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Use of data storage tags to reveal aspects of
fish behaviour CM 2006/Q:13

Observations of cod behaviour reveal insights into the function and properties of the swimbladder under pressure.

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ABSTRACT

Atlantic cod (*Gadus morhua* L.) is a highly adaptive boreal species with a broad distribution through different ecosystems in the North Atlantic. Diet, environmental factors and population dynamics vary enormously throughout this range, and behaviours are therefore extremely plastic. However, the behaviour of cod will always be constrained by physiology, be it temperature tolerance, swimming speeds or buoyancy control. Cod, like other gadoids, are physoclists, i.e. they have a closed compliant swimbladder that can be filled or emptied in order to achieve neutral buoyancy at any depth. Pressure changes caused by vertical movements lead to expansion and compression of the swimbladder as individuals ascend or descend respectively. Over time, changes in the volume of the swimbladder will occur so that individuals can maintain neutral buoyancy with the minimum effort. Here, we have used data collected by cod tagged with electronic tags and released in five different regions of the NE Atlantic to investigate the neutrally buoyant descent rates of cod that are moving from shallow residence depths to deeper ones. First, we describe the patterns of vertical movement and rates of descent in the recuperation period following tagging, when the swimbladder is re-inflating to achieve neutral buoyancy at capture depth. Using this recuperation behaviour as an indication of swimbladder inflation during extreme depth changes, we then describe similar patterns of natural behaviour during medium-term transitions from shallow to deeper depths as cod migrate between different areas. Third, we assess the significance of behaviour of this kind, its relationship to environmental variables and how it varies between regions and seasons.

INTRODUCTION

Atlantic cod (*Gadus morhua*) is a highly adaptive boreal species with a broad distribution through different ecosystems. Diet, environmental factors and population dynamics vary enormously throughout this range, and behaviours are therefore extremely plastic. However, the behaviour of cod will always be constrained by physiology, be it temperature tolerance, swimming speeds or buoyancy control.

Cod, like other gadoids and species such as bass (*Dicentrarchus labrax*), redfish (*Sebastes* spp.), horse mackerel (*Trachurus* spp.), and capelin (*Mallotus villosus*), are physoclists, i.e. they have a closed compliant swimbladder that can be filled or emptied in order to achieve neutral buoyancy at any depth (Arnold & Greer-Walker, 1992). In cod, the swimbladder occupies between 4-5% of the volume of the fish. Pressure changes caused by vertical movements lead to expansion and compression of the swimbladder as individuals ascend or descend respectively. Over time, changes in the volume of the swimbladder will occur so that individuals can maintain neutral buoyancy with the minimum effort (Strand *et al.*, 2005). In cod, this is achieved by the secretion or excretion of gas by two specialised vascular structures in the swimbladder. Secretion of gas to the swimbladder occurs through a gas gland and is a chemical process, which therefore varies with temperature (Scholander & van Dam, 1954). Resorption is a solely physical process that occurs through a specialist organ called the oval, and is only limited by the oval's supply of blood. Resorption is therefore faster than secretion and increases with hydrostatic pressure (Harden Jones & Scholes, 1985). However, as gas secretion and resorption proceed slowly, relative to the short-term (seconds to minutes) vertical movements of cod (Heffernan *et al.*, 2004), it follows that there must be some restriction on the extent and speed of the changes in depth a cod can make whilst still enjoying the advantages of neutral buoyancy. Arnold & Greer-Walker (1992) describe a free vertical range (FVR), within which a cod can use compensatory swimming movements to move freely without needing to change the volume of gas in the swimbladder. The FVR has been shown experimentally to be at pressures 25% less and 50% more than the pressure at the depth at which neutral buoyancy is achieved (Harden Jones & Scholes, 1984).

Nonetheless, changes in the depth of neutral buoyancy are likely to take place at all times as the swimbladder and associated organs respond to medium-term (hours) changes in residence depth (Strand *et al.*, 2005). At times or in places where seabed depth changes rapidly, for example during off-shore migrations (Godø & Michalsen, 2000), compensatory swimming will not be sufficient for buoyancy control, and significant changes in residence depth on a time-scale of hours to days will require changes in the gas volume in the swimbladder if energy expenditure on buoyancy control is to be minimised (Strand *et al.*, 2005). Aside from the energetic considerations of buoyancy control (Strand *et al.*, 2005), and the limits that this imposes upon cod behaviour (Arnold & Greer-Walker, 1992; Godø & Michalsen, 2000; Heffernan *et al.*, 2004), understanding the buoyancy control of cod in more detail has great relevance to the design of acoustic surveys because of the correlation

between swimbladder volume and target strength (e.g. for cod: Godø & Michalsen 2000; Righton *et al.*, 2001; Heffernan *et al.*, 2004; and for other species: e.g. McClatchie *et al.*, 1996a & b, Rose & Porter 1996).

The difficulties of obtaining reliable estimates of the rate of gas exchange in swimbladders are well documented (Strand *et al.* 2005, Arnold & Greer-Walker, 1992). Here, we have used data collected by cod tagged with electronic tags and released across the NE Atlantic to investigate the neutrally buoyant descent rates of cod that are moving from shallow residence depths to deeper ones. First, we describe the patterns of vertical movement and rates of descent in the recuperation period following tagging, when the swimbladder is re-inflating to achieve neutral buoyancy at capture depth. Using this recuperation behaviour as an indication of swimbladder inflation during extreme depth changes, we describe similar patterns of natural behaviour during medium-term transitions from shallow depths to deeper depths as cod move across different areas during migrations.

MATERIALS AND METHODS

Tagging programme

Atlantic cod (*Gadus morhua*, L.) were tagged with electronic data storage tags (DSTs) at various locations in the eastern Atlantic between 1999 and 2004. Data from 342 of these tags had been returned by early 2006 (Table 1) and were available for analysis.

