

Fol. 41 W

Not to be cited without prior reference to the authors

23 DES. 1997

The Catching Performance of Fishing Gears Used in Surveys
ICES C.M. 1997/W:18

ICES Annual Science Conference
Baltimore, Maryland, USA, 25 Sep-4 Oct 1997.

THE USE OF DATA STORAGE TAGS TO STUDY COD NATURAL BEHAVIOUR AND
AVAILABILITY TO ABUNDANCE SURVEYS IN THE BARENTS SEA

Olav Rune Godø and Kathrine Michalsen¹
Institute of Marine Research,
P.O. Box 1870, N-5024 Bergen, Norway

ABSTRACT

Vertical movements of fish stocks can be studied by means of acoustic data from surveys, and diurnal related cycles in behaviour is often reported. To what extent the movements observed by this method reflect behaviour of individual fish, or alternatively, reflect probabilities of fish to be distributed at bottom or in the pelagic zone at specific time periods is unknown. Improved knowledge of fish natural behaviour is essential to understand variation in availability and efficiency of survey trawls as well as the actual target strength used in acoustical surveys. Data storage tags (DST) represent a new tool to observe individual fish behaviour in relation to environmental factors like temperature, depth and light.

In this paper the results from tags attached to North-East Arctic cod, released at spawning ground and during feeding, are presented and analysed with emphasise on implication of fish behaviour on efficiency of abundance surveys.

Keywords: abundance surveys, data storage tags, environmental factors, fish behaviour, vertical movements

¹ Authorship equal

5126 / 6 4410

INTRODUCTION

Cod in the Barents Sea, managed as the North-East Arctic cod stock, conduct horizontal as well as vertical migrations. The majority of mature specimens, more than 7 years of age, migrate to the spawning grounds in the Lofoten area or further south in November-February (Woodhead and Woodhead 1965, Mehl *et al.* 1985). During the summer and early autumn they move further north and east to feed on capelin. A similar migration, though less in extent, takes place for the largest immature fish, ages 3-6 years (Mehl *et al.* 1985). Throughout the whole year cod distribute vertically from the bottom to far up in the water column (Hysten *et al.* 1986, Godø and Wespestad 1993). The distribution is apparently affected by a number of factors such as density, depth, light, current etc. (Godø and Wespestad 1993, Michalsen *et al.* 1996). A varying vertical distribution and migration cause uncertainty about those methods that combine information from bottom trawl and hydro-acoustic abundance surveys (Aglen 1994, 1996, Godø 1994). The lack of understanding of the mechanisms controlling the vertical migrations as well as data to model its variation normally restricts compensation for its effects on surveys estimates.

A recorded collective pattern in vertical distribution, e.g. as observed by acoustics (Michalsen *et al.* 1996, Aglen *et al.* in prep.), is not necessarily caused by an identical pattern in movement of individual fish, but may rather be explained by some kind of probability function or by a distribution pattern. Available information strongly indicate that the dynamics is size dependent (Michalsen *et al.* 1996, Godø *et al.* 1997, Aglen *et al.* in prep.). To understand variability in vertical distribution dynamics of cod, it is necessary to improve the data on movements of individual fish of different size and during different season etc.

The gas-filled swimbladder is responsible for 90-95% of the total reflected energy (Foote 1980a) and the target-strength function is based on the assumption that the swimbladder acts as an ideal buoyancy organ, independent of depth changes (Foote 1980b). However, due to the relatively slow rates of gas secretion and resorption it has been argued that fish undertaking large vertical migrations only can be neutrally buoyant at the top of their vertical range (Alexander 1971, Arnold and Greer Walker 1992).

New technology, i.e. application of data storage tags (DST) (Arnold *et al.* 1994, Gunn *et al.* 1994, Thorsteinsson 1995), has now opened the possibility to alternative methods for studies of vertical distribution and behaviour. In this paper we will present data from DSTs in an experiment designed to study dynamics of vertical movement of cod older than 3 years in the Barents Sea.. The vertical movements will be analysed with particular emphasis on the physiological limitation of the cod to maintain neutral buoyancy under pressure changes. The results will be discussed in relation to variability in target strength in acoustic surveys and availability of cod to bottom trawl surveys. Problems connected to application of this methodology in behaviour studies will be elucidated.

MATERIAL AND METHODS

Data storage tags

The data storage tags (DST) are produced by Star Oddi, Iceland, are slightly positively buoyant, and measure 56 mm in length and 17 mm in diameter. The tag is small and, although attached externally, unlikely to impede the swimming performance of the fish significantly (Arnold and Holford, 1978). During the six first days of the week temperature and depth were recorded every 2 hours, while on the seventh day recordings were every 12 hours. This weekly pattern was repeated during the time the fish spent in the sea before it was caught. Precision of the temperature and depth records are ± 0.2 °C and ± 1 bar respectively according to calibration done for each individual tag by the producer.

Fish and tagging

In March -April 1996 158 tagged cod were released off the Norwegian coast (71°N, 25°E), while 42 cod were tagged on the Lofoten spawning grounds (Figure 1). The fish were captured at 50-100 m depth by bottom and pelagic trawls which were taken slowly to the surface. There was no evidence of the swimbladder being inverted through the mouth. The fish were kept in tanks for visual inspection before and after tagging to secure optimal survival after release. The tags were attached through the muscles in front of the first dorsal fin (Figure 2) with a mono filament line in the same way as done during conventional tagging with Lea tags (Anon. 1953, Godø 1989). All fish were measured to the nearest cm below before tagging. As with conventional experimental tagging methods, recovery of these tags are through the commercial fishery. Vertical profiles of the temperature at the two release sites are shown in Figure 3.

Analysis

To study dynamics in vertical movement of individual fish, with regard to diurnal or semidiurnal cycles, the depth variation was analysed by time series methods (SAS 1993). To expand the time series for each tag data for every 2 hour were interpolated for the seventh day of (using Proc expand, SAS 1993). Within defined sequences of relatively stable behaviour, variation of the individual tag data was tested in relation to random walk models and models with any kind of repeating feature by studies of the auto-correlation and partial auto-correlation functions and their residuals (SAS 1993).

The buoyancy of the fish depends on the extent of the vertical movements compared to the gas secretion and resorption capacity in the swimbladder. To be in neutral buoyancy at all depths, the secretion of gas into the swimbladder will limit the descent of cod to roughly 1 m h^{-1} at 10° C (Harden Jones and Scholes 1985). The resorption of gas out of the swimbladder is faster than the secretion and the time (t) needed to maintain neutral buoyancy when moving from deep to shallow water is

$$t = B \ln (P1/P2)$$

where B is the slope of the regression line when time for adaptation is plotted against $\ln(P1/P2)$. P1 and P2 are the pressures in atmospheres at the greater and lesser depths respectively.

