Life under pressure: insights from electronic data-storage tags into cod swimbladder function

Jeroen van der Kooij, David Righton, Espen Strand, Kathrine Michalsen, Vilhjalmur Thorsteinsson, Henrik Svedäng, Francis C. Neat, and Stefan Neuenfeldt

The behavioural response of cod (*Gadus morhua*) to sudden pressure reductions was investigated in a large electronic-tagging experiment using data collected from 141 cod tagged in five different areas of the Northeast Atlantic. More than 40% of cod exhibited a characteristic equilibration behaviour after a rapid pressure reduction caused either by capture before tagging, or by pressure reduction during a rapid ascent from the seabed, or when migrating to deeper water. The equilibration allowed the cod to regain demersal residence. The rate of descent averaged 10 m d^{-1} (ranging from 2 to 23 m d^{-1}) over periods of less than a day to 1 month. Descent rates for cod on the Icelandic shelf were inversely related to fish length, i.e. smaller fish descended more rapidly, findings consistent with results achieved in the past under laboratory conditions. Modelling of swimbladder volume during equilibration suggested that cod were negatively buoyant for most of the time. The results imply that swimbladder functionality is retained after the probable barotrauma that would follow a large and rapid ascent, and that rates of gas exchange into the swimbladder may be naturally variable. These findings have implications for assumptions on discard mortality, the interpretation of cod behaviour, and its impact on biomass estimates obtained from acoustic surveys.

Keywords: behaviour, buoyancy, cod, discard, physoclists.

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J. van der Kooij and D. Righton: Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK. E. Strand: Department of Biology, University of Bergen, PO Box 7800, N-5020 Bergen, Norway. K. Michalsen: Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway. V. Thorsteinsson: Marine Research Institute, Skúlagata 4, PO Box 1390, 121 Reykjavík, Iceland. H. Svedäng: Swedish Board of Fisheries, Institute of Marine Research, PO Box 4, S-453 21 Lysekil, Sweden. F. C. Neat: Marine Laboratory, Fisheries Research Services, 375 Victoria Road, 101, AB11 9DB Aberdeen, UK. S. Neuenfeldt: Danish Institute for Fisheries Research, Charlottenlund Castle, 2920 Charlottenlund, Denmark. Correspondence to J. van der Kooij: tel: +44 1502 524416; fax: +44 1502 513865; e-mail: jeroen.vanderkooij@cefas.co.uk.

Introduction

The Atlantic cod (*Gadus morhua*) is a highly adaptive boreal species with a broad distribution through different ecosystems, from temperate waters at the southern limit of its latitudinal range to Subarctic waters at its northern limits. Diet, environmental factors, and population dynamics vary enormously throughout this range, and behaviours are extremely plastic. However, the behaviour of cod will always be constrained by physiology, be it temperature tolerance, swimming speed, or buoyancy control.

Cod, like other gadoids and species such as bass (*Dicentrarchus labrax*), redfish (*Sebastes* spp.), and horse mackerel (*Trachurus* spp.), are physoclists, i.e. they have a closed, compliant swimbladder that can be filled or emptied to achieve neutral buoyancy at any depth (Arnold and Greer-Walker, 1992). In cod, the swimbladder occupies between 4% and 5% of the volume of the fish. Pressure changes caused by vertical movements lead to expansion and compression of the swimbladder as fish ascend or descend, respectively. Over time, the amount of gas in the swimbladder will change so that individuals can maintain neutral buoyancy with minimum effort (Strand *et al.*, 2005). In cod, this is achieved

by the secretion or excretion of gas by two specialized vascular structures in the swimbladder. Gas is secreted to the swimbladder through a gas gland, and is a chemical process, so it varies with temperature (Scholander, 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 and 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 while still enjoying the advantages of neutral buoyancy. Arnold and 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 and Scholes, 1985).

Nonetheless, changes in the depth of neutral buoyancy are likely at all times because the swimbladder and associated organs respond to medium-term (hours to days) changes in residence depth (Strand *et al.*, 2005). At times or in places where seabed depth changes rapidly, e.g. during offshore migration (Godø and 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 amount of gas in the swimbladder, if energy expenditure on buoyancy control is to be minimized (Strand *et al.*, 2005). Aside from the energetic considerations of buoyancy control (Strand *et al.*, 2005), and the limits that this imposes on cod behaviour (Arnold and Greer-Walker, 1992; Godø and Michalsen, 2000; Heffernan *et al.*, 2004), understanding the buoyancy control of cod in more detail has relevance to the design of acoustic surveys and the interpretation of acoustic data, because of the correlation between swimbladder volume and target strength (MacLennan and Simmonds, 1992; Rose and Porter, 1996; Godø and Michalsen, 2000; Heffernan *et al.*, 2004).

The difficulties of obtaining reliable estimates of the rate of gas exchange in swimbladders are well documented (Arnold and Greer-Walker, 1992; Strand *et al.*, 2005). Here, we used data collected from cod tagged with electronic tags and released across the various regions of the Northeast Atlantic to investigate the neutrally buoyant descent rates of cod moving from shallow depths of residence to deeper ones. First, we describe the patterns of this equilibration behaviour in terms of vertical movement and rates of descent in the recuperation period following tagging, when the swimbladder is re-inflating to compensate for loss of gas due to pressure reduction during capture, and to achieve neutral buoyancy at capture depth. Second, using this recuperation behaviour as an indication of swimbladder inflation during extreme depth changes, we describe and compare similar patterns of natural-equilibration behaviour during medium-term transitions from shallow to deeper water, as cod move across different areas during migration, and following rapid ascents from the seabed. Third, we investigate the energetic costs associated with behaviour of this type, and assess the null hypothesis that this is the most energetically efficient way of coping with large transitions in depth. Finally, we estimate the buoyancy status of cod during

these transitory phases, and both assess and discuss the implications for acoustic surveys.