Data Storage Tags

Several different types of tag were used in this study: the LTD_1200, the LTD_2400 (LOTEK Marine Technologies, St Johns, Newfoundland, Canada, www.lotek.com), the DST_300, the DST Milli and the DST Centi (Star-Oddi Corporation, Vatnagardar 14, 104 Reykjavik, Iceland, www.star-oddi.com). DSTs were programmed to record depth and temperature at intervals between 10 s and 15 min.

Cod were caught using different methods depending on the location of tagging, prevailing conditions and the particular expertise of the fishermen. In the southern North Sea, cod were caught in shallow water (>25 m) by rod or longline (Righton *et al.*, 2006). In the northern North Sea, cod were caught in deep water (>60 m) using a BT 158 Jackson Rock-hopper trawl (Neat *et al.*, 2006). In the Skagerrak, cod were caught in cages or by 30 minute trawls (Svedäng *et al.* 2006). Cod in the Irish Sea were caught using rod and line in water of 75-90 m depth (Righton & Metcalfe, 2002). In the Barents Sea, cod were caught at 200 m using ground trawl and purse seine (Godø & Michalsen, 2000). On the Iceland shelf, cod were caught at between 50 to 100 m using a gill net (Palsson & Thorsteinsson, 2004). In all cases, captured fish were brought slowly to the surface to optimise post-tagging survival.

Captured cod were transferred to tanks supplied with running seawater and were retained in the tank only long enough to determine if they were in a suitable condition for tagging. Typically, these were cod that could maintain

buoyancy near the bottom of the tank without apparent difficulty and without external injury, such as bloodied fins or net-marks. Healthy cod were then measured to the nearest centimetre total length (TL). Cod of approximately 50 cm or greater in length were considered suitable for tagging. Fish were tagged either externally or internally (Table 1). External tags were attached by threading monofilament line or wire from the attachment points of the DST through the muscles anterior to the first dorsal fin and fastening the ends securely on the other side (see Godø & Michalsen, 2000; Palsson & Thorsteinsson, 2004; Righton *et al.*, 2006, for details). In the case of internal tagging, individuals were first placed in a shallow (~20 cm) bath, containing anaesthetic until light anaesthesia was achieved. Subsequently, a small (1.5 cm) incision was made in the skin of the belly, just behind the ventral fins, and a DST was inserted. The incision was then stitched twice with absorbable sutures and the wound smeared with antibiotic powder mixed with orahesive. All surgical instruments were sterilized before use on each individual.

Tag recovery

Fish recaptures were made through the commercial fishery, with a financial incentive offered for their return. Capture information included latitude, longitude, depth, and date of capture. Specimen information included fish length, sex, and fish weight.

Definition of equilibration behaviour

Equilibration behaviour is characterised by a series of large depth fluctuations occurring over a period of days, during which the depth attained on successive ascends linearly increases as a cod increases its neutrally-buoyant depth (Fig 1a). The starting point is the shallowest depth on this theoretical slope. This behaviour often occurs immediately after tagging (see also Heffernan *et al.*, 2004; Nichol & Chilton, 2006), but is also associated with transitions from shallow water to deeper water. Those records that contained evidence of this behaviour were examined in detail (Table 1).

Region	Tags returned	Tags examined	Equilibration
Barents Sea	31	25	8
North Sea	115	71	31
Skagerrak	80	11	1*
Icelandic shelf	112	13	11
Irish Sea	4	4	4
Total	342	124	55

Table 1. Metadata of all cod DST returned, examined and those used for analyses of equilibration behaviour. *Most Skagerrak tags were set to record in telescoped intervals and only one DST had regular recording intervals throughout the whole equilibration period. More examples were found but could not be used for further analyses.

Analysis of descent rate and equilibration period

The recording frequency of the DSTs varied per region, and was standardized to 10 min intervals for the analyses, either by re-sampling at a lower frequency or interpolating data to a higher frequency. A total of 124 DST records from five different regions were investigated for the presence of depth adaptation.

The depth time-series was scrutinized to identify times of rapid transitions to deeper water. Examples of equilibration behaviour were then extracted. For each example, the starting point of equilibration was taken as the time and depth of the shallowest point at the start of the descent (Figure 1a). The maximum depth attained during this descent was typically the depth to which the individual would then become resident. In some occasions the seabed depth changed during the equilibration period suggesting the fish was migrating as it equilibrated. The end-point of equilibration was taken to be when the individual ceased to undertake large ascents away from the new residence depth into mid-water. The descent rate over the equilibration period was then estimated by plotting a line of best fit that extended through the uppermost portion of the depth range (Figure 1b) of each adaptation period, based on the assumption that cod were neutrally buoyant only at the upper limit of their depth range (Harden Jones & Scholes 1985, Arnold & Greer-Walker 1992). We then identified all the points that fell within the free vertical range (FVR: Arnold & Greer-Walker 1992) defined by this line of neutral buoyancy (Fig. 1b). From all examined records, 73 specimens displayed a total of 134 equilibration behaviours. These examples were scrutinized and only the clearest 83 examples (from 55 specimens) were used for further analyses.

For each equilibration example a number of variables were extracted: start and end time and depth, rate of descent, mean temperature, intercept, fish length and weight. As examples of equilibration behaviour were found not just after release but also further along in the record, we distinguished between “post-tagging” and “mid-record” examples. Post-tagging consisted of those cases that occurred straight after (within days) of release, and were not preceded by any other clear behavioural pattern. Mid-record examples occurred later on in the DST record. In some instances this was within a week after release, but in all these cases the fish had resumed “normal” behavioural patterns prior to equilibration, suggesting complete recuperation following potential effects of tagging. These preceding vertical patterns were for example migration, feeding and sometimes equilibration behaviours.

