Escape mortality of cod, saithe, and haddock in a Barents Sea trawl fishery

Ólafur Arnar Ingólfsson, Aud Vold Soldal, Irene Huse, and Mike Breen

Ingólfsson, Ó. A., Soldal, A. V., Huse, I., and Breen, M. 2007. Escape mortality of cod, saithe, and haddock in a Barents Sea trawl fishery. – ICES Journal of Marine Science, 64: 1836–1844.

We investigated the survival of gadoid fish in the Barents Sea escaping from a demersal trawl during commercial fishing conditions, with and without a sorting grid, at high and low levels of fishing intensity. The mortality of cod and saithe was negligible and unrelated to experimental conditions. Haddock mortality was generally greater than observed in earlier experiments and inversely related to fish length. Any possible effects of experimental conditions were hidden by large variability in the observed rates of mortality. We conclude that the observed mortality of haddock is confounded by methodological problems, particularly the instability of the observation cages, and does not reflect the true escape mortality. Cod and saithe are capable of surviving the stress of passage through, and escape from, the trawl, whereas haddock are more vulnerable, despite being a closely related species.

Keywords: cod, codend, escape mortality, fishing intensity, haddock, saithe, Sort-V.

Received 4 July 2007; accepted 30 August 2007; advance access publication 4 October 2007.

Ó. A. Ingólfsson, A. V. Soldal, and I. Huse: Institute of Marine Research, PO Box 1870, Nordnes, 5817 Bergen, Norway. M. Breen: Fisheries Research Services, Marine Laboratory, PO Box 101, Aberdeen, UK. Correspondence to Ó. A. Ingólfsson: Present address: Marine Research Institute, Árnagata 2-4, 400 Ísafjördur, Iceland; tel: +354 575 2303; fax: +354 450 3005; e-mail: olafur@hafro.is.

Introduction

Stock assessment and fisheries management rely on the use of technical conservation measures such as mesh size restrictions and size selective grids to minimize discard of unwanted and undersized fish, and are based on the simple, but unproven, assumption that all fish escaping from fishing gears survive and remain in the population. However, a number of studies have demonstrated that this assumption may be incorrect (Soldal *et al.*, 1993; Sangster *et al.*, 1996; Suuronen *et al.*, 1996a; Anon., 2000). A proportion of escaping fish, in particular the smallest ones (Sangster *et al.*, 1996; Suuronen *et al.*, 1996b; Wileman *et al.*, 1999), may die after passing through trawl codends. A precise, quantitative description of this escape mortality is essential to determining the effectiveness of such technical measures for fisheries management.

There have been several studies of escape mortality over the past 15 years (Anon., 2000). However, survival values have been affected by inferior methods of collecting, transporting, and monitoring escapees (e.g. Sangster *et al.* 1996; Suuronen *et al.*, 1996b; Breen *et al.*, 2002), and experiments rarely reflect commercial fishing conditions in terms of towing depth, speed and duration, catch size, area, and season (Main and Sangster, 1990; Soldal *et al.*, 1993; Sangster *et al.*, 1996; Suuronen *et al.*, 1996a, b; Wileman *et al.*, 1999; Suuronen, 2005). Therefore, commercial fishers often criticize the experiments because they do not reflect true fishing practices and have limited confidence in the survival estimates. However, as the results of this study will demonstrate, offshore survival experiments carried out during full-scale commercial conditions offer tremendous methodological challenges.

It is clear from earlier experiments that the ability of fish species to withstand the physical injury and fatigue associated with capture and escape vary markedly. Low and medium survival rates have been observed for small pelagic species such as herring (*Clupea harengus*) (Suuronen *et al.*, 1996a, b), walleye pollock (*Theragra chalcogramma*) (Pikitch *et al.*, 2002), and vendace (*Coregonus albula*) (Suuronen *et al.*, 1995), but the mortality rates of flatfish (DeAlteris and Reifsteck, 1993) and gadoids (Main and Sangster, 1990; Jacobsen *et al.*, 1992; Soldal *et al.*, 1993; Suuronen *et al.*, 1996a, 2005) are generally better. However, among closely related gadoid species, the estimates of escape mortality are highly variable and inconsistent. Although cod (*Gadus morhua*) and saithe (*Pollachius virens*) seem to suffer negligible mortality after escaping from fishing gear (Jacobsen *et al.*, 1992; DeAlteris and Reifsteck, 1993; Soldal *et al.*, 1993; Suuronen *et al.*, 2005), the mortality of haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) are highly variable (Soldal *et al.*, 1993; Sangster *et al.*, 1996; Wileman *et al.*, 1999).

The intensity of fishing activities and effort can vary considerably among seasons, regions, and fishing grounds. Juvenile fish living in areas exposed to greater fishing effort are more likely to be herded by a trawl and escape from it, and therefore have a greater average daily expenditure of energy. This and the increased stresses of repeated capture and escape are likely to affect the physical condition of the juvenile population, and potentially their escape survival. Fish may die as a result of stress and muscular fatigue incurred during entrainment and escape through trawl codends (Beamish, 1966; Wood *et al.*, 1983). Also, stressors that do not directly kill fish may still cause indirect mortality, such as behavioural impairment making the escapee more vulnerable to predation (Ryer, 2002; Sneddon *et al.*, 2003; Ryer *et al.*, 2004; Davis, 2005).

This project was designed to provide improved survival data for different gadoid species escaping from a bottom trawl with and without sorting grids during true commercial fishing conditions in the Barents Sea, as well as to study the effect of fishing intensity on escape survival.

Material and methods

Two experiments were conducted out of Varanger Peninsula in Norway at depths of 45–90 m during the periods 16 April–5 May 2004, and 28 March–18 April 2005 (Figure 1). The first part of each experiment (a low-intensity fishery) was carried out in an area which had no history of trawling activities. The high-intensity fishery was simulated with two trawlers towing for 18 h d^{-1} in a circular area with a radius of 3 nautical miles in 2004 and a rectangular area of 3 × 3 nautical miles in 2005. The high-fishing-intensity level was based on commercial effort statistics from 2000 to 2002 and therefore representative of the Barents Sea trawl fisheries.

The experimental protocol for collecting and monitoring fish escaping from the demersal trawl was similar to the method described by Lehtonen *et al.* (1998), with some modifications. The trawler that performed the experimental hauls in 2004 had a 1790 kW main engine, and was rigged with a two-panel bottom trawl ("Alfredo Maxi") with 120 m sweeps. The codend was made of 2 × 5 mm braided Magnet-PE twine with a nominal mesh size of 135 mm. The overall length of the codend was 9.4 m and its circumference was 62 meshes. The tapered extension between the trawl and the codend was 8 m long. In 2005, a sister ship to that used in 2004 was chartered, and it had a 1543 kW engine and a similar trawl ("Alfredo 4") with 90 m sweeps.