Material and methods
Tags and tagging
Atlantic cod were tagged with electronic data-storage tags (DSTs) at various locations in the Northeast Atlantic between 1999 and 2004. Data from 342 of these tags had been returned by early 2006 and were available for analysis.

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 Reykjavík, Iceland, www.star-oddi.com). DSTs were programmed to record depth and temperature at intervals between 10 s and 15 min.

Capture methods
Cod were caught using different methods depending on the location of tagging, prevailing conditions, and the particular expertise of the fishers involved (Table 1). In the southern North Sea, cod were caught in shallow water ($\sim$25 m) by rod or longline (Righton *et al.*, 2006). In the northern North Sea, cod were caught in deeper water ($>$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-min trawl (Svedäng *et al.*, 2006), and in the Irish Sea, cod were caught using rod and line in water 75–90 m deep (Righton and Metcalfe, 2002). In the Barents Sea, cod were caught in 100 m of water using bottom trawl or purse-seine (Michalsen *et al.*, 2006), and on the Iceland shelf, cod were caught 20–110 m deep using a gillnet or Danish seine (Pálsson and Thorsteinsson, 2003). Baltic Sea cod were caught by longline 30–40 m deep (Neuenfeldt *et al.*, in press). Always, captured cod were brought slowly to the surface to optimize post-tagging survival.

Captured cod were transferred to tanks supplied with running seawater and were retained in the tank only long enough to determine whether 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

Table 1. Methods of cod capture, capture depth, tagging method, number of DSTs examined, the number of cod used for analyses of equilibration behaviour, the mean temperature experienced by cod during equilibration, and the total fish length at release for cod that underwent equilibration.

Region	Capture methods	Capture depth (m)	Tagging method	Number examined	Number equilibrating	Temperature (°C) and (s.d.)	Length (cm) and (s.d.)
Baltic sea	Longline	30–40	External	17	0	N/A	N/A
Barents sea	Trawl/purse-seine	100	Internal/external	25	8	5.3 ($\pm$2.2)	72.9 ($\pm$10.3)
Icelandic shelf	Gillnet/Danish seine	20–110	Internal	13	11	7.2 ($\pm$1.9)	97.0 ($\pm$5.6)
Irish sea	Rod	75–90	External	4	4	8.3 ($\pm$0.9)	64.5 ($\pm$7.3)
North sea							
Southern	Longline/rod	25	Internal/external	61	27	7.3 ($\pm$2.1)	61.1 ($\pm$6.6)
Northern	Trawl	$>$60	Internal	10	4	7.0 ($\pm$0.43)	67.0 ($\pm$4.2)
Skagerrak[a]	Trawl/cages	$>$50	External	11	1[a]	7.1	53
Total	–	–	–	141	55	–	–

[a]Most Skagerrak tags were set to record at irregular intervals, and only the data from one DST covered the whole equilibration period in regular recording intervals. More examples were found, but only one complete example could be used for analysis.
N/A, not applicable.

external injury, such as bloodied fins or net-marks. Healthy cod were then measured to the nearest centimetre total length (TL). Skagerrak cod >37 cm, owing to the exclusive use of the smaller, Lotek 2400 tags, and in other regions >50 cm, 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 (Godø and Michalsen, 2000; Righton *et al.*, 2006; Neuenfeldt *et al.*, in press). For internal tagging, individuals at all release locations except the Icelandic plateau 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 (for detail, see Pálsson and Thorsteinsson, 2003; Neat *et al.* 2006; Righton *et al.* 2006). All surgical instruments were sterilized before use on each fish.

Tagging was conducted under Government licence and always adhering to national regulations on the treatment of experimental animals.

Tag recovery

Fish were recaptured by the commercial fishery, with a financial incentive offered for their return. Capture information requested included location, date, and water depth. Specimen information included fish length, weight, and sex.

Definition of equilibration behaviour

Previously described as recuperation (Nichol and Chilton, 2006) and depth adaptation (Heffernan *et al.*, 2004), we redefined the typical post-release patterns of gradual descent as equilibration behaviour, because we found the same behaviour occurring naturally well after release. Equilibration behaviour is characterized by a series of large depth fluctuations over a period of days, during which the depth attained on successive ascents increases linearly as a cod increases its neutrally buoyant depth (Figure 1). The starting point is the shallowest depth on this theoretical slope. As examples of equilibration behaviour were found not just after release (recuperation *sensu* Nichol and Chilton, 2006) but also further along in the record, we distinguished between "post-tagging" and "mid-record" examples. Post-tagging comprised those cases that occurred straight after (within days of) release,
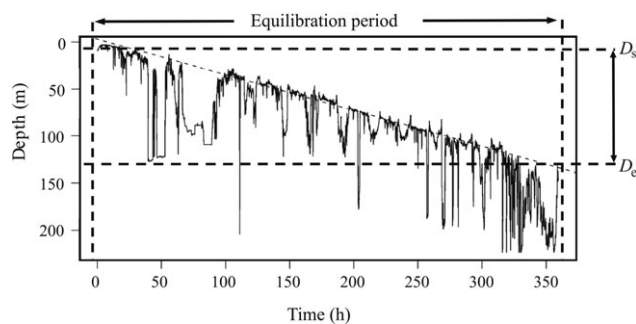