RESULTS

Patterns of equilibration

In the 138 tags examined for this paper, 55 specimens showed clear examples of equilibration behaviour. From these 47 specimens displayed post-release equilibration and a total number of 36 mid-record examples were found. Figure 2 shows examples of three different types of equilibration behaviour found both post-tagging and mid-record. The same definition for

equilibration behaviour applies to all three types but they are differentiated by the relative amount of time the cod spends in mid-water and the seabed. 'Seabed equilibration' is characterized by the fish spending more time on the seabed than in mid-water, 'Mid-water' directed equilibration by more time in mid-water than near the seabed and in 'neutral equilibration' approximately equal amounts of time are spent in mid-water and near the seabed. All three types were found in equal proportions in all regions and in both post-tagging and mid-record equilibration periods.

The duration of the equilibration behaviour varied between 0.34 days and 28.33 days with an average of 3.81 days (s.d. \pm 4.54). There was some linear relation between the equilibration duration and the change in depth experienced during this behaviour (Fig. 3). With increasing duration however the range of depth change experienced by different individuals increased. The specimens that underwent the longest equilibration periods showed relatively small changes in residence depth.

Mid-record equilibration behaviour was found to occur in nearly all months of the year (Fig. 4). Post-release equilibration data were removed in this figure, as they would bias towards those seasons when fish were released. Although April had the highest frequency of occurrence, the histogram was not corrected for days at liberty and most data are from this month.

Description of rates of descent

Descent rates ranged from 1.44 to 24 m day⁻¹ with an average of 10.20 m day⁻¹ (s.d. \pm 4.88) (Fig 5). The highest descent rates (slope) were also amongst the shorter descents, and the slope of descent of those specimens that underwent the longest equilibration periods, were less steep (Fig. 6). Neither cod length (Fig. 7) nor temperature (Fig. 8) appeared to have an effect on the descent rate.

DISCUSSION

The characteristic vertical patterns of gradual descent, here described as equilibration behaviour, were found to be common among the 138 cod DST records examined (40%). Apart from in the Baltic Sea, examples were found in cod from all the explored regions. In 47 specimens this behaviour was observed immediately or shortly after the fish being released and a total of 36 mid-record examples were identified. The results of the analyses of this behaviour imply that duration of the behaviour, fish length, temperature and proportional pressure increase have no effect on the rate of descent.

Significance of re-equilibration behaviour

The ubiquity of this behavioural pattern suggests that post-tagging equilibration is an extreme version of re-establishment of a behavioural (the need to be demersal) and physiological (the need to be neutrally buoyant) equilibrium. The patterns are associated with re-inflation of the swimbladder to obtain neutral buoyancy at capture depth, after apparent loss of gas from the swimbladder during the preceding capture and tagging process. It has

therefore been postulated that analyses of this behaviour could be useful for getting estimates of rate of neutrally buoyant descent, and the rate of gas secretion into the swimbladder (Heffernan *et al.*, 2004). It is, however, possible that the capture process caused physical trauma resulting from a rapid reduction in pressure, leading to abnormal behaviour and the anomalous rates of descent. However, the estimates from mid-record equilibration suggest that the rate of neutral buoyant descent is very similar to those observed in post-tagging equilibration, 10.3 m (s.d. \pm 5.3) day⁻¹ and 10.1 (s.d. \pm 4.4) m day⁻¹ respectively.

No clear patterns were observed in the rate of equilibration between regions, but this is likely to be due to the fact that several of the parameters were different between various sampling regions, such as fish length (see e.g. much larger size of Icelandic fish in Fig. 6) and depth of residence (neutral buoyancy). Damage to the swimbladder after capture is also likely to influence the results, yet difficult to quantify or record. In addition equilibration is likely to be super-imposed on other behavioural patterns like spawning and particularly migration.

Comparison with other studies

Given the temperature range, the rates of descent during equilibration found for cod in our study areas are consistent with the rate of gas-gland secretion necessary to maintain neutral buoyancy (Harden Jones & Scholes 1985, Thorsteinsson 1995, Heffernan *et al* 2004, Nichol & Chilton 2006). The range of descent rates is quite large (Fig. 5), probably due to the variability of secretion of gasses into the swimbladder. Again, the regional differences will add to this.

As expected a positive relation was found between the duration of the equilibration period and the depth change during the behaviour. The rate of gradual descent is physiologically limited by the rate of gas-gland secretion. However, none of the other factors explored in this paper showed any clear effects on descent rate. Gas-secretion rates are dependent on fish size (Harden Jones & Scholes 1985), but we found no clear relationship between fish length and slope (Fig. 7). Nichol & Chilton (2006) found for Pacific cod (*Gadus macrocephalus*) that smaller fish tended to descent faster. In our study area, the cod that descended fastest were indeed the smaller fish, but possibly because of the regional differences in fish size, no overall significant relationship was found between the two variables. Secretion rates into the swimbladder are directly related to water temperature (Harden Jones & Scholes 1985). Being a chemical process it is temperature dependent and an increase in descent rate was expected with increasing temperature. However, despite a large range of temperatures in our regions no such effect was observed. Regression plots exploring relationships between the various parameters and descent rate, as used in this study have the advantage that they provide an instant visual guide. However the different conditions in the various regions dictate the use of other methods, which will be explored in future studies.

Nichol & Chilton (2006) found that the descent rate in most of the Pacific cod decreased in time and they explained this curvilinearity by increasing diffusion

and leakage of gasses from the swimbladder with depth. The descent rates of the majority of the Atlantic cod from our study areas were more or less linear and we have made no further attempt to fit curvilinear regressions slopes. Only a few examples showed some curvilinearity: Cod 1362 from the Irish Sea has a decreasing descent rate (Fig. 2); cod 514 from the Icelandic shelf shows an increase (between 70-120 h) followed by a decrease (120 h-end) in the descent rate (Fig. 2). The fact that most descent rates were linear could be explained by the fact that several of the equilibration periods were too short for curvilinearity to be detected.