To collect grid escapees, a Sort-V stainless steel sorting grid with 55-mm bar spacing was fitted to the trawl (Figure 2). Escaping fish were collected in cages attached to covernets, either covering the codend to catch codend escapees and escape-control fish (Figure 3) or opening the sorting grid (Figure 4) to

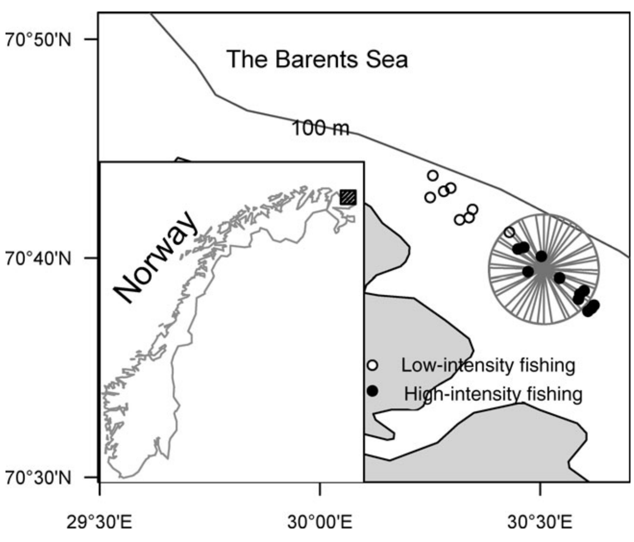

Figure 1. The experimental area off the Varanger peninsula in 2004. The open and filled circles show where the cages were set. The transects in the circle show the tracks of the trawlers simulating the high-intensity fishing.

catch grid escapees. The cages were based on a design by Fisheries Research Services, Marine Laboratory, Aberdeen (MB, unpublished), which minimizes the effects of water flow on the captive fish in the cover. They were 5 × 2 × 2 m in dimension and constructed from tubing frames of 70 mm aluminium. The front 3.75 m of the cage was lined with knotless square mesh PA-netting, 15 mm bar length in front, gradually decreasing to 4 mm. The aft 1.25 m and the rear door of the cage were lined with a PVC canvas. In 2004, all sides had a triangular shaped canvas (Figure 3b), but these were removed in 2005 because video shots showed that the captured fish avoided the canvas area. Two acoustic releases (AR 661 B2S from Oceano Technologies) were used to control the closing of the cage gate and release of the cage from the trawl. They were mounted on the covernet in front of the cage. Some technical difficulties were experienced in 2004, in particular with the hydrodynamic stability of the cage/cover assembly when attached to the trawl, and with the closing, release, and anchoring of the cages securely to the seabed after sampling. Changes were introduced in 2005 to overcome these difficulties. First, to improve closing of the cages at the front, a curtain of knotless PA netting with a steel bar fitted to the bottom edge was attached to the front frame of the cage. During towing and sampling, the curtain was coiled at the ceiling. When triggering the acoustic release to detach the cage from the trawl, the curtain would drop, closing the front cross section of the cage. Second, the flotation of the cages was increased to compensate for the weight of the curtains. Third, depth and temperature loggers were fitted to the cages to monitor possible vertical movements of the cages during towing and anchoring, as well as to monitor environmental changes.

Fish were sampled from three categories of escaping fish: (i) grid escapees, (ii) mesh escapees, and (iii) controls. The control group passed through the trawl and entered the cover/cage assembly, without encountering a grid or a codend. The control group therefore demonstrates the effect of the escape process *per se*. To minimize the effects caused by variations in fish density over time, the categories were dispersed throughout the experimental period. The trawler towed for ~0.5 h at a speed of 1.8–2 m s^{-1} (3.5–4 knots) with the cage open at the rear, allowing all fish to pass through it. To start sampling, a signal was sent to the first acoustic-release unit, which released and closed the rear door of the cage. After a sampling period of 2–15 min, dependent on the fish density in the trawl path, the cage was released from the covernet (simultaneously with closing the curtain in 2005) with a signal to the second acoustic-release. Sampling time was defined as the time between the confirmation signals from first and second acoustic-releases. Floats lifted the rope and camera cable to the surface, which maintained tension at the front of the cage and kept it closed (see Figure 4 for the chronological order of grid-cage release). The cages were anchored to the seabed at the release site after confirming by video camera the presence of an adequate number of required species in the cage.

The observation period was set to 6 d, based on experience from earlier experiments with gadoids (Main and Sangster, 1990; Soldal *et al.*, 1993) which showed peak mortality on day 1, followed by a gradual decrease in mortality over the next few days, after which secondary infections, thought to be caused by captivity, started to appear after ~1 week. The rough weather conditions in the Barents Sea in addition to the anchoring depths prevented divers from monitoring the cages. Daily monitoring of the cages

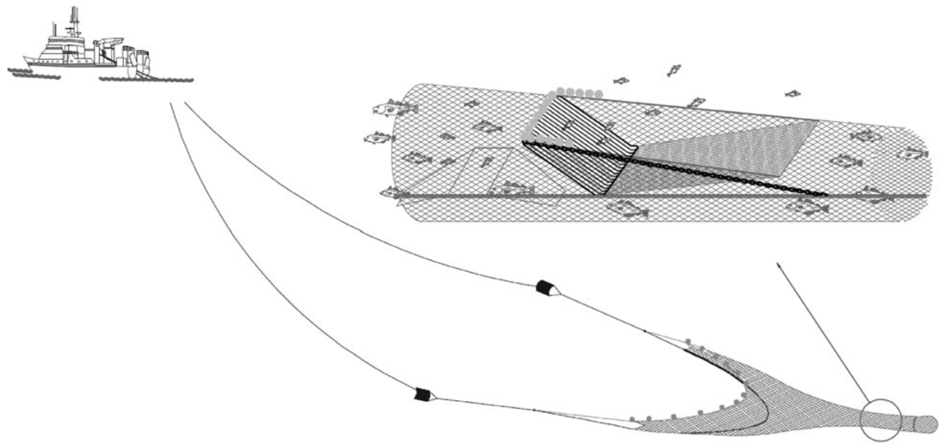

Figure 2. The Sort-V grid, and its positioning in the trawl.

was conducted remotely by wireless from the auxiliary vessel, using the cameras mounted in the cages, connected to an antenna at the surface via cable running along the rope to the surface buoy (Figure 5). This method did not allow us to count the number of dead fish, but the images did provide a general impression of fish well-being and behaviour during the observation phase. Because water temperatures were $<4°C$, we believed there to be a low risk of disease spreading from degrading dead fish to live ones.