Figure 1. Post-tagging example of equilibration behaviour in cod 11788 (Skagerrak), including start and end time, and start depth (D_s) and end depth (D_e) of equilibration.

and that were not preceded by any other clear behavioural pattern. Mid-record examples were later in the DST record, and were associated with transitions from shallow to deeper water and following rapid ascents away from the seabed. Although in some instances mid-record equilibration took place within a week of release, they were distinguished from post-tagging cases by the fact that the fish had resumed other behavioural patterns before equilibration. This suggested complete recuperation following potential effects of tagging, and that the equilibration was natural. Those records that contained evidence of this behaviour were examined in detail (Table 1). We distinguished between three types of equilibration. The same definition for equilibration behaviour applied to all three types, but they could be differentiated by the relative amount of time the cod spent in midwater and near the seabed. The seabed depth here was assumed to be the maximum depth reached by the cod within any 24-h period (as for Arnold and Greer-Walker, 1992; Hobson *et al.*, in press). Seabed equilibration is characterized by the fish spending more time on the seabed than in midwater, midwater equilibration by more time in midwater than near the seabed, and neutral equilibration by approximately equal amounts of time spent in midwater and near the seabed (Figure 2).

Analysis of descent rate and equilibration period

The recording frequency of the DSTs varied by region, but was standardized to 10-min intervals for the analyses, either by re-sampling at a lower frequency or interpolating data to a higher frequency. In all, 141 DST records from six different regions were investigated for the presence of depth adaptation.

Each depth time-series was scrutinized to identify times of rapid transition to deeper water, and 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 1). The maximum depth attained during this descent was typically the depth at which the individual would become resident. In several cases, the assumed seabed depth changed during the equilibration period, suggesting that the fish was migrating as it equilibrated. The end-point of equilibration was taken to be when the individual ceased to undertake vertical migration away from the new residence depth. The descent rate over the equilibration period was estimated by manually fitting a line that extended through the uppermost portion of the depth range (Figure 1) of each equilibration period, based on the assumption that cod were neutrally buoyant only at the upper limit of their depth range (Harden Jones and Scholes, 1985; Arnold and Greer-Walker, 1992). Although we also applied a linear regression to the data during equilibration, visual comparison indicated that the lines fitted manually followed the uppermost points more accurately, and were therefore selected for further analyses. Nichol and Chilton (2006) found that the descent rate in most of the Pacific cod (*Gadus macrocephalus*) they analysed decreased in time, and they attributed this curvilinearity to increasing diffusion and leakage of gas from the swimbladder with depth. Initial examination of our equilibration data showed that only a few examples showed curvilinear descent rates: cod 514 from the Icelandic shelf first shows an increase in the descent rate (between 70 and 120 h) followed by a decrease (120 h to the end Figure 2). As the descent rates of most Atlantic cod from our study areas were more or less linear, we made no further attempt to fit curvilinear regressions slopes.
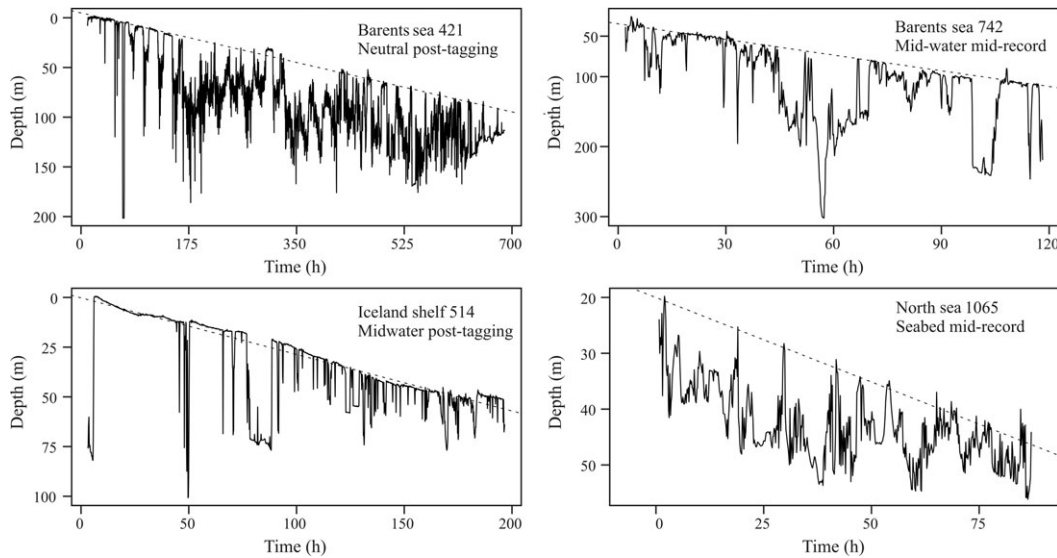
Figure 2. Post-tagging and mid-record examples of three types of equilibration behaviour from different regions (with tag-identity code). The *x*-axis represents the time since the start of the equilibration behaviour and the *y*-axis the depth (m). The dotted line represents the regression of the rate of neutral descent. Seabed, midwater, and neutral describe the different patterns observed, and post-tagging and mid-record indicate the location of the behaviour in the DST record.

