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

Ólafur Arnar Ingólfsson   Aud Vold Soldal   Irene Huse   Mike Breen

Abstract

Experiments are described to investigate the survival of gadoid fish in the Barents Sea escaping from a demersal trawl, with and without a sorting grid, at high and low levels of fishing intensity. The mortality for cod (*Gadus morhua*) and saithe (*Pollachius virens*) was negligible and unrelated to the experimental parameters: selection device (codend meshes and sorting grid) or fishing intensity. Haddock (*Melanogrammus aeglefinus*) mortality was generally higher, more variable and inversely related to fish length, and was neither related to selection device nor fishing intensity. The mortality of haddock escaping through the selective devices in the trawl was not significantly different from that of the control group, which avoided passing through either the codend meshes or selection grid, suggesting that the escape per se is not the main cause of mortality. It is concluded that the observed mortality of haddock is confounded by methodological problems, in particular instability of the observation cages, and does not reflect the true escape mortality.

Introduction

Stock assessment and management of fisheries build upon the use of technical conservation measures by fisheries management to minimise discarding of unwanted and undersized fish, and is based on the simple, but unproven, assumption that all fish escaping from fishing gears survive and live on to promote the exploited population. However, a number of studies have demonstrated that this assumption may be untrue (Anon, 2000; Sangster et al., 1996; Soldal et al., 1993; Suuronen et al., 1996a). A proportion of escaping fish, in particular the smallest ones (Ingólfsson et al., III; Sangster et al., 1996; Suuronen et al., 1996b; Wileman et al., 1999), may die after escaping from trawl codends. A precise, quantitative description of this escape mortality is essential for determining the effectiveness of these technical measures.

There have been a substantial number of escape mortality investigations over the past 15 years (Anon, 2000). While some gadoids, namely cod and saithe, have been shown to suffer negligible mortality (Soldal et al., 1993; DeAlteris and Reifsteck, 1993; Suuronen et al., 2005) the estimates of escape mortality have proved to be highly variable and inconsistent for other species like haddock, whiting (Ingólfsson et al., III; Soldal et al., 1993; Sangster et al., 1996; Wileman et al.,

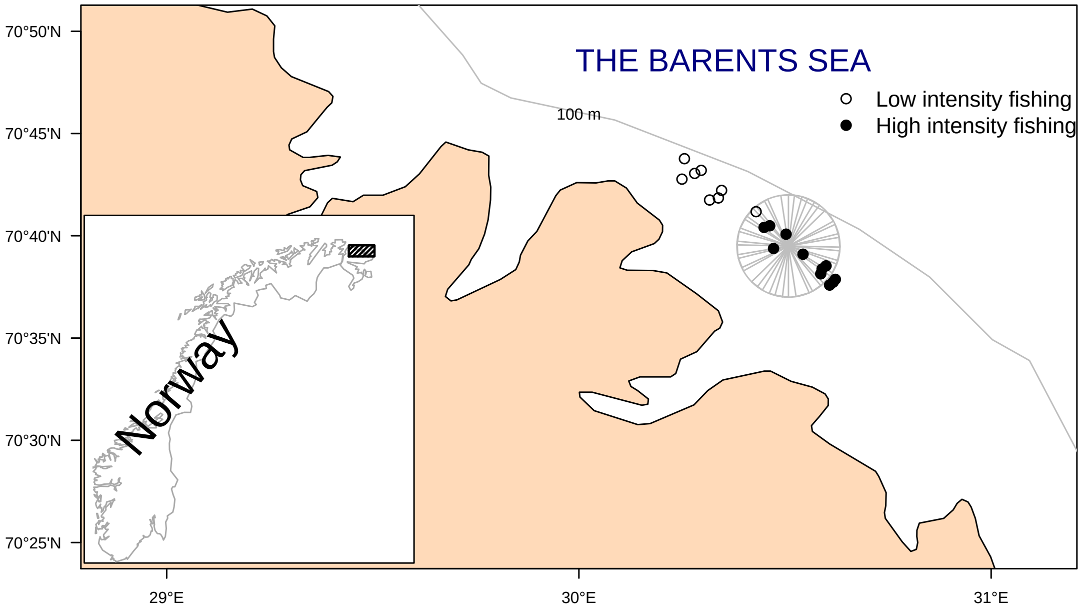

Figure 1: The experimental area out of Varanger peninsula in 2004. The open and filled dots show where the cages were set out. The transects in the drawn circle show the tracks of the trawlers simulating the high intensity fishing

1999) and Baltic herring (Suuronen et al., 1996a,b). The mortalities observed in survival experiments are easily influenced by the methods used to collect, transport and monitor escapees (Suuronen et al., 1996b), and the variability in earlier studies indicates that methodological errors have affected the results. Breen et al. (2002) demonstrated that haddock mortality is correlated with time spent in the cover/cage during towing, i.e. sampling time.

The intensity of fishing activities and effort can vary considerably between seasons, areas 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 have an impact on the physical condition of the juvenile population, and potentially their escape survival. It has been shown that fish may die as a result of stress and muscular fatigue (Beamish, 1966; Wood et al., 1983) incurred during entrainment and escape through trawl codends (Beamish, 1966). Also, stressors that do not directly kill fish may still cause indirect mortality, such as behavioural impairment making the escaped fish more vulnerable to predation (Davis, 2005; Ryer, 2002; Ryer et al., 2004; Sneddon et al., 1993).

This project was designed to develop sampling techniques that overcome current biases in escape mortality estimation, and to use these techniques to provide improved survival data for gadoid species escaping from a bottom trawl with and without sorting grid in the Barents Sea, as well as to study the effect of fishing intensity on escape survival.