At the end of the observation period, the cages were brought to the surface and live and dead fish counted and measured to the nearest centimetre below. When the total number of live or dead haddock was estimated to exceed 500 ($>$10 baskets), the contents of at least five baskets ($\sim$250 fish) were measured by randomly selecting them and counting the remaining fish.

Data analysis

For cod and saithe, for which mortality was negligible, the number of living and dead fish along with information of their size ranges, mean length, and standard deviation (s.d.) of the size distribution are provided.

Haddock survival data were analysed using generalized linear mixed models (GLMM). Mixed-effects models (Pinheiro and Bates, 2000) provide a flexible and powerful tool for analysing grouped data. A model with both fixed effects (parameters associated with a population or repeatable levels of experimental factors, i.e. catch composition, cage category, high/low fishing intensity, etc.) and random effects (associated with individual experimental units, i.e. cages) is called a mixed-effects model. Because death and survival are binary events, we selected a model with binomial error distribution and logit-link function.

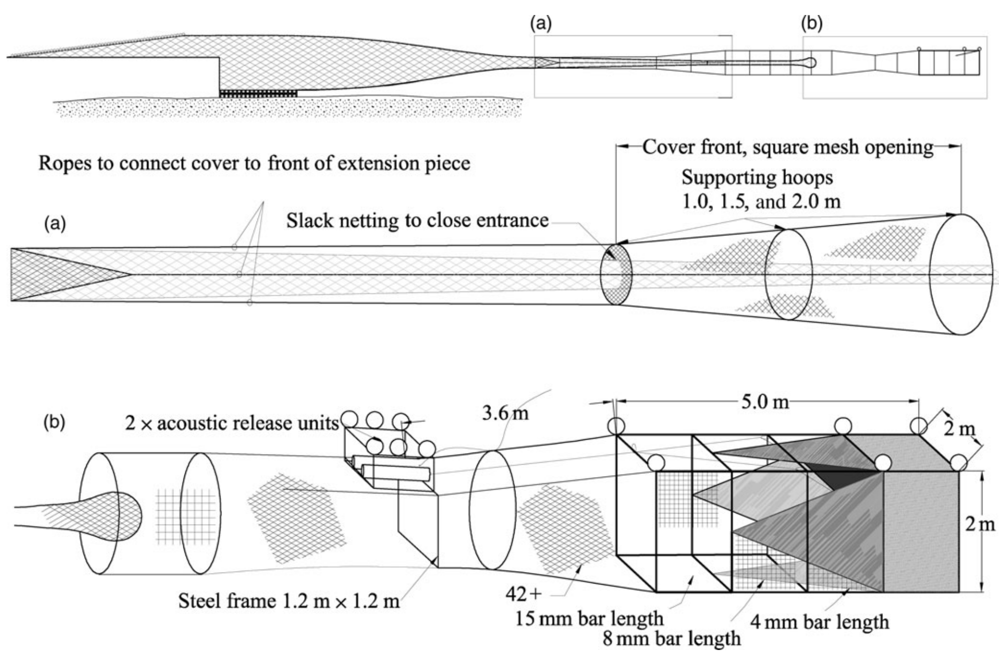

Figure 3. The attachment of the codend cover and cage to the trawl: (a) detail of cover attachment to the trawl extension; (b) detachable cage and attachment to the cover.

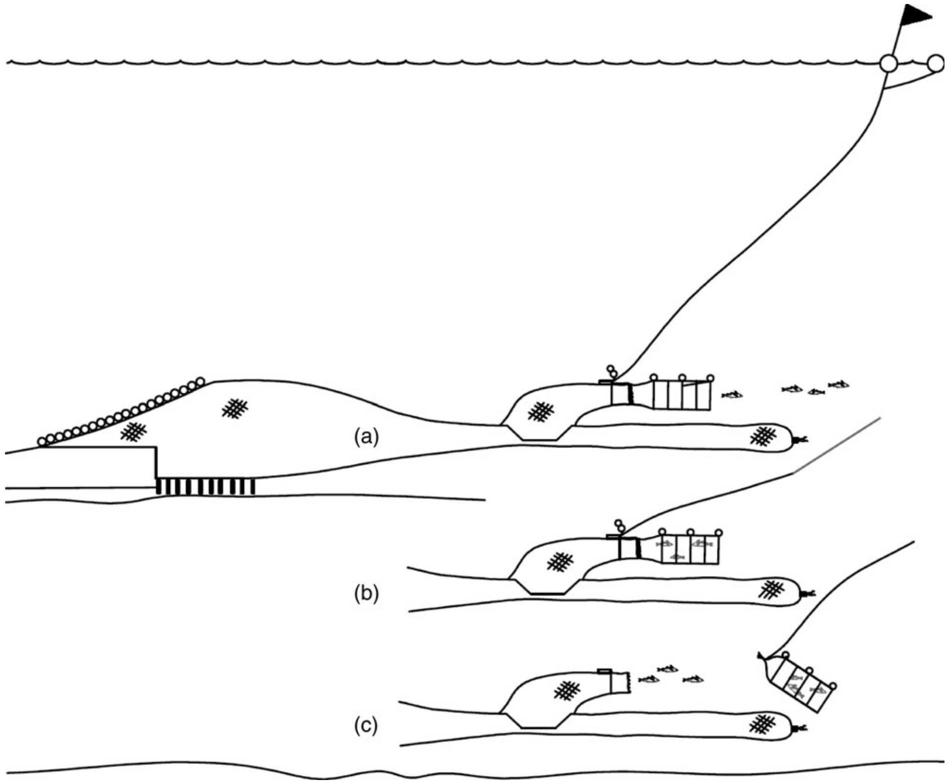

Figure 4. Chronological order of grid-cage release: (a) towed with cage open, covernet encloses the Sort-V grid; (b) the door has been released by acoustic release and the sampling begins; (c) the cage has been released and closed in front by acoustic release.