From all the records we examined, 73 cod displayed a total of 134 equilibration behaviours. These examples were scrutinized carefully and only the clearest 83 examples (from 55 fish) were used for further analyses. For each equilibration example, several variables were collected: start and end time and depth, rate of descent, mean temperature, and fish length. Scatterplots were produced to explore the relationships between variables. Multiple linear regression was then used to relate the descent rate during equilibration to independent variables from all regions using

$$Y = a + b_1X_1 + b_2X_2 + \cdots + b_pX_p, \tag{1}$$

where the dependent Y variable (descent rate in m d^{-1}) was expressed in terms of a constant (a) and a slope (b) times the X_n variable. The independent explanatory variables used were fish length, water temperature during equilibration (both continuous variables), and region (categorical variable), as well as their various interactions. Region was included to explore the regional effects of temperature and length.

Modelling energy expenditure and neutral buoyancy

We used a bioenergetic model (Strand *et al.*, 2005) to explore buoyancy regulation, including its restrictions and energetic costs. The model was parameterized for Atlantic cod and based on the integration of existing theory and experimental data on bioenergetics, physiology, and hydromechanics. As the swimbladder is subject to the physical laws for gases, swimbladder dynamics and gas exchange in particular are dependent on depth, body size, and temperature. Input variables in the model were therefore the individual vertical depth and temperature profile from the DST, standardized to 10-min intervals, as well as cod length and weight upon release. For each depth profile, the model calculates swimbladder buoyancy status relative to the neutrally buoyant state (1 is neutrally buoyant, i.e. perfect volume, 0 an empty swimbladder, and 2 double the neutrally buoyant volume) and energy

expenditure (in J kg^{-1} s^{-1}). These energetic costs calculated by the model consisted of standard metabolic rate and those costs exclusively involved in maintaining neutral buoyancy: gas secretion into the swimbladder and compensatory swimming (see Strand *et al.*, 2005, for more detail). The bioenergetic model was run on the time, depth and temperature data of 20 pre-selected cod, each with one or more cases of equilibration. The model assumed the starting state of the swimbladder upon release to be neutrally buoyant and fully functioning.

We also ran the model on two theoretical post-tagging scenarios to explore the energetic efficiency of equilibration behaviour: one cod that went straight to the seabed after release, and one cod that gradually descended at the same rate as observed in a "real cod" profile (Irish Sea Tag 1362), but without intermittent vertical excursions to the seabed.

Results
Patterns of equilibration
Of the 141 cod examined, 55 showed clear examples of equilibration behaviour. Of these, 47 displayed post-release equilibration, and there were 36 mid-record examples. None of the Baltic Sea cod showed equilibration. The three types of equilibration identified (neutral, seabed, and midwater equilibration) were found in similar proportions in all regions (except in the Baltic) and in both post-tagging and mid-record equilibration episodes (see Figure 2 for examples).

The duration of the equilibration period varied between 0.34 and 28.33 d, with an average of 3.81 d (s.d. ± 4.54). As expected, there was a positive linear relationship ($r^2 = 0.46$, d.f. = 1, 81, $p < 0.0001$) between the change in depth during the equilibration period [$D_s - D_e(m)$] and the duration of equilibration (Figure 3). With increasing depth change, the length of equilibration period increased.

Mid-record equilibration behaviour was found in all months of the year except November (Figure 4). As most data from the DSTs covered spring and early summer, the frequency occurrence of
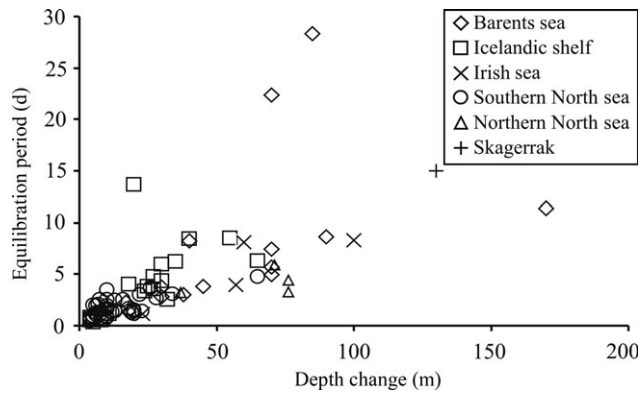
Figure 3. Relationship between depth change during equilibration and the equilibration period for the different regions ($r^2 = 0.46$, d.f. = 1, 81, $p < 0.0000$).
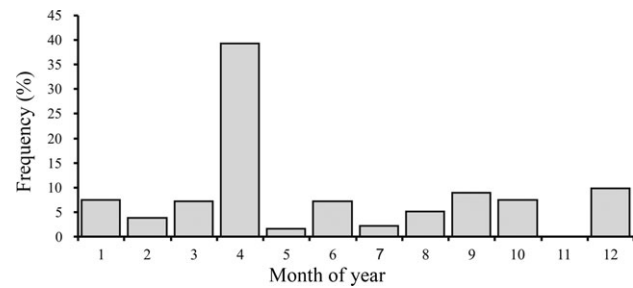

Figure 4. Percentage occurrence of mid-record equilibration by month. The proportions were corrected by available cod data per month by dividing the number of examples of equilibration in each month by the number of cod at liberty in that month. Post-release equilibration data were removed, because they would bias towards early spring, when most fish were released.

equilibration was corrected for cod data available by month. Some 39% of equilibration behaviour was observed in April, mainly cod from the southern North Sea and the Barents Sea.