Insights into swimbladder function

Descent rates suggest full swimbladder functionality as soon as cod began the gradual descents, although some of the residence depths at which cod were captured and hauled up imply that damage was inevitable (Hetherington, pers. comm.). This suggests that cod have very quick repair mechanism (Nichol & Chilton 2006). Indeed the similarity between post-tagging and mid-record descent rates confirms this. These similarities allow for cautious comparison and can aid in understanding the natural occurrence of equilibration, which is one of the few patterns found across the various regions and even across different physoclists species such as Pacific cod (Nichol & Chilton 2006) and bass (Quayle, pers. comm.). Some preliminary explorations indicate natural occurrence when cod move from shallow to deeper depths. Mid-record (or natural) equilibration did not seem bound by season (Fig. 4), suggesting it is not associated with a particular behaviour like e.g. spawning. More work in particularly the functioning of the swimbladder, could reveal, for example, energetic advantages of this behaviour.

ACKNOWLEDGEMENT

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FIGURES

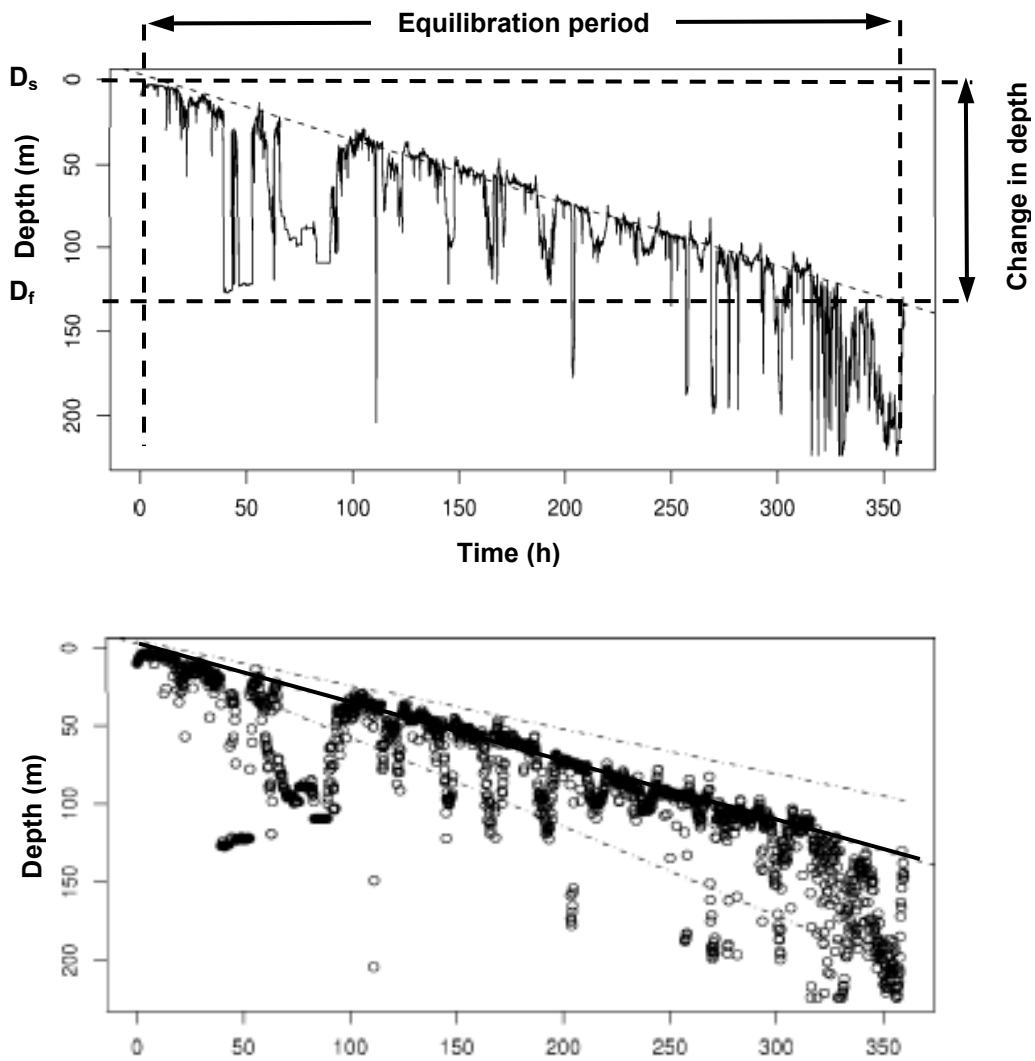
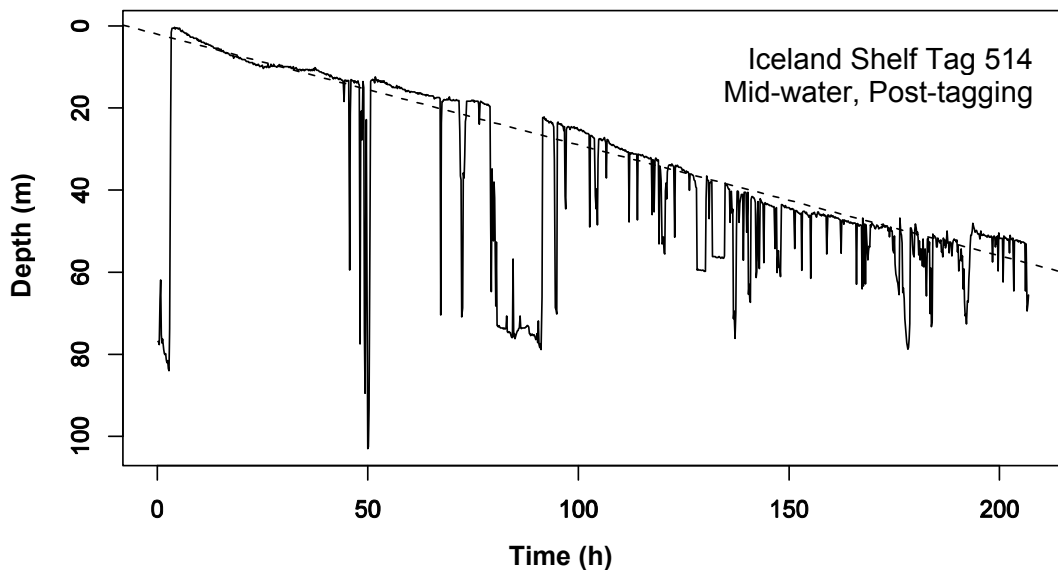
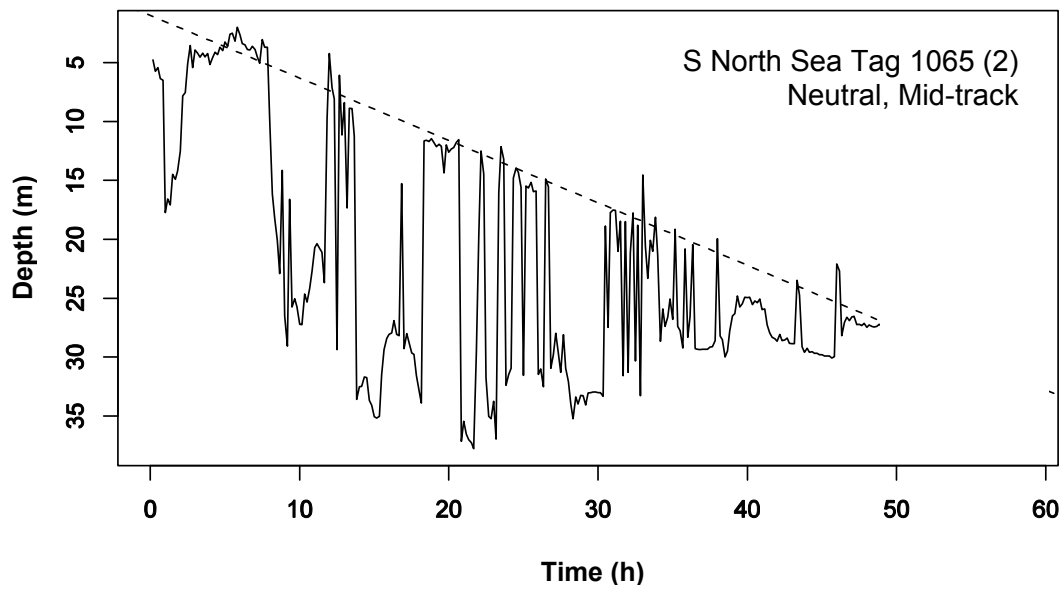
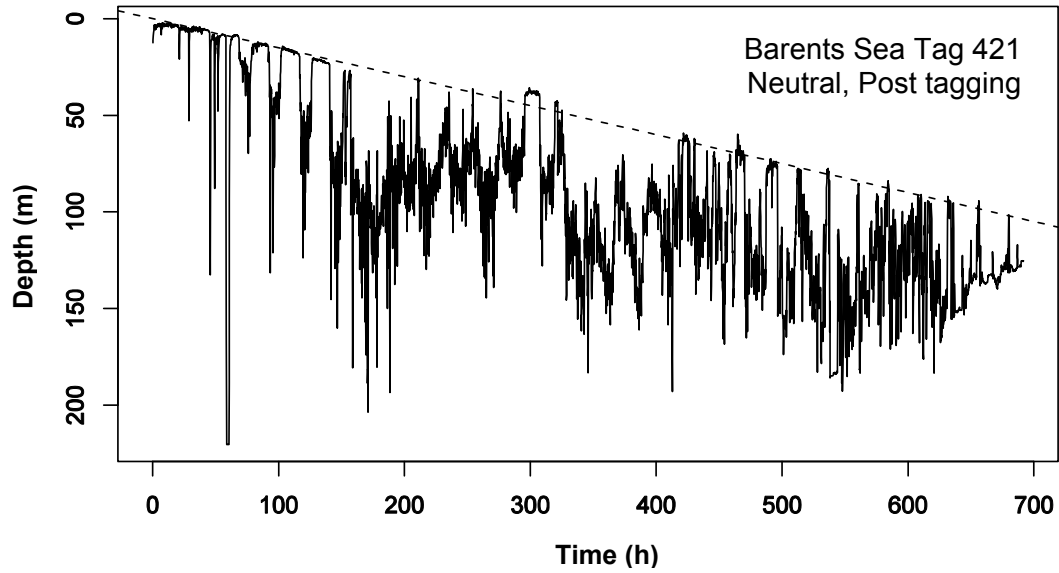