According to the experiments of Harden Jones and Scholes (1985) $B=254$, which is the value used in our tests of stability in buoyancy during ascents.

RESULTS

Size composition and horizontal migration

The length compositions of the tagged fish from the two areas are shown in Figure 4. According to additional sampling from the two areas, cod from the spawning ground in Lofoten were mature fish, while the bulk of the fish from North Cape Bank were immature specimen.

Within 12 months after release off the Norwegian coast and in the Lofoten area, a total number of 18 and 9 tagged fish respectively, have been recaptured (Figure 1, Table 1).

After release behaviour

Although not consistent, the behaviour during the first two weeks after release differ from what appeared thereafter. Some of the fish conducted rapid descents and ascents with gradually decreasing oscillations (Figure 5, type 1 behaviour), while other fish dived directly towards the bottom (or preferred depth level), before doing repeated ascends to shallower waters for short time intervals (Figure 5b, type 2 behaviour). Some individuals waited several hours or even days before diving towards bottom, while others descended within few hours after release. Although both behaviour patterns was observed, the type 2 behaviour dominated among the mature fish released in Lofoten, while the cod released off the Norwegian coast mainly showed type 1 behaviour. In addition to variation in behaviour pattern the time used before the fish appear to be acclimatised to a preferred depth level varied from 4 to about 13 days.

Vertical movements after acclimatisation

After 13 days in freedom we consider all fish to be acclimatised. The vertical movements of the cod after this period are categorised in two types of behaviour.

Some fish remain at one depth with very limited vertical movements for periods over several days/weeks, i.e. they kept within a vertical "migration channel". An extensive change in depth of the "channel", with small shift in the amplitude of the short term movements is what we call Type 3 behaviour (Figure 6). In one occasion a change in depth of the "channel" was preceded by rapid vertical movements of 250 m.

Type 4 behaviour is exemplified with a gradual change in the depth of the "channel" with abrupt shift in the amplitude of the short term movements (Figure 6). A shift in the amplitude of almost 100 m within short time could be observed.

The difference in depth within different time intervals describes the dynamics of the vertical movements (Table 2). Cod from both release sites showed that for all time periods, most of the movements kept within depths of 10 m. With increasing time periods the difference in depth

increases slightly. In the Lofoten experiment fish was observed to exceed 100 m within a two hours interval at three occasions, while such dramatic jumps were more frequent in the Norwegian Coast experiment (40 occasions). Larger amplitudes apparently occur sporadically, and often during special situations, e.g. when a general change in depth occurred (type 3 behaviour). The mean depth differences during descent were greater than during ascents for all time intervals.

The direction of movements within two time periods (each with an interval of 2 hours), as observed after acclimatisation are compared in Table 3. The fish may change direction every two hour interval (Case 1, 2 options). Alternatively, the fish may continue a descent or ascent over the two periods (Case 2, 2 options). The remaining measurements (5 options), i.e. when depth remained constant in one or both of the periods are defined as Case 3. If the fish moved randomly we could expect frequencies of 22, 22 and 56%, respectively. The results shows that in the two first cases the fish moved vertically to a higher degree than the expected 22% and most frequently the fish changed the direction of their vertical movements during the two time periods compared to the continued descend or ascend (28.3% in case 1 compared to 28.8 % in case 2). On the other hand, cases where the fish kept at the same depth in one or both of the two following observation periods were underrepresented (32,9% compared with 56%)

Diurnal behaviour

All recaptures were analysed for any kind of diurnal or semidiurnal variation dynamics in vertical movements by time series analysis. When selecting periods of relative stability in movements, a significant semidiurnal effect on the vertical distribution was observed for some of the fish. The model explained vertical movements in the order of 1 to 2 m, and could thus be related to a tidal effect for fish staying close to bottom. Even though no diurnal differences could be documented in these analysis, Table 2 show that the average diurnal differences in depth is about the double of the average 2 hour difference for both the Lofoten and the Norwegian coast experiments.

Buoyancy

Acoustic target strength of fish is dependent on the amount of gas in the swimbladder and the angle at which the swimbladder is exposed to the echo sounder transducer. Both factors are dependent on the ability of cod to keep neutral buoyancy under substantial vertical movements. The time needed to level out the pressure difference between two succeeding observations to maintain in a constant buoyant state was calculated for all two hours intervals after the acclimatisation period. Table 4 show that fish can not regulate the gas level fast enough to be neutrally buoyant at all times. In 28.9% of all cases (i.e. close to 60% of the descents) the fish needed 3 hours or more to obtain neutral buoyancy. In extreme situations, several days would have been needed to stabilise buoyancy. Only occasionally the ascent exceeded the limit for the resorption capacity. The average descent differences are larger than the ascent (Table 2), and it is believed that this could be a result of the physical limitations the swimbladder expansion put on fish ascend.

Migration and temperature

For tags which had logged temperature during six months or more, the general trend is that the cod experience the warmest environment during early spring (February - March) and the coldest during Autumn (September - October) (Fig. 7). The exception is the only recapture from the spawning ground (tag 44) which showed temperature peaks both during spawning and in September. Also, a fish with a 2- months delay in temperature drop compared to the rest show that the time when cod move into colder water may vary.

More remarkable than the seasonal change in temperature is the abrupt shifts within a day. For tag 131 (Figure 8) average daily temperature varied from less than -1°C to about 4.5°C . In about 20% of the days a difference between daily maximum and minimum temperatures (dift in Figure 8) above 1.0°C was recorded, however, periodically the difference was as much as 3°C . For the tags remaining in sea after the acclimatisation time (Table 5) the maximum difference in temperature between neighbouring measurements (2 hours) varied from 0.5 to 5.6°C . There seems to be no apparent connection between maximum in depth and temperature differences (Table 5).

DISCUSSION

Vertical movement of fish create variability in the availability of fish to bottom trawl (Godø and Wespestad 1993, Aglen 1996, Michalsen *et al.* 1996), and for actual target strength to be used in acoustic surveys (Arnold and Greer Walker 1992, Harden Jones and Scholes, 1981). There is, however, a lack of understanding of the dynamics of the vertical movements as well as the mechanisms controlling them. Most reports are on population movements (see Introduction), although the last years patterns of single fish behaviour have been described based on data from cod tagged with acoustic tags (ie. Arnold *et al.* 1994, Godø 1996). The applicability of these experiments is, however, restricted by the low number of fish observed and the short period of observation of each fish, making it difficult to draw general conclusions from such experiments. By using data storage tags, which rely on recovery through the commercial fisheries, it is possible to tag a much higher number of fish and to get long term, high resolution data on vertical migration dynamics of fish. The tags have been used on several free-ranging fish in the open sea, included tuna, salmon, cod and plaice (Arnold *et al.* 1994). Thorsteinsson (1995) reports data on vertical distribution of cod off Iceland as observed with DSTs, but the time between recordings (8-9 hours) was too long to identify diurnal patterns.