If π_{ij} is the survival probability in the jth length class in the ith cage, and x_{ij} the corresponding value of the covariate, the logit for an analysis of covariance model with a random effect ζ_i can be written as

$$\log\left(\frac{\pi_{ij}}{1-\pi_{ij}}\right) = x_{ij}\beta + z_{ij}\zeta_i, \qquad (1)$$

where β is the p-dimensional vector of fixed effects, and ζ_i the two-dimensional vector of random effects. The parameter z_{ij} is a subset of x_{ij} (two-dimensional vector of 1s and fish length j within cage i). The variance is denoted σ_ζ^2 for the "among cages" variability, i.e.

$$\zeta_i \sim N(0, \sigma_\zeta^2). \qquad (2)$$

This model combines a random-effects model for analysis of categorical data with a regression model.

The covariates tested were fish length, fishing intensity (high/low), cage category (grid, mesh, control), number of fish in each cage (by species and pooled), number of cod >50 cm (for a

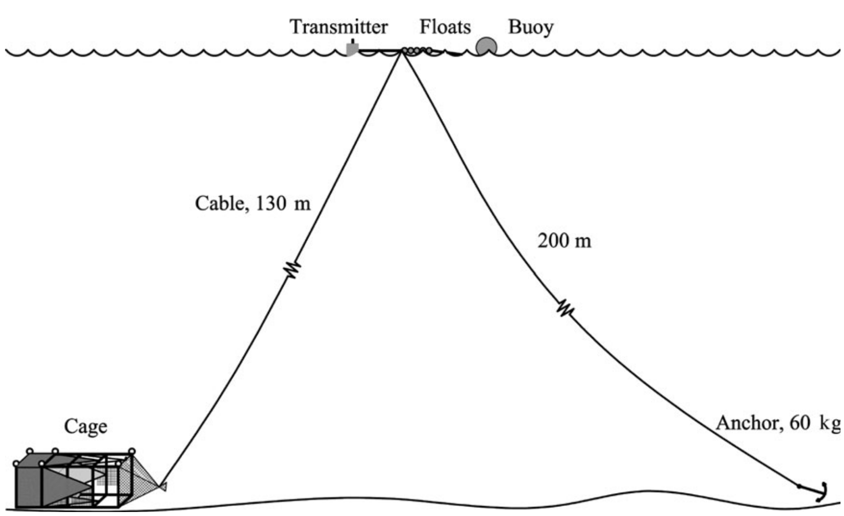

Figure 5. Rigging of cages on the seabed, after release from the trawl.

predator effect), sampling time, number of fish per unit sampling time, anchoring depth, vertical movement of cages (Δ-depth, recorded as the depth range throughout the observation period, measured by depth logger), maximum tidal range (as a measure of current speed), and maximum wind speed (m s^{-1}) during the first 24 h after setting out the cages. Interaction terms were added to the model. Both backward-elimination and forward-selection procedures were applied for variable selection, based on *p*-values for estimated parameters.

All statistical analysis and graphics production were carried out using the R statistical program (R Development Core Team, 2007). For model fitting, the GLMMPQL routine (Venables and Ripley, 2002) was applied.

Results

The results of the GLMM analyses for 2004 and 2005 showed that mortality differed between years. Exploratory analysis revealed that the difference may be explained by larger horizontal and vertical movements of the cages during the observation period in 2005. The data from each year were therefore treated separately.

2004 experiments

Trawl escapees were successfully sampled in 19 experimental cages. Of those, eight were collected during low-intensity fishing (three controls, two grid escapes, and three mesh escapes), and 11 during high-intensity fishing (three controls, three grid escapes, and five mesh escapes). The chronological order of cage-release and time at sea are shown in Figure 6. All cages were retrieved on the 6th day at sea except for the first high-intensity fishing cage (a grid cage), which was taken up on day 7 because of inclement weather at the time. Bottom temperature, recorded from equipment mounted on the trawl, was about 4°C.

Table 1 shows the treatment and the number of fish of each species in the cages. In all, 1369 cod, ranging in length from 22 to 94 cm (mean = 44.9 cm, s.d. = 8.59 cm), were captured during the experiments. Four of these, ranging from 30 to 46 cm, were found dead, not in the same cage, but in three of the 19 cages. Two were in low-intensity grid cage 2, one in high-intensity mesh cage 5, and one in grid cage 1, resulting in cod mortalities of 6.3, 0.6, and 0.4%, respectively, in those cages, and an average pooled mortality of 0.3%.

A total of 570 saithe, ranging in length from 26 to 68 cm (mean = 42.3 cm, s.d. = 6.27 cm) was captured. Nine, ranging from 34 to 56 cm, were found dead in four of the cages: one in low-intensity mesh cage 1, six in escape control cage 3, and one each in high-intensity mesh cage 1 and escape control cage 2, resulting in mortality rates of 1.9, 1.7, 6.7, and 3.1% for saithe in those cages, respectively, and an average pooled mortality of 1.6%.

Many more haddock, 12 571 in all, ranging in length from 12 to 61 cm (mean = 34.6 cm, s.d. = 6.64 cm), were sampled during the experiments. Of these, 1823 haddock died. The mortality rate was related to fish length, with mortality greatest among the smallest fish (Figure 7); the GLMM analysis showed increased survival rate with fish length (Table 2). The model also showed that anchoring depth affected survival in a negative manner (Figure 8). There was no difference in survival rate between escape control and experimental groups, indicating that survival was independent of selectivity device (mesh or sorting grid). Nor did mortality seem to increase with fishing intensity. The variability in the estimates, however, may have overwhelmed subtle differences between groups. The other experimental covariates tested (number of fish in the cage by species and pooled, number of cod >50 cm, i.e. the predator effect, sampling time, number of fish per unit sampling time, and maximum wind speed the next 24 h after setting out the cages) did not influence haddock survival.

2005 experiments

In 2005, harsh sea conditions limited the experiments, and just seven valid cages could be collected. After a difficult start to the experiment, we abandoned the mesh-escape category in an attempt to obtain sufficient numbers of replicates from the other categories. The cages were fitted with depth and temperature loggers, which demonstrated that they had moved vertically and/or horizontally during the observation (see the Δ-depth column in Table 3). The horizontal movements were recognized from the depth loggers as gradual changes in depth during the observation period, suggesting that the cages had drifted with the currents along the seabed. The current speed measured at the sites frequently reached 0.5 m s^{-1}, with a maximum of 0.6 m s^{-1}.