Materials and methods

Two experiments were conducted out of Varanger peninsula in Norway at 45-90 meter depth (Figure 1) during 16 April to 5 May 2004 and 28 March to 18 April 2005. The first half of each experiment (low intensity fishery) was done in an area with no 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 square area 3 × 3 nautical miles in 2005. The criteria for high intensity fishing was based on trawl catch statistics from 2000 to 2002.

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 single two-panel bottom trawls ('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 (including selvedges). The tapered extension between the trawl and codend was 8 m long. In 2005 a sister ship of that used in 2004 was hired. It had a 1543 kW main engine and a similar trawl ('Alfredo 4') with 90 m sweeps.

To collect grid escapees, a Sort-V stainless steel sorting grid (Figure 2) with 55 mm bar spacing was fitted to the trawl. Escaping fish were collected in cages attached to cover nets, either covering the codend in order to catch codend escapees and control fish (Figure 3) or the opening of the sorting grid (Figure 4) to catch grid escapees. The cages were 5 × 2 × 2 m in dimension and constructed from 70 mm aluminium tubing frames. The foremost 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. All sides had a triangular shaped canvas (Figure 3B). This is based on a design by Fisheries Research Services, Marine Laboratory (unpublished results), which minimizes the effects of water-flow on the captive fish in the cover. In each cage a camera and light with ~130 meter cable was fitted so that fish could be monitored at the anchoring depth during the experiment. Two acoustic releases (AR 661 B2S from Oceano Technologies) were mounted on the cover net in front of

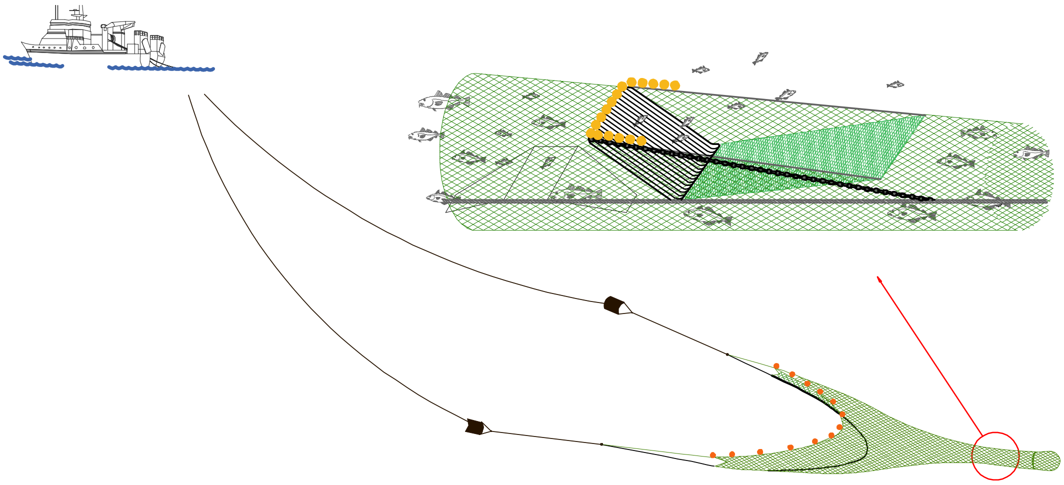

Figure 2: The Sort-V grid and the positioning in the trawl

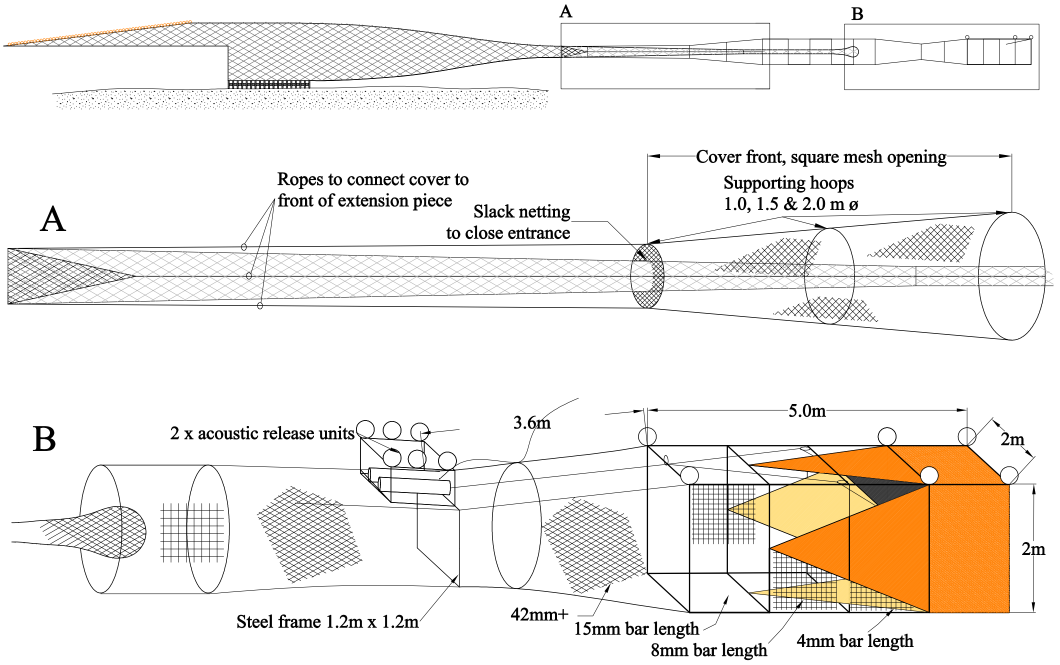

Figure 3: Attachment of codend cover and cage to the trawl. A: Detail of cover attachment to trawl extension. B: Detachable cage and attachment to the cover

the cage, which were used to control the closing of the cage gate and release of the cage from the trawl. During the development of the protocols, a number of technical difficulties were experienced, 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. Some changes were introduced in 2005 to overcome these difficulties: fitting a curtain into the foremost frame of the cage to improve closing at the front end, increased floatation of the cages due to increased weight of cage with curtain, and including depth and temperature loggers on the cages.