Acclimatisation

The fish were all caught by trawl at depths of less than 100 m and brought slowly to the surface. If the fish was in neutrally buoyant state when caught, the abrupt elevation of the fish to surface, could have damaged the swimbladder, as the fish can not resorb gas out of the swimbladder fast enough to prevent rupture of the swimbladder wall (Tytler and Blaxter 1973, Harden Jones and Scholes 1985). We assume the fast up and down movements observed during the acclimatisation period is possible because the fish is not yet restricted by a functional swimbladder. Survival tests in experiments for long term commercial storage of living cod, have shown that all swimbladders

are broken when fish are caught at deep waters like in our experiment. Healing starts after few days and in these tests fish obtained an gas filled, functional swimbladder after 4-5 days (B. Isaksen, Institute of Marine Research, Bergen, pers. comm.). In a study of pressure sensitivity of saithe where the swimbladder was emptied by a needle, the threshold was restored to near normal after 15-18 hours (Tytler and Blaxter 1977). Even though the healing is supposed to be obtained within few days, repeatedly vertical movements (which do not give the stable pressure conditions as for fish held at constant depth) could delay this process. Extensive vertical movements may even cause new damage to the swimbladder. This might explain the large variation, from 4 to 13 days, in time needed for acclimatisation for free-ranging fish. Even though the behavioural signals indicate that swimbladder in most fish are healed after 13 days, it can not be concluded that the swimbladder function is fully restored at that point. A controlled experiment which simulates the capture and tagging process as well as fish vertical movements after release would have improved our knowledge on the healing process and secured a proper analysis of the results.

Vertical movements

Fish perform vertical movements to minimise predation and optimise food search (Neilson and Perry 1990). In addition some species utilize current speed for transport, by passive or by modulated drift, and occasionally attend those depths which have the highest water currents (Arnold *et al.* 1993, Michalsen *et al.* 1996). On the other hand, by moving down to the bottom high current speed might be avoided.

The data show that cod after acclimatisation normally kept within a limited migration window. In most cases the cod moved vertically less than 10 m during the two hours between each measurement. The lack of the expected diurnal pattern in the time series analysis could be caused by the variability of short term search movements for food. If the search movements in extent are of the same order of magnitude, a possible diurnal pattern could be difficult to distinguish. The resolution of 2 hours apparently can not fully uncover the whole dynamics, and an improved resolution might improve the understanding of the vertical movements.

Buoyancy and target strength

The cod has a closed swimbladder (physoclist) which occupies 5% of the body volume when the fish is adapted to neutral buoyancy (Harden Jones and Marshall, 1953; Sand and Hawkins, 1974). Pressure changes caused by vertical movements leads to expansion and compression of the swimbladder gas and the fish responds to the changes in density with resorption or secretion of gas, respectively (Harden Jones and Scholes, 1981, 1985). The swimbladder wall expands uniformly and reversibly with pressure reductions up to 50% of the pressure at which the fish is adapted, but burst if the pressure falls below 60-70% (Tytler and Blaxter, 1973). Because the dorsal surface of the swimbladder is attached to the backbone and pleural ribs, most of the contraction occurs in the dorso-ventral plane, reducing the effect of pressure on the target strength. However, expansion of adjacent organs, such as the stomach and gonads, will reduce its volume of 35% of normal size and thereby also the average target strength by 2-5 dB (Ona, 1990).

The rate of resorption of gas out of the swimbladder, which is a physical process, increases with hydrostatic pressure to which the fish were adapted (Harden Jones and Scholes, 1985), but seems to be limited by the supply of blood (Ross, 1979a,b). Secretion of gas into the swimbladder is a chemical process, which increases markedly with temperature, slightly with pressure and decreases with weight of the fish. This process is much slower than the resorption and there is a difference between the rates of the two processes which will increase with depth. Under experimental conditions, small cod (less than 1440 g) can cope with reductions of 25% and increases of 50% of the pressure to which they were originally adapted without experiencing any exceptional buoyancy problem (Harden Jones and Scholes, 1985), while larger cod probably can compensate for 70-90% of the swimbladder lift (Ona, 1990) by using their pectoral fins (Alexander, 1971) and altering the angle of attack of the body (Harden Jones and Scholes, 1985). Since a change in aspect angle of only a few degrees have a marked effect on the target strength, which increases when the head is tilted down and decreases when it is tilted up (Nakken and Olsen 1977, Rose and Porter, 1996), a combination of negative buoyancy and a head up position could cause a dramatic reduction in the target strength measurements and lead to a masking of the proportion of fish close to the bottom.

This study shows that the cod probably are under-buoyant for most of the time. The conditions experienced by the fish in this experiment is substantially different from the experiment conditions described by Harden Jones and Scholes (1985). The rough approximation of buoyant descent capability of 1 m h^{-1} due to secretion limitation in our experiment is considered to be an overestimate, due to bigger fish, colder water and higher pressure levels. What effects the under buoyancy have on tilt angle and swimbladder volume is difficult to evaluate from the available data. Data storage tags which include a tilt sensor in addition to the depth and temperature sensors, will strongly improve the basis for answering some of these questions. The importance of improved information on fish orientation is stressed by McClatchie *et al.* (1996) who studied potential impact of tilt angle on target strength variability.

The analysis of the vertical movements so far indicate no diurnal pattern and hence no systematic variation in TS. The average diurnal differences in depth (Table 4) is difficult to analyse because, as discussed above, the resolution of the observations might hide potential diurnal pattern in the data. Further, the great geographical distribution of the tagged cod (Fig. 1) involve high uncertainty on the actual length of day experienced by the individual fish. It has been speculated if a light sensor would be exposed to enough light when the fish during summer approach 100 m depth.

To increase the reliability of the survey-based abundance estimates it is necessary to acquire better information on fish behaviour, natural as well as vessel affected, as well as how behaviour vary with species and size. The present experiment show the potential of using DSTs to approach these problems. We think that improved tags with more storing capacity, improved resolution utilising new sensors as discussed above, represent an important step forward in methods for studying fish behaviour and its effect on survey stock assessment.