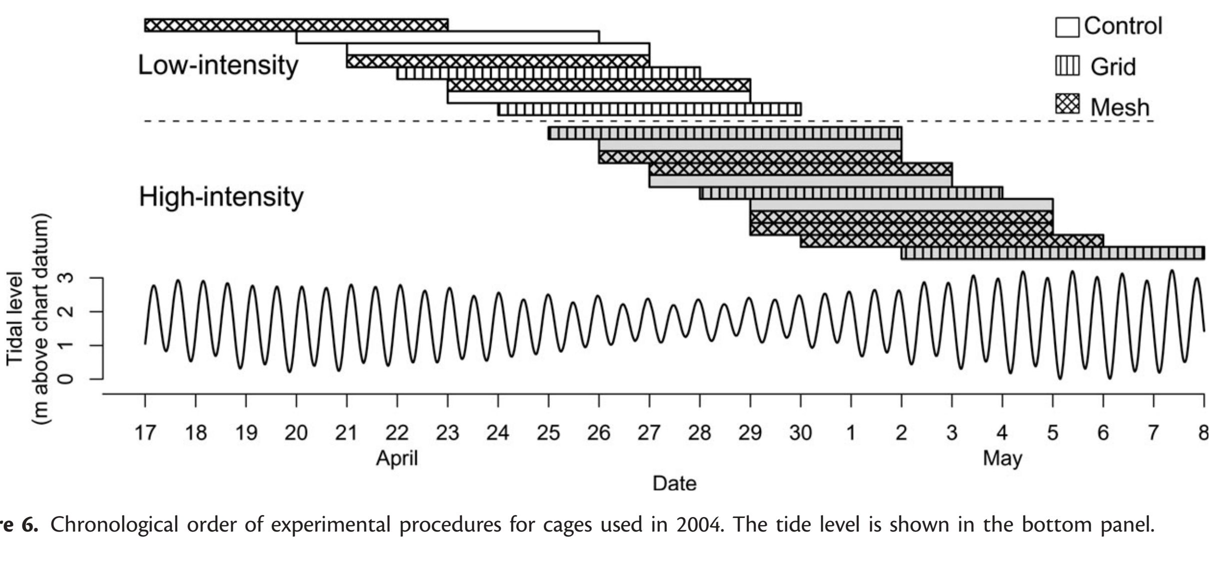

Figure 6. Chronological order of experimental procedures for cages used in 2004. The tide level is shown in the bottom panel.

Table 1. Data from the observation period in the 2004 experiment.

Category	Fishing intensity	No.	Number of fish				Haddock				Sampling time (min)	Anchoring depth (m)	Tide difference (m)
			Cod	Haddock	Saithe	Total	Mean length	Min length	Max length	% mortality			
Mesh	Low	1	8	502	53	563	37.5	14	51	56.0	11	87	2.52
Mesh	Low	2	149	1 499	0	1 648	34.8	21	49	2.1	14	47	2.33
Mesh	Low	3	9	83	1	93	32.1	24	45	65.1	7	80	1.89
Mesh	High	1	18	819	15	853	34.9	23	53	1.1	3	71	1.29
Mesh	High	2	10	216	14	240	39.2	25	53	2.8	3	81	1.32
Mesh	High	3	35	155	8	203	36.5	22	53	11.0	5	75	1.52
Mesh	High	4	10	139	1	153	35.8	25	55	4.3	6	73	1.53
Mesh	High	5	182	703	5	898	35.6	24	52	26.6	15	67	1.54
Grid	Low	1	100	181	56	337	38.1	22	53	12.2	10	90	1.62
Grid	Low	2	32	91	1	134	36.8	26	57	9.9	8	80	2.12
Grid	High	1	259	1 452	21	1 803	35.1	22	53	5.7	14	71	1.31
Grid	High	2	54	42	30	154	38.4	25	52	35.7	10	76	1.32
Grid	High	3	16	1 858	0	1 995	30.1	12	49	12.7	14	88	2.50
Control	Low	1	8	87	24	119	41.3	25	54	16.1	5	60	2.45
Control	Low	2	2	33	0	35	37.2	26	53	9.1	10	70	2.33
Control	Low	3	108	116	99	324	42.3	32	57	12.9	7	90	1.89
Control	High	1	38	2 294	10	2 354	33.6	21	61	33.0	3	78	1.29
Control	High	2	152	1 522	32	1 707	36.5	24	56	1.9	2	57	1.32
Control	High	3	174	771	7	1 119	35.5	23	56	5.6	8	70	1.54

The "No." column shows the chronological order within category and intensity as in Figure 7. The total number of fish includes species (mainly flatfish) other than those mentioned in the table.

Table 3 lists the number of fish of each species in the valid cages. In low-intensity grid cage 2, one cod out of 32 died, i.e. a 3.1% mortality. There was no mortality of cod in the other cages, giving an overall pooled mortality rate of 0.8%. Except for low-intensity escape control cage 1, the numbers of saithe were low (Table 3). One saithe out of 299 in that cage died, resulting in a pooled mortality rate of 0.3%.

In all, 2943 haddock were caught in the cages during the 2005 experiment. As in the previous year, the variability in mortality estimates was great, and the mortality did not differ significantly between grid and escape control categories, nor between high- and low-intensity fishing. Again mortality was greatest among the smallest fish (Figure 9, Table 4). Of the two grid cages that rose to the surface, low-intensity cage 2 had greater mortality

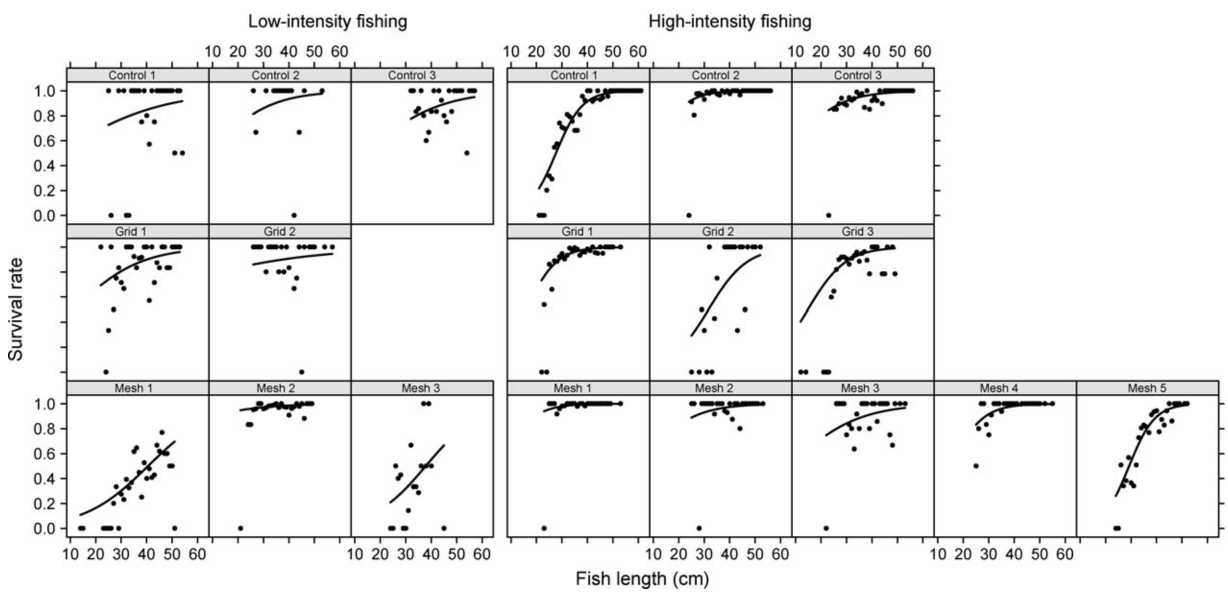

Figure 7. Haddock survival rates from individual cages in 2004 along with fitted values from the GLMM model.

Table 2. Results from GLMM analysis of haddock mortality in 2004, with random effects for intercept and slope (for length).

Explanatory variable	Parameter estimate	s.e.	d.f.	*p*-value
Intercept	2.45	2.05	502	0.231
Fish length	0.113	0.018	42	<0.001
Anchoring depth	-0.057	0.026	17	0.043
$\sigma_{\text{intercept}}$	2.33	–	–	–
$\sigma_{\text{fish length}}$	0.062	–	–	–

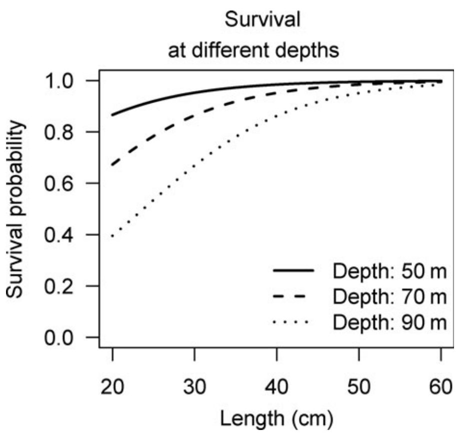

Figure 8. Predicted values for survival rates of haddock, showing the effect of anchoring depth in 2004.

than high-intensity cage 1. The time spent at depths less than half the bottom depth was 160 and 60 min, respectively. The anchoring depth range was narrower than the previous year and was not a significant explanatory factor for haddock survival. The temperature in the cages ranged from 3.4°C to 3.8°C.

Discussion

The mortality of cod and saithe in the cages was low and appears to be unrelated to the experimental conditions of escape category or fishing intensity. This low mortality agrees with previous observations of escape mortality for those species (DeAlteris and Reifsteck, 1993; Soldal *et al.*, 1993; Suuronen *et al.*, 2005). We conclude that the mortality of cod and saithe following their escape from either the codend or selection grid of a demersal trawl is negligible. Also, mortality was not affected by fishing intensity. In experiments run simultaneously to the high-intensity fishing experiment, cod tagged with electronic tags repeatedly encountered and passed through trawls (IH, unpublished). Of $>$3500 cod tagged and released alive during two subsequent seasons, the probability of being recaptured was $\sim$0.1, and of being recaptured twice during 5 d, $\sim$0.01. This, however, could not be shown to affect the escape mortality of cod and saithe.

Haddock mortality was generally greater, more variable, and inversely related to length. Moreover, the variation was not related to escape category, suggesting that the escape *per se* may not be the most important cause of mortality. Mortality was not related to fishing intensity, but any possible differences between groups may have been masked by the large variability in the haddock mortality. The greater mortality of haddock in comparison with cod and saithe is consistent with the results of earlier experiments (Soldal *et al.*, 1993; Sangster *et al.*, 1996; Soldal and Engås, 1997; Wileman *et al.*, 1999), although the haddock mortality rates we observed were greater than those documented for previous studies, particularly our values for 2005.

Length-dependent mortality in haddock escaping from towed fishing gear has been observed by Soldal *et al.* (1991) and Sangster *et al.* (1996), and for herring (*C. harengus*) by Suuronen *et al.* (1996b). An inverse relationship between length and mortality suggests that the poorer swimming ability of smaller fish (Breen *et al.*, 2004) makes them more susceptible to post-exhaustion stress and injury during and after their escape from fishing gear (Sangster *et al.*, 1996; Suuronen *et al.*, 1996b).

During the development of the protocols used in the 2004 experiment, a number of technical difficulties were experienced, bringing about some changes in the cage design for the following year. However, it is suspected that these modifications, in particular the increased buoyancy, may have increased the mobility of the cages during the monitoring period. Gradual alterations in cage deployment depth throughout the monitoring period, as shown by the depth loggers, suggest that there was considerable horizontal movement of some cages. Moreover, the depth loggers showed large vertical movements in two of the cages (Table 3).

Although depth loggers were not used in 2004, we suspect that there were also horizontal movements and vertical instability of the cages, as in 2005. The GLMM models showed that mortality rates in 2004 were dependent on the anchoring depth of the cages. That depth is unlikely to be a direct mortality factor, but

Table 3. Data from the observation period in the 2005 experiment.

Category	Fishing intensity	No.	Number of fish				Haddock				Sampling time (min)	Anchoring depth (m)	Δ-depth (m)
			Cod	Haddock	Saithe	Total	Mean length	Min length	Max length	% mortality			
Grid	Low	1	9	166	1	323	38.3	23	56	52.12	10	70	*
Grid	Low	2	32	185	0	324	36.9	23	51	79.46	11	77	S
Grid	High	1	24	573	0	825	33.9	23	49	52.18	14	58	S
Grid	High	2	37	1 453	0	1 904	34.1	23	50	45.77	20	78	11
Control	Low	1	1	46	299	350	36.5	23	55	52.17	9	75	2
Control	Low	2	22	102	0	154	31.8	22	47	45.45	23	75	13
Control	Low	3	19	92	1	193	35.7	26	49	32.97	10	75	3

In addition to the information corresponding to Table 1, the Δ-depth column includes the range for recorded vertical movement during the observation period (S, cage lifted to surface; *, no depth data, but cage had drifted 1.5 nautical miles).