The cover connecting the cage to the trawl was attached to the front of the tapered extension (Figure 3A). The purpose of this was to minimise any restriction of the passage through the narrow extension caused by the increased load from the drag of the cover/cage assembly. Recent studies (Ingólfsson and Jørgensen, er I) have shown that a considerable proportion of fish in the trawl opening passes underneath the trawl. To eliminate the possibility of that fish to enter the cages, the foremost part of the cover was closed in front by attaching it to the trawl extension with a slack netting in such a way that there was no strain on the extension. To minimize effects of the cover on water flow around the codend, the tapered front of the cover was made of a larger mesh size (50 mm) and thinner twine (1.1 mm dynex) than that used in the cage, and was hung on the lines with 71% hanging ratio (square mesh opening).

Fish were sampled from three categories of escaping fish: (i) grid escapees; (ii) mesh escapees; and (iii) control fish. The control group fish simply passed through the trawl and directly into the cover/cage as-

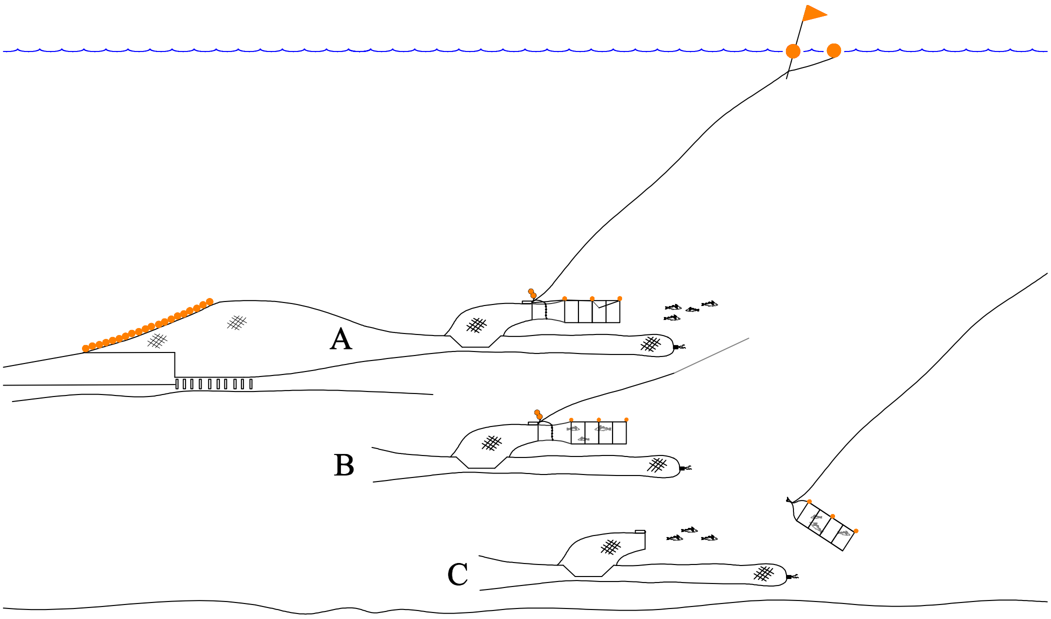

Figure 4: Chronological order of grid-cage release. A: Towed with cage open, cover net encloses the Sort-V grid. B: The door has been released by acoustic release and the sampling begins. C: Cage released and closed in front by acoustic release

sembly, without encountering the grid or codend. To minimize variation in fish density over time, the categories were randomly dispersed throughout the experimental period. The trawler towed for approximately 0.5 h at a speed of 1.8 to 2 ms^{-1} (3.5 to 4 knots) with the cage open at the rear, allowing all the fish to pass through it. To start sampling escapees, a signal was sent to the first acoustic-release unit, which released and closed the door at the rear end of the cage. After 2 to 15 min sampling period, the cage was released from the cover net with a signal to the second acoustic-release. Sampling time was defined as the time between the confirmation signals from first and the second acoustic-releases. Floats lifted the rope and camera-cable to the surface, which maintained tension at the front end of the cage and kept it closed (see Figure 4 for chronological order of grid-cage release). For added security, the closing strop was threaded through a 5 kg steel disc. The cages were anchored on the bottom where they had been released from the trawl.

During an observation period of six days, the cages were monitored wireless from the auxiliary vessel, by use of cameras mounted in the cages, connected to an antenna at the surface via cable running along the ∼130 m rope to the surface buoy (Figure 5).

At the end of the observation period, the cages were brought to the surface and live and dead fish were counted and measured to the nearest cm. When total number of alive or dead haddock were estimated to exceed 500 (>10 baskets), a minimum of 5 baskets (∼250 fish) were measured by randomly picking baskets and the remaining fish were counted.