REFERENCES

- Aglen, A. 1994. Sources of error in Acoustic estimation of fish abundance. *In* Marine fish behaviour in capture and abundance estimation, pp. 107-129. Ed. by A. Fernö and S. Olsen. Fishing News Books.
- Aglen, A. 1996. Impact of fish distribution and species composition on the relationship between acoustic and swept-area estimates of fish density. *ICES Journal of Marine Science*, 53: 501-505.
- Alexander, R. 1971. Swimbladder gas secretion and energy expenditure in vertical migrating fishes. *In* International symposium on biological sound scattering in the ocean, pp. 74-85. Ed. by G. B. Farquhar. US Government Printing Office, Washington, 629 pp.
- Anon., 1953. A guide to fish marks. *J. Couns. Int. Explor. Mer.*, 19: 241-289.
- Arnold, G. P., and Holford, B. H. 1978. The physical effects of an acoustic tag on the swimming performance of plaice and cod. *J. Couns. Int. Explor. Mer.* 38: 189-200.
- 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 Journal of Marine Science* 49: 357-372.
- Arnold, G. P, Greer Walker, M. Emerson, L.S. and Holford, B.H. 1994. Movements of cod (*Gadus morhua* L.) in relation to tidal streams in the southern North Sea. *ICES Journal of Marine Science*, 51: 207-232.
- Arnold, G. P., Lundgren, B. and Godø, O. R. 1994a. Electronic tags in fisheries research and management. Report on a workshop held at Fisheries Laboratory, Lowestoft, UK. 14-17 November 1994. 61pp.
- Engås, A. and Godø, O.R. 1986. Influence of trawl geometry and vertical distribution of fish on sampling with bottom trawl. *J. Northw. Fish. Sci.* (7): 35-42.
- Foote, K. G. 1980a. Averaging of fish target strength functions. *Journal of the Acoustical Society of America*, 67: 504-515.
- Foote, K. G. 1980b. Effect of fish behaviour on echo energy: the need for measurements of orientation distributions. *Journal du Conseil International pour l'Exploration of the sea*, 144, 69pp.
- Godø, O.R. 1989. The use of tagging studies to determine the optimal time for estimating Acoustic abundance of spawning cod. *Fisheries Research*, 8: 129-140.

Godø, O. R. 1994. Factors affecting the reliability of groundfish abundance estimates from bottom trawl surveys. *In* Marine fish behaviour in capture and abundance estimation, pp. 166-199. Ed. by A. Fernö and S. Olsen. Fishing News Books.

Godø, O. R. 1995. Transplantation-tagging-experiments in preliminary studies of migration of cod off Norway. *ICES Journal of Marine Science.*, 52: 953-960.

Godø, O.R. and Wespestad, V. 1993. Monitoring changes in abundance of gadoids with varying availability to surveys. *ICES Journal of Marine Science*, 50: 39-51.

Godø, O.R., Karp, W.A. and Totland, A. 1997. Effects of trawl sampling variability on precision of acoustic abundance estimates of gadoids from the Barents Sea and the Gulf of Alaska. *ICES Journal of Marine Science*, (in press).

Gunn, J. S., Polacheck, T. Davis, T. L. O., Sherlock, M. and 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 C.M. 1994/Mini:21*. 23pp. (mimeo).

Harden Jones, F.R. and Marshall, N. B. 1953. The structure and function of the teleostean swimbladder. *Biol. Rev.* 28: 16-83.

Harden Jones, F.R. and Scholes, P. 1981. The swimbladder, vertical movements and the target strength of fish. *In* Meeting on hydroacoustical methods for estimation of marine fish populations, 25-29 June 1979. II: Contributed papers, discussion and comments. The Charles Stark Draper Laboratory, Inc. Cambridge, Massachusetts, USA. p157-181.

Harden Jones, F.R. and Scholes, P. 1985. Gas secretion and resorption in the swimbladder of cod *Gadus morhua*. *Journal of Comparative Physiology* 155b: 319-331.

Hysten, A., Nakken, O. and Sunnanå, K. 1986. The use of acoustic and bottom trawl surveys in the assessment of North-east Arctic cod and haddock stock. *In* a workshop on comparative biology, assessment and management of gadoids from the North Pacific and Atlantic Oceans, pp. 473-498. Ed. by M. Alton. Seattle, Washington, June 1985.

McCleave, J. D., Harden Jones, F. R., Legget, W. C., and Northcote, T. G. 1984. Fish migration studies: future directions. *In* McCleave, J. D., Arnold, G. P., Dodson, J. J. & Neill, W. H. (eds.), *Mechanisms of migration in fishes*. Plenum Press, New York, pp.545-554.

McClatchie, S., Aslop, J., Ye, Z., and Coombs, R. 1996. Consequences of swimbladder model choices and fish orientation to target strength of three New Zealand fish species. *ICES Journal of Marine Science*, 53: 847-862.

Mehl, S., Nakken, O., Tjelmeland, S. and Ulltang, Ø. 1985. The construction of a multispecies model for the Barents Sea with special reference to the cod-capelin interactions. *Cont. Workshop*

comparative biology, assessment and management of gadoids from the North Pacific and Atlantic Oceans. Seattle, 24.- 28 June 1985. pp1-25.

Michalsen, K., Godø, O.R. and Fernø, A. 1996. Diel variation in the catchability of gadoids and its influence on the reliability of abundance indices. ICES Journal of Marine Science, 53: 389-395.

Ona, E. 1990. Physiological factors causing natural variations in acoustic target strength of fish. Journal of the Marine Biological Association of the UK, 70: 107-127.

Ross, L. G. 1979a. The haemodynamics of gas resorption from the physoclist swimbladder: the structure and morphometrics of the oval in *Pollachinus virens* (L.). J. Fish. Biol. 14: 261-266.

Ross, L. G. 1979b. The haemodynamics of gas resorption from the physoclist swimbladder II. The determination of blood flow rate in the oval of *Pollachinus virens* (L.) using radiolabelled microspheres. J. Fish. Biol. 14: 389-393.

Sand, O., and Hawkin, A. D. 1974. Measurements of swimbladder volume and pressure in the cod. Norw. J. Zool. 22: 31-34.

SAS Institute Inc. 1993. SAS/ETS Users's Guide, Version 6, Second Edition. Cary, NC, USA. 1022 pp.

Torsteinsson, 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 C.M. 1995/B:19: 1-15.

Tytler, P., and Blaxter, J. H. S. 1973. Adaption by cod and saithe to pressure changes, Netherlands Journal of Sea Research, 7:31-45.

Tytler, P., and Blaxter, J. H. S. 1977. The effect of swimbladder deflation on pressure sensitivity in the saithe *Pollachinus virens*. Journal of the Marine Biology Workshop report 1995.

Woodhead, P. M. J., and Woodhead, A. D. 1965. Seasonal changes in the physiology of the Barents Sea Cod *Gadus morhua* L., in relation to its environment. II. Physiology reactions to low temperatures. ICNAF Special Publication, 6: 717-734.

Table 1. Information on release and recapture of cod off the Norwegian coast (N) and in the Lofoten area (L).