Description of rates of descent

Descent rates ranged from 1.44 to 24 m d^{-1} (Figure 5) with an average of 10.3 m d^{-1} (s.d. $\pm$ 5.24) for post-tagging cases, and 10.6 (s.d. $\pm$ 5.26) for mid-record cases. To test whether post-tagging equilibration differed from mid-record equilibration, we applied a Mann–Whitney *U*-test to the descent rates. The results reject the null hypothesis that there is a difference between the
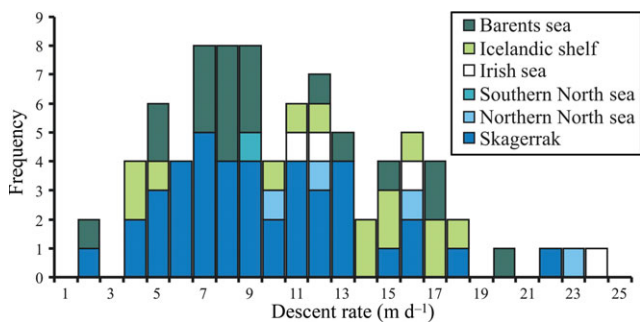

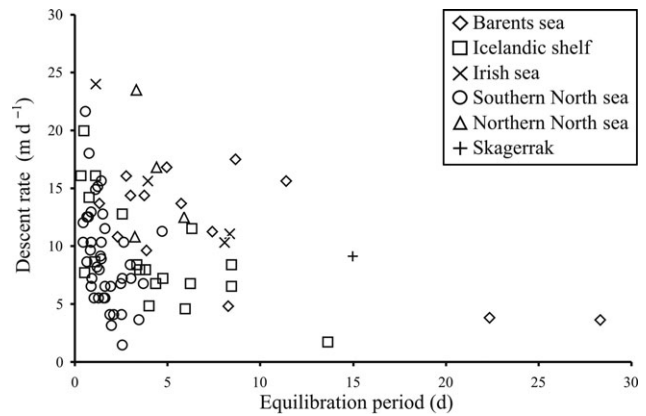**Figure 5.** Frequency histogram of descent rate.

Figure 6. Relationship between descent rate and equilibration period.

two [Rank sum (PT) = 1571.5, (MR) = 1614.5; $z = 0.1603$; $p = 0.8726$). The fastest descent rates (the steepest slopes) were also among the shorter descents, and the rates of descent of those cod that underwent the longest equilibration periods were slower (Figure 6). Neither cod length (Figure 7) nor temperature (Figure 8) appeared to have an effect on the descent rate. This was supported by the results of the multivariate analyses, when these variables and their interactions were used in the model (Table 2). Only the region "Iceland" significantly contributed to the model in interaction terms with temperature, length, and temperature combined with length. Backward, stepwise elimination of non-significant variables and interactions resulted in a model with only data from that area and length, temperature, and length–temperature interaction all highly significant (Table 3). Descent rate increased the smaller the fish and with lower temperature.

Bioenergetic model

The outputs from the model confirmed the expectations that during equilibration, neutral buoyancy is maintained at the top of the cod's position in the water column, and that cod are negatively buoyant most of the time. The slope of this descent was
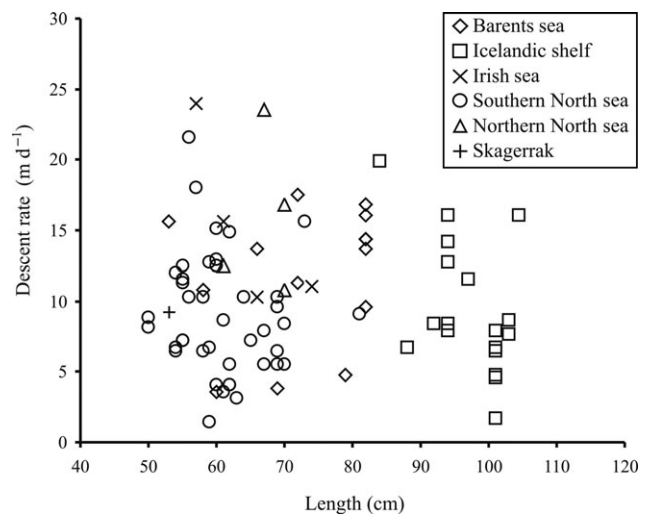

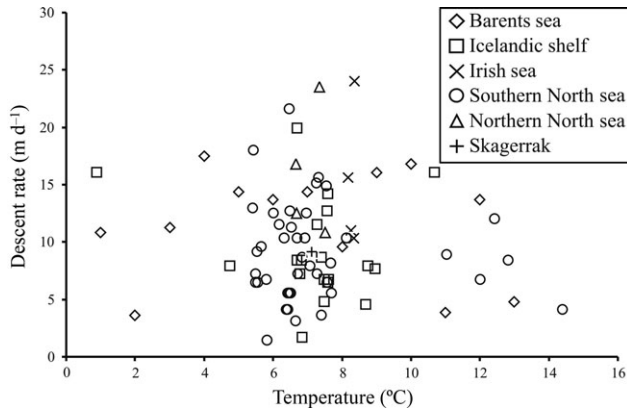**Figure 7.** Relationship between descent rate and fish length.

