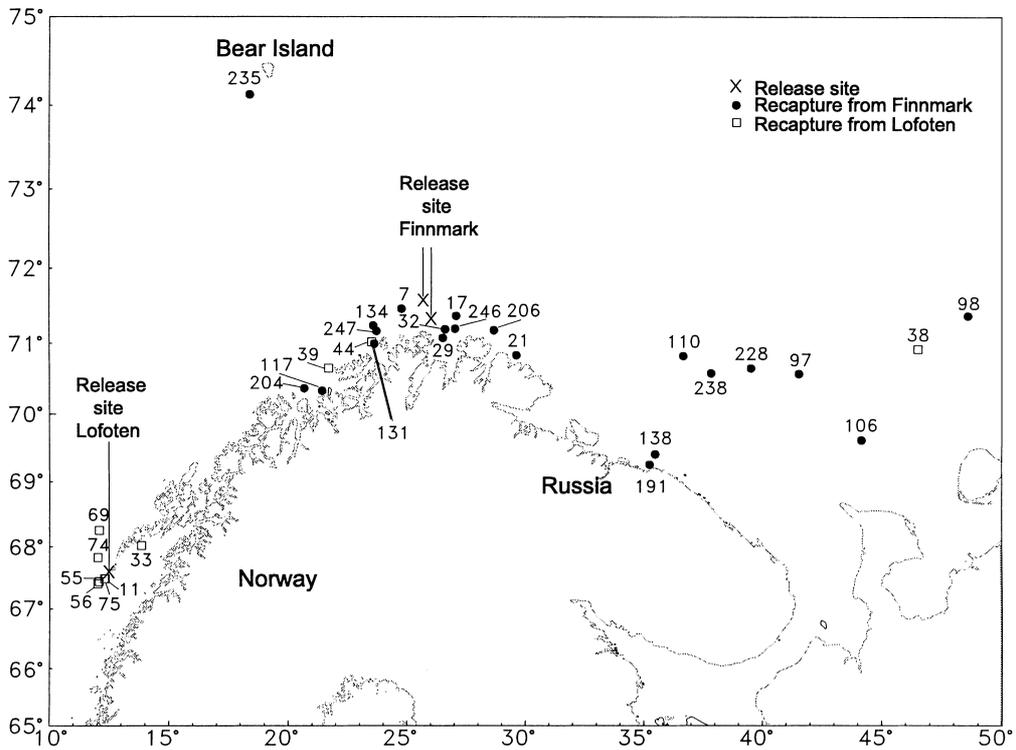


Fig. 1. Location of the two release sites (x), off the Finnmark coast and at the Lofoten spawning grounds. Position of the recaptured fish, released from the two release sites are marked with dots and squares, respectively. Identification of the individual fish is given by tag number.

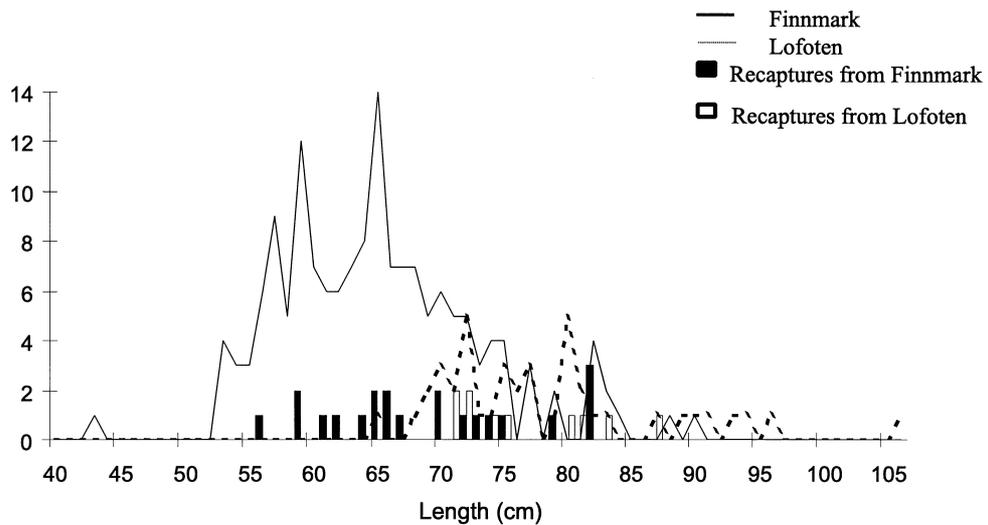


Fig. 2. Length composition of fish released off the Finnmark coast (line) and at the Lofoten spawning grounds (dotted line). Number of recaptured fish in the different length groups are shown as black and white columns, respectively.

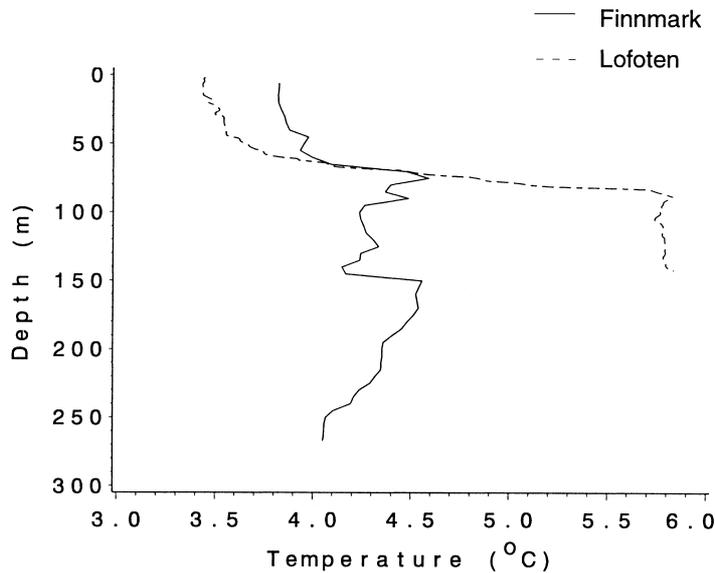


Fig. 3. Temperature profiles at the release locations off the Finnmark coast and in the Lofoten area.