Release site	Tag no.	Date of release	Date of recapture	Length at release (cm)	Days in sea
N	7	17.03.96	24.03.96	66	7
N	17	17.03.96	26.03.96	82	9
N	134	16.03.96	29.03.96	61	13
N	29	13.03.96	11.04.96	82	29
N	247	14.03.96	13.04.96	70	30
N	32	17.03.96	09.05.96	79	53
N	21	17.03.96	30.05.96	62	74
N	235	16.03.96	16.06.96	70	92
N	138	14.03.96	24.06.96	65	102
N	228	16.03.96	16.07.96	66	122
N	246	16.03.96	21.07.96	64	127
N	238	14.03.96	21.07.96	67	129
N	97	18.03.96	21.09.96	97	187
N	98	18.03.96	21.10.96	59	217
N	110	18.03.96	18.11.96	82	245
N	106	16.03.96	26.11.96	59	255
N	117	17.03.96	18.03.97	74	366
N	131	17.03.96	02.04.97	72	381
L	75	28.03.96	30.03.96	72	2
L	11	28.03.96	30.03.96	71	2
L	55	28.03.96	02.04.96	83	5
L	74	28.03.96	02.04.96	74	5
L	56	28.03.96	11.04.96	72	14
L	69	28.03.96	17.04.96	71	20
L	33	28.03.96	21.05.96	87	54
L	38	28.03.96	10.08.96	75	135
L	44	28.03.96	05.02.97	81	314

Table 2 Difference in depth (m) within different time intervals from cod after the acclimation period, presented as percentages a) off the Norwegian coast and b) in the Lofoten area, presented as percentages within each depth and time interval. Mean ascent and descent are average depth difference observed during ascent and descent respectively.

a)

Interval(hr)	Depth (m)								Ascent(m) difference	Descent(m) difference
	0-9	10-19	20-29	30-39	40-49	50-99	100-199	200+		
2	10,00	2,31	1,06	0,55	0,34	0,57	0,08	0,00	8	11
4	9,99	2,81	1,42	0,68	0,49	0,75	0,14	0,00	10	13
6	9,78	3,02	1,60	0,81	0,56	0,93	0,15	0,01	12	15
8	9,50	3,20	1,79	0,88	0,62	0,99	0,21	0,01	13	16
12	8,71	3,37	1,83	1,09	0,69	1,09	0,23	0,02	14	18
24	7,86	3,66	2,30	1,32	0,84	1,43	0,26	0,03	17	21
ALL	55,84	18,37	9,99	5,33	3,54	5,76	1,08	0,09	12	16

b)

Interval(hr)	Depth (m)								Ascent difference	Descent difference
	0-9	10-19	20-29	30-39	40-49	50-99	100-199	200+		
2	9,37	2,86	1,37	0,73	0,43	0,55	0,03	-	9	13
4	8,69	3,13	1,79	1,02	0,61	0,82	0,07	-	12	15
6	7,99	3,45	2,27	1,11	0,70	1,05	0,08	-	15	17
8	7,57	3,95	2,23	1,19	0,70	1,17	0,10	-	16	18
12	6,97	4,35	2,38	1,37	0,69	1,26	0,14	-	17	19
24	6,80	4,44	2,17	1,32	1,04	1,71	0,34	-	20	21
ALL	47,39	22,17	12,21	6,75	4,18	6,55	0,76	-	15	17

Table 3 Direction of movements between two time periods, as recorded in all tags after the acclimation period.

	Case 1	Case 2	Case3
Observations (N)	11454	8620	9847
Percentage	38.3%	28.8%	32.9%

Table 4. Number of hours (hr) needed for achieving neutral buoyancy after descent (negative hr) and ascent (positive hr). Frequency, percent, and cumulative frequency and percent reflect numbers of occurrence and percents under the different hr categories. The -12 hr category include descents where secretion of gas takes 12 hours and more.

HR	Frequency	Percent	Cumulative frequency	Cumulative percent
-12	2475	11.4	2475	11.4
-11	301	1.4	2776	12.8
-10	95	0.4	2871	13.3
-9	429	2.0	3300	15.3
-8	51	0.2	3351	15.5
-7	593	2.7	3944	18.2
-6	207	1.0	4151	19.2
-5	664	3.1	4815	22.3
-4	400	1.8	5215	24.1
-3	1045	4.8	6260	28.9
-2	854	3.9	7114	32.9
-1	1438	6.6	8552	39.5
0	7619	35.2	16171	74.8
1	4926	22.8	21097	97.6
2	425	2.0	21522	99.5
3	94	0.4	21616	100.0
4	10	0.0	21626	100.0

Table 5. Mean depth and temperatures recorded after the acclimatisation period. Dif. min. and max. are minimum and maximum differences for neighbouring observations of depth and temperature (2 hours intervals).

Tag no.	Mean depth (m)	Dif. max depth (m)	Dif. min depth (m).	Mean temp. (°C)	Dif. max temp. (°C).	Dif. min temp. (°C).
21	128.9	128.4	105.4	3.3	1.0	1.3
29	114.4	172.0	50.0	3.9	0.9	1.1
32	186.7	70.0	77.8	4.0	0.7	0.5
33	277.3	120.6	124.5	4.5	1.8	2.2
38	183.4	154.9	154.9	3.8	0.9	1.0
44	128.6	100.8	88.9	2.9	3.1	3.5
69	98.9	34.7	29.3	5.5	1.0	0.7
97	151.3	98.0	107.8	3.1	2.6	2.6
98 *	221.9	-	-	2.3	-	-
106	180.6	88.8	110.1	2.3	3.5	5.6
110	204.1	207.9	158.3	2.3	1.4	1.4
117	238.4	196.8	245.9	3.0	2.1	2.4
131	207.2	122.6	133.7	2.1	2.8	2.8
138	244.5	71.9	301.3	2.8	1.2	0.9
228	178.3	70.2	73.5	3.3	2.1	2.3
235	281.6	131.5	129.8	3.7	0.6	0.7
238	278.0	96.1	102.5	2.1	2.5	3.0
246	235.5	138.2	128.9	2.3	2.1	2.3
247	288.0	59.1	52.3	4.5	0.6	0.6

* Incorrect time interval, no min and max calculations done.