Data analysis

For cod and saithe, where the mortality was negligible, the number of living and dead fish, along with information of their size range, mean length and standard deviation (sd) of the size distribution are given in Tables 1

and 3.
Haddock survival data was analysed using generalized linear mixed models (glmm). Mixed-effects models (Pinheiro and Bates, 2000) provide a flexible and powerful tool for the analysis of 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. Since the event of dead vs. alive is binary, a model with binomial distribution and logit-link becomes our choice.
If π_{ij} is the survival probability in the j-th length class in the i-th cage and x_{ij} is the corresponding value of the covariate, the logit for an analysis of covariance model with a random effect ζ_i for the intercept and slope (for fish length) can be written:

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

where β is the p-dimensional vector of fixed effects, ζ_i is the 2-dimensional vector of random effects, z_{ij} is a subset of x_{ij} (2-dimensional vector of 1's and fish length j within cage i). The variances are denoted σ^2_ζ, for the between cage variability. That is,

$$\zeta_i \sim \mathcal{N}(0, \sigma^2_\zeta)$$

This model combines a random-effects model for analysis of categorized data with a regression model.
The covariates tested were fish length, fishing intensity (high/low), cage category (grid, mesh, control), number of fish in cage (by species and pooled), number of cod above 50 cm (predator effect), sampling time, number of fish per unit sampling time, anchoring depth, maximum tidal range (as a measure of current speed) and maximum wind speed (ms^{-1}) the first 24 hours after setting out the cages. Interaction terms were added to the model. Both forward selection and backward elimination were applied to select the best subsets of covariates. The final models include only significant ($p<0.05$) covariates and interaction terms. All statistical analysis and graphics were done in the R statistical program (R Development Core Team, 2005). For model fitting, the glmmPQL routine (Venables and Ripley, 2002) was applied.

Results

The results from running glmm analyses on the data from 2004 and 2005 show that mortality differs between years. Further analysis revealed that this 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 analysed separately.

2004 experiments

Trawl escapees were successfully sampled in a total of 19 experimental cages. Of those, 8 were sampled during low intensity fishing (3 controls, 2 grid escapes and 3 mesh escapes) and 11 during high intensity fishing (3 controls, 3 grid escapes and 5 mesh escapes). See Figure 6 for chronological order of cage-release and time in sea before taken up. All the cages were taken up on the sixth day in the sea except for the first high intensity cage (a grid cage), which was taken up on day seven due to weather restrictions. 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. A total of 1369 cod, whose length ranged from 22 to 94 cm (mean = 44.9 cm, sd = 8.59 cm), were captured during the experiments. Four of these, ranging from 30 to 46 cm, were found dead in three of the 19 cages. Two were found in low intensity grid cage no. 2, one in high intensity mesh cage no. 5 and one in grid cage no. 1, giving 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 623 saithe, whose length ranged from 26 to 68 cm (mean = 42.3 cm, sd = 6.27 cm) were captured. Nine saithe, ranging from 34 to 56 cm were found dead in four of the cages: One in

Table 1: Data from the observation period in the 2004 experiment. The 'No' column shows chronological order within category and intensity and is the same as in Figure 7. The total number of fish includes other species than mentioned in the table, mainly flatfish

			Number of fish				Haddock				Sampling	Anchoring	Tidal
	Fishing						Mean	Min	Max	%	time	depth	difference
Category	intensity	No.	Cod	Haddock	Saithe	Total	Length	Length	Length	Mortality	(min)	(m)	(m)
Mesh	Low	1	8	502	53	563	37.5	14	51	56.0	11	87	2.52
Mesh	Low	2	149	1499	0	1648	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	1452	21	1803	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	1858	0	1995	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	345	570	42.3	32	57	12.9	7	90	1.89
Control	High	1	38	2294	10	2354	33.6	21	61	33.0	3	78	1.29
Control	High	2	152	1522	32	1707	36.5	24	56	1.9	2	57	1.32
Control	High	3	174	771	7	1119	35.5	23	56	5.6	8	70	1.54

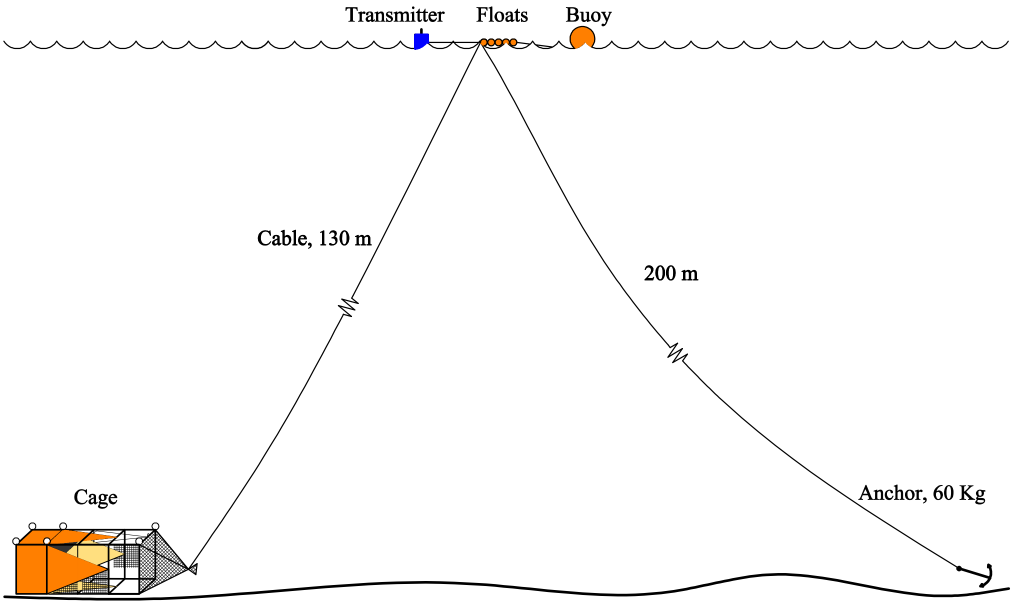

Figure 5: Rigging of cages on the seabed, after release from the trawl

low intensity mesh cage no. 1 and six in control cage no. 3, one in high intensity mesh cage no. 1 and control cage no. 2, giving respectively 1.9, 1.7, 6.7 and 3.1% saithe mortality in those cages and an average pooled mortality of 1.4%.

A total of 12571 haddock, with length ranging from 12 to 61 cm (mean = 34.6 cm, sd = 6.64 cm) were sampled during the experiments. A total of 1823 haddock died. The mortality rate was related to fish length with the highest mortality among the smallest fish (Figure 7). There was no difference in survival rate between the control and the experimental groups, indicating that survival was independent of selectivity device (mesh or sorting grid). Nor did mortality increase with fishing intensity. The glmm analysis showed that the survival rate increased with fish length (Table 2). The model also showed that interaction between anchoring depth and tidal range affected survival in a negative manner. Tidal range was correlated to fishing intensity (Figure 6.) with the widest tidal range (and thus strongest currents) during the low intensity fishing period, and there was a ten-

Table 2: Results from glmm analysis on haddock survival with random effects for both intercept and slope (for length) for the 2004 data

Explanatory variable	Estimate	Std. error	DF	p-value
Intercept	0.717	1.155	502	0.535
Fish length	0.112	0.018	502	0.000
Anchoring depth × tidal difference	-0.019	0.007	17	0.015
$\sigma_{Intercept}$	2.652			
σ_{Length}	0.061			

Table 3: Data from the observation period in 2005. In addition to the information corresponding to Table 1, the 'Δ-depth' column includes recorded vertical movement m during the observation period (S: Cage lifted to surface, *: No depth data, but cage had drifted 1.5 nm)

			Number of fish				Haddock				Sampling	Anchoring	Δ-depth
	Fishing						Mean	Min	Max	%	time	depth	
Category	intensity	No.	Cod	Haddock	Saithe	Total	Length	Length	Length	Mortality	(min)	(m)	(m)
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	1453	0	1904	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

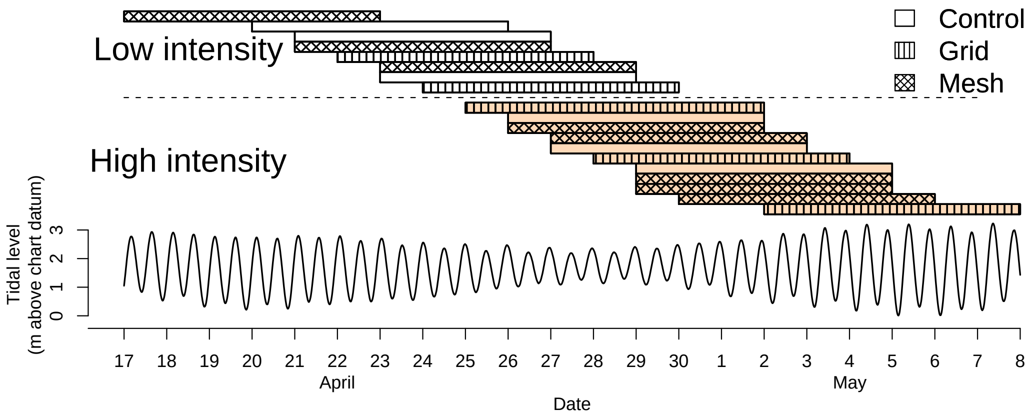

Figure 6: Chronological order of setting out and taking up cages in 2004. The tidal level is shown in the figure

Table 4: Results from glmm analysis on haddock survival with random effects for intercept and slope (for length), for the 2005 data

Explanatory variable	Estimate	Std. error	DF	p-value
Intercept	-2.080	0.951	187	0.030
Length	0.142	0.015	187	0.000
Factor (Vertical movement)	-3.142	0.836	6	0.011
$\sigma_{Intercept}$	1.472			
σ_{Length}	0.057			

dency towards higher survival rates during the high intensity fishing period. Figure 8 shows predicted survival rates, and illustrates how depth range affects haddock survival.

The other experimental covariates tested (number of fish in the cage by species and pooled, number of cod larger than 50 cm (predator effect), sampling time, number of fish per unit sampling time, and maximum wind speed the next 24 h after setting out the cages) were not shown to influence the survival of haddock (p>0.05).

2005 experiments

In 2005, the weather inhibited the experiments severely, and only seven valid cages were obtained. After a troublesome start of the experiment, it was decided to abandon the mesh escape category in an attempt to get sufficient numbers of replicates from the other categories. All the valid cages were fitted with depth and temperature loggers, which proved that they had moved vertically and/or horizontally during the observation period when they were supposed to stand steady on the bottom (see the 'Δ-depth' column in Table 3). The horizontal movements were recognized by the depth loggers as gradual changes in depth during the observation period, suggesting that the cages had drifted with the currents along the bottom. The current speed, measured at the sites frequently reached 0.5 ms^{-1}, with a maximum of 0.6 ms^{-1}.