Vertical profiles of the temperature at the two release sites (Fig. 3) were used to verify the temperature recorded by the tag immediately after release.

For three of the recaptured cod, otoliths were collected (tag nos. 32, 33 and 110). For one tag (no. 98) irregularities in the time interval were discovered and this tag was excluded. For four tags, the number of recordings was limited by the battery capacity (up to 383 days or 3900 recordings).

Plots of depth and temperature over time were made for each specimen. Differences between the vertical movements recorded shortly after release and those occurring later have been defined as after release behaviour. At maximum, this period lasted 14 days and in the following analysis data from this period have been excluded.

### 2.3. Variations in depth and temperature

Daily mean values of depth ( $d$ ) and temperature ( $t$ ) per tag were calculated as

$$\bar{d}_{\text{day, tag}} = \sum_{i=1}^n \frac{d_{i, \text{day, tag}}}{n_{\text{day, tag}}}, \quad (1)$$

$$\bar{t}_{\text{day, tag}} = \sum_{i=1}^n \frac{t_{i, \text{day, tag}}}{n_{\text{day, tag}}}, \quad (2)$$

where  $n$  is the number of observations per day for each tag.

Monthly mean values of depth ( $d$ ) and temperature ( $t$ ) for each tag were calculated as

$$\bar{d}_{\text{month, tag}} = \sum_{i=1}^n \frac{d_{i, \text{month, tag}}}{n_{\text{month, tag}}}, \quad (3)$$

$$\bar{t}_{\text{month, tag}} = \sum_{i=1}^n \frac{t_{i, \text{month, tag}}}{n_{\text{month, tag}}}, \quad (4)$$

where  $n$  is the number of observations per month for each tag.

### 2.4. Dynamics of the vertical movements

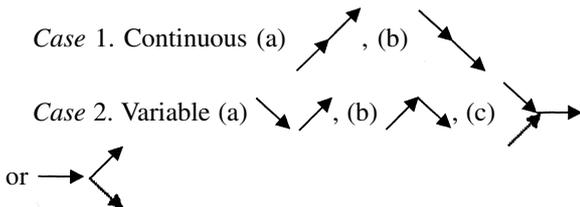
Variation in vertical movements was studied by calculating the vertical excursion executed by a specimen in a given time interval. Thus, a new data set with vertical excursions is established for each new time interval. The observations from these data sets were put in a  $8 \times 6$  frequency table corresponding to eight vertical excursion classes and six time intervals. The eight excursion classes were: category “0–9” which includes fish that migrated from 0–9 m from start to finish within the interval, and similarly for the other categories 10–19, 20–29, 40–49, 50–99, 100–199, and 200+ m. Category

“200+” includes excursions of 200 m and more. The six time intervals had different range and varied from 2 to 24 h (see Table 2). Only days with 2 h recording intervals have been used. The percentages ( $p_{td}$ ) of the total number of observations falling into specific categories of time and excursion were calculated for all tags as follows:

$$p_{td} = \frac{\sum_{m=1}^n n_{td}}{\sum_{m=1}^n n_{tg}}, \quad (5)$$

where  $n_{td}$  is the number of observations from a specific tag falling into a specific category and  $n_{tg}$  is the total number of observations in this tag.

If fish do have a distinct time cycle in their vertical movements, continuous ascends, descends or constant depth are expected to dominate, even between as few as three successive recordings (within two successive time intervals of 2 h, which is equivalent to 4 h). The vertical migration patterns were grouped as continuous (Case 1) or variable (Case 2), as described below:



By selecting data with progressively larger vertical movements, in either (Case 2(c)) or both of the two time intervals (Case 1(a) and (b), Case 2(a) and (b)), the dynamics of the successive ascents and descents were studied. Since the precision of the depth recording is approximately 10 m (1 ATA), only depth ranges above this level were chosen.

### 2.5. Buoyancy

The swimbladder of cod is elastic. When a neutrally buoyant fish ascends, the outside pressures decreases and the volume of the swimbladder increases. The reverse takes place when fish descends. Thus, the buoyancy of the fish depends on the magnitude of the vertical movement and the gas secretion and resorption capacity of the swimbladder. Based on laboratory studies, Harden Jones and Scholes (1985) quantified the time (min) needed for the fish to counterbalance changes in pressure during descents

( $t_d$ ) and ascents ( $t_a$ ):

$$t_d = (D_2 - D_1)60, \quad (6)$$

$$t_a = B \ln\left(\frac{P_1}{P_2}\right), \quad (7)$$

where  $D_1$  and  $D_2$  are the depths in the beginning and the end of the time interval, respectively,  $B$  is the slope of the regression line when time for adaptation is plotted against  $\ln(P_1/P_2)$ , and  $P_1$  and  $P_2$  are the pressures in atmospheres at the greater and lesser depths, respectively. According to those experiments,  $B=254$ , which is the value used in our tests of stability in buoyancy during ascents.

## 3. Results

At present a total of 21 (Finnmark) and 10 (Lofoten) tagged fish have been recaptured (Table 1).

### 3.1. Acclimatisation

Due to the rough handling of the fish during capture and tagging, close attention should be paid to the data recorded during the first period after release. During the first 2 weeks the behaviour of the fish differed from what appeared thereafter. Some of the fish conducted descents and ascents with gradually decreasing oscillations (Fig. 4a, type 1 behaviour, fish no. 33). Other fish dived directly towards the bottom (or the preferred depth level), before ascending repeatedly to shallower waters for short time intervals (Fig. 4b, type 2 behaviour, fish no. 17). Some individuals waited several hours or even days before descending, while others descended within a few hours after release. In addition to variation in behaviour pattern, the time before the exhibited “normal behaviour” varied between individuals. After 14 days in the sea, the characteristic abnormal movements described above were no longer apparent. The data from this acclimatisation period have consequently been excluded from the analysis.