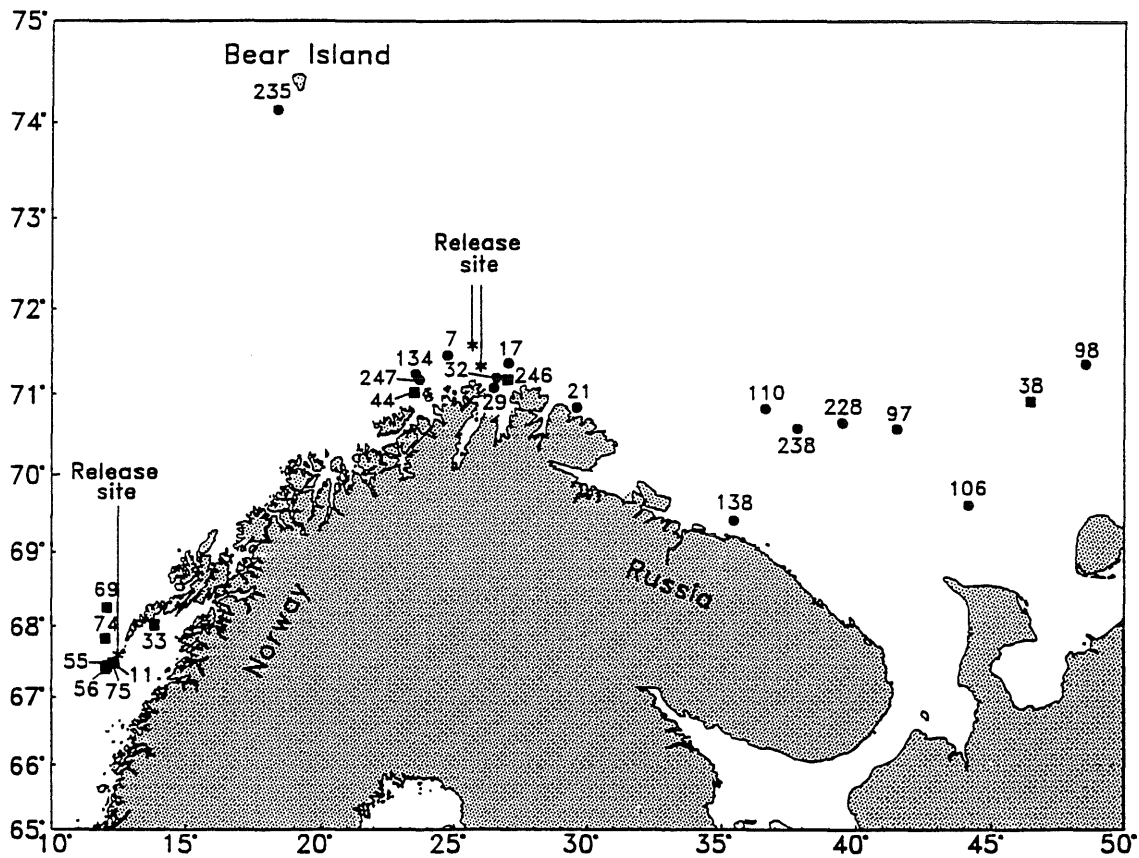


Figure 1. Tagging locations off the Norwegian coast and in the Lofoten area (stars). Recaptures are indicated with dots and squares respectively. Tag number is given for each recapture.

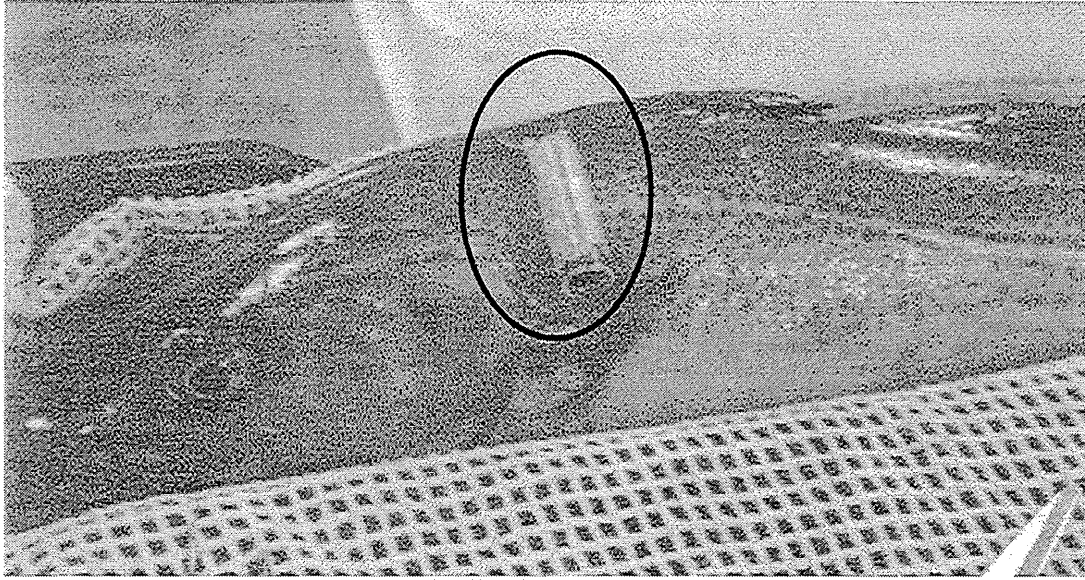


Figure 2. The Star Oddi data storage tags externally attached to a cod.

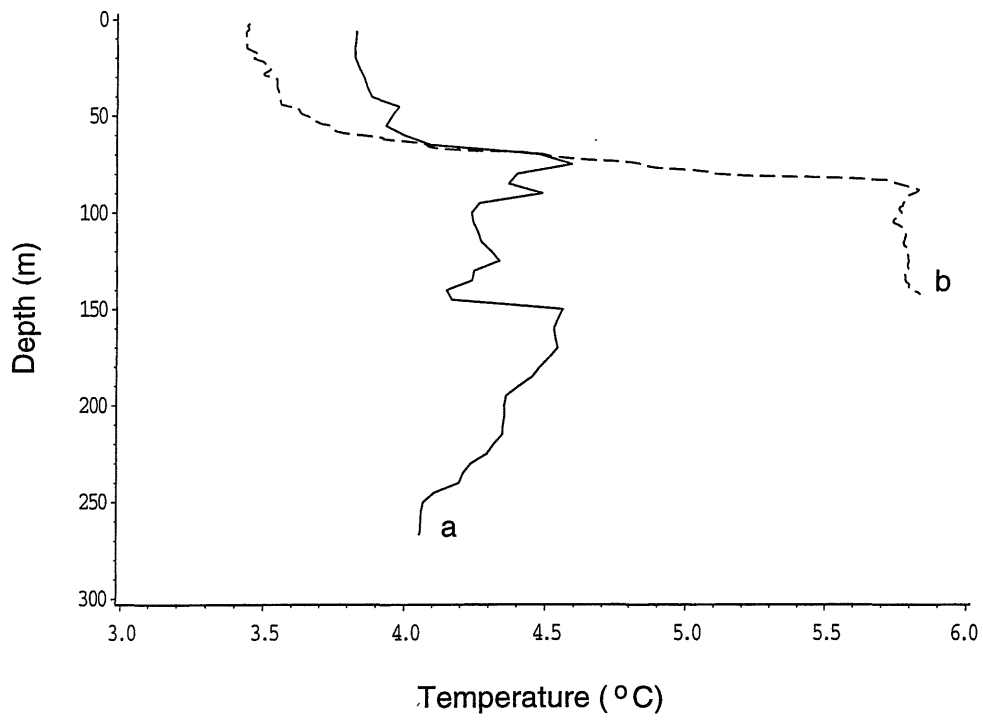
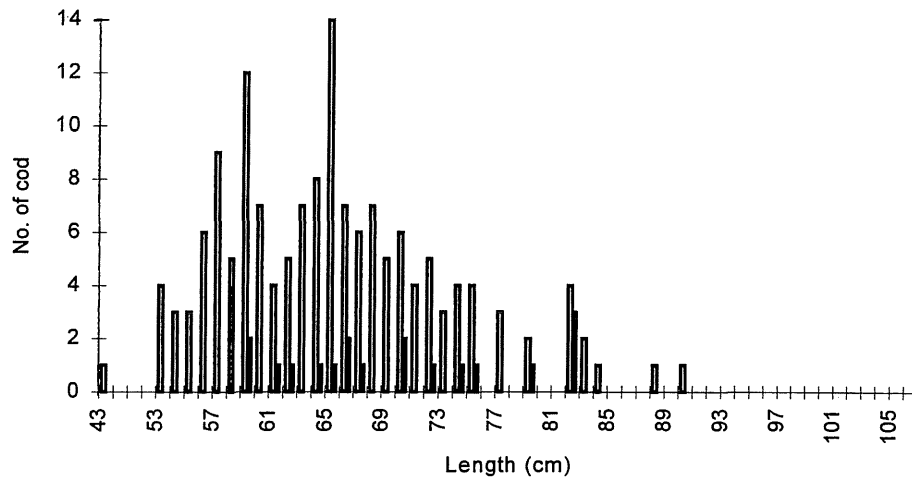