Figure 8. Relationship between descent rate and mean ambient temperature during equilibration.

usually in agreement with the speed of the cod's ability to maintain neutral buoyancy. Figure 9 a shows the first 10 d of the depth profile of an Irish Sea cod after release and its corresponding calculated swimbladder volume (Figure 9b; horizontal line at swimbladder volume = 1 represents the neutrally buoyant state) and energy expenditure (Figure 9c), which included secretion, compensatory swimming, and the standard metabolic rate. The

Table 2. Regression summary of descent rate, as a function of region, fish length, mean water temperature, and their interactions.

Variable	Estimate	*p*-value
Intercept	0.69	0.3793
Region		
Iceland	**13.89**	**0.0160**
Irish sea	−248.70	0.1724
Northern North sea	−126.30	0.0519
Skagerrak	0.06	0.8567
Southern North sea	−0.49	0.7059
Length	0.00	0.8585
Temperature	−0.11	0.5298
Region interaction with length		
Iceland	**−0.01**	**0.0167**
Irish sea	0.41	0.1722
Northern North sea	0.18	0.0528
Southern North sea	0.00	0.8212
Region interaction with temperature		
Iceland	**−1.57**	**0.0414**
Irish sea	30.38	0.1678
Northern North sea	18.76	0.0515
Southern North sea	0.19	0.3950
Length: temperature interaction	0.00	0.5510
Region interaction with length and with temperature		
Iceland	**0.00**	**0.0489**
Irish sea	−0.05	0.1683
Northern North sea	−0.03	0.0526
Southern North sea	0.00	0.4241

Temperature and length are continuous variables, region a categorical variable. Emboldened variables are significant. Model $F = 1.76$, d.f. = 20, 62, $r^2 = 0.362$, $p = 0.04691$, $n = 83$.

Table 3. Regression summary of the descent rate for Icelandic cod as a function of fish length, mean water temperature, and the length–temperature interaction.

Variable	Estimate (b_i)	*p*-value
Intercept	14.57461	0.00203
Length	−0.014791	0.00257
Temperature	−1.676729	0.00519
Length–temperature interaction	0.001743	0.00520

Temperature and length are both continuous variables. Model $F = 6.05$, d.f. = 3, 14, $r^2 = 0.565$, $p = 0.0073$, $n = 18$.

starting state of the swimbladder (i.e. neutrally or negatively buoyant) had little effect on the swimbladder volume and energy-expenditure patterns: after ∼24 h, there was little difference in volume and energy expenditure, and after 60 h they were equal for both scenarios. The model output from the theoretical "cod depth" profiles (Figure 10) revealed that a gradual linear descent, at the same rate as observed in cod 1362, without the rapid, intermittent, vertical excursions to the seabed (Figure 10a, solid line) was within the swimbladder's ability to maintain neutral buoyancy throughout the equilibration period. The energetic costs involved in this descent were limited to the standard metabolic rate and gas secretion. A dive straight to the seabed after release (Figure 10a, dotted line) required several days
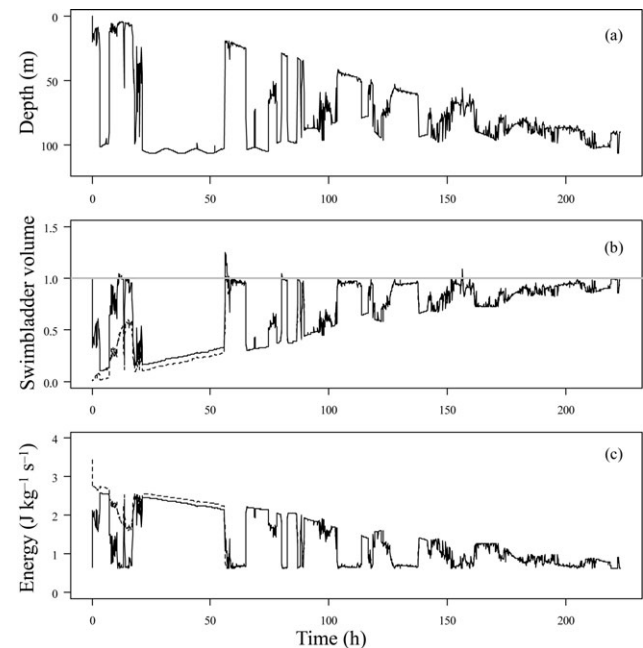