Table 3 shows the number of fish of each species in the valid cages in 2005. In low intensity grid cage no. 2, one cod out of 32 died, i.e. 3.1% mortality. There was no mortality of cod in the other cages, giving an overall total mortality of 0.8%. Except for low inten-

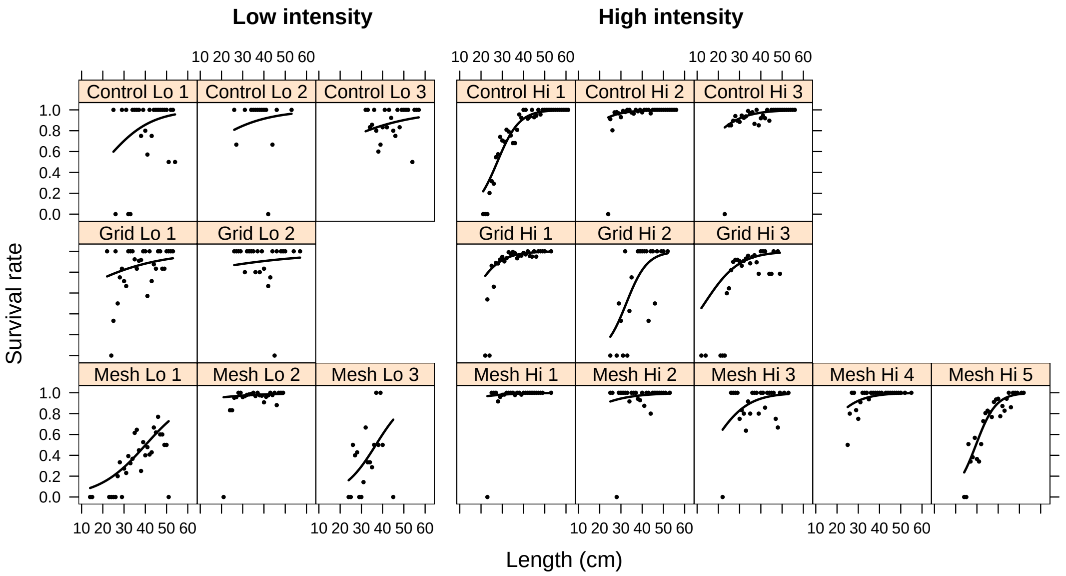

Figure 7: Haddock survival rates from individual cages in 2004 along with fitted values from the glmm model

sity control cage no. 1, the numbers of saithe were low (Table 3). One saithe out of 299 in that cage died, giving 0.3% mortality.

A total of 2943 haddock were caught in the cages in 2005. As in the previous year, mortality did not differ significantly between grid and control categories, nor between high and low intensity fishing. The mortality was highest among the smallest fish, with vertical movement of the cages during the observation period adding significantly to the mortality. (Figure 9, Table 4). Of the two grid cages that rose to the surface, the low intensity cage no. 2 had higher mortality than the high intensity cage no. 1. The time spent at less depths than half the bottom depth was 2h 40m and 1h, respectively. The anchoring depth range was narrower than the previous year and was not a significant explanatory factor on haddock survival. The temperature in the cages ranged from 3.4 to 3.8°C.

Discussion

Cod and saithe mortality

The observed mortality for cod and saithe was low and appears to be unrelated to the experimental parameters: escape category or fishing intensity. This low mortality agrees with observations of escape mortality from earlier experiments with these species (Soldal et al., 1993; DeAlteris and Reifsteck, 1993; Suuronen et al., 2005). It can be concluded that the mortality of cod and saithe following their escape from either the codend or selection grid of a demersal trawl is negligible, irrespective of selectivity device and the intensity of the fishing operations at the time.

Haddock mortality

Haddock mortality was generally higher, more variable and inversely related to length. Moreover, this variation is neither related to escape category nor fishing intensity. The high mortality of haddock in comparison to other gadoids (cod and saithe) is consistent with results of other experiments (Sangster et al., 1996; Soldal et al., 1993; Soldal and

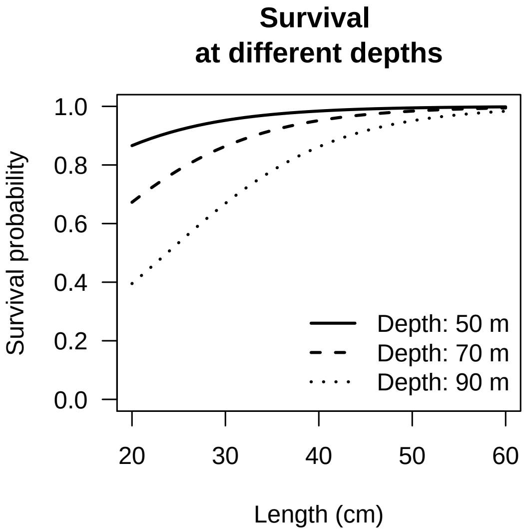

Figure 8: Predicted values for survival rate of haddock, showing the effect of anchoring depth in the 2004 experiment

Engås, 1997; Wileman et al., 1999) although the observed haddock mortality in this experiment was higher both years, but particularly in 2005, than observed in these previous studies. The mortality of haddock escaping through grid or mesh was not significantly different from that of the control group, which avoided passing through either the codend meshes or selection grid, suggesting that the escape per se is not the main cause of mortality.

Length-related mortality in haddock escaping from towed fishing gear has been observed in previous experiments (Soldal et al., 1991; Sangster et al., 1996). A similar relationship has also been observed in other species, such as herring (*Clupea harengus* L.) (Suuronen et al., 1996b). An inverse relationship between length and mortality have suggests that the poorer swimming ability of smaller fish (Breen et al., 2004), mean they are more susceptible to post-exhaustion stresses and injuries during and after their escape from the fishing gear (Sangster et al., 1996; Suuronen et al., 1996b).