Figure 3. Temperature profiles on release locations a) off the Norwegian coast, b) in the Lofoten area.

a)



b)

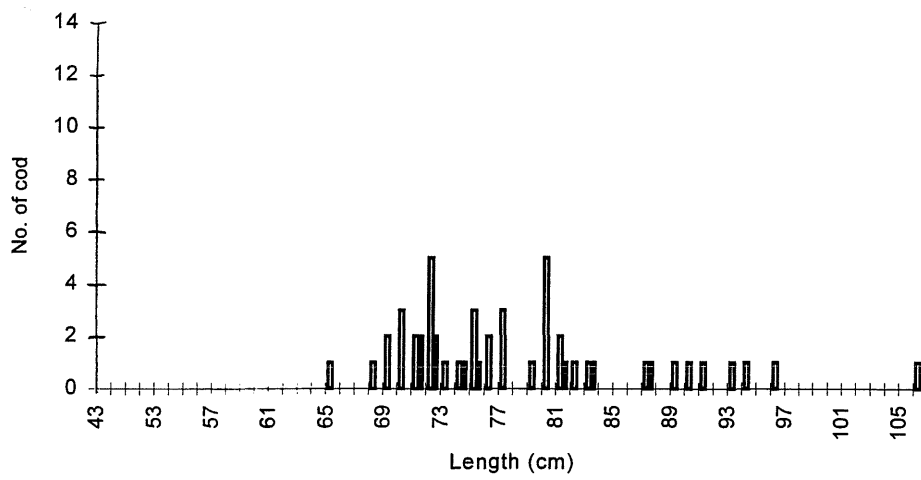


Figure 4. Length compositions of released (white column) and recaptured (black column) cod from the two tagging locations a) off the Norwegian coast, b) in the Lofoten area.

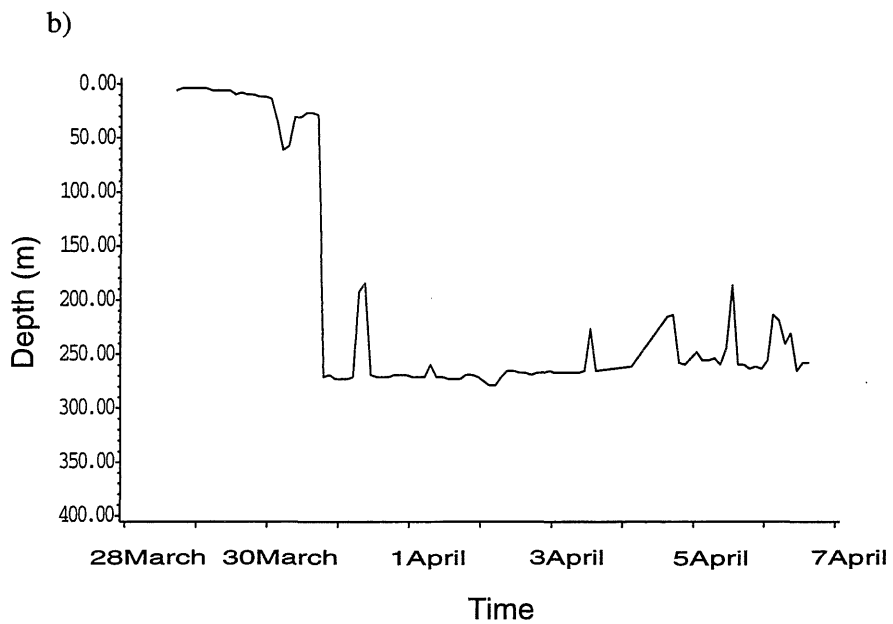
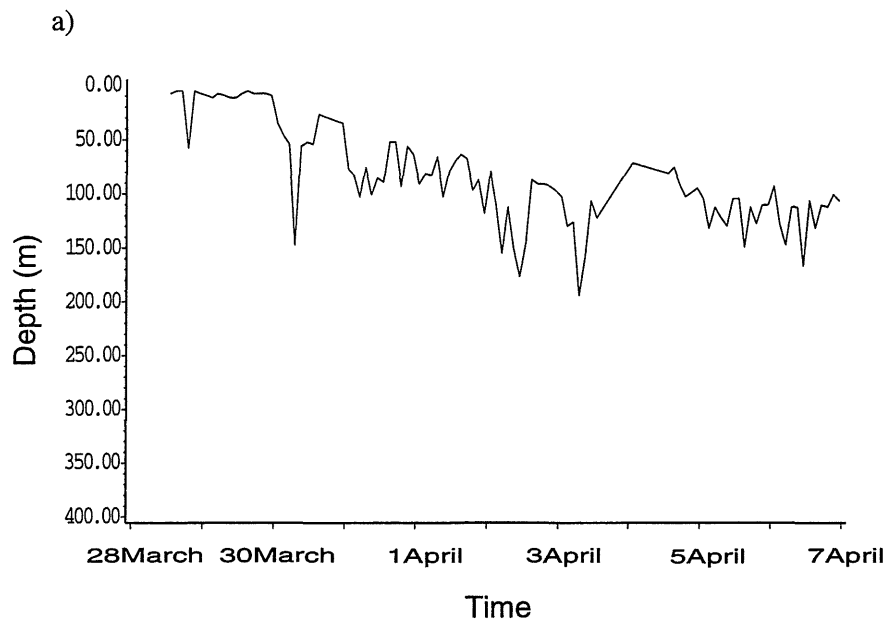


Figure 5. After release behaviour. Depth of fish by date. a) Type 1 behaviour, b) Type 2 behaviour.