### 3.2. Short term patterns in vertical movements

The first impression from the plots of depth and temperature over time is that there is a substantial difference between specimens, but some general

Table 1

Information on release and recapture of cod off the Norwegian coast (N) and in the Lofoten area (L)

Release site	Tag number	Date of release	Date of recapture	Length at release (cm)	Recording time (days)
N	7	17/3/96	24/3/96	66	7
N	17	17/3/96	26/3/96	82	9
N	134	16/3/96	29/3/96	61	13
N	29	13/3/96	11/4/96	82	29
N	247	14/3/96	13/4/96	70	30
N	32	17/3/96	9/5/96	79	53
N	21	17/3/96	30/5/96	62	74
N	235	16/3/96	16/6/96	70	92
N	138	14/3/96	24/6/96	65	102
N	228	16/3/96	16/7/96	66	122
N	238	14/3/96	21/7/96	67	129
N	97	18/3/96	21/9/96	75	187
N	98	18/3/96	21/10/96	59	217 <sup>a</sup>
N	110	18/3/96	18/11/96	82	245
N	106	16/3/96	26/11/96	59	255
N	246	16/3/96	11/2/97	64	337
N	117	17/3/96	18/3/97	74	366
N	131	17/3/96	2/4/97	72	381
N	204	14/3/96	31/3/97	65	382 <sup>b</sup>
N	191	14/3/96	5/8/97	56	383 <sup>b</sup>
N	206	16/3/96	8/12/97	73	383 <sup>b</sup>
L	75	28/3/96	30/3/96	72	2
L	11	28/3/96	30/3/96	71	2
L	55	28/3/96	2/4/96	83	5
L	74	28/3/96	2/4/96	74	5
L	56	28/3/96	11/4/96	72	14
L	69	28/3/96	17/4/96	71	20
L	33	28/3/96	21/5/96	87	54 <sup>c</sup>
L	38	28/3/96	10/8/96	75	135
L	44	28/3/96	5/2/97	81	314
L	39	28/3/96	29/9/97	80	382 <sup>b</sup>

<sup>a</sup> Incorrect time interval, all data excluded from further analysis.

<sup>b</sup> Recording time stopped as a result of battery failure.

<sup>c</sup> Recording time was limited by excessive pressure of the tag.

patterns could be extracted, as is demonstrated by the specimens with the tag no. 131 (Fig. 5) and 44 (Fig. 6). The extent of the vertical movements varied during the year (Fig. 5a). For certain periods, the fish with tag no. 131 remained at almost the same depth with very limited vertical movements. In other periods, mainly during spring and autumn, excursions of 100 m were frequently observed. For some fish, sporadic and rapid movements of up to 250 m within a 2 h interval were recorded. There was no clear relationship between the extent of the vertical movements and the daily mean depth (Fig. 5b). Within restricted periods, some of the fish moved vertically with a distinct 24 h cycle (Fig. 6). In this case the fish between 130 (14 ATA) and 30 m (4

ATA), experienced pressure reductions above 50% in several occasions.

In general the fish were kept within the pressure tolerance of the tags (480 m), but one fish (tag no. 33) exceeded this depth, so the capsule collapsed and the recordings were terminated. The vertical migrations were within a depth interval of 10 m in about 55% of the situations (Table 2). Within all depth intervals, excluding the lowest one (0–9 m), the percentage of occurrence increased with increasing time intervals. Although no diel pattern in vertical movements appeared from this broad scale presentation, the mean differences in depth for both the ascents and descents within a 24 h interval were about twice the difference

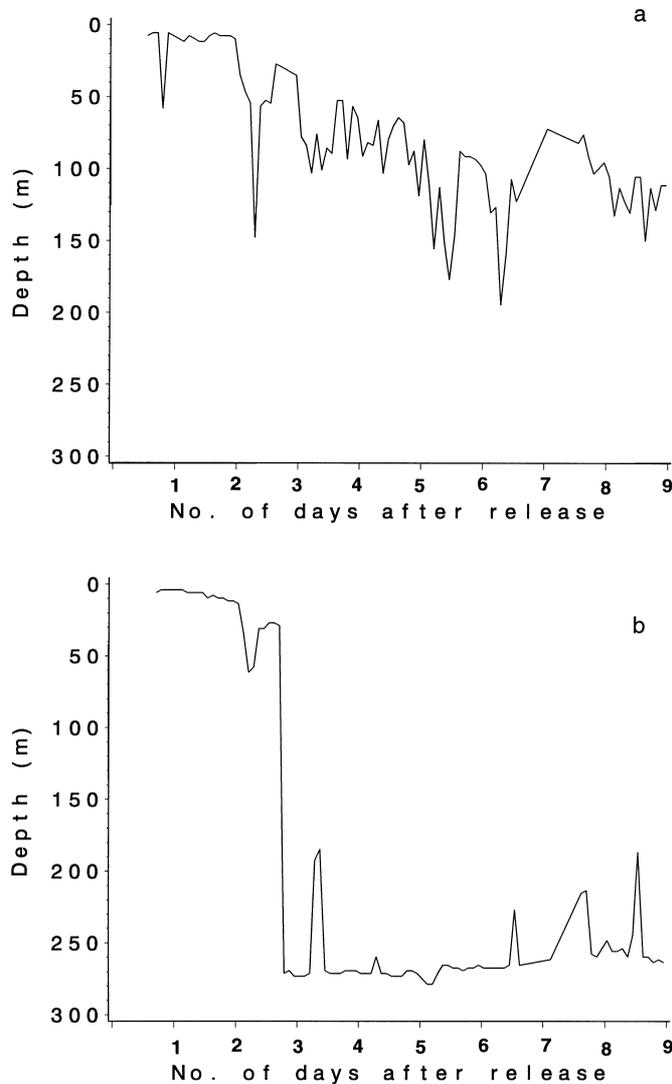


Fig. 4. After release behaviour. Depth of fish by number of days after release: (a) type 1 behaviour, tag no. 33; (b) type 2 behaviour, tag no. 17.

observed for the 2 h interval (Table 2). Further, it should be noted that the total mean distance is 1–4 m larger for the descents than for the ascents. The data indicate no difference between mature and immature fish vertical migration (Table 2).