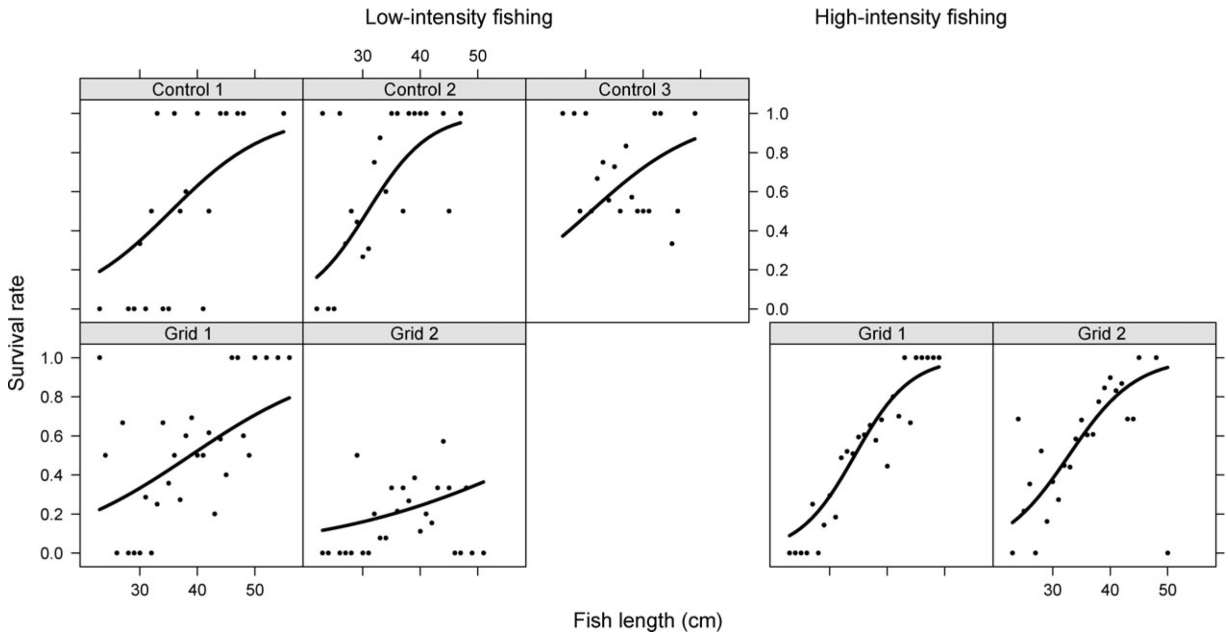

Figure 9. Haddock survival rates from individual cages in 2005, and fitted values from the GLMM model.

Table 4. Results from GLMM analysis of haddock mortality in 2005, with random effects for intercept and slope (for length).

Explanatory variable	Parameter estimate	s.e.	d.f.	*p*-value
Intercept	−4.60	0.96	164	<0.001
Fish length	0.131	0.030	42	<0.001
$\sigma_{intercept}$	2.01	–	–	–
$\sigma_{fish\ length}$	0.062	–	–	–

may be associated with technical problems, such as vertical instability of the cages. The anchoring depths varied from 47 to 90 m, whereas the length of the cable from the cage to the surface buoy was ~130 m. The slack in the cables was therefore considerably less for the cages anchored at greater depth. The resultant vertical lift vector created by the cable drag might therefore have been greater for the cages anchored at the greatest depths, so we suspect that vertical instability is one of the major reasons for the high rates of mortality of haddock observed.

Although it is clear that the mortality data for haddock from these experiments have been compromised as a result of additional and unwarranted stressors during the sampling and monitoring of escapees, it is equally apparent that cod and saithe were capable of surviving the stress of passage through and escape from the trawl, in addition to these experimentally induced captivity stressors. This raises an important question: why are cod and saithe able to survive these stresses, and haddock cannot? There are three likely causes of the observed haddock mortality in these experiments: (i) stress and exhaustion because of passage through the trawl, (ii) injury and stress as a result of decompression, and (iii) stress related to captivity.

Studies show that haddock have less swimming capability than saithe and cod of similar size (He and Wardle, 1988; Breen *et al.*, 2004). However, there is limited knowledge of the swimming capabilities of fatigued fish entering and escaping from a trawlnet. Such fish are likely to have reduced swimming capacity because respiratory substrates in the white muscle will be depleted. Moreover, in a study of haddock swimming endurance, 9 of 40 fish died within 24 h of swimming to a "fatigued" state (Breen *et al.*, 2004), implying that post-exhaustion stresses may affect the mortality rates of haddock after escaping from trawls.

The greatest mortality in the 2005 experiments was in cages lifted to the surface during the observation period (Table 3). Tytler and Blaxter (1973) showed that when reducing the ambient pressure, the swimbladder wall expanded reversibly and uniformly to a point where the pressure differential had reached four-fifths of the rupture pressure. Subsequently, there was irreversible "ballooning", leading to rupture of the swimbladder, usually into the peritoneal lining. According to Tytler and Blaxter (1973), this took place at mean pressure reductions of 70% for cod, 67% for saithe, and 58% for haddock. Therefore, when the cages were lifted from the seabed by strong currents, the pressure changes may have had a more detrimental effect on haddock than on the other species. However, the results of Tytler and Blaxter (1973) were based on only four haddock. We therefore suggest that before firm conclusions can be drawn concerning the importance of pressure changes on survival, further study of the tolerance of the different gadoid species to changing pressure should be carried out.

After passing through and escaping from the trawl, the escapees were collected in a codend cover and held in cages for an observation period of 6 d. Captivity can be stressful for fish (Wardle, 1981; Wedemeyer, 1997), and can lead to the death of the experimental subjects (Bayne, 1985). Cod and saithe clearly survive confinement in cages well. Little is known about the tolerance of haddock to captivity, but our analysis did not indicate that the number of fish in the cages, or the number of large cod or other predators in the cages (the predator effect) affected survival negatively. However, Martin-Robichaud (2003) noted that wild-caught haddock are easily stressed, leading to swimbladder dysfunction and mortality while being transferred to captivity. Therefore, captivity stress may have contributed to the mortality of haddock we observed in this experiment.

Acknowledgements

This project was part of the project Q5RS-2002-01603 "Survival" funded by The EU Commission. We thank the editor and two anonymous reviewers for valuable comments on the manuscript, our colleagues from IMR and Marine Laboratories, and the crews of the vessels "Havglans", "Kågtind", and "Riston" for valuable assistance during the cruises.

References

Anon. 2000. Report of the FTFB Topic Group on Unaccounted Mortality in Fisheries. ICES Document CM 2000/B: 3. pp. 34–105.

Bayne, B. L. 1985. Responses to environmental stress: tolerance, resistance and adaptation. *In* Marine Biology of Polar Regions and Effects of Stress on Marine Organisms, pp. 331–349. Ed. by J. S. Gray and M. E. Christiansen. John Wiley, New York.