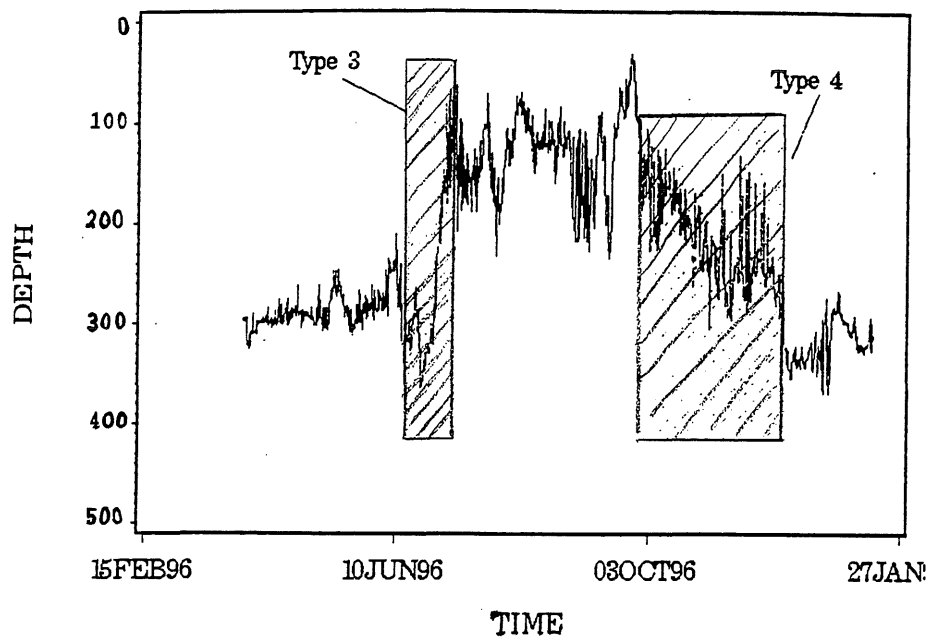


Figure 6. Behaviour after acclimatisation. Depth of fish by date. Type 3 behaviour exemplify extensive change in depth, with small shifts in the amplitude of the short time movements. Type 4 behaviour exemplify gradual change in depth level but with abrupt shift in the amplitude of the short time movements.

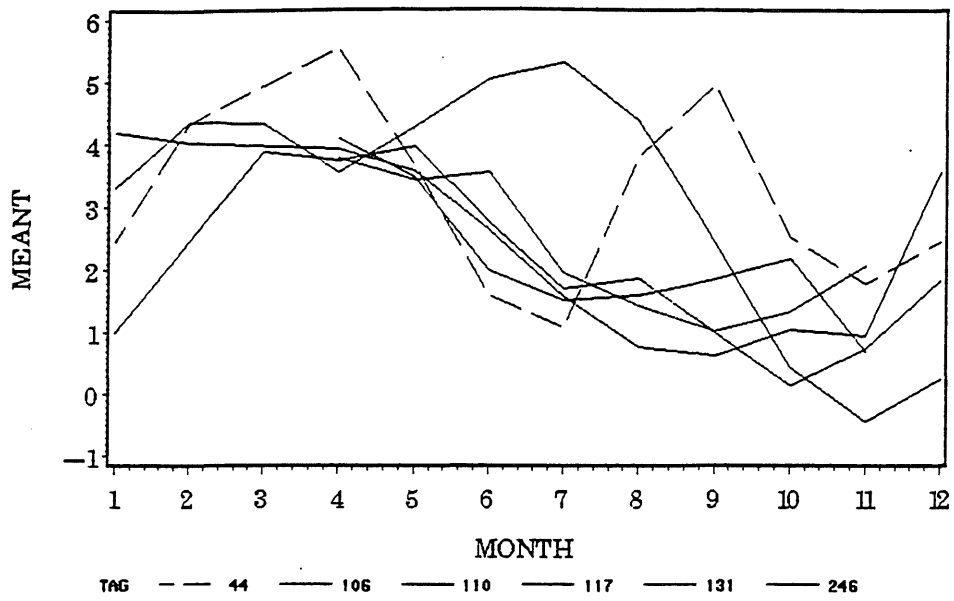


Figure 7. Seasonal changes in temperature for tagged fish with more than 6 months in sea.

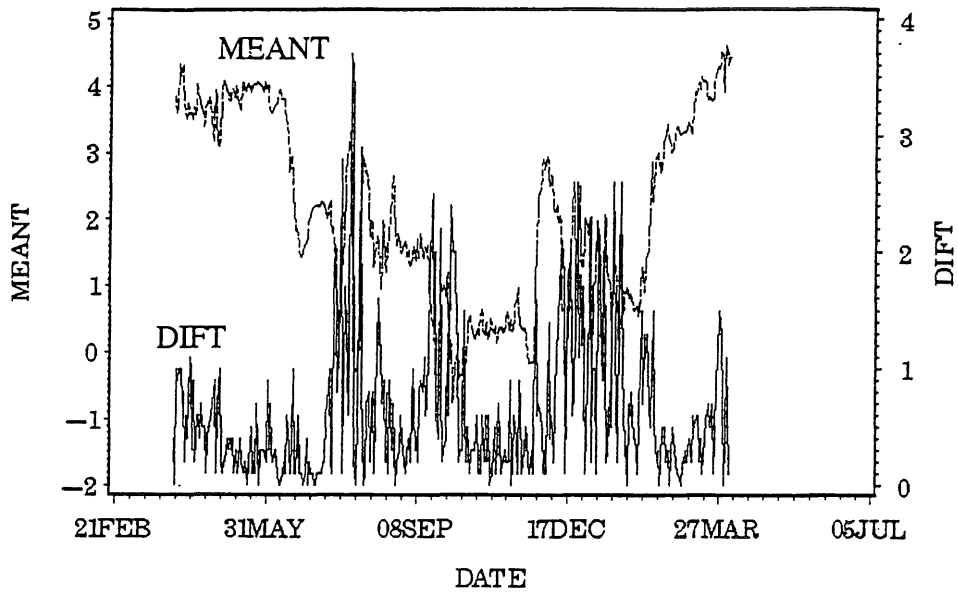


Figure 8. Mean temperature (Meant) per day and the daily difference between maximum and minimum observations of temperature (Dift) for tag no. 131.