The percentages of the various migration patterns within periods of 4 h are presented in Fig. 7. As shown earlier, most of the observations were kept within depths of 10 m. This is within the level of precision of the tag depth sensor, and is not included in the graph. The variable movements (Case 2(a) and (b)) are

dominant in all five groups of depth difference. The more extensive the excursions, the more dominant is the Case 2 behaviour pattern. Only one recording of continuous migration occurred at excursions of more than 100 m. From the few records of more than 100 m, Case 2b pattern dominated, i.e., rapid and long upward movements succeeded by a decent. In other words, more often, cod tend to make short excursions to shallower water with successive return than in the opposite direction (excursion to deeper water with immediate return).

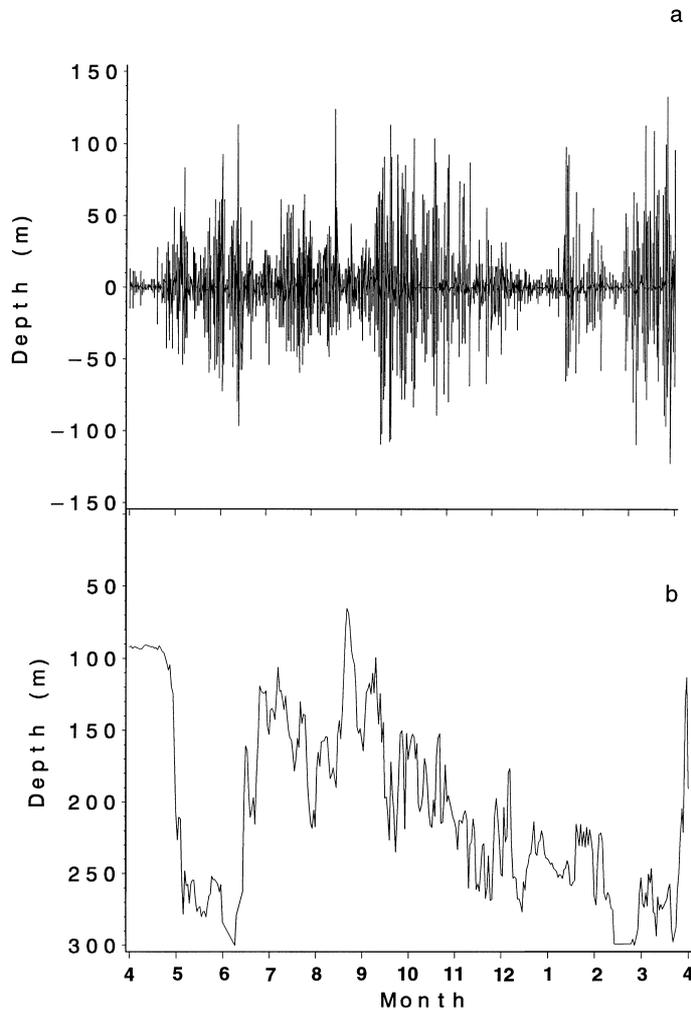


Fig. 5. Depth recordings for tag no. 131 presented as (a) changes in depth within 2 h intervals and as (b) mean depth per day.

### 3.3. Seasonal migration and temperature

Mean depth per day varied between the individual tagged fish (Fig. 8a). In general, the fish stayed deeper/closer to the bottom during winter and spring than during summer and autumn. The temperature difference between the individual fish was highest during the summer/autumn (Fig. 8b). To study seasonal variations in depth and temperature for the individual fish, mean values per month were calculated. In Fig. 9, recordings from some of the individuals released off the Finnmark coast, which had stayed in the sea for more than 3 months are shown. As shown in Fig. 8 the

fish stayed closer to the surface in autumn than in the rest of the year (Fig. 9a). The corresponding temperatures were lower during the autumn than during the winter/spring (Fig. 9b).

### 3.4. Buoyancy and target strength

The time necessary to compensate for the change in the gas pressure in the swimbladder between two succeeding observations was calculated for each observation according to Eqs. (6) and (7) (Table 3). Apparently fish cannot regulate the gas pressure fast enough to be always neutrally buoyant. In 28.9% of all

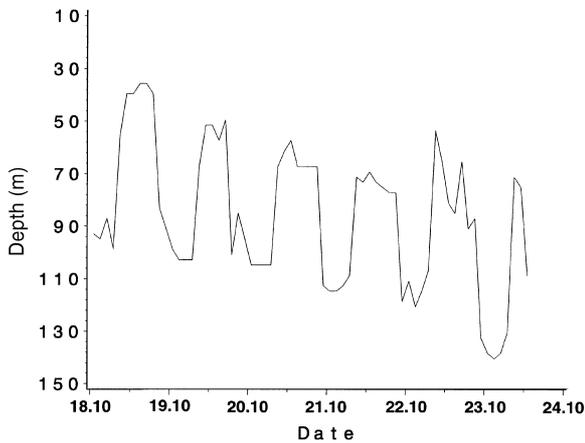


Fig. 6. An example of a 24 h cycle in the vertical movements (tag no. 44) in the period October 18–24, 1995.

cases (i.e., close to 60% of the descents) the fish required 3 h or more to obtain neutral buoyancy. In extreme situations, several days would have been needed to neutralise the buoyancy. Only occasionally

did the ascent exceed the calculated limit regarding the resorption capacity.