Technical difficulties

A substantial mortality was observed for haddock in all experimental categories, but the considerable variation between the observed mortality in individual cages was not significantly related to the escape category (codend mesh, selection grid or control) nor the fishing intensity. During the development of the protocols used in this experiment, a number of technical difficulties were experienced, 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. To overcome these difficulties, in 2005, floatation of the cages was increased to prevent unintentional contact with the seabed while towing, a curtain was fitted into the cage to improve closing of the front end, and depth and temperature loggers were fitted on the cages. However, it is suspected that these modifications, in particular the increased buoyancy, may have increased the potential 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

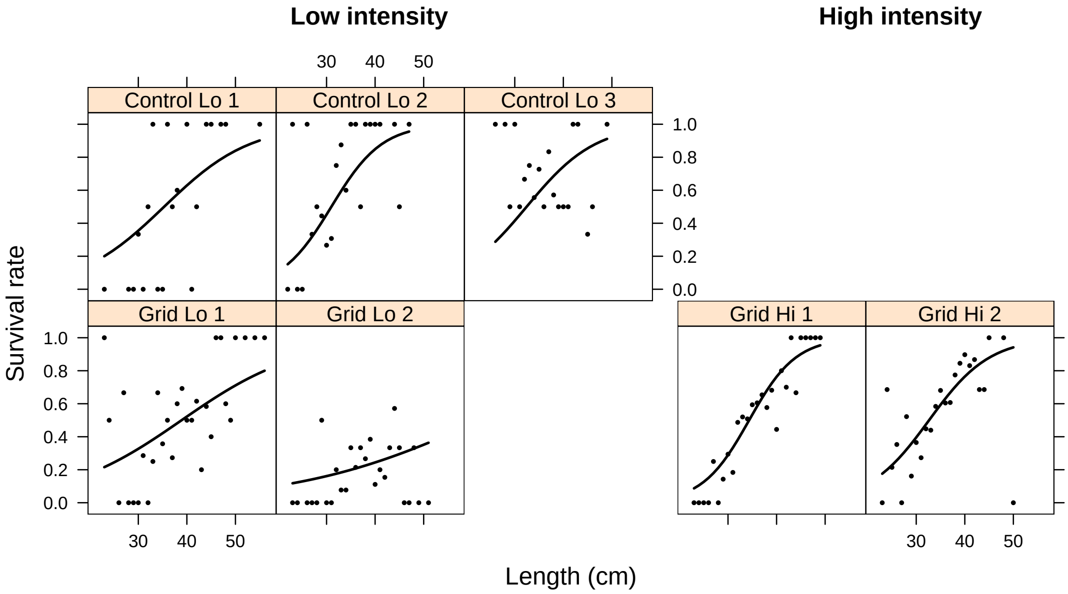

Figure 9: Haddock survival rates from individual cages in 2005 along with fitted values from the glmm model

that there were considerable horizontal movement of some cages. Moreover, data obtained from the depth loggers in the same year show large vertical movements in two of the cages: both from the grid category, one from low and one from high intensity fishing (Table 3). Although depth loggers were not used in 2004, we suspect movements and instability of the cages also this year. Analysis of the mortality data suggests that some of the observed mortality in haddock may be the result of these disturbances.

The glmm models used for analysing the mortality data showed that mortality was induced upon the anchoring depth of the cages and current strength. Both factors support the hypothesis that mortality was linked to the instability of the cages. The currents in the experimental area are strong and frequently exceeded 0.5 ms^{-1} in 2005. Moreover, the tidal range, and thus the current strength, were correlated to fishing intensity with the strongest currents during the low intensity fishing period in 2004 (Figure 3). The anchoring depths varied from 47 to 90 m, while 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 larger depths than for those anchored in shallower waters. The resultant vertical lift vector created by the cable drag must therefore have been greater for the cages anchored on the largest depths, and also largest during the heaviest currents, increasing their instability and risk of being dragged along or even lifted from the bottom during strong tidal currents. We therefore suspect cage instability to be one of the major reasons for the observed mortality of haddock.

Why do haddock die when cod and saithe do not?

While it is clear that the mortality data for haddock from these experiments have been compromised due to additional and unwarranted stressors during the sampling and monitoring of the escapees, it is equally apparent that the cod and saithe were capable of surviving the stress of passage through and escape from the trawl, in addition to these experimental induced captivity stressors. This raises an important question: why are cod and saithe able to survive these stresses, when the closely related gadoid, haddock, cannot? There are three likely causes of the observed haddock mortality in these experiments: (1) Stress and exhaustion due to trawl passage, (2) injury and stress due to decompression, and (3) stress related to captivity.

Stress and exhaustion due to trawl passage

Studies show that haddock has a lower swimming capability than saithe and cod of similar sizes (He and Wardle, 1988; Breen et al., 2004). However, little investigation has been carried out to study the swimming capabilities of fatigued fish entering and escaping from the trawl net. These fish are likely to have a much reduced swimming capacity as respiratory substrates in the white muscle will be depleted. Furthermore, in a study investigating the swimming endurance of haddock, 9 out of 40 fish died within 24 h of swimming to a 'fatigued' state (Breen et al., 2004); implying post-exhaustion stresses may affect the mortality rates of haddock after escaping from trawls. In addition, fish escaping trawl codends may suffer swimming impairment and behavioural deficits that subject them to elevated predation risk and reduced feeding success (Davis, 2005; Ryer, 2002; Ryer et al., 2004; Sneddon et al., 1993).