Beamish, F. W. 1966. Muscular fatigue and mortality in haddock caught by otter trawl. Journal of the Fisheries Research Board of Canada, 23: 1507–1519.

Breen, M., Dyson, J., O'Neill, F. G., Jones, E., and Haigh, M. 2004. Swimming endurance of haddock at prolonged and sustained swimming speeds, and its role in their capture by towed fishing gears. ICES Journal of Marine Science, 61: 1071–1079.

Breen, M., Sangster, G., O'Neill, B., Kynoch, R., Jones, E., and Soldal, A. V. 2002. Evidence of sampling induced biases in mortality estimates from experiments investigating mortality in fish escaping from towed fishing gears. ICES Document CM 2002/V: 25. 5 pp.

Davis, M. W. 2005. Behaviour impairment in captured and released sablefish: ecological consequences and possible substitute measures for delayed discard mortality. Journal of Fish Biology, 66: 254–265.

DeAlteris, J. T., and Reifsteck, D. M. 1993. Escapement and survival of fish from the codend of a demersal trawl. ICES Marine Science Symposia, 196: 128–131.

He, P., and Wardle, C. S. 1988. Endurance at intermediate swimming speeds of Atlantic mackerel, *Scomber scombrus* L., herring, *Clupea harengus* L., and saithe, *Pollachius virens* L. Journal of Fish Biology, 33: 255–266.

Jacobsen, J. A., Thomsen, B., and Isaksen, B. 1992. Survival of saithe (*Pollachius virens*) escaping through trawl meshes. ICES Document CM 1992/B: 29. 10 pp.

Lehtonen, E., Tschernij, V., and Suuronen, P. 1998. An improved method for studying survival of fish that escape trawl-codend meshes. Fisheries Research, 38: 303–306.

Main, J., and Sangster, G. I. 1990. An assessment of the scale damage to and survival rates of young fish escaping from the codend of a demersal trawl. Scottish Fisheries Research Report, 46/90. 28 pp.

Martin-Robichaud, D. J. 2003. Haddock broodstock management. *In* Early Rearing of Haddock: State of the Art. Proceedings of a Workshop, 16–17 October 2002, pp. 17–22. Ed. by D. E. Aiken. Aquaculture Association of Canada Special Publication 7. St. Andrews, NB, Canada. 136 pp.

Pikitch, E., Erickson, D., Suuronen, P., Lehtonen, E., Rose, C., and Bublitz, C. 2002. Mortality of walleye pollock escaping from the codend and intermediate (extension) section of a pelagic trawl. ICES Document CM 2002/V: 15. 30 pp.

Pinheiro, J. C., and Bates, D. M. 2000. Mixed-Effects Models in S and S-PLUS. Springer, New York. 528 pp.

R Development Core Team. 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org.

Ryer, C. H. 2002. Trawl stress and escape vulnerability to predation in juvenile walleye pollock: is there an unobserved bycatch of behaviourally impaired escapees? Marine Ecology Progress Series, 232: 269–279.

Ryer, C. H., Ottmar, M. L., and Sturm, E. A. 2004. Behavioral impairment after escape from trawl codends may not be limited to fragile fish species. Fisheries Research, 66: 261–269.

Sangster, G. I., Lehmann, K., and Breen, M. 1996. Commercial fishing experiments to assess the survival of haddock and whiting after escape from four sizes of diamond mesh codends. Fisheries Research, 25: 323–345.

Sneddon, L. U., Braithwaite, V. A., and Gentle, M. J. 2003. Novel object test: examining nociception and fear in the rainbow trout. Journal of Pain, 4: 431–440.

Soldal, A. V., and Engås, A. 1997. Survival of young gadoids excluded from a shrimp trawl by a rigid deflecting grid. ICES Journal of Marine Science, 54: 117–124.

Soldal, A. V., Engås, A., and Isaksen, B. 1993. Survival of gadoids that escape from a demersal trawl. ICES Marine Science Symposia, 196: 122–127.

Soldal, A. V., Isaksen, B., Marteinsson, J. E., and Engås, A. 1991. Scale damage and survival of cod and haddock escaping from a demersal trawl. ICES Document CM 1991/B: 44. 7 pp.

Suuronen, P. 2005. Mortality of fish escaping trawl gears. FAO Fisheries Technical Paper, 478. 72 pp.

Suuronen, P., Erickson, D., and Orrensalo, A. 1996a. Mortality of herring escaping from pelagic trawl cod-ends. Fisheries Research, 25: 305–321.

Suuronen, P., Lehtonen, E., and Jounela, P. 2005. Escape mortality of trawl-caught Baltic cod (*Gadus morhua*) – the effect of water temperature, fish size and codend catch. Fisheries Research, 71: 151–163.

Suuronen, P., Perez-Comas, J. A., Lehtonen, E., and Tschernij, V. 1996b. Size-related mortality of herring (*Clupea harengus* L.) escaping through a rigid sorting grid and trawl codend meshes. ICES Journal of Marine Science, 53: 691–700.

Suuronen, P., Turunen, T., Kiviniemi, M., and Karjalainen, J. 1995. Survival of vendace (*Coregonus albula* L.) escaping from a trawl codend. Canadian Journal of Fisheries and Aquatic Sciences, 52: 2527–2533.

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

Venables, W. N., and Ripley, B. D. 2002. Modern Applied Statistics with S, 4th edn. Springer, New York. 495 pp.

Wardle, C. S. 1981. Physiological stress in captive fish. *In* Aquarium Systems, pp. 403–414. Ed. by A. D. Hawkins. Academic Press, London. 452 pp.

Wedemeyer, G. A. 1997. Effects of rearing conditions on the health and physiological quality of fish in intensive culture. *In* Fish Stress and Health in Aquaculture, pp. 35–71. Ed. by G. K. Iwama, A. D. Pickering, J. P. Sumpter, and C. B Schreck. Society for Experimental Biology, Seminar Series 62. Cambridge University Press. 478 pp.

Wileman, D. A., Sangster, G. I., Breen, M., Ulmestrand, M., Soldal, A. V., and Harris, R. R. 1999. Roundfish and *Nephrops* survival after escape from commercial fishing gear. Final Report EC Contract FAIR-CT95-0753.141 pp.

Wood, C. M., Turner, J. D., and Graham, M. S. 1983. Why do fish die after severe exercise? Journal of Fish Biology, 22: 189–201.

doi:10.1093/icesjms/fsm150