#### 4. Discussion

During capture, the fish were brought to the surface from depths of 50–200 m. If neutral buoyant at these depths, following Harden Jones and Scholes (1985), a retrieval time of 7–12 h is necessary for the fish to maintain buoyancy under the reduced pressure. Since hauling took only 1–1.5 h, the gas resorption was not fast enough to prevent rupture of the swimbladder wall under such pressure changes, and all tagged fish probably had a damaged swimbladder at release. Survival tests in experiments for long term commercial storage of living cod have shown that all swimbladders were broken when fish were caught at depths similar to those in our study. In these tests healing started after a few days and fish obtained a gas filled, apparently functional, swimbladder 4–5 days after the

Table 2

Distance of vertical movements (m) presented as percentage of occurrence within different time intervals (h) for fish released: (a) off the Norwegian coast and (b) in the Lofoten area<sup>a</sup>

Time interval (h)	Distance (m)								Ascent (m)	Descent (m)
	0–9	10–19	20–29	30–39	40–49	50–99	100–199	200+		
<i>Norwegian coast</i>										
2	10.3	2.4	1.1	0.5	0.3	0.5	0.1	0.0	8.0	12.0
4	10.1	2.9	1.4	0.7	0.5	0.7	0.1	0.0	10.0	14.0
6	9.7	3.1	1.7	0.9	0.5	0.9	0.1	0.0	12.0	15.0
8	9.3	3.4	1.7	0.9	0.6	1.0	0.2	0.0	13.0	16.0
12	8.6	3.5	1.8	1.1	0.6	1.1	0.2	0.0	14.0	18.0
24	7.7	3.6	2.2	1.3	0.8	1.4	0.3	0.0	17.0	20.0
Total (%)	55.6	18.9	9.9	5.5	3.4	5.7	1.0	0.0		
Total number of observations	37073	12604	6595	3690	2269	3805	638	27		
Total mean									12.0	16.0
<i>Lofoten area</i>										
2	10.4	3.2	1.0	0.6	0.3	0.4	0.0	0.0	8.0	11.0
4	9.7	3.7	1.4	0.7	0.4	0.6	0.0	0.0	10.0	13.0
6	9.6	3.8	1.6	0.9	0.4	0.7	0.0	0.0	11.0	14.0
8	9.1	4.0	1.6	1.0	0.5	0.7	0.1	0.0	12.0	15.0
12	8.5	4.0	1.9	1.1	0.6	0.8	0.1	0.0	13.0	16.0
24	8.6	3.6	1.8	1.0	0.5	1.0	0.1	0.0	14.0	17.0
Total (%)	56.0	22.3	9.3	5.3	2.7	4.2	0.3	0.0		
Total number of observations	10677	4249	1776	1009	509	798	63	0		
Total mean									11.0	15.0

<sup>a</sup> Total percentage and total number of observations within each depth interval are given. Ascent and descent represents the mean depth difference observed during ascents and descents, respectively, within the various time intervals as well as the total mean.

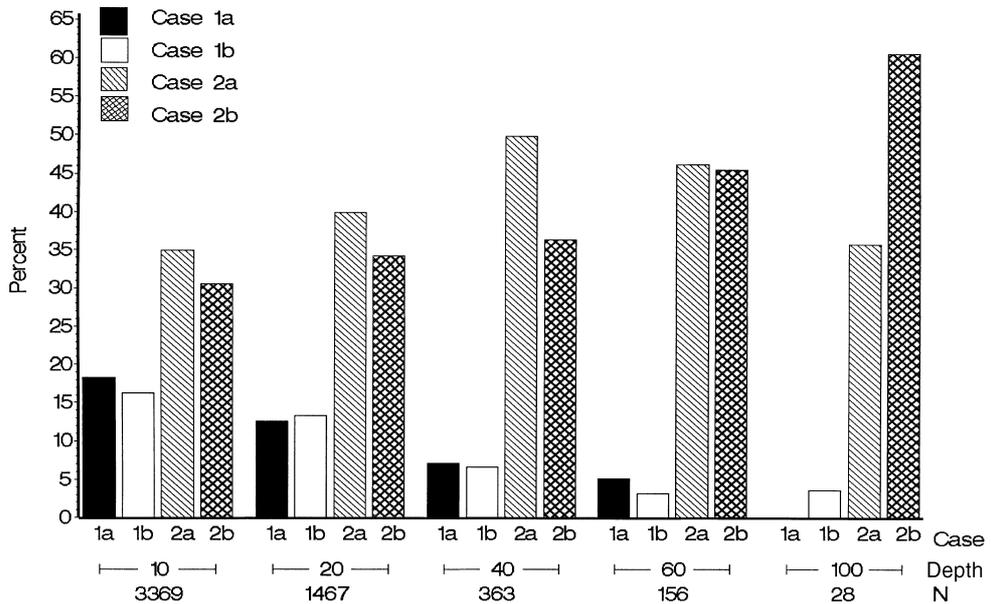


Fig. 7. The percentages of the various migration patterns, within periods of 4 h, grouped as continuous (Case 1) and variable (Case 2). The extent (in m) of the vertical movements (depth) and the number of observations (*N*) for each migration pattern are given.

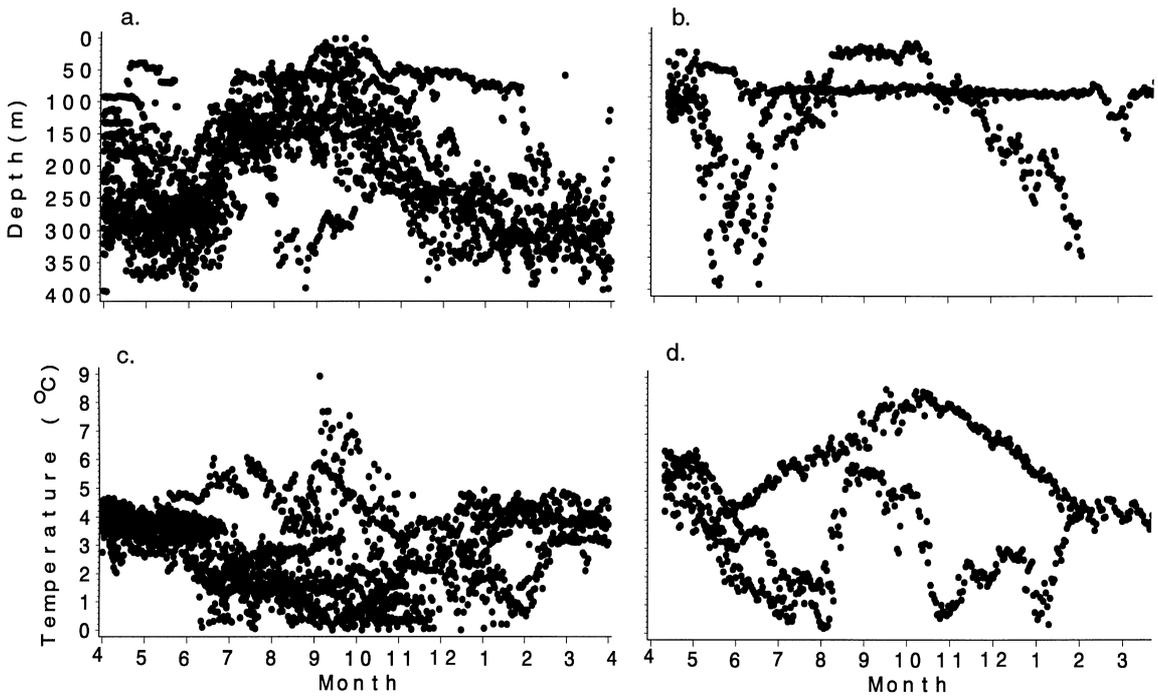


Fig. 8. Mean values per day for the depth of each tag released off the Finnmark coast (a) and in the Lofoten area (b), and mean daily temperatures of each tag released off the Finnmark coast (c) and in the Lofoten area (d).

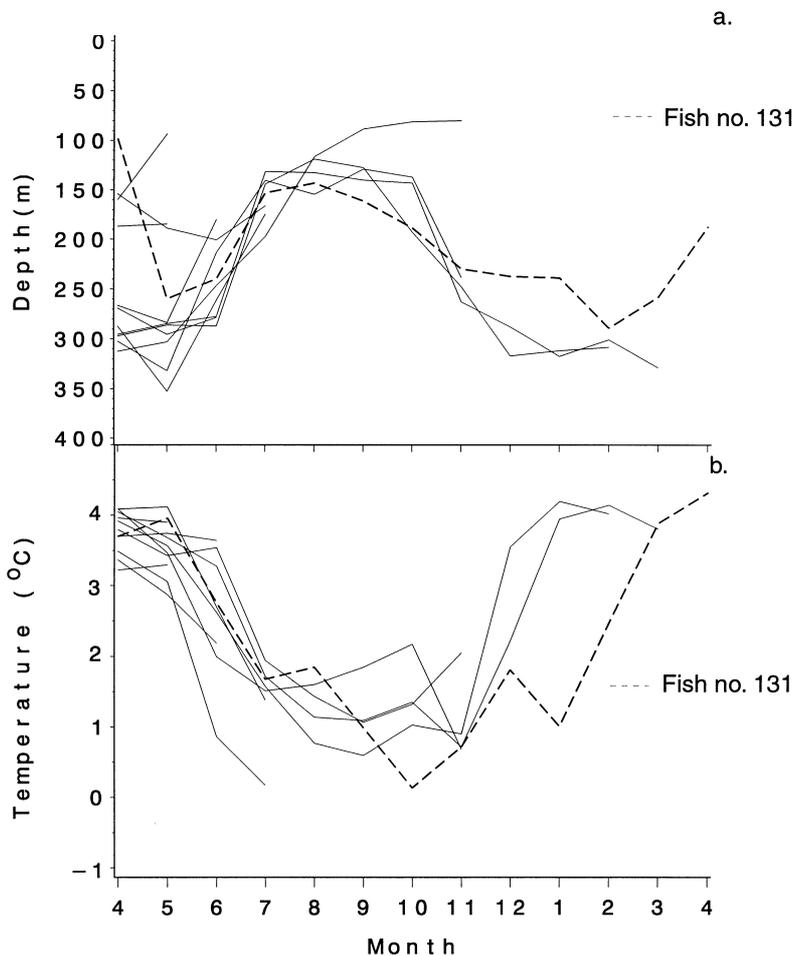


Fig. 9. Mean values per month for individual fish (a) temperature and (b) depth. Data from fish no. 131 is marked with a dotted line.

initial injury (Bjørnar Isaksen, Institute of Marine Research, Bergen, pers. comm.). In a study of pressure sensitivity of saithe, where the swimbladder was emptied using a hyperdermic needle, the threshold was restored to near normal after 15–18 h (Tytler and Blaxter, 1977). Although the wall of the swimbladder is healed within a few days, repeated vertical movements, which do not provide the stable pressure conditions, will probably disturb the healing process. This might explain the large variation in time, from 4 to 13 days, necessary for acclimatisation of free-ranging fish. Even though the observed behaviour indicates that swimbladders of most fish are healed after 13 days, it cannot be concluded that the swimbladder function is fully restored at that point. A controlled

experiment, which simulates the capture process as well as the vertical movements of the fish after release, is required to obtain more detailed knowledge about the healing process.

Since these tags do not have a sensor for bottom detection, the depth recordings could describe either changes in bottom depths along the horizontal migration route or active vertical movements of the fish in the pelagic zone. As the Barents Sea is a shelf area, and as we know that cod often are recorded acoustically well above the bottom (see e.g. Godø, 1994), it is assumed that the frequent, short term changes in depth are representative for the vertical movements of the fish. The long-term changes could, on the other hand, be a result of horizontal migration.

Table 3  
Time (h) needed to achieve neutral buoyancy after descents and ascents<sup>a</sup>

Movement	HR	Frequency	Per cent	Cumulative frequency	Cumulative per cent
Descend	12	4494	11.6	4494	11.6
Descend	11	583	1.5	5077	13.1
Descend	10	131	0.3	5208	13.4
Descend	9	735	1.9	5943	15.3
Descend	8	317	0.8	6260	16.1
Descend	7	758	2.0	7018	18.1
Descend	6	652	1.7	7670	19.8
Descend	5	907	2.3	8577	22.1
Descend	4	887	2.3	9464	24.4
Descend	3	1865	4.8	11329	29.2
Descend	2	1281	3.3	12610	32.5
Descend	1	2847	7.3	15457	39.8
	0	12998	33.5	28455	73.3
Ascend	1	9010	23.2	37465	96.5
Ascend	2	1184	3.0	38649	99.5
Ascend	3	137	0.4	38786	99.9
Ascend	4	36	0.1	38822	100.0

<sup>a</sup> Frequency, per cent, cumulative frequency and cumulative per cent are given for the different time intervals. The 12 h interval includes descents where secretion of gas takes more than 12 h.