Decompression stress / injury

The highest mortality in the 2005 experiments was in cages that had lifted to the surface during the observation period (Table 3). Similarly, the results from Ingólfsson et al. (III) observed the highest mortality of haddock in cages that were accidentally raised to a depth corresponding to more than the preset safety limit of 50% pressure reduction. The safety limit of 50% pressure reduction was suggested by Tytler and Blaxter (1973), who showed that when reducing the ambient pressure, the swimbladder wall expanded reversibly and uniformly to a point where the pressure differential had reached 4/5 of the rupture pressure. Subsequently irreversible 'ballooning' occurred, leading to rupture, usually into the peritoneal lining. Mean values for pressure reduction leading to rupture were 70% for 18 cod, 67% for 16 saithe and 58% for four haddock. These data indicate that haddock are more sensitive to pressure changes than cod and saithe. Therefore, when the cages were lifted from the seabed during strong currents, the pressure changes may have had a more detrimental effect on haddock than on the other species; where the expanded swim bladder may have caused damage to internal organs and/or additional stress due to loss of buoyancy control. But it must be born in mind that the results of Tytler and Blaxter (1973) were based on four haddock only, and before more firm conclusions can be drawn on the importance of pressure changes on survival, the tolerance of the difference gadoids species should be investigated in detail.

Captivity stress

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 six days. Captivity can be detrimentally stressful for fish (eg. Wardle 1981 and Wedemeyer 1997) and can lead to the death of the experimental subjects (Bayne, 1985). We have seen that cod and saithe survive confinement in cages well. Little is known as to the tolerance of haddock to captivity stress, but our analysis did not manifest that number of fish in cages, number of large cod or wolffish in cages (predator effect) affected survival in a negative manner. It has however been noted that wild caught haddock are 'easily stressed' leading to swimbladder dysfunction and mortality while transferred to captivity (Martin-Robichaud, 2003). Therefore captivity stress may have contributed to the observed mortality of the fish in this experiment – in particular the haddock - through a number of potential stressors, including cage volume, shape and stability.

Conclusions

Only a negligible mortality was observed among cod and saithe escapees in these experiments, and no effect of selection device or fishing intensity on mortality rate was found. However, the mortality of haddock was highly variable, and frequently higher than in previous experiments. The observed mortality of haddock is thought not to reflect the true escape mortality, but is confounded by methodological problems – in particularly cage instability - that may have induced potentially fatal captivity stresses. It is apparent that the cod and saithe are capable of surviving the stress of passage through and escape from the trawl, in addition to the experimental induced captivity stressors, while haddock are not, despite being a closely related gadoid and having a similar life-style. Further investigations should be carried out to explore the causes of these inter-specific differences in tolerance of gadoids to capture and captivity stresses.

Acknowledgements

We thank the editor and two anonymous referees for valuable comments on the manuscript, our colleagues from IMR and Marine Laboratories, and the crews of the vessels "Havglans", "Kågtind" and "Riston" for invaluable assistance during the cruises.

References

Anon 2000. Report of the FTFB topic group on unaccounted mortality in fisheries. FTFB working group, Haarlem, The Netherlands, 10-11 April 2000. ICES CM 2000/B:1.

Bayne, B. 1985. Responses to environmental stress: tolerance, resistance and adaptation. In Gray, J. S. and Christiansen, M. E., editors, *Marine biology of polar regions and effects of stress on marine organisms*, pages 463–495. 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(7):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 CM 2002/V:25.

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 Symposium*, 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.

Ingólfsson, O. A. and Jørgensen, T. Paper I. Escapement of gadoid fish beneath a commercial bottom trawl: relevance to the overall trawl selectivity. *Fisheries Research*. In press.

Ingólfsson, O. A., Soldal, A. V., and Huse, I. Paper III. Gadoids escaping codends and sorting grids: Survival and injuries. *Manuscript*.

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

Martin-Robichaud, D. J. 2003. Haddock broodstock management. In Aquaculture Association of Canada Special Publication: Early Rearing of Haddock: State of the art. Proc. Workshop 16-17 Oct 2002, St. Andrews, Canada, no. 7: 17-22.

Pinheiro, J. C. and Bates, D. B. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag, New York.

R Development Core Team 2005. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Ryer, C. H. 2002. Trawl stress and escape vulnerability to predation in juvenile walleye pollock: Is there an unobserved bycatch of behaviourally impaired escapees? *Mar. Ecol. Prog. Ser.*, 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. 1993. Novel object test: Examining nociception and fear in the rainbow trout. *Journal of Pain*, 4(8):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 Symposium*, 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 Fish Capture Committee, CM 1991/B:44, 12 pp.

Suuronen, P., Erickson, D., and Orrensalo, A. 1996a. Mortality of herring escaping from pelagic trawl cod-ends. *Fisheries Research*, 3–4:305–321.

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*, 70:151–163.

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.

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

Venables, W. N. and Ripley, B. D. 2002. *Modern Applied Statistics with S*. Springer, New York, fourth edition. ISBN 0-387-95457-0.

Wardle, C. S. 1981. Physiological Stress in Captive Fish. In Hawkins, A. D., editor, *Aquarium Systems*. Academic Press, London.

Wedemeyer, G. A. 1997. Effects of rearing conditions on the health and physiological quality of fish in intensive culture. In by G. K. Iwama, Pickering, A. D., Sumpter, J. P., and Schreck, C. B., editors, *Fish Stress and Health in Aquaculture*, volume 62, page 278. Cambridge University Press. Society for Experimental Biology, Seminar Series.

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. EC Contract No: FAIR-CT95-0753. Final report 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.