Figure 9. (a) The observed post-tagging equilibration depth profile of Irish Sea cod 1362. (b) The model's predicted swimbladder-buoyancy status of the same cod relative to neutral buoyancy, 1 being neutrally buoyant (optimal volume), 0 representing an empty swimbladder, and 2 would be double the neutrally buoyant swimbladder volume. The solid line is the buoyancy status when the cod was neutral at time 0, and the dashed line the status when the cod swimbladder was empty (negatively buoyant) at time 0. (c) The corresponding energy consumption, consisting exclusively of standard metabolic rate, gas secretion into the swimbladder, and compensatory swimming (solid line for neutrally buoyant start status, and dashed line for negatively buoyant start status).
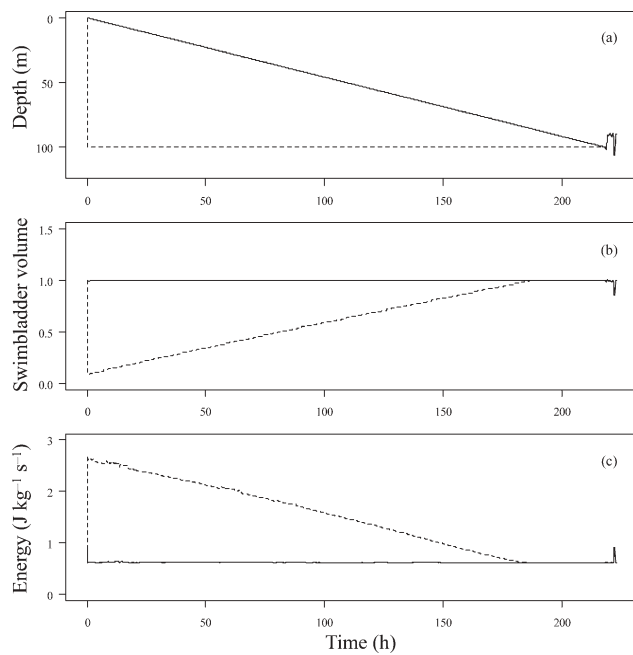
Figure 10. (a) Two theoretical post-tagging scenarios of a cod descending to the seabed at the same rate as cod 1362 (11.04 m d^{-1}), but without the vertical excursions (solid line), and of a cod that heads straight down to the seabed after release (dashed line). (b) The model's predicted swimbladder-buoyancy status of the same two theoretical scenarios, 1 being neutrally buoyant (optimal volume), 0 representing an empty swimbladder, and 2 would be double the neutrally buoyant swimbladder volume. (c) The corresponding energy consumption of the two scenarios. Summed energetic costs of scenario 1 where the cod descends gradually were 840.4 J kg^{-1} s^{-1}, and for scenario 2 were 1973.23 J kg^{-1} s^{-1}. Energetic costs of observed post-tagging descent (Figure 9c) were 1791.79 J kg^{-1} s^{-1}.

($\sim$185 h) of swimbladder adaptation before neutral buoyancy was achieved, and was energetically relatively costly because of the additional compensatory swimming.

Discussion

The characteristic vertical patterns of gradual descent punctuated by bouts of extensive vertical movement, here described as equilibration behaviour, were found in 55 of 141 cod (39%) from all regions examined, though 42% if Baltic cod are removed from the analysis. The behaviour was not solely associated with post-tagging recovery of neutral buoyancy. In some cases ($n = 16$), individual cod performed the equilibration behaviour more than once. Cod equilibrated to depth changes of between 4 and 170 m (mean = 30 m, s.d. $\pm$ 31), at a mean descent rate of 10.5 m d^{-1} (s.d. $\pm$ 5.28), and the duration of equilibration ranged from 8 h to nearly a month. The post-tagging equilibration rates calculated from the tag data suggested full swimbladder functionality, supported by the fact that there was no significant difference from natural mid-record descent rates. On this assumption, our modelling of swimbladder volume suggested that neutral buoyancy was maintained only at the top of the cod's position in the water column. The descent rate during equilibration was therefore determined by a cod's ability to increase its neutrally buoyant depth.

Rates of equilibration and gas secretion

Given the temperature range during equilibration, the rates of descent found for cod in our study areas are consistent with the rate of gas secretion for the gas gland necessary to maintain neutral buoyancy (Harden Jones and Scholes, 1985; Thorsteinsson, 1995; Heffernan *et al.*, 2004; Nichol and Chilton, 2006). The range in descent rates was probably caused by variability in the rate of secretion of gases into the swimbladder, but also by regional differences in fish length, ambient temperature, and seabed depth. In addition, cod might not always equilibrate at the maximum possible rate. We expected a negative relationship between fish length and descent rate, and the cod that descended fastest were mainly smaller fish in the southern North Sea. However, there was no overall relationship between length and descent rate when data from all regions were combined. With region included as a categorical variable in the multivariate analysis, a negative relation was found between fish length and descent rate for Icelandic cod (Tables 2 and 3), as for Harden Jones and Scholes (1985, using cod no larger than 50 cm). However, this relationship was absent for all other regions and suggests that, in the natural environment, there may be little or no difference in the realized gas secretion rate of small and large fish (50–100 cm in our study).

We expected a positive relationship between water temperature and the rate of equilibration because gas secretion to the swimbladder is an active biochemical process. However, descent rate was not related to water temperature when data from all regions were combined, and there was a significant negative relationship for the Icelandic region and temperature (Tables 2 and 3). Nichol and Chilton (2006) found no temperature dependence and attributed this to the narrow temperature range in their study area. In our case, the temperatures experienced by the tagged cod covered a wide range (mean temperature during equilibration ranging from 0.4°C to 14.4°C). One possible reason why we did not find the expected relationship between temperature and gas secretion rate is that the number of cod that exhibited equilibration in some of the regions was small, so the statistical power of the dataset was limited. Again, regional differences between factors other than length and temperature are likely to have had an effect on the descent rates.

Any damage to the swimbladder as a result of catching the fish from deep water in the more northerly areas (Barents Sea, Icelandic Sea) may have influenced the results. However, the post-tagging equilibration rates calculated from the tag data suggest full swimbladder functionality even though the pressure reduction during the capture of the cod was likely to have caused damage to it. This suggests that, like Pacific cod (Nichol and Chilton, 2006), Atlantic cod have very quick swimbladder-repair mechanisms. This is supported by a recent study by Midling *et al.* (2006) on Atlantic cod, describing the presence of a membrane that lines the swimbladder and restores swimbladder functionality when damaged. This would explain the similarity between the post-release equilibration descent rates and those from natural (mid-record) observations. It is unlikely that the swimbladder-repair mechanism developed in response to fishing; it is more likely to be the result of evolutionary selection. However, it does suggest that cod experience extreme pressure reductions, and consequent barotrauma, naturally, as a consequence of sudden ascents during, for example, foraging or predator-avoidance behaviour.

Interpreting equilibration behaviour

Given the plasticity in vertical movement behaviour that characterizes cod (Righton *et al.*, 2001), the near ubiquity of equilibration behaviour is notable. The results of the swimbladder modelling suggest that cod were only either neutrally buoyant at the top of their vertical range or significantly negatively buoyant when they returned to the (assumed) seabed. Neither of these states would appear ideal, so the behaviour was probably a compromise between two preferred states: the physiological state of neutral buoyancy and the behavioural state of demersal residence. Again, such conjecture is supported by the swimbladder modelling, because those results suggest that the equilibration observed is not the most energetically advantageous pattern of vertical movement: the theoretical scenario where cod gradually descend without occasional sudden vertical descents was energetically cheaper than with the swift descents, although by a relatively small amount. To put this in perspective, the energy content of, for example, a 10 cm sand eel (*Ammodytes* spp.) or herring (*Clupea harengus*) is ∼20 and 60 kJ, respectively (Wanless *et al.* 2005), two orders of magnitude greater than the difference in energetic costs of the different descent scenarios, and could be considered relatively trivial. Therefore, whereas some examples of equilibration indicate that prolonged periods (>8 h) are indeed spent efficiently in midwater, all our examples, as well as examples from similar studies (Heffernan *et al.*, 2004; Nichol and Chilton, 2006), show frequent excursions to the seabed. It is therefore likely that cod descend to the seabed for other reasons, superimposed on the equilibration behaviour at slight energetic cost. This might be, for instance, a requirement to feed on demersal prey, or they may need to descend to obtain a positional reference. On the other hand, cod may have a natural preference for demersal residence, or perhaps wish to return to the depth at which they were originally adapted, i.e. before capture.

No examples of equilibration were found in cod from the Baltic Sea, most cod appearing, in this case, to return to their capture depth immediately after release. This could be because Baltic cod did not need to equilibrate after tagging because of the comparatively shallow depth of capture. Although cod caught and released in the similarly shallow southern North Sea did display equilibration, Baltic cod may not be as strongly associated with the seabed, because of the restricting effect of the physical environment there. The hostile low salinity and oxygen conditions (Neuenfeldt and Beyer, 2003) near the seabed may inhibit the manifestation of demersal residence.

The significance of equilibration

Although equilibration behaviour after tagging is undoubtedly an extreme version of the re-establishment of a behavioural (the need to be demersal or semi-pelagic) and physiological (the need to be neutrally buoyant) equilibrium, it is also likely to be natural when cod move between different water strata, as confirmed by the occurrence of equilibration many months after tagging. Although we found equilibration in nearly all months of the year, most mid-record equilibration examples were recorded in April and were mainly data from the southern North Sea. This coincides with a period when southern North Sea cod migrate to deeper offshore water after spawning (Righton *et al.*, 2001, 2007). Most Barents Sea examples were in December and January, when Northeast Atlantic cod move from shallow coastal regions to deeper water (Michalsen *et al.*, 2006). In some other instances, natural equilibration took place after sudden expeditions away from the seabed to midwater. Perhaps the presence of pelagic prey, such as herring or capelin (*Mallotus villosus*), triggered these rapid reductions in residence depth. The distribution and abundance of different prey types is an important factor determining the vertical migration patterns of top predators such as cod (Strand *et al.*, 2005). As cod can reduce the amount of gas in the swimbladder faster than they can increase it, rapid reductions resulting from large ascents to feed on pelagic or semi-pelagic prey would require cod to re-fill the swimbladder, i.e. to re-equilibrate once the midwater foraging had ended. Alternatively, large ascents perhaps in response to attempted predation might cause rupture of the swimbladder and require subsequent re-inflation.

The similarity (i.e. similar rates of descent) between post-tagging and natural (mid-record) equilibration also suggests that although there may be barotrauma during capture, a cod is capable physically and physiologically of adapting to the effects of associated pressure reduction and of resuming normal behaviour shortly after release. This finding has implications in, for example, discard mortality, and suggests that barotrauma of captured cod may not have an impact on mortality as significant as previously thought. Unfortunately, there is limited information on the existence of equilibration or similar patterns in other physoclist species, but information on Pacific cod (Nichol and Chilton, 2006) and sea bass (*Dicentrarchus labrax*; DR, unpublished data) suggests that equilibration may be common to other physoclists too.

The insight that our observations of post-tagging and natural equilibration behaviour provide is useful for making estimates of the rate of neutrally buoyant descent, and the rate of gas secretion into the swimbladder. In turn, these results could be helpful in validating, for example, individual-based models on cod behaviour (Strand *et al.*, 2005), which can help in understanding vertical patterns and supporting the calculation of correction factors necessary to fine-tune the results of acoustic and trawl stock-assessment surveys (Foote, 1980; MacLennan and Simmonds, 1992; Aglen *et al.*, 1999). Tilt angle and the physiological state of the swimbladder have a large effect on target strength, and are highly variable during patterns of behaviour such as equilibration. Spatial and temporal knowledge of this pattern will aid the design of survey methodologies and improve the accuracy of acoustic-biomass calculations.

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