The diet of north-east Arctic cod consists mainly of fish, with capelin as the dominant species (Mehl, 1989). Since the species composition of the diet varies during the season (Burgos and Mehl, 1987), the observed variation in the frequency and extent of the vertical movements could be a reflection of the seasonal variations in availability of the different prey species. The rare appearance of clear diel or semi-diel vertical migration patterns could be explained by the long time required (5–6 days) to digest a meal of capelin (dos Santos, 1990), as well as by the slow and energy demanding process of adjusting for pressure changes (Alexander, 1971, 1972; Harden Jones and Scholes, 1985). Despite the lack of clear diel signals in the data, other systematical patterns were observed. Within a 4 h period, the fish usually reversed the direction of their movement (see Fig. 7), a tendency which increases with increasing span in the vertical movements. The explanation of the observed fast undulating behaviour without a systematic pattern is not obvious. With the physical constraints caused by the gas filled swimbladder, a smooth, longer-term vertical movement pattern would be more reasonable. However, the observed pattern could be an effective food search modus. This kind of movement might also indicate that cod are able to suppress positive buoy-

ancy through muscular activity, improving its ability to extend the range of the “search channel”. What we have defined as a variable migration pattern could thus reflect a systematic approach to optimise the search for food.

The collective diurnal pattern in vertical distribution, apparent from bottom trawl and acoustic measurements, is not necessarily caused by an identical diel pattern in the movement of the individual fish. To obtain detailed knowledge about possible cycles in the vertical movements, it appears from this study that data collection with much higher resolution in time is necessary. Comprehensive statistical analyses may provide more quantitative information about the vertical movements. Such studies are necessary in order to produce behaviour models representative of the whole population, which finally can be compared with collective behaviour patterns emerging from trawl and acoustic surveys.

Geographical position of the tagged fish during migration is essential for establishment of better migration models. A rough position of the fish could possibly be determined by combining temperature and depth data from the fish with information about topography and temperature of the Barents Sea. However, technological development targeting determination of

tag position is carried out by several institutions, and a solution to this problem will substantially improve the data with respect to migration and behaviour modelling.

The monthly mean temperatures experienced by cod in this study were higher during the winter than during the summer/autumn. The divergence of this cycle compared to normal seasonality is mainly because the fish are distributed in the cold northern and eastern parts of the Barents Sea during summer and autumn, while they migrate to the warmer southwestern part during winter and spring. The temperature in the Barents Sea is relatively stable at depths deeper than 100 m (Ottersen and Ådlandsvik, 1993), and therefore the seasonal variation has a minor influence compared to the geographical differences in the distribution area of cod. The present results are in accordance with Ottersen et al. (1998) and Michalsen et al. (1998), who came to the same conclusion by comparing the general seasonal migration patterns of cod and the observed environmental variability. Using data storage tags, it has for the first time become possible to confirm from observation the earlier predictions that individual cod are experiencing higher temperatures during winter than during summer.

Temperature is important for all biological processes. In the assessment of north-east Arctic cod, temperature is used as input to consumption models. The observations from this study demonstrate the complexity involved in establishing a correct ambient temperature throughout the year. More extensive use of DST could help establish more precise annual temperature cycles and hence, improve the analysis where temperature is involved.

Experiments have shown that the process of gas secretion is much slower than the process of gas resorption, and that it increases with temperature and is inversely related to the weight of the fish (Harden Jones and Scholes, 1985). Since the tagged fish were larger and experienced colder water than those used in the experiment by Harden Jones and Scholes (1985), the secretion capacity of the swimbladder has been overestimated in our calculations. Despite this overestimate, the calculations showed that the tagged cod were negatively buoyant for most of the time. These findings agree with the argument of Alexander (1971), which later on was proved under

controlled condition by Harden Jones and Scholes (1985) and verified in the field by Arnold and Greer Walker (1992): the process of maintaining neutral buoyancy at all depths is energy demanding, and fish that are neutrally buoyant only at the top of their vertical range and rest on the bottom for part of the time will thus save energy.

Large cod can compensate for reduction in the swimbladder lift by swimming (Ona, 1990), using their pectoral fins (Alexander, 1971) or altering the angle of attack of the body (Harden Jones and Scholes, 1985). Since the greatest potential source of variation in target strength is the orientation of the fish relative to the horizontal plane (the tilt angle, Aglen, 1994), compensation for negative buoyancy by altering the angle of attack of the body, a combination of negative buoyancy and a head up position could cause a substantial reduction in the target strength measurements and lead to a masking of the proportion of fish close to the bottom. From the available data it was not possible to evaluate the effect of vertical movements on the tilt angle and thus the target strength of the fish. Several authors (e.g. Aglen, 1994; McClatchie et al., 1996) have stressed the importance of improved information on fish movements to study the potential impact of tilt angle distribution on target strength variability. It is hoped that data storage tags with a tilt sensor will improve the basis for answering some of these questions.

To increase the reliability of the survey estimates of fish abundance, better information is needed on fish behaviour, natural and vessel affected, as well as on how behaviour may vary between species and size groups. In this context a better understanding of the individual behaviour is essential. The present paper shows the potential for using data storage tags to approach these problems. An improved tag with larger battery capacity/memory, higher resolution and new sensors, could be an important tool for studying fish behaviour and its effect on survey assessment in the future.

### Acknowledgements

The technical staff, and captain and crew aboard R/V G.O. Sars and R/V Michal Sars are thanked for skilful treatment of the fish during tagging and

Hildegunn Mjanger for preparation of recapture maps. We are also grateful for valuable suggestions and comments to the manuscript from G.P. Arnold and M. Pennington. The Research Council of Norway and the Nordic Council of Ministers have financially supported the work.