Figure 1. Post-tagging example of equilibration behaviour in cod 11788 (Skagerrak), showing start and end points, and start depth (D_s) and end depth (D_f) of equilibration (top figure). Depth profile of the same cod showing the slope of the equilibration regression (solid line) and the upper and lower limit of the Free Vertical Range (dotted line).



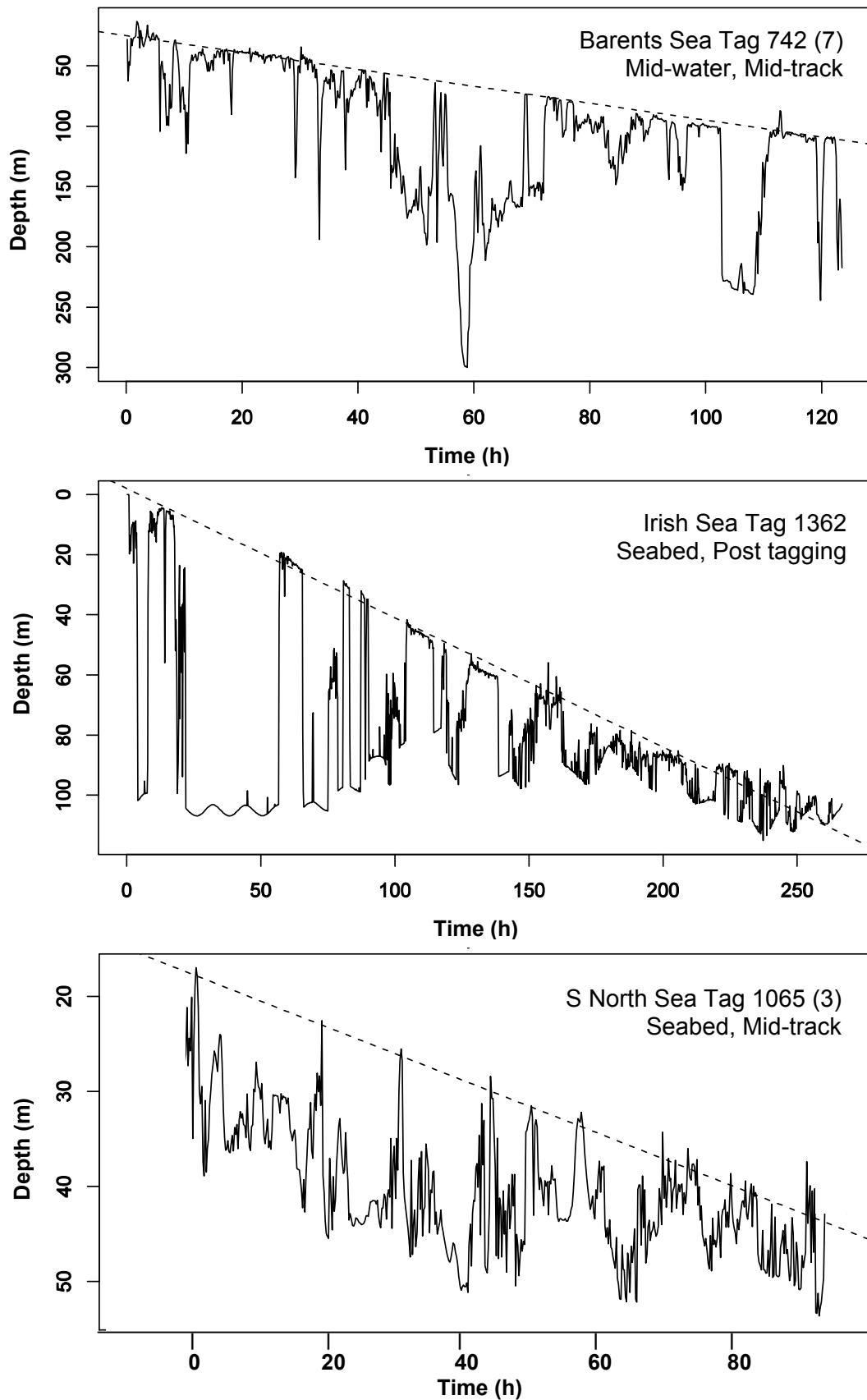


Figure 2. Post-tagging and mid-record examples of three types of equilibration behaviour from different regions. X-axis represents time (in hours) since start of the equilibration behaviour and y-axis depth (m). Dotted line represents regression of rate of neutral descent.

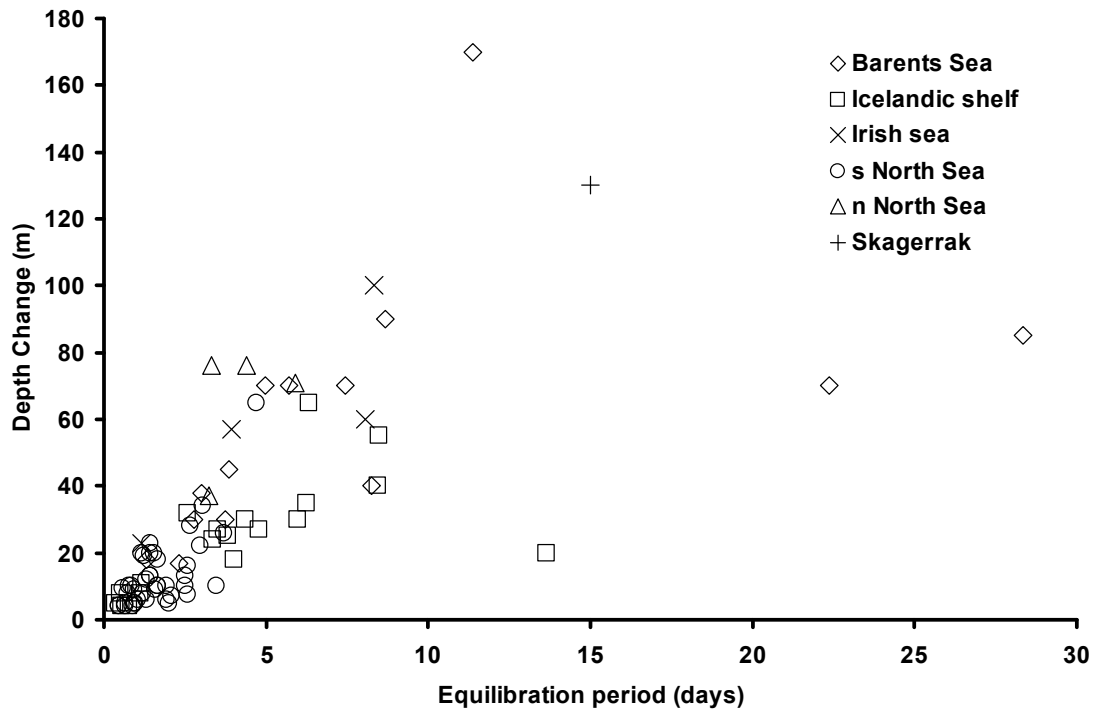


Figure 3. Relation between duration of equilibration and depth change for the different regions.

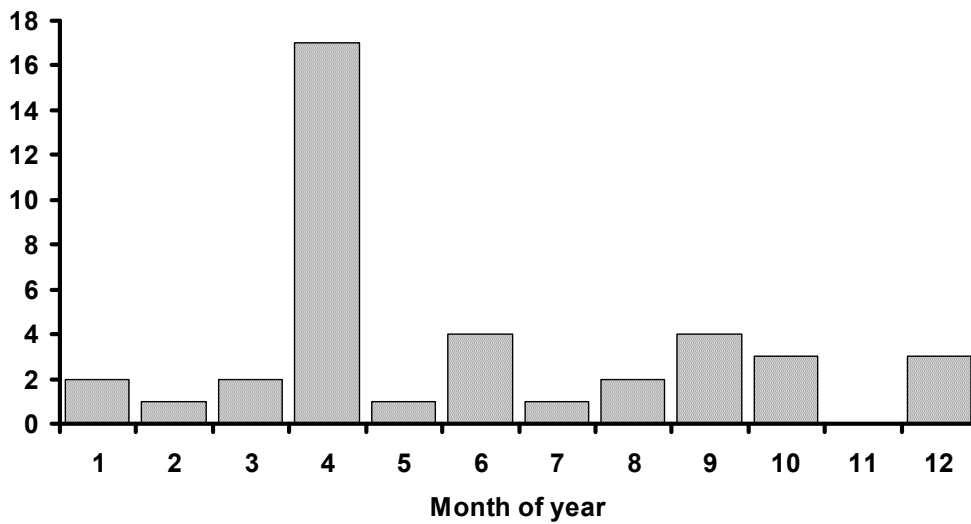


Figure 4. Frequency occurrence of mid-record equilibration by month.

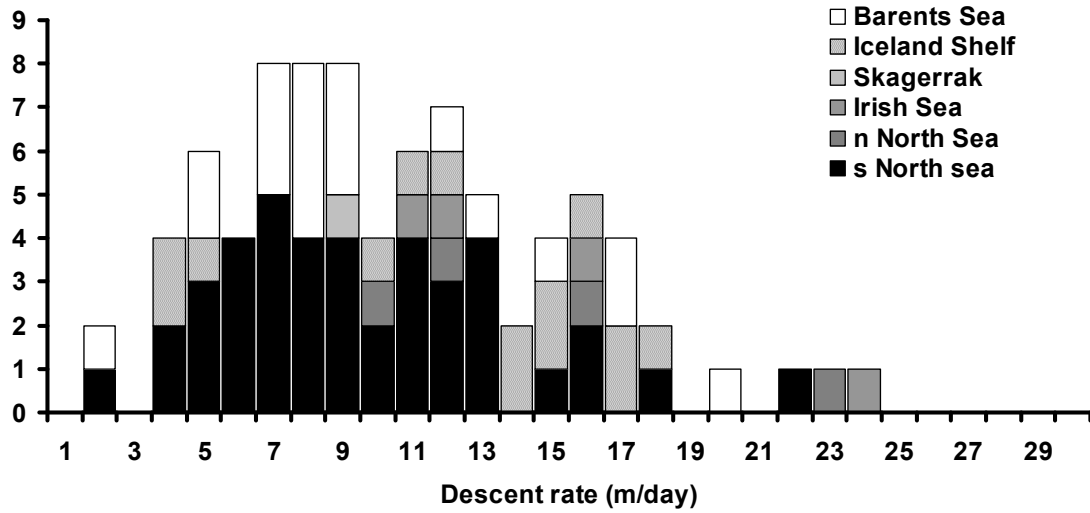


Figure 5. Frequency histogram of descent rate (m day^{-1}).

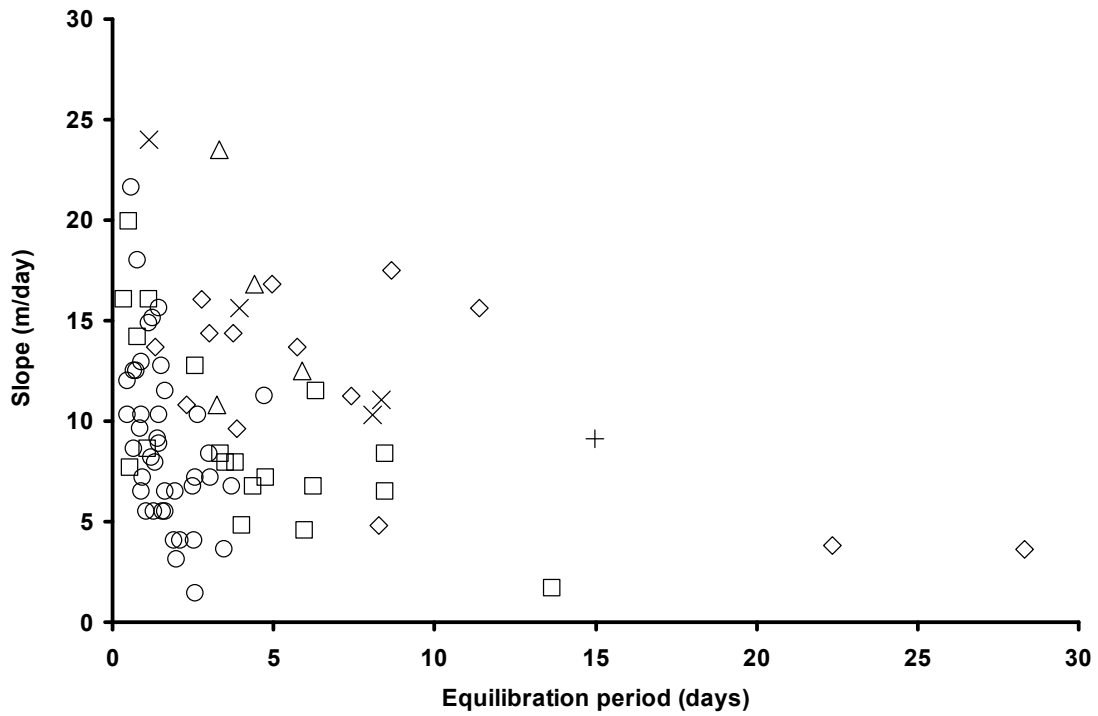


Figure 6. Relation between descent rate (m day^{-1}) and equilibration period (days). For legend please see Fig. 3.

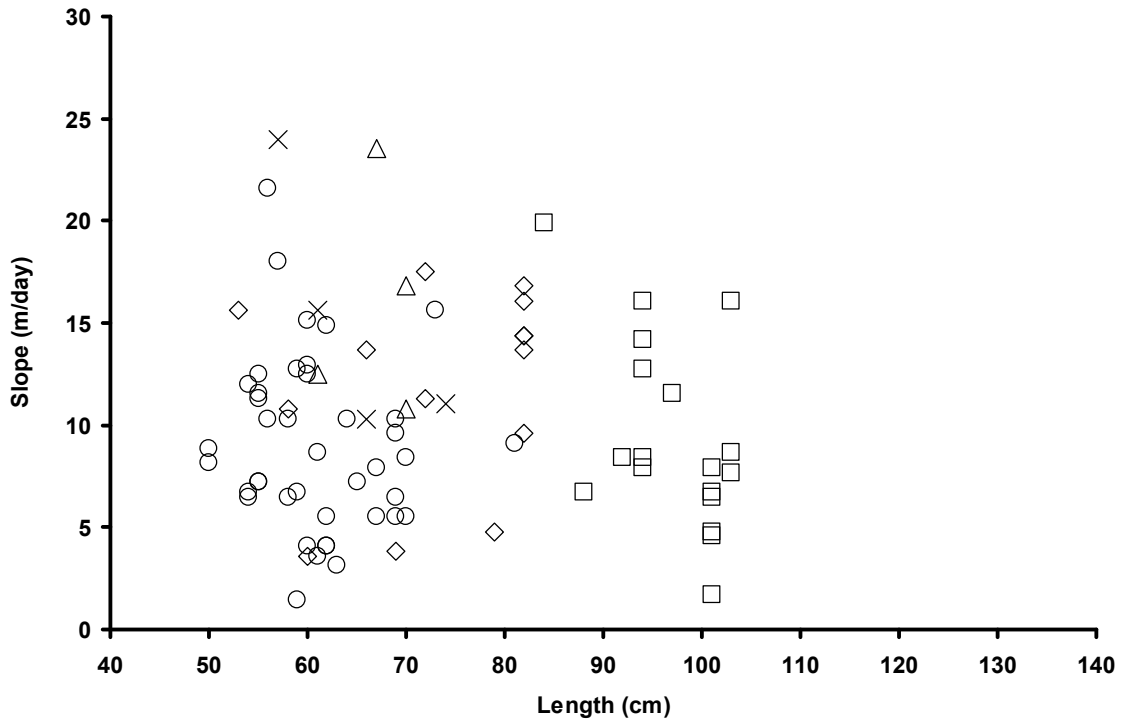


Figure 7. Relation between descent rate (m day^{-1}) and fish length (cm). For legend please see Fig. 3.

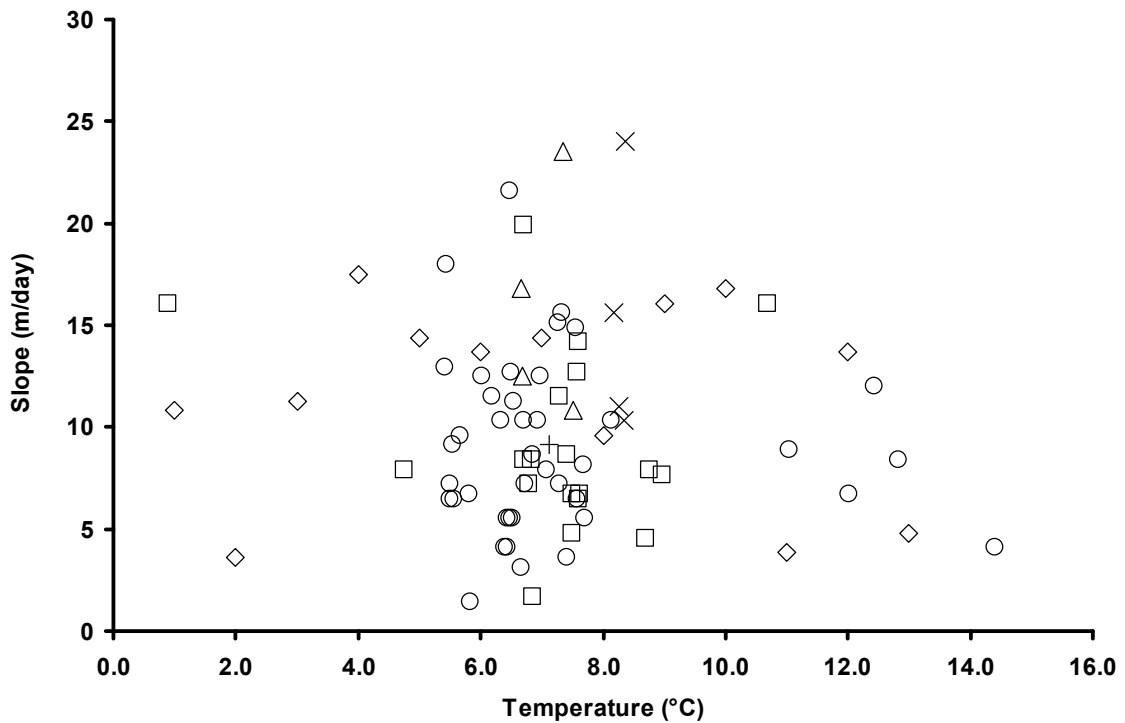


Figure 8. Relation between descent rate (m day^{-1}) and to temperature ($^{\circ}\text{C}$). For legend please see Fig. 3.