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Dead or alive—estimating post-release mortality of Atlantic cod in the recreational fishery

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Atlantic cod (*Gadus morhua*) is one of the most important commercial and recreational target species in European marine waters. Recent recreational fisheries surveys revealed that recreational cod catches and release rates are substantial compared to the commercial fishery, particularly in the western Baltic Sea. Despite high release rates, no literature exists exploring the post-release mortality of cod and potential sublethal effects after catch-and-release in recreational fisheries. This study investigates (i) the post-release mortality of undersized cod, (ii) potential factors affecting mortality, and (iii) consequences of the catch-and-release process on cod. During four experimental trials, western Baltic Sea cod were angled from a charter vessel and thereafter observed together with control fish in netpens for 10 d at holding temperatures between 6.2 and 19.8°C. Adjusted mortality rates for angled cod ranged from 0.0–27.3% (overall mean 11.2%). A logistic regression analysis revealed that bleeding and holding-water temperature were the only significant predictors of mortality. Slow hook injury healing (>10 d) and bacterial wound infections were observed in some surviving cod. The results will help to increase the accuracy of recreational cod removal estimates and thereby improve the management of western Baltic cod stock.

Keywords: angling, catch-and-release, *Gadus morhua*, hooking mortality, post-release survival, sustainable recreational fishing, western Baltic cod.

Introduction

The influence of recreational fisheries (particular angling) on marine fish stocks and ecosystems has become an increasingly important topic for fishery management, and research efforts have recently begun to increase across Europe (e.g. Post *et al*., 2002; Coleman *et al*., 2004; Cooke and Cowx, 2004, 2006; Lewin *et al*., 2006; Arlinghaus *et al*., 2007; Pawson *et al*., 2008).

In 2001, the regular collection of marine recreational fishery data was initiated by the European Council, and since 2008, EU Member States have been obliged to assess recreational cod (*Gadus morhua* L.) catches (CEC, 2001, 2008). Atlantic cod is one of the most important commercial and recreational target species in European marine waters (Pawson *et al*., 2007; ICES, 2010). Previous surveys from various European countries (e.g. Netherlands, Sweden, Denmark, and Germany) have indicated that recreational cod catches are substantial compared to commercial catches. This seems particularly relevant for the cod stock in the western Baltic Sea (ICES, 2010; Dorow and Arlinghaus, 2011; Sparrevohn and Storr-Paulsen, 2012; Strehlow *et al*., 2012; van der Hammen and de Graaf, 2012). For example, Strehlow *et al*. (2012) estimated that between 2005 and 2010, the annual German recreational cod harvest from the western Baltic Sea (ICES Subdivisions 22 and 24) ranged from 34–70% of the German commercial fishery landings.

Release rates in the north and central European recreational cod fishery typically vary between 25 and >60% (Sparrevohn *et al*., 2011; Ferter *et al*., 2012, 2013; ICES, 2012; Strehlow *et al*., 2012; van der Hammen and de Graaf, 2012). Reasons for release are legal restrictions (e.g. minimum sizes) or the practice of voluntary catch-and-release. The German marine recreational fishing survey revealed that 375 t (2009) and 405 t (2010) of undersized cod (<38 cm) were released in the Baltic recreational fishery, corresponding to 2.2 and 1.3 million cod, respectively. Therefore, