ICES Journal of Marine Science Advance Access published June 4, 2015

ICES Journal of Marine Science

ICES International Council for the Exploration of the Sea
CIEM Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science; doi:10.1093/icesjms/fsv102

Dive to survive: effects of capture depth on barotrauma and post-release survival of Atlantic cod (*Gadus morhua*) in recreational fisheries

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Ferter, K., Weltersbach, M. S., Humborstad, O-B., Fjelldal, P. G., Sambraus, F., Strehlow, H. V., and Vølstad, J. H. Dive to survive: effects of capture depth on barotrauma and post-release survival of Atlantic cod (*Gadus morhua*) in recreational fisheries. – ICES Journal of Marine Science, doi: 10.1093/icesjms/fsv102.

Received 20 March 2015; revised 7 May 2015; accepted 11 May 2015.

Atlantic cod (*Gadus morhua*) caught in recreational fisheries are commonly released, often with barotrauma after rapid decompression. Mouth-hooked, non-bleeding cod kept in a floating net pen showed mortalities $\geq$40% when angled from >50 m depth, likely because of cumulative stress from ongoing barotrauma and exposure to warm surface water. In a natural setting, however, cod have the opportunity to descend after release and are not restricted to the surface. In a follow-up study, 97.8% of similarly selected cod managed to dive following immediate release, whereas 2.2% were floaters. No mortality was observed for divers kept in cages, which were lowered to capture depth for 72 h. While the floaters would likely have died in a natural setting, no mortality was observed when they were recompressed and kept at capture depth for 72 h. The occurrence of swim bladder ruptures, swollen coelomic cavities, venous gas embolisms, and gas release around the anus was significantly influenced by capture depth (range 0–90 m). A supplementary radiology study showed inflated swim bladders in 87% of the cod after 72 h, and most barotrauma signs had disappeared after 1 month. This study encourages investigation of survival potential for physoclistous species when high mortalities are assumed but undocumented. Matching natural post-release and containment environment is essential in the experimental setup, as failure to do so may bias survival estimates, particularly when a thermocline is present. Assuming minimal predation, short-term mortality of cod experiencing barotrauma is negligible if cod submerge quickly by themselves and are otherwise not substantially injured. Survival of floaters may be increased by forced recompression to capture depth. Sublethal and long-term impacts of barotrauma remain to be studied. To ensure that cod have sufficient energy to submerge, anglers are encouraged to avoid fighting the fish to exhaustion and to minimize handling before release.

Keywords: barotrauma signs, catch-and-release, containment study, gas embolism, post-release mortality, recreational fishing, swim bladder rupture.

Introduction

Atlantic cod (*Gadus morhua*, hereinafter: cod) is one of the most important marine recreational target species in the North Atlantic, the North Sea, and the Baltic Sea (Vølstad *et al.*, 2011; Sparrevohn and Storr-Paulsen, 2012; Strehlow *et al.*, 2012; van der Hammen and de Graaf, 2012; Armstrong and Hyder, 2013; NEFSC, 2013; Brownscombe *et al.*, 2014a). Landings by recreational anglers account for a significant part of the total landings (e.g. up to 70% of the commercial cod landings in the Baltic Sea; Strehlow *et al.*, 2012). Consequently, German recreational catches have been

included in the western Baltic cod assessment since 2013 (ICES, 2013). A recent review by Ferter *et al.* (2013a) showed that release rates (by numbers of fish) for this species are >50% in several European recreational fisheries. Similar release rates have also been reported for the Gulf of Maine recreational fishery (NEFSC, 2013) in the Northwest Atlantic. The high release percentages can be explained by regulatory catch-and-release (C&R) practice, i.e. release of catches due to harvest regulations such as minimum landing sizes or bag limits, and/or voluntary C&R, i.e. when anglers decide to release their catch, although it could have been harvested legally (Arlinghaus *et al.*, 2007; Ferter *et al.*, 2013a).

Considering the high C&R rates documented for cod, post-release mortalities may have to be accounted for to ensure reliable stock assessments (Eero *et al.*, 2015). Post-release mortalities coupled with high release rates can have a negative impact on fish stocks if ignored in stock assessments (Kerns *et al.*, 2012). Coggins *et al.* (2007) showed that unaccounted post-release mortalities of ca. 30% made harvest regulations ineffective. Post-release mortalities vary significantly between species and fisheries, and depend on many factors including anatomical hooking location, water temperature, and capture depth (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Arlinghaus *et al.*, 2007; Cooke and Wilde, 2007; Hühn and Arlinghaus, 2011). Besides post-release mortalities, released fish can also experience sublethal impacts which can, among others, increase the risk of predation (Cooke and Philipp, 2004) or reduce reproductive success (Suski *et al.*, 2003). While several studies on escape and discard mortalities of cod in a commercial fishery context have been published (e.g. Milliken *et al.*, 1999, 2009; Pálsson *et al.*, 2003; Suuronen *et al.*, 2005; Humborstad *et al.*, 2009), only a few studies have investigated the impacts of C&R on cod in recreational fisheries. Weltersbach and Strehlow (2013) studied the post-release mortality of cod in the German Baltic Sea recreational charter boat fishery. They estimated an average post-release mortality of 11.2% (after correcting for handling and caging effects), which is in the lower range of reported post-release mortalities [compare Bartholomew and Bohnsack (2005)]. Moreover, they found that bleeding and holding-water temperature were the main factors influencing post-release mortality of cod in their experiment. Another study by Ferter *et al.* (2015) examined the sublethal C&R effects on cod following best-release practice in recreational angling. They found that some cod showed altered swimming behaviour after being released, but that these returned to pre-release behaviour within 10–15 h. Both of these studies showed that cod is generally resilient to C&R in shallow waters (<20 m), if the fish do not have substantial hooking injuries. Many cod are captured and released in waters <20 m, e.g. in the German Baltic Sea (Strehlow *et al.*, 2012) or from shore in the UK (Armstrong and Hyder, 2013); however, there are other recreational fisheries where cod are captured in significantly deeper waters. These fisheries include, among others, the Dutch recreational fishery where cod are often captured on wrecks below 20 m in the North Sea [T. van der Hammen, pers. comm.; 24% released (van der Hammen and de Graaf, 2012)] and the northern Norwegian recreational fishery where cod are captured down to >100 m [66% released in the tourist fishery (Ferter *et al.*, 2013b)].

Cod have closed (physoclistous) swim bladders and experience barotrauma when brought up from deeper water (Midling *et al.*, 2012). Barotrauma occurs when gas in the swim bladder expands due to rapid reduction of ambient pressure and cannot be reabsorbed by diffusion, which ultimately leads to swim bladder rupture and other barotrauma signs (e.g. Rummer and Bennett, 2005; Nichol and Chilton, 2006; Hannah *et al.*, 2008a; Humborstad and Mangor-Jensen, 2013). Barotrauma has been shown to increase post-release mortalities in several species (e.g. Collins *et al.*, 1999; St John and Syers, 2005; Alós, 2008; Hannah *et al.*, 2008b), but to the best of our knowledge, no study has investigated the effects of barotrauma on post-release mortality of angled cod. The increase in post-release mortality with increasing capture depth has for various species been attributed to different barotrauma signs, including stomach protrusion, gas bubble formation in the blood vessels causing embolisms, and damage to internal organs (Rummer and Bennett, 2005; Hannah *et al.*, 2008b). Moreover, fish may become positively buoyant beyond behavioural control and thus have difficulties submerging, which makes them vulnerable to avian predation and exposes them to warmer surface water temperatures (Bettoli and Osborne, 1998; Hannah *et al.*, 2008b). Methods to mitigate these barotrauma effects have been developed, e.g. venting needles to relieve excess gas (Keniry *et al.*, 1996; Roach *et al.*, 2011) and release weights to lower fish to capture depth (Butcher *et al.*, 2012). Yet, the effectiveness of these devices varies between species (Collins *et al.*, 1999) and has been questioned (Wilde, 2009). Several studies have demonstrated that cod have the ability to recover from barotrauma after being brought up from deep water (Godø and Michalsen, 2000; van der Kooij *et al.*, 2007; Midling *et al.*, 2012; Humborstad and Mangor-Jensen, 2013), but none of these has systematically quantified post-release mortalities or occurrence of internal and external barotrauma signs with increasing capture depth. However, such information is important if post-release mortalities are to be included in stock assessments and for the development of release guidelines for anglers, e.g. recommended capture depth for release of fish.

Using a range of field experiments and a supplementary radiology study, the present study describes different external and internal barotrauma signs in cod after rapid decompression from capture depths up to 90 m and the recovery process from these. Moreover, this study quantifies the effect of capture depth (down to 90 m) on short-term post-release mortality of angled cod–without substantial hooking injuries–using different study designs (i.e. containment in a floating net pen vs. submerged cages).

Material and methods

Study locations

Several field experiments were conducted in Kattfjorden (69°38′N 18°12′E) west of Tromsø, Norway and its adjacent fjords during summers of 2013 and 2014. The Kattfjord is a relatively sheltered fjord with a maximum depth of ca. 140 m and three main connections to the open sea that ensure regular water exchange. The Kattfjord and its adjacent fjords are popular for both commercial and recreational fishing and have several large angling tourism businesses (Vølstad *et al.*, 2011) along the shoreline.

A supplementary radiology experiment was conducted at the Institute of Marine Research, Matre Research Station, Matredal, Norway. Cod for this experiment were captured in Masfjorden (60°52′N 5°33′E).

All experimental procedures were conducted in accordance with the Norwegian regulation on animal experimentation (Forskrift om forsøk med dyr) and were approved by the Norwegian animal research authority (Forsøksdyrutvalget; FOTS ID 4993 and 5796).

Holding-time determination (floating-net-pen study)

A floating-net-pen study was conducted in July and August 2013 to estimate the maximum time until short-term mortality occurs in cod due to rapid decompression (Table 1). For the experimental design of the submerged-cage study in 2014, it was necessary to estimate the maximum time in which short-term mortality occurs after rapid decompression. For this, a containment study design (Pollock and Pine, 2007) using a floating net pen was chosen, recognizing that the mortality estimates would not be representative of a real C&R event (i.e. potentially biased upwards) because in a natural setting the released fish would usually submerge and not remain at the surface for a longer period. The study was limited to a maximum depth of 90 m due to low cod catch rates below 90 m.

For the treatment group, a total of 316 cod (21–83 cm; mean 42.02 cm) captured on angling gear from depths of 4–90 m were selected with the aim to cover all depth groups evenly. Only cod captured on the bottom for which the capture depth was known exactly were included in the experiment. Capture depth was determined using a conventional echosounder (FCV-620, Furuno Electric Co. Ltd, Nishinomiya, Japan). Moreover, only mouth-hooked cod without significant hooking injuries, i.e. not belly- or deep-hooked and not bleeding from the gills, were included in the experiment as these injuries could have led to additional mortality not caused by rapid decompression (Weltersbach and Strehlow, 2013).

For the control group, 50 cod (18–78 cm; mean 32.14 cm) were captured $\leq$10 m with two-chamber fish pots [150 × 100 × 120 cm, 28.5-mm mesh size; see Furevik *et al.* (2008)] to account for the effects of handling, tagging, and containment. The control group was restricted to fish without injuries or signs of barotrauma, but no selection was performed in terms of other conditions (e.g. parasite presence or relative weight index).

The total lengths (TLs) of all fish were measured to the nearest lower cm, and each fish was tagged with an individually numbered T-Bar anchor tag (TBA-1, Hallprint Pty. Ltd, Holden Hill, South Australia) below the anterior dorsal fin. Data were recorded for: time of capture, TL, capture depth, lure type, hook type, hooking position, bleeding, and air exposure duration. After tagging, fish were placed into a 310-l on-board holding tank supplied with flow-through surface seawater, where they were held for 5–330 min. Dissolved oxygen was monitored using an oxygen meter (Handy Polaris, OxyGuard International AS, Farum, Denmark). After each angling session, the fish were transferred into a flat-bottom floating net pen [400 × 400 × 400 cm, see Isaksen *et al.* (2010) for more details] anchored in a protected bay with good water exchange and 12 m depth. Following release into the net pen, fish were observed to see if they submerged to the bottom of the net pen (divers) or if they floated at the surface (floaters). The floating net pen was inspected at least once a day, and dead fish were removed. The total holding time for surviving fish ranged from 6 to 21 d. Water temperature was measured every 15 min using a data-storage tag placed at 2 m depth in the net pen. A temperature/depth profile was taken on 4 August 2013 using a data-storage tag (DST-milli TD, Star-Oddi, Reykjavik, Iceland) in the centre of the Kattfjord, which was applied to all fish.

A total of 17 cod <30 cm in length could not be recovered from the net pen at the end of the experiment (most likely due to escapement and cannibalism). Therefore, analysis of the mortality data from the floating-net-pen study was restricted to fish $\geq$30 cm to avoid bias. This left 256 cod in the treatment group and 25 cod in the control group for the analysis of the mortality data.

Quantification of post-release mortality and floaters (submerged-cage study)

A submerged-cage study was conducted during July and August 2014 to (i) estimate short-term, post-release mortality for cod after rapid decompression and (ii) quantify the proportion of floaters under representative conditions (Table 1). In general, the

Table 1. Summary of the different study aims (as ordered in the Material and methods section), periods of studies, a short description of each study, and the statistical tests used for analysis.

Study aim	Period	Study description	Statistical analysis
Holding-time determination	Jul 2013 – Aug 2013	Estimation of the maximum time until short-term mortality occurs due to rapid decompression using a floating net pen to design the submerged-cage study (potential bias due to restriction to the surface).	GLM, Pearson correlation
Quantification of post-release mortality and floaters	Jul 2014 – Aug 2014	Estimation of short-term post-release mortality for cod after rapid decompression in submerged cages (simulating the cod's natural descent). Quantification of floaters and divers under representative conditions.	–
Investigation of short-term post-release behaviour	Jul 2014 – Aug 2014	Study if cod classified as divers return to their capture depth, another depth or resurface after submergence using data-storage tags.	–
Quantification of external barotrauma signs	Jul 2014 – Aug 2014	Quantification of external barotrauma signs of cod in the treatment group in the submerged-cage study to be able to link those signs to potential post-release mortality.	GLM
Quantification of internal barotrauma signs	Jul 2013 – Aug 2014	Quantification of internal barotrauma signs with increasing capture depth during field dissections. Study of internal barotrauma signs in the laboratory using radiology.	GLM, χ^2
Investigation of healing process	Jul 2013 – Jan 2014	Investigation of the swim bladder-healing potential for surviving cod in the floating-net-pen study. Study of the healing process of internal barotrauma signs in the laboratory using radiology.	MLR

GLM, generalized linear model; Pearson correlation, Pearson product–moment correlation coefficient (ρ); χ^2, Chi-squared test; MLR, multiple linear regression.

sampling protocol followed the procedures of the floating-net-pen study (e.g. all fish were tagged and length measured after capture). However, divers and floaters were classified directly after capture, and cod were kept in submerged net cages (at ≥capture depth) to simulate the cod's natural decent after release.

For the treatment group, a total of 275 cod (22–85 cm; mean 46.47 cm) were captured between 7 and 90 m; for the control group, 32 cod (21–57 cm; mean 32.28 cm) were captured from a depth of 10 m. Again, only mouth-hooked fish without severe hooking injuries or bleeding were included. To study submergence success of released cod (i.e. quantify floaters), a 5-m long cylindrical diving channel connected to a submersible cage was used (Figure 1). Immediately after capture, cod were released into the diving channel next to the boat. Following a period of 1–75 min (mean 32 min) after capture, the submersible cage was retrieved to the surface. All cod that had stayed in the channel, and had not managed to dive into the cage, were noted and classified as floaters. The cage was then detached from the channel. To determine the survival of floaters after forced recompression, they were placed into the cage together with the successfully submerged cod (divers). Thereafter, the cage was lowered to at least capture depth. As the floating-net-pen study showed that all mortalities (except for three floaters that died later) occurred within 50 h after capture [see also Humborstad *et al.* (2009)], the cages were retrieved after a minimum of 72 h. All cod were classified as dead (i.e. no activity) or alive (i.e. active swimming and operculum movement) at the surface under water before lifting the cage into the boat. One cod in the treatment group could not be recovered from the cage (probably because of cannibalism) and was, therefore, removed from the post-release mortality dataset, leaving 274 individuals in the treatment group. A temperature/depth profile was taken on 6 August 2014 using a CTD (Starmon mini CTD, Star-Oddi, Reykjavik, Iceland) in the centre of the Kattfjord. Additional temperature/depth profiles were taken at the capture locations whenever a cage was lowered to capture depth to account for potential temperature variations.

Short-term post-release behaviour

To study whether cod classified as divers returned to their capture depth, another depth, or resurfaced, a supplementary behavioural experiment was conducted as part of the 2014 field study (Table 1). A diving cod was defined as a fish which descended to a minimum depth of 5 m directly after release (corresponding to the length of the diving channel in the submerged-cage study). A DST-milli tag (weight in water: 5 g) was used to monitor depth and temperature during capture, release, and submergence. Typical angling gear was used for the experiment, and the tag was fixed on the fishing line (0.19 mm diameter) above the swivel to which the lure was attached. Once hooked ($n = 10$; 36–60 cm; mean 48.3 cm; capture depths 40–85 m), a fish was retrieved, quickly dehooked, and the TL measured. A flexible rubber band was fixed around the tail of the cod, and then connected to the swivel (including the DST, but without the lure). Thereafter, the cod was released and allowed to swim freely for 5 min, after which the fishing line was retrieved to break the rubber band and recover the data-storage tag.

Quantification of barotrauma signs and healing process

To quantify external barotrauma signs, the occurrences of swollen coelomic cavity, gas release around the anal opening, gut eversion, stomach eversion, subcutaneous gas bubbles, and exophthalmia (eye protrusion) were noted for each cod in the treatment group immediately after capture during the submerged-cage study in 2014 (Table 1).

To quantify internal barotrauma signs, a total of 91 cod (22–70 cm; mean 41.11 cm) were captured for dissection from depths of 6–88 m using angling gear during the 2013 and 2014 field studies (Table 1). Only cod that were hooked in the lip or mouth were used. These cod were immediately killed with a blow to the head (percussive stunning) and the TL measured. Each fish was dissected within 2 h after capture to detect the presence or absence of gas in at least one of three veins (i.e. *Vena cardinalis communis*, *Vena hepatica*, and *Vena cardinalis caudalis*) and under the peritoneum. Subsequently, the peritoneum was removed and the swim bladder examined for its inflation status (i.e. inflated or not inflated), signs of ruptures and, if present, hole location(s).

To collect information on swim bladder healing for surviving cod, 7–12 fish were randomly selected from the net pen for each 10-m capture depth interval (0–10, 11–20, etc.) at the end of the floating-net-pen study in 2013 (Table 1). These fish were killed with a blow to the head (percussive stunning), opened ventrally, and the organs and peritoneum lining were removed to expose the swim bladder. To test swim bladder pressure tolerance, the swim bladder was inflated with a modified blood pressure meter (Precisa N, Rudolf Riester GmbH, Jungingen, Germany), and the maximum atmospheric pressure (mmHg) at the time of its rupture was recorded [see Midling *et al.* (2012) for detailed method description].

To identify internal barotrauma signs not easily observed during the dissections conducted in the field, a radiology study was conducted in two sampling rounds during winter 2013/2014. To assess the healing process of internal barotrauma signs, the same individuals were X-rayed several times before and after rapid decompression (Table 1). In total, 21 cod (28–67 cm; mean 49.73 cm) were captured in fyke nets (due to low catch rates on angling gear) in <10 m depth. Immediately after capture, each cod was radiographed using a portable high frequency X-ray unit (Porta 100 HF, Eickemeyer Medizintechnik für Tierärzte KG, Tuttlingen, Germany) with 50 kV and 10 mA s at a distance of 70 cm. A 35 × 43 cm image plate placed into a protective rigid cassette (Dürr Medical, Bietigheim-Bissingen, Germany) was used to take the pictures. The image plate was scanned using an X-ray scanner (CR 35 VET, Dürr Medical), and the digital image was converted into a TIFF file (Vet-Exam Plus Software, version 4.14.0.). The TIFF files were colour-inverted and further processed (i.e. contrast adjustment and white background) using Adobe InDesgin and Photoshop CS5. After X-ray, all cod were placed into a submersible cage (150 × 100 × 120 cm, 28.5-mm mesh size) and lowered to 44 m depth. After an acclimatization period of 11 d, the cage was rapidly pulled to the surface (ca. 0.2 m s^{-1}) to induce barotrauma. Twenty cod were X-rayed (one cod died during the acclimatization period) and placed into a 500-l tank supplied with flow-through seawater. Additional X-ray pictures were taken 3 and 32 d after decompression following the same procedure. All fish were anaesthetized using MS222 (15 g 100 ml^{-1}) before each X-ray session. Following the second X-ray examination, 5 cod were dissected to verify the X-ray pictures.

Data analysis

The influences of each predictor variable on the mortality of cod during the floating-net-pen study were analysed by fitting a generalized linear model (GLM) to the data to describe the relationship between total mortality observed (binary response variable) and capture depth, TL, duration of air exposure, transportation

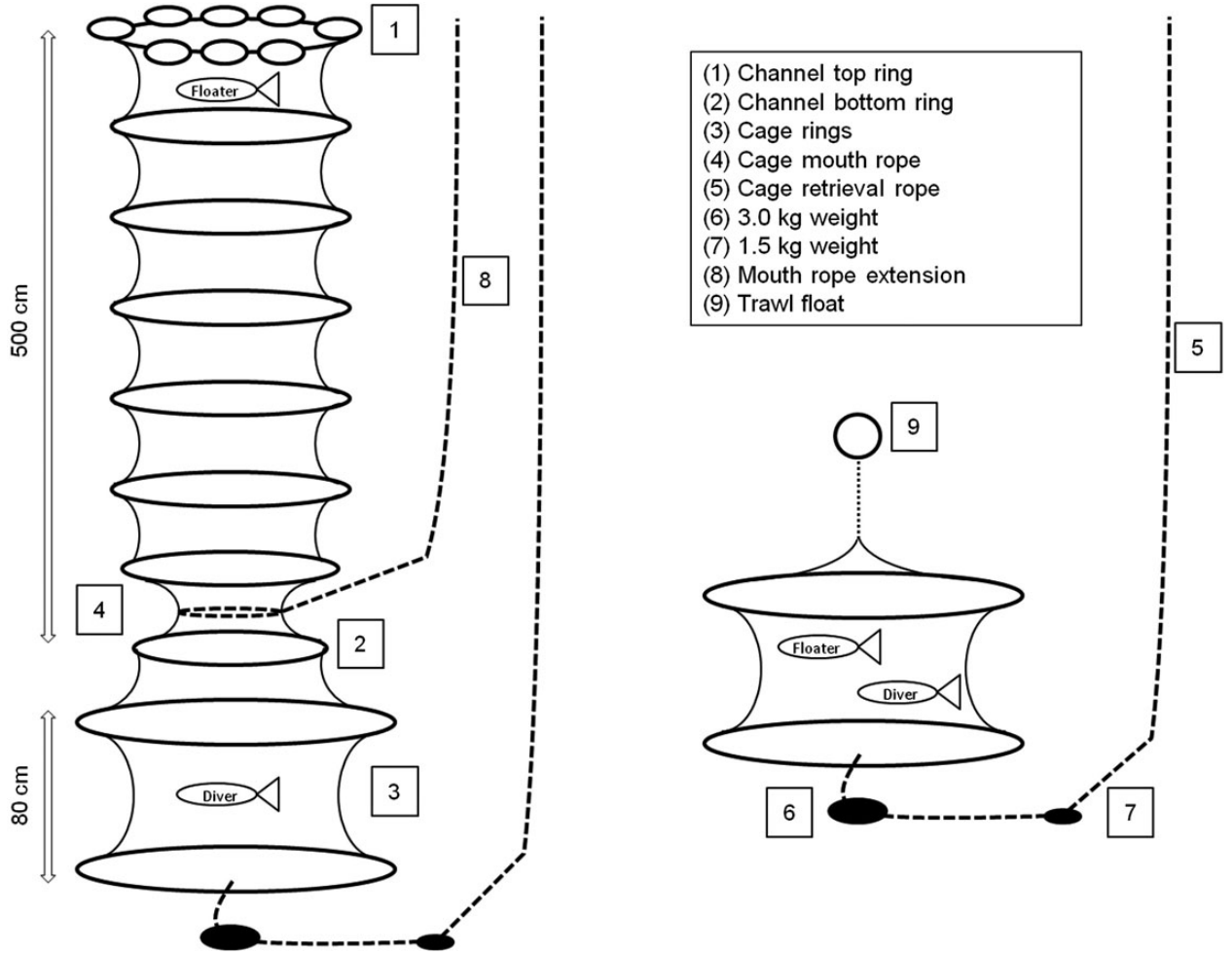

Figure 1. Diving channel and cage setup in the submerged-cage study. The channel was 500 cm in length and consisted of black knotless netting (20-mm mesh size). The channel was stabilized by eight rings which had a diameter ranging from 70 cm in the top (1) to 55 cm on the bottom (2). Directly above the lower end of the channel, a round net cage was attached which consisted of black knotless netting. The cage was stabilized by two rings [90 cm in diameter (3)], which were 80 cm apart from each other, i.e. the approximate cage height was 80 cm. At the top of the cage mouth, there was 75 cm of excess netting which could be closed by a mouth rope (4), which was drawn through the net meshes. The cage was attached to the diving channel by putting the excess net over the lowest ring of the channel and tightening the cage mouth to a diameter of 30 cm using the mouth rope (4). At the bottom of the cage, a cage retrieval rope (5) with a 3-kg weight (6) was attached (90 cm of the rope between cage bottom and weight). Additionally, a 1.5-kg weight (7) was fixed 1 m apart from the 3-kg weight to buffer potential wave action after cage submersion. The cage could be retrieved to the surface by pulling on an extension (8) of the mouth rope, which closed the cage mouth. After detachment of the cage from the channel, a small trawl float (9) was attached to the mouth rope to keep the cage upright after submersion. When the cage was lowered to the bottom, the retrieval rope was held at the surface using a large trawl float.

time (continuous variables), and the presence/absence of floating (categorical variable) as potential explanatory variables. In addition, the Pearson product–moment correlation coefficient (ρ) was calculated to evaluate the correlation between water depth and temperature.

In the study of external barotrauma signs, four GLMs were used to analyse the effects of capture depth and TL as potentially significant predictors on the occurrence of barotrauma in general (data pooled and at least one sign occurred) and for each of the three most common external barotrauma signs (swollen coelomic cavity, gas release, and gut eversion).

In the study of internal barotrauma signs, a GLM was used to describe the relationship between the presence/absence of swim bladder rupture as a binary response variable and TL and capture depth as continuous explanatory variables. A Chi-squared test for given probabilities was used to determine whether holes in ruptured swim bladders occurred with equal probabilities on the right and the left side. Another GLM was developed to analyse the relationship between the occurrence of venous gas embolisms (binary response variable) and capture depth and TL of cod (explanatory variables).

To evaluate the swim bladder-healing process, a multiple linear regression (MLR) analysis was used to describe the relationship between maximum pressure tolerance of the swim bladder as a proxy for the swim bladder-healing process (dependent variable) and time after catch, capture depth, and TL (independent variables). For this purpose, cod from $\geq$19 m were used, since these could be assumed to have ruptured swim bladders after capture (see Results).

All GLMs were fitted to the data using maximum-likelihood estimations and the ordinary least-squares estimation procedure for the MLR. Binomial probability distributions were assumed for

all GLMs due to the binary nature of the response variables, and logit links were used as link functions. Model selections (GLMs and MLR) were based on stepwise backward eliminations using the Akaike information criterion. The Wald test was performed for significance testing of the estimated model coefficients for all GLMs and the *t*-test for the MLR. The 95% Wilson's confidence intervals were calculated for the mortality percentages in both the floating-net-pen study and the submerged-cage study (Agresti and Coull, 1998). All statistical analyses were conducted using the software R version 2.15.3 (R Development Core Team, 2013).

Results

Holding time, post-release mortality, and submergence success

In the floating-net-pen study, all mortalities (dead cod: treatment group $n = 81$; control group $n = 1$) occurred within 50 h after capture (except for three floaters that died later), indicating that the holding time in the submerged-cage study should be at least 50 h. Mortalities >40% were observed in depth intervals ≥50 m (Figure 2). The mortality in the control group was 4%. The overall percentage of floaters in the treatment group was 23.4% after transfer from the on-board tank to the floating net pen, of which 88.3% died. Mortality increased significantly with capture depth (GLM: $p < 0.001$) in the floating-net-pen study. However, there was a strong correlation between water depth and temperature (Pearson's correlation: $\rho = -0.98$, d.f. = 267, $p < 0.001$), suggesting that the mortality estimate was confounded by temperature effects. The maximum temperature difference between capture depth and holding depth (at 2 m) was 8.6°C at 90 m capture depth. TL, duration of air exposure, and on-board transportation time were non-significant predictors of mortality in the floating-net-pen study (GLM: all $p > 0.05$).

In the submerged-cage study, no mortality was observed for divers in either of the depth intervals or in the control group during the observation period (Table 2). In total, 2.2% of the cod in the treatment group were classified as floaters under representative conditions, and floaters only occurred in depths >50 m. After these floaters were observed alive for 10–45 min in the diving channel, they were submerged to capture depth and survived the experimental observation period of 72 h.

The supplementary post-release behaviour study showed that none of the cod classified as divers returned to the surface within the monitoring period of 5 min (Figure 3). Following a steep escape dive after release, most of the cod stayed at a stable water depth, except two fish which returned to shallower water depths. All 10 cod had submerged deeper than 12 m within 5 min of release. In fact, five cod had returned close to their initial capture depth (±10 m) 5 min after release. Five cod did not submerge to their initial capture depth within 5 min, but three of those had descended to deeper than 33 m (initial capture depths: 56–85 m). One cod caught at 71 m and 1 caught at 50 m stayed at 12 and 16 m, respectively, 5 min after release.

External barotrauma signs

The occurrence of barotrauma signs in general, and a swollen coelomic cavity and gas release around the anus in particular, was significantly influenced by capture depth (GLMs: all three $p < 0.001$). Moreover, smaller cod had a higher frequency of swollen coelomic cavities than larger cod (GLM: $p < 0.05$), but neither the presence/absence of external barotrauma signs in general nor the occurrence of gas release were significantly affected by TL (GLMs: both $p > 0.05$). For capture depths of 0–10 m, 50% of the cod showed no external signs of barotrauma, whereas the other 50% had a swollen coelomic cavity caused by an expansion of the swim bladder (Figure 4). In capture depths ≥11 m, the percentage of fish with no external barotrauma signs decreased, reaching 0% in the 41- to 50-m depth interval. At the same time, the percentage of fish with swollen coelomic cavities increased from 50% in the 0- to 10-m interval to a maximum of 73% in the 11- to 20-m depth interval, and then decreased to ~20% for the deepest capture depth intervals. The decrease in the percentage of cod with swollen coelomic cavities was accompanied by an increase in the percentage of fish that released gas around the anus (based on the prediction from the GLM, there was a 50% chance for gas release

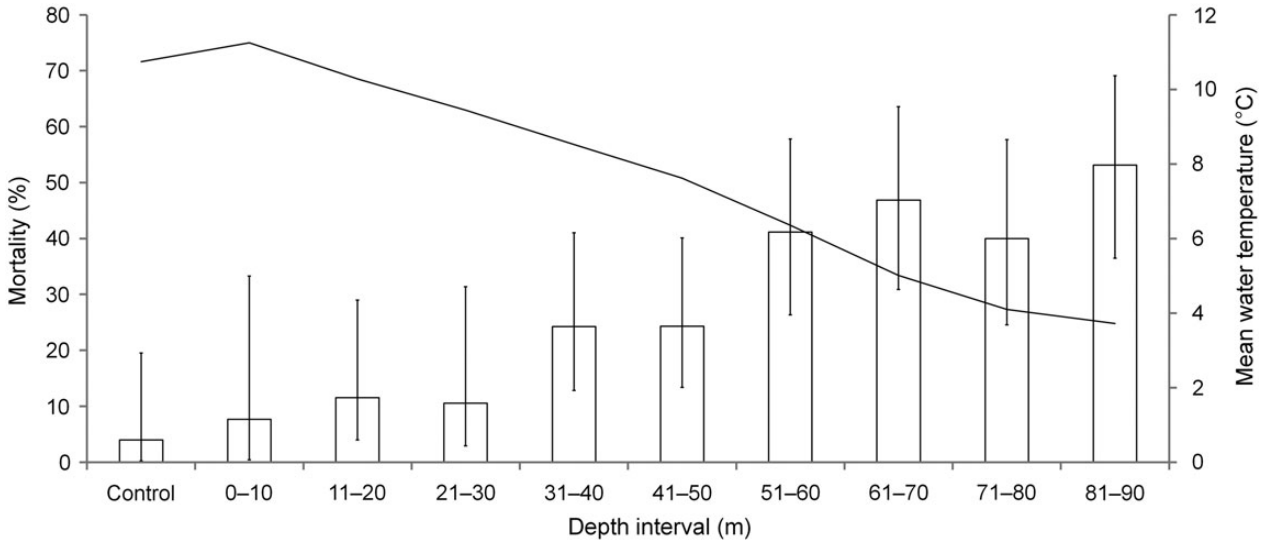

Figure 2. Mortality of cod in the floating-net-pen study by depth interval (open bars). Error bars indicate the 95% upper and lower Wilson's confidence intervals. The continuous line shows the temperature at capture depth of the control group (10 m), and the mean temperatures in each of the depth intervals (based on the temperature/depth profile in the centre of the Kattfjord on 4 August 2013).

Table 2. Overview and mortality of cod in the submerged-cage study.

Depth (m)	Temp. (°C)	N_{all}	Length (cm)	SE	$N_{floaters}$	$Mortality_{divers}$ (%)	LCI	UCI	$Mortality_{floaters}$ (%)	LCI	UCI
Control	10.3	32	32.28	1.47	–	0	0	10.7	–	–	–
0–10	11.1	30	33.73	1.58	0	0	0	11.4	–	–	–
11–20	9.5	30	38.93	1.51	0	0	0	11.4	–	–	–
21–30	8.5	30	43.60	1.90	0	0	0	11.4	–	–	–
31–40	7.6	30	47.00	2.64	0	0	0	11.4	–	–	–
41–50	7.0	30	53.10	2.61	0	0	0	11.4	–	–	–
51–60	6.3	31	47.39	1.56	1	0	0	11.4	0	0	94.9
61–70	5.8	31	53.74	2.14	1	0	0	11.4	0	0	94.9
71–80	5.6	31	48.06	2.12	3	0	0	12.1	0	0	56.1
81–90	5.5	31	52.58	2.69	1	0	0	11.4	0	0	94.9

Depth, capture depth interval; Temp., temperature at capture depth of the control group (10 m), and the mean temperatures in each of the depth intervals (based on the temperature/depth profile in the centre of the Kattfjord on 6 August 2014); N_{all}, number of individuals; Length, total length; SE, standard error; $N_{floaters}$, number of fish that failed to submerge; $Mortality_{divers}$, percentage of divers that died within 72 h; $Mortality_{floaters}$, percentage of floaters that died within 72 h after being recompressed; LCI, lower Wilson's confidence interval; UCI, upper Wilson's confidence interval.

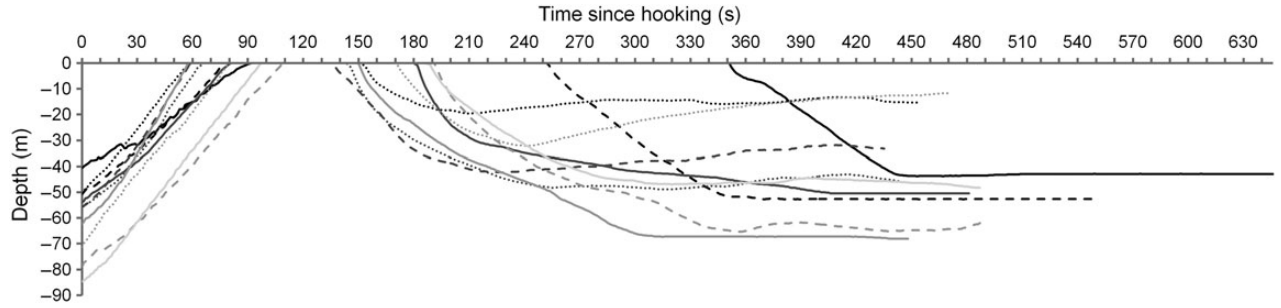

Figure 3. Capture profile and short-term, post-release behaviour of cod classified as divers ($n = 10$). After release, each cod was monitored for 5 min.

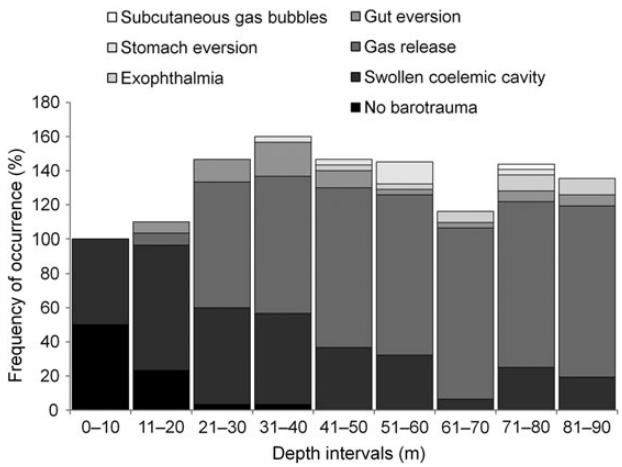

Figure 4. The occurrence of external barotrauma signs in angled cod for each 10-m depth interval (from 0 to 90 m). As several individuals had more than one barotrauma sign, the sum of occurrence adds up to >100%.

around the anus at 27.4 m). From >41 m, >90% of the captured cod were observed to release gas around the anus. Eversion of the gut through the anus was first observed in the 11- to 20-m depth interval and was observed most commonly in the 31- to 40-m depth interval; however, there was no significant effect of capture depth or TL (GLMs: both $p > 0.05$). Only a few fish showed other external barotrauma signs such as exophthalmia, stomach eversions, and subcutaneous gas bubbles (<15% for each of these signs in any of the capture depth intervals).

Internal barotrauma signs

Internal barotrauma signs observed during field dissections were ruptured swim bladders, gas under the peritoneum, and gas bubble formation in the venous blood system. The first swim bladder rupture was observed for a cod caught at a depth of 7 m (Figure 5a), and the incidence increased significantly with depth (GLM: $p < 0.05$). The prediction from the GLM showed that there was a 50% chance of swim bladder rupture at 13.1-m depth. For capture depths ≥19 m, 100% of the cod were observed to have swim bladder ruptures. Most of the cod had ruptures on only one side of the swim bladder (91%), with a non-significant predominance of ruptures on the left side (i.e. in 58% of the cod with ruptures on one side; $\chi^2 = 1.95$, d.f. $= 1$, $p > 0.05$). The likelihood of rupture was independent of TL (GLM: $p > 0.05$). All fish with swim bladder rupture had gas under the peritoneum. The occurrence of venous gas embolisms increased significantly with capture depth (GLM: $p < 0.001$; Figure 5b), whereas TL was an insignificant predictor of the presence of gas embolisms (GLM: $p > 0.05$). The first gas embolism was observed at 10-m capture depth. According to the prediction from the GLM, there was a 50% chance of gas embolism at 19.7-m capture depth. Gas embolisms were mainly observed in the *V. cardinalis communis*, *V. hepatica*, and *V. cardinalis caudalis* (Figure 6).

The radiology study uncovered additional internal barotrauma signs that were not observed in the field dissections (Table 3 and Figure 7). In cases where cod did not release gas around the anus, large amounts of gas were trapped in the coelomic cavity [Figure 7, cod a, (2)]. However, in 95% of the radiographed cod,

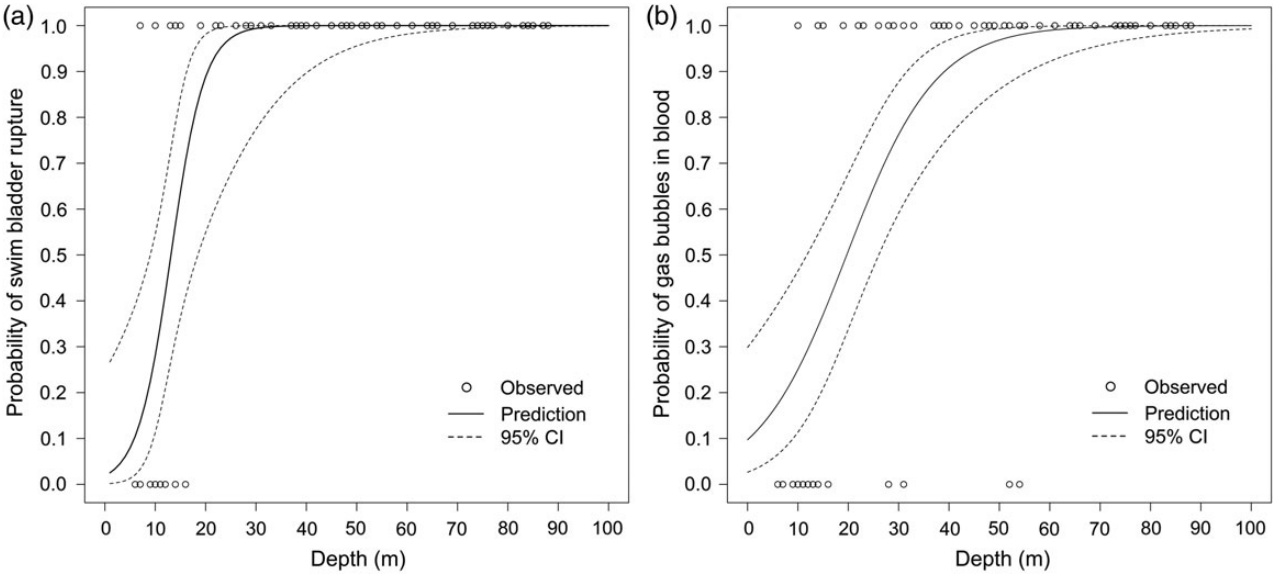

Figure 5. The probability of (a) swim bladder rupture and (b) gas bubble formation in the venous blood system (venous gas embolism) in angled cod with increasing capture depth. Points represent individual fish present (1) and absent (0) data (many points overlap). The continuous lines show the model predictions and the dotted lines the range of the 95% confidence intervals.

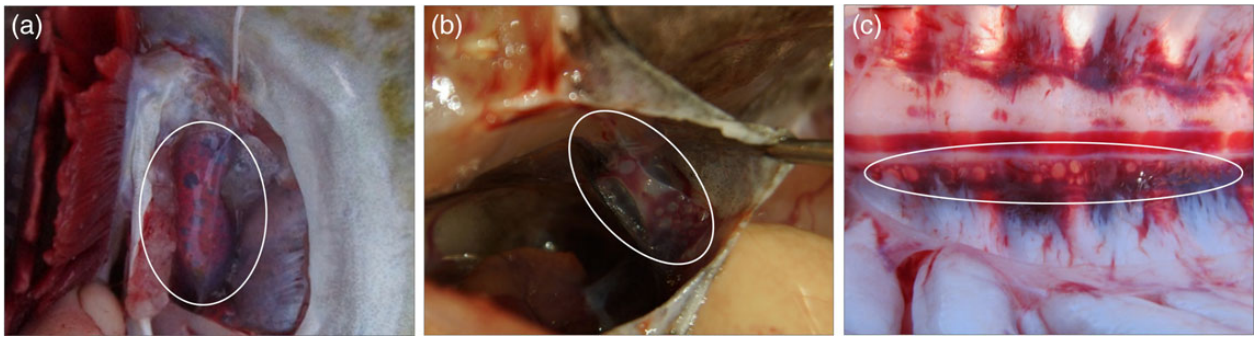

Figure 6. Pictures of gas embolisms in the (a) *V. cardinalis communis*, (b) *V. hepatica*, and (c) *V. cardinalis caudalis* of cod with barotrauma after rapid decompression. The affected veins are encircled with white rings.

Table 3. Overview of internal barotrauma signs in cod observed in the radiology study 10 d before and at 0, 3, and 32 d after rapid decompression from 44 m.

Internal barotraumas signs	Before decompression	Days after decompression		
		0	3	32
$N_{radiographed}$	21	20	15	15
Inflated swim bladder (%)	100	60	87	100
Gas outside swim bladder (%)	0	90	60	20
Gas exit pathway (%)	0	95[a]	69[a]	0
Gas "channel" over spinal cord (%)	0	80	47	0

[a]Based on 19 cod on day 0 and 13 cod on day 3, because of poor picture quality making it difficult to determine the presence or absence of a gas exit pathway in some individuals.

an exit pathway from the posterior end of the swim bladder to the anus was formed, through which excess gas escaped [Figure 7, cod b, (3)]. Another internal barotrauma sign observed by radiology was a gas-filled channel above the spinal cord [Figure 7, cod b, (4)], spanning from the head to the tail. This sign was found in 80% of the radiographed cod immediately after decompression. For ca. two-thirds of the cod, gas embolisms were detectable in the *V. cardinalis communis*.

Healing process after barotrauma

After a holding time of at least 6 d in the floating net pen, all tested swim bladders withstood a minimum pressure of 40 mmHg (except for two cases with severely ruptured swim bladders). The maximum measured pressure tolerance was 240 mmHg. The maximum pressure tolerance of the swim bladder was independent of TL or capture depth (MLR: both $p > 0.05$), but increased significantly with time after capture (MLR: $p < 0.001$; adj. $r^2 = 0.17$; Figure 8). According to the model predictions, the maximum pressure tolerance increased by 0.25 mmHg (s.e. = 0.06) on average for every 1 h increase in time after capture. However, even several days after the rupture, there was a large variation in the maximum pressure tolerance.

In the radiology study, the exit pathway to the anus and the gas-filled channel above the spinal cord had, in all cases, disappeared 32 d after decompression (Figure 7 and Table 3). Moreover, all fish

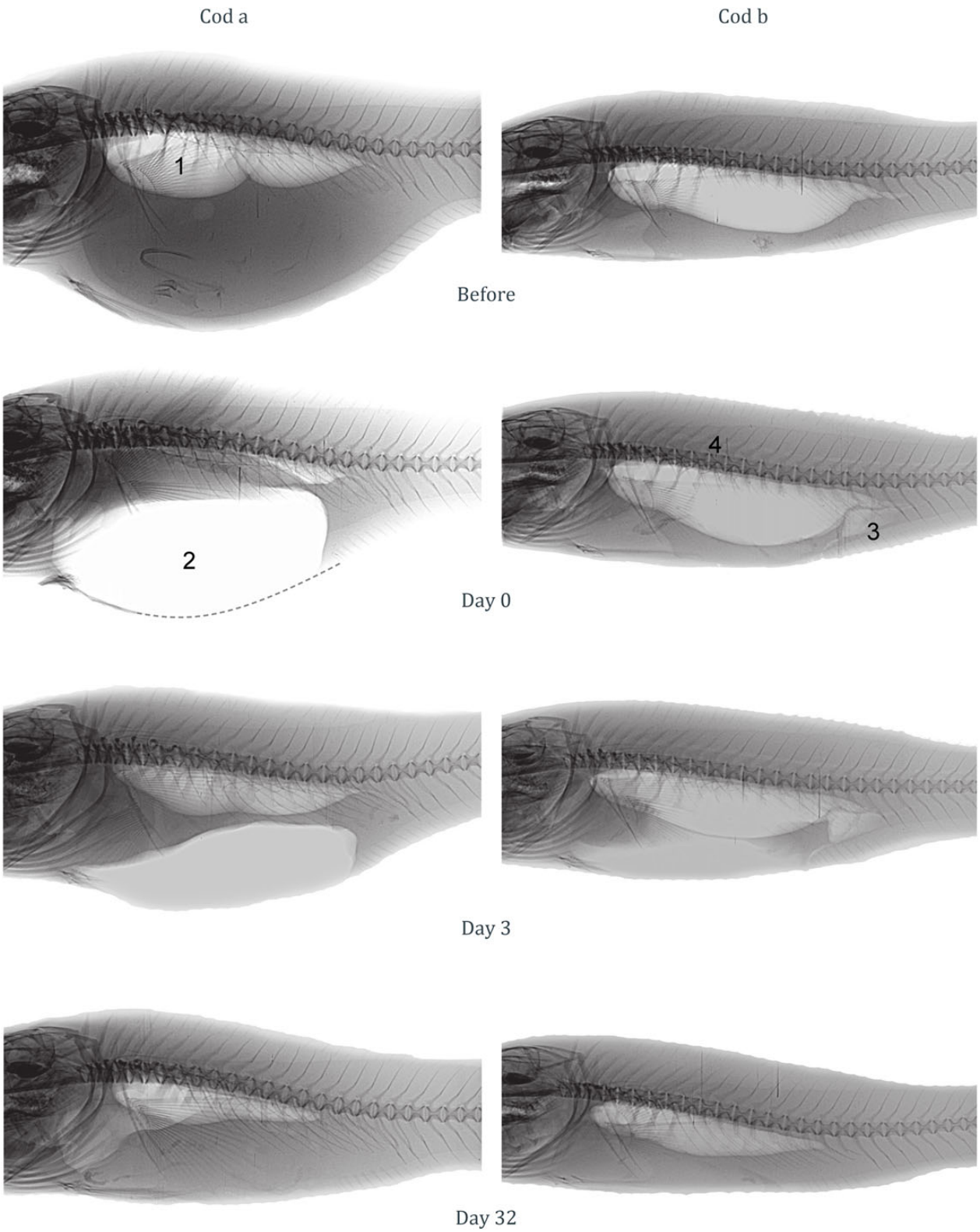

Figure 7. Lateral radiographs of two cod 10 d before and 0, 3, and 32 d after rapid decompression from 44 m. Lighter areas indicate the presence of gas. After the rapid decompression, "cod a" did not release gas from the anal region, whereas "cod b" released gas. Examples of (1) an inflated swim bladder, (2) gas outside the swim bladder, (3) the presence of a gas exit pathway, and (4) the presence of a gas channel above the spinal cord are marked with numbers. The dotted line shows the reconstructed edge of the belly (not visible due to overexposure on original picture).

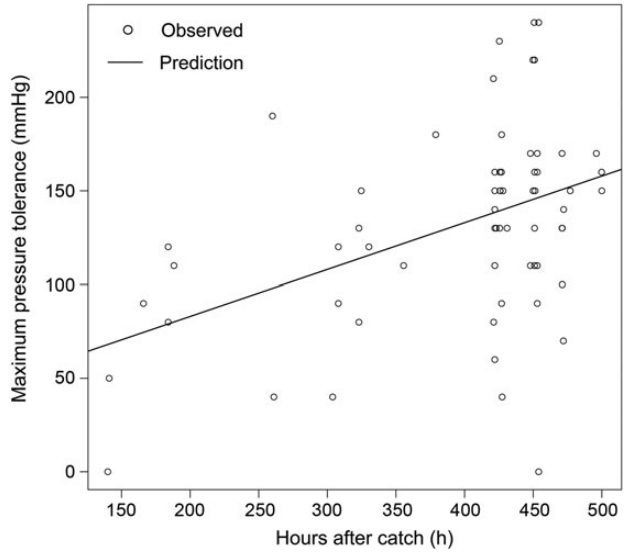

Figure 8. Maximum pressure tolerance (mmHg) of the swim bladder of cod following swim bladder rupture. Only cod captured from ≥19 m ($n = 68$) were included to ensure that the swim bladder had ruptured.

had an inflated swim bladder, but 20% still had some residual gas outside the swim bladder. Gas which was detectable in the *V. cardinalis communis* of several cod right after decompression was only detectable in one fish after 3 d. None of the fish had gas embolisms in the *V. cardinalis communis* 32 d after decompression.

Discussion

Post-release mortality of fish is highly species- and fishery-specific (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Hannah *et al.*, 2014) and is largely driven by biological, environmental, and fishery-specific factors (Davis, 2002; Arlinghaus *et al.*, 2007; Cooke and Wilde, 2007; Hühn and Arlinghaus, 2011). The results from this study show that barotrauma has no adverse effects on the short-term, post-release survival of cod if the fish manage to submerge quickly on their own, do not have substantial hooking injuries, and are subject to only minimal predation risk. Furthermore, the submerged-cage study, combined with the radiology and swim bladder-healing study, showed the physical formation of an excess gas-release pathway and recovery from barotrauma in cod. The findings in this study are consistent with previous studies that have described cod as a resilient species, which is able to recover quickly from barotrauma after successful submergence (van der Kooij *et al.*, 2007; Midling *et al.*, 2012; Humborstad and Mangor-Jensen, 2013). Moreover, this study emphasizes the importance of taking the species' post-release behaviour into account when designing experiments to estimate post-release mortality after rapid decompression. When fish with barotrauma are able to return to capture depth on their own after release, and when the water column is temperature-stratified, submerged cages are more suitable than floating net pens to study post-release survival.

Post-release mortality

Independent of initial capture depth, all cod that submerged successfully survived the C&R event. Even cod with severe signs of barotrauma showed none within a relatively short period. Quick release after capture is of utmost importance as prolonged surface holding exacerbates barotrauma effects (e.g. blockage of blood flow because of gas embolisms) and increases mortality substantially as shown in the floating-net-pen study [compare Jarvis and Lowe (2008)]. This becomes particularly relevant when the cod are brought up from colder deep water and exposed to warmer surface water, which can lead to cumulative stress (Davis and Ryer, 2003). If cod are not allowed to submerge to colder water shortly after capture, this will lead to substantial amounts of mortality [compare Weltersbach and Strehlow (2013)]. Similarly, Syme *et al.* (2013) showed that cardiac function in cod was impaired when water temperatures were increased rapidly from 10 to 20°C. Pérez-Casanova *et al.* (2008) observed a range of stress responses (e.g. increased blood cortisol levels) and substantial mortality when cod acclimatized to 10°C were exposed to increasing water temperatures. Milliken *et al.* (2009) observed an increase in post-release mortality of cod caught with longline and angling gear when surface temperatures were high (>9°C), although they kept the fish in cages submerged to capture depth. Their finding differs from the findings in the present study where no mortality occurred for cod kept in cages lowered to capture depth, although the temperature difference between the surface and the maximum capture depth was higher than 6°C. A possible explanation for this difference may be different experimental procedures, as the cod in the study by Milliken *et al.* (2009) were kept in an on-board holding tank before they were transferred to the submersible cage. Although the water of the on-board holding tanks was cooled approximately to capture-depth temperature, holding in on-board holding tanks above the surface may have led to additional cumulative stress (Davis and Ryer, 2003) and exacerbation of barotrauma resulting in increased post-release mortality.

Sublethal effects were not investigated in this study, but potentially play an important role in long-term survival and need to be considered (e.g. Butcher *et al.*, 2012). Behavioural changes during the recovery phase (van der Kooij *et al.*, 2007; Ferter *et al.*, 2015) can lead to indirect post-release predation by larger fish or marine mammals (Brownscombe *et al.*, 2014b).

Barotrauma signs and recovery

The most commonly observed external barotrauma signs were swollen coelomic cavities and gas release around the anus. Interestingly, after an initial high frequency of swollen coelomic cavities in cod from rather shallow capture depths, this barotrauma sign became less pronounced with increasing capture depth. On the other hand, the percentage of cod that released gas around the anus increased substantially from capture depths >20 m and was observed in most of the cod from deeper water depths (Figure 4). As an example, a cod brought up from 50 m experiences a larger decrease in atmospheric pressure than one from 20 m. Although the swim bladder will expand and most likely rupture in both cases (Figure 5a) leading to a swollen coelomic cavity, the pressure inside the coelomic cavity may not be large enough to induce rupture around the anus in the cod from 20 m. In contrast, the internal pressure in the cod from 50 m is large enough to induce rupture around the anus, leading to pressure relief from the coelomic cavity due to gas release around the anus during ascent. This may explain the decreasing percentage of cod with swollen coelomic cavities with increasing capture depth. Similarly, Brown *et al.* (2010) found extreme barotrauma signs in red emporer (*Lutjanus sebae*) less frequently in fish from great water depths than from intermediate water depths. Humborstad and Mangor-Jensen (2013) argued

that the gas-release pathway in cod is not via the intestines, but through an opening which may be analogous to the abdominal pores in cyclostomata and salmonides. In fact, the formation of a gas-filled pathway leading from the posterior end of the swim bladder to the anal opening was observed in cod that released gas around the anus directly after rapid decompression in the radiology study (Figure 7). This gas-release mechanism may also explain the infrequent occurrence of other external barotrauma signs in cod. In other capture situations where cod cannot orientate themselves freely, e.g. in a trawl codend, this gas-release mechanism might not work as well as observed in the present study, e.g. when the cod is entangled in the net or squeezed with other fish (Suuronen *et al.*, 2005). Other closely related benthic fish species like tusk (*Brosme brosme*) or ling (*Molva molva*) do not seem to have the same gas-release mechanism since these species often show subcutaneous gas bubbles, exophthalmia, and stomach eversions caused by barotrauma (Humborstad and Mangor-Jensen, 2013). The same may be true for many other marine fish species that show exophthalmia and stomach eversion more frequently than cod after rapid decompression (e.g. Rummer and Bennett, 2005; Kerwath *et al.*, 2013). In cases where cod did not release any or very little gas around the anus, although they were brought to the surface from great capture depth, their coelomic cavities were bloated due to excess residual gas, and these cod had difficulty submerging after release. This was the case for 2.2% of the angled cod in the submerged-cage study, which is rather low compared with a study by Midling *et al.* (2012) where 20% of the cod captured in Danish seines were floaters. A popular belief is that a slower hauling speed from capture depth to the surface may be linked to a lower incidence of floaters, because the fish can reabsorb some of the gas by controlled passive diffusion via the oval in the swim bladder. However, this is unlikely because a sufficient pressure reduction via gas resorption would take several hours (Harden Jones and Scholes, 1985; Arnold and Greer Walker, 1992). It is more likely that the cod have more time to release gas around the anus when hauled up slowly. However, in the present study, no direct relationship between retrieval speed and flotation status of the cod was observed.

Swim bladder ruptures and gas under the peritoneum were the most obvious barotrauma signs inside the coelomic cavity. All cod captured at $\geq$19 m had a ruptured swim bladder; based on GLM predictions, there was a 50% chance of rupture at 13.1 m. Thus, swim bladder ruptures can even occur in fisheries where barotrauma issues have previously been neglected because of rather shallow fishing depths, e.g. in the German Baltic Sea fishery (Weltersbach and Strehlow, 2013). There was a slight, though insignificant, prevalence of rupture holes on the left side which is consistent with previous findings by Midling *et al.* (2012). Swim bladder rupture in cod and the recovery process have been studied extensively (e.g. van der Kooij *et al.*, 2007; Midling *et al.*, 2012; Humborstad and Mangor-Jensen, 2013). Midling *et al.* (2012) showed that cod have an instant repair mechanism, which can restore swim bladder function immediately after rupture. Nevertheless, they also showed that the maximum pressure tolerance increased with time after rupture, which is consistent with the findings in the present study. Yet, even 1 week after rupture, there was a large variation in maximum pressure tolerance among the surviving fish (Figure 8), most likely linked to variation in hole size (Midling *et al.*, 2012). This was also reflected by the low percentage of response variable variation that was explained by the linear model ($r^2 = 0.17$). A variation in the healing process was also observed in the radiology study. While most cod had managed to refill their swim bladder after 3 d, two cod had refilled their swim bladders only 1 month after decompression (Table 3). Although swim bladder rupture does not directly lead to short-term mortality if the cod submerges successfully after release, it has been shown to have effects on the post-release behaviour. For example, Nichol and Chilton (2006) showed that Pacific cod (*Gadus macrocephalus*) returned to shallower water after an initial escape dive to refill their swim bladders while being neutrally buoyant, followed by a gradual descent which can take several days (a recuperation period). Similar behaviour has also been described for Atlantic cod (van der Kooij *et al.*, 2007).

In-depth dissections in the field and the radiology study revealed gas bubbles in the venous blood stream after rapid decompression (Figure 6). Formation of gas embolisms in the blood stream has been described for several species, e.g. Chinook salmon (*Oncorhynchus tshawytscha*) (Brown *et al.*, 2012) and largemouth bass (*Micropterus salmoides*) (Feathers and Knable, 1983). Two possible origins of gas embolisms have been discussed: formation of gas bubbles from dissolved gases in the blood (Henry's law) or from already existing gas (i.e. inside swim bladder), which expands and escapes into the blood stream (Boyle's law) (Brown *et al.*, 2012). Brown *et al.* (2012) investigated the origin of gas bubbles in the blood stream of juvenile Chinook salmon after rapid decompression and concluded that the observed gas embolisms originated from gas inside the swim bladder rather than from dissolved gas in the blood stream. This is also most likely the case for cod, as gas embolisms in the *V. cardinalis caudalis* were often associated with bleedings from that vein in the area of the oval. Surprisingly, the venous gas embolisms did not cause any mortality in the submerged-cage study, although most of the cod had gas embolisms when captured from $\geq$20 m and blood flow was constrained. One reason could be that the gas got recompressed when the fish were lowered to capture depth (simulating a natural descent) and thus most likely disappeared from the blood stream. However, even in the floating-net-pen study and the radiology study, where the cod were not recompressed, a significant percentage of the fish (with documented gas bubbles in the blood stream) survived, contributing to the impression of cod generally being a robust species (Humborstad *et al.*, 2006; Humborstad and Mangor-Jensen, 2013). The radiology study showed that the gas had disappeared from the venous blood stream within 32 d after rapid decompression, although the fish were kept in an onshore tank.

One barotrauma sign which was observed in the radiology study, but not in the field dissections, was the formation of a gas-filled channel above the spinal cord. To the best of our knowledge, this barotrauma sign has not previously been described for cod. Brown *et al.* (2012) showed gas-filled channels mainly between the coelomic cavity and the dorsal fin in juvenile Chinook salmon after rapid decompression using radiology. However, the location and extent of these channels appeared to be rather random within the tissue. In the present radiology study, the gas-filled channel occurred consistently at the same location and to the same extent in 80% of the cod. In all cod, this line had disappeared after 32 d in the radiology study. Humborstad *et al.* (in prep.) observed a gradual development of exophthalmia in cod which were held in tanks for several weeks after rapid decompression (caused by gas formation behind the eyes). One possible cause may be the gas-filled channel described here. In a natural setting where cod are allowed to return to capture depth, the development of exophthalmia in the long term is less likely because the excessive gas will most likely be recompressed.

Implications for fisheries management

The present study suggests that harvest regulations such as minimum landing sizes and bag limits can also work as efficient management tools for cod that are captured in water depths >20 m. This holds true as long as the fish are released quickly after capture, submerge successfully on their own, are otherwise not substantially injured (e.g. not bleeding; Weltersbach and Strehlow, 2013), and predation risk is low.

Although the percentage of floaters in the submerged-cage study was low (2.2%), this issue requires consideration by managers because the percentage of floaters may be higher at other times of the year, e.g. during spawning season (M. Åhlund, pers. comm.). The floating-net-pen study showed that most of the floaters (>80%) died even with avian predation excluded. Taking avian predation into account (Milliken *et al.*, 1999), one can assume a mortality percentage close to 100% for these floaters. One way to avoid floaters is a slower retrieval speed or bringing the fish up in stages (Keniry *et al.*, 1996), so that they have time to release excess gas during ascent. However, very slow retrieval to the surface exhausts the fish extensively (authors' own observation), which is why a decompression stop at ~10 m following normal retrieval may be more beneficial than very slow retrieval. Recompression of floaters using release weights (shot-lining; e.g. Butcher *et al.*, 2013) or cages (e.g. Hannah and Matteson, 2007) may be an efficient treatment option, because all recompressed floaters survived in the submerged-cage study. Venting or fizzing (e.g. Scyphers *et al.*, 2013) may be another option to treat barotrauma in floating cod, but its efficiency is not tested thoroughly for this species. For example, Roach *et al.* (2011) showed that recompression is the preferred method over venting for treating barotrauma signs in Australian bass (*Macquaria novemaculeata*). However, for both methods, concerns remain regarding angler acceptance and animal welfare, and there would be a strong need for angler education to ensure appropriate implementation (Scyphers *et al.*, 2013).

Animal welfare issues are relevant (Cooke and Sneddon, 2007) as cod may experience some form of pain or discomfort [reviewed by Rose *et al.* (2014)] during the rapid decompression and recovery process. Thus, although C&R of cod captured at depths >20 m may, under the discussed circumstances, be unproblematic from a purely biological and fisheries assessment point of view, ethical challenges remain (Arlinghaus, 2008). This concerns the practice of voluntary C&R of cod experiencing signs of barotrauma in particular. While regulatory C&R is generally accepted as long as the released fish survive and do not suffer substantial sublethal impacts, voluntary C&R often leads to conflicts and public debates (Aas *et al.*, 2002; Arlinghaus, 2007). Thus, the voluntary release of cod experiencing severe barotrauma should be discussed from an animal welfare perspective by carefully balancing ethical, biological, and socio-economic interests.

Study limitations and future studies

The short-term, post-release mortality estimates in this study are based on a containment experiment and may thus be influenced by general caging effects and by excluding post-release predation (Pollock and Pine, 2007; Donaldson *et al.*, 2008; Raby *et al.*, 2014). Caging did not lead to mortality in the submerged-cage study as all cod survived, but a few fish showed some external injuries (e.g. damaged fin rays and keratitis), which were most likely caused by caging (McLaughlin *et al.*, 1997). Post-release predation may play an important role for smaller individuals in particular, as these can be easily swallowed by larger fish or aquatic mammals. As most marine recreational anglers in Norway release cod because they are too small (Ferter *et al.*, 2013b; A. R. Kleiven, K. Ferter, and J. H. Vølstad, unpublished data), future studies should, therefore, investigate post-release predation of cod during descent to capture depth and the recovery phase after barotrauma. This can, for example, be done in a tagging study, in which cod with barotrauma are released into their natural environment where they are exposed to natural predators (Hochhalter and Reed, 2011; Rudershausen *et al.*, 2013). A telemetry project investigating post-release mortality of cod caught on angling gear at 44.5–83 m depth and released into their natural environment has been initiated in the Gulf of Maine (Mandelman *et al.*, 2014). Furthermore, sublethal effects, e.g. stress responses, due to rapid decompression should be investigated in future studies. This could be done by measuring physiological stress responses in the blood, e.g. cortisol levels, in fish that are exposed to simulated capture depth changes (Pribyl *et al.*, 2012).

The mortality estimates in this study are limited to cod without bleeding or substantial hooking damage. However, bleeding has been shown to increase post-release mortality in cod (Weltersbach and Strehlow, 2013). Also, other studies have shown that hooking injury, specifically deep hooking, is the main predictor for post-release mortality of fish [reviewed in Muoneke and Childress (1994); Bartholomew and Bohnsack (2005); Arlinghaus *et al.* (2007); Cooke and Wilde (2007); Hühn and Arlinghaus (2011)]. Thus, the results would have been different if all kinds of anatomical hooking locations were included in this study. Barotrauma might also increase the mortality of bleeding fish (i.e. because of synergistic effects), but this was outside the scope of this study. It would be helpful to investigate the effects of gear and bait types on hooking injuries and size selectivity in future studies to reduce release rates and post-release mortality of cod.

The field studies were conducted during summer in northern Norway when surface water temperatures are highest. Summer is also the peak season for many recreational anglers and particularly for marine angling tourism in northern Norway (Borch *et al.*, 2011). Thus, in terms of warm surface water temperatures in northern Norway, the post-release estimates in this study are considered conservative. However, if the temperature difference between the bottom and the surface is higher in other regions, the mortality estimates of this study may not be representative for these regions. Moreover, the occurrence and degree of barotrauma signs could be different at other times of the year, e.g. during spawning season when the gonads are enlarged.

The short-term, post-mortality estimates are based on an observation period of 72 h. This monitoring period was chosen because the floating-net-pen study showed that all mortality (except for three floaters) occurred within 50 h of capture. Potential mortality due to barotrauma could have occurred earlier due to cumulative stress (e.g. from warm surface water) in the floating-net-pen study, which is why we added an extra day to the holding time in the submerged-cage study. In addition, several other studies that investigated post-capture mortalities of cod have shown that most of the short-term mortality occurred within the first 72 h (e.g. Humborstad *et al.*, 2009; Weltersbach and Strehlow, 2013; Benoît *et al.*, 2015). A longer holding time could have led to exacerbation of caging effects and potentially caused additional mortality (Pollock and Pine, 2007). Yet, long-term effects could occur, including bacterial infections and inflammation of the gut, which were averted because of the barotrauma (Butcher *et al.*, 2012). Acoustic telemetry could be used to study long-term effects of barotrauma.

However, to obtain representative results, one would either have to separate tagging and the C&R event (Ferter *et al.*, 2015) or use a non-invasive tagging method (Bridger and Booth, 2003). Surgical implantation of an acoustic tag could treat barotrauma signs (similarly to venting), but could also have negative effects on post-release survival and behaviour (Donaldson *et al.*, 2008).

The conclusions of the present study are based on the post-release mortality estimates from the submerged-cage study rather than the floating-net-pen study, because the estimates from the submerged-cage study are assumed to more accurately reflect the post-release survival potential for cod with barotrauma. An underlying assumption of the submerged-cage study was that cod classified as divers would manage to descend by themselves. If cod classified as divers had remained just below the surface or even resurfaced after release in a natural setting, the mortality estimates in the submerged-cage study would have been biased downwards (see results from the floating-net-pen study) because the fish were recompressed by lowering them to capture depth (Brown *et al.*, 2010). This assumption was validated in the short-term, post-release behaviour study. None of the 10 cod that submerged deeper than 5 m after release (corresponding to the length of the diving channel) resurfaced within the 5-min observation period. While five cod returned close to their capture depth or deeper, the other five remained shallower (Figure 3). The potential effect of fishing line drag and DST weight on descending success is assumed to be minimal because of thin line and low tag weight. The short-term behaviour study was conducted at a steep slope where the water depth increased rapidly from >80 to <30 m depth. As the boat drifted towards shallower waters during the experiment, descending cod might have sought shelter in shallower water once they caught sight of the bottom structure without moving to deeper areas. This might have been the case for the three cod that remained shallower than capture depth, but still descended to at least 33 m. A possible reason why the two remaining cod were recorded at 12 and 16 m 5 min after release could be that these fish had remained at a depth where they were neutrally buoyant (i.e. shallower than capture depth because of gas loss; Humborstad and Mangor-Jensen, 2013) and would have exhibited a gradual equilibrium behaviour (van der Kooij *et al.*, 2007). As the volume of gases is already halved at 10 m relative to the surface (Harden Jones and Scholes, 1985), one can assume that all cod classified as divers descended to depths which were deep enough to recompress them sufficiently. However, it would be interesting to investigate descending behaviour of cod in relation to different angling practices (e.g. different retrieval speeds and decompression stops) in future studies. Such studies could also increase the understanding of the occurrence of floaters.

Conclusion

This study showed that cod are generally resilient to barotrauma impacts. Although most cod that were brought up from >20 m depth showed substantial barotrauma signs, e.g. swim bladder rupture and gas bubble formation in the blood, none of them died during the short-term submerged-cage study (simulating the cod's natural descent). Moreover, swim bladder function was usually restored, and most barotrauma signs disappeared within a month. Thus, the survival potential for other physoclistous species may also be high, and further investigations are encouraged when high mortalities are assumed, but have not been documented. From a biological and stock assessment point of view, post-release mortality of cod experiencing barotrauma is negligible if the fish manage to submerge quickly on their own, are otherwise not substantially injured (e.g. not bleeding), and predation risk is low. However, animal welfare issues remain as the fish most likely experience capture and post-release stress. Managers are encouraged to consider C&R in future management decisions and promote best practice guidelines, which can be used by anglers to reduce unwanted bycatch and to mitigate negative impacts of barotrauma in cod. To ensure that cod have enough energy to submerge, anglers are encouraged to avoid fighting the fish to exhaustion and to minimize handling before release.

Acknowledgements

This research has been funded by the Institute of Marine Research and the University of Bergen. MSW and HVS were funded by the European Commission's Data Collection Framework (DCF). The authors are grateful to Harald Næss for his extraordinary assistance before and during the field studies, and Tone Vågseth and Britt Sværen Daae for their help during the radiology experiment. Tessa Bargmann provided valuable comments on an earlier draft of this manuscript, and Annemarie Schütz kindly helped with graphical design. Moreover, the authors thank the teams at "Sjøtun Brygge" and "Lauklines Kystferie" for their practical support, and Bjørnar Isaksen for providing equipment for the field study. The authors also thank two anonymous reviewers for providing constructive feedback to this manuscript.

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Handling editor: Emory Anderson