## References

- Aglen, A., 1994. Sources of errors in acoustic estimation of fish abundance. In: Fernö, A., Olsen, S. (Eds.), *Marine Fish Behaviour in Capture and Abundance Estimation*. Fishing News Books, Oxford, pp. 107–133.
- Aglen, A., Engås, A., Huse, I., Michalsen, K., Stensholt, B., 1999. How vertical fish distribution may affect surveys results. *ICES J. Mar. Sci.* 56, 345–360.
- Alexander, R., 1971. Swimbladder gas secretion and energy expenditure in vertical migrating fishes. In: Farquhar, G.B. (Ed.), *International Symposium on Biological Sound Scattering in the Ocean*. US Government Printing Office, Washington, pp. 74–85.
- Alexander, R.M., 1972. The energetics of vertical migration by fishes. In: Sleight, M.A., MacDonald, A.G. (Eds.), *The Effect of Pressure on Organisms*. Symposia of the Society for Experimental Biology, pp. 273–294.
- Anon., 1953. A guide to fish marks. *J. Cons. Int. Explor. Mer.* 19, 241–289.
- Arnold, G.P., Greer Walker, M., 1992. Vertical movements of cod (*Gadus morhua* L.) in the open sea and the hydrostatic function of the swimbladder. *ICES J. Mar. Sci.* 49, 357–372.
- Arnold, G.P., Greer Walker, M., Emerson, L.S., Holford, B.H., 1994. Movements of cod (*Gadus morhua* L.) in relation to tidal streams in the southern North Sea. *ICES J. Mar. Sci.* 51, 207–232.
- Arnold, G.P., Holford, B.H., 1978. The physical effects of an acoustic tag on the swimming performance of plaice and cod. *J. Cons. Int. Explor. Mer.* 38, 189–200.
- Beltestad, A.K., 1974. Feeding, vertical migrations and schooling of 0-group herring (*Clupea harengus* L.) in relation to light intensity. Cand. Real. Thesis. University of Bergen, Bergen, Norway, 80 pp. (in Norwegian).
- Burgos, G., Mehl, S., 1987. Diet overlap between north-east Arctic cod and haddock in the southern part of the Barents Sea in 1984–1986. *ICES CM/G:50*.
- dos Santos, J., 1990. Aspects of the eco-physiology of predation in Atlantic cod (*Gadus morhua* L.). Dr. Scient. Thesis. The Norwegian College of Fishery Science, University of Tromsø, 116 pp.
- Engås, A., Soldal, A.V., 1992. Diurnal variations in bottom trawl catches of cod and haddock and their influence on abundance indices. *ICES J. Mar. Sci.* 49, 89–95.
- Foote, K., 1980. Averaging fish target strength functions. *J. Acoust. Soc. Am.* 67, 504–515.
- Godø, O.R., 1989. The use of tagging studies to determine the optimal time for estimating acoustic abundance of spawning cod. *Fish. Res.* 8, 129–140.
- Godø, O.R., 1994. Factors affecting the reliability of groundfish abundance estimates from bottom trawl surveys. In: Fernö, A., Olsen, S. (Eds.), *Marine Fish Behaviour in Capture and Abundance Estimation*. Fishing News Books, Oxford, pp. 166–199.
- Godø, O.R., 1995. Transplantation–tagging–experiments in preliminary studies of migration of cod off Norway. *ICES J. Mar. Sci.* 52, 953–960.
- Gunn, J.S., Polacheck, T., Davis, T.L.O., Sherlock, M., Betlehem, A., 1994. The application of archival tags to study the movement, behaviour and physiology of southern bluefin tuna, with comments on the transfer of the technology to groundfish research. *ICES CM 1994/Mini:21*, 23 pp. (mimeo).
- Harden Jones, F.R., Scholes, P., 1985. Gas secretion and resorption in the swimbladder of cod *Gadus morhua*. *J. Comp. Physiol. B* 155, 319–331.
- Huse, I., Ona, E., 1996. Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring. *ICES J. Mar. Sci.* 53, 863–873.
- Karlsson, L., Ikonen, E., Westerberg, H., Sturlaugsson, J., 1996. Use of data storage tags to study the spawning migration of Baltic salmon (*Salmo salar* L.) in the Gulf of Bothnia. *ICES CM 1996/M:9*, 15 pp. (mimeo).
- McClatchie, S., Aslop, J., Coombs, R., 1996. Consequences of swimbladder model choices and fish orientation to target strength of three New Zealand fish species. *ICES J. Mar. Sci.* 53, 847–862.
- Mehl, S., 1989. The Northeast Arctic cod stock's consumption of commercially exploited prey species in 1984–1986. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.* 188, 185–205.
- Metcalfe, J.D., Arnold, G.P., 1997. Tracking fish with electronic tags. *Nature* 387, 665–666.
- Michalsen, K., Godø, O.R., Fernö, A., 1996. Diel variation in the catchability of gadoids and its influence on the reliability of abundance indices. *ICES J. Mar. Sci.* 53, 389–395.
- Michalsen, K., Ottersen, G., Nakken, O., 1998. Growth of north-east Arctic cod (*Gadus morhua* L.) in relation to ambient temperature. *ICES J. Mar. Sci.* 55, 863–877.
- Ona, E., 1990. Physiological factors causing natural variations in acoustic target strength of fish. *J. Mar. Biol. Assoc. UK* 70, 107–127.
- Ottersen, G., Ådlandsvik, B., 1993. Climatological temperature and salinity fields for the Nordic Seas. Report No. 8. Institute of Marine Research, Department of Marine Environment, 1993, 121 pp.
- Ottersen, G., Michalsen, K., Nakken, O., 1998. Ambient temperature and distribution of north-east Arctic cod. *ICES J. Mar. Sci.* 55, 67–85.
- Thorsteinsson, W., 1995. Tagging experiments using conventional tags and electronic data storage tags for the observations of migration, homing and habitat choice in the Icelandic spawning stock of cod. *ICES CM 1995/B:19*, pp. 1–15.
- Tytler, P., Blaxter, J.H.S., 1977. The effect of swimbladder deflation on pressure sensitivity in the saithe *Pollachinus virens*. *J. Mar. Biol. Assoc. UK* 57, 1057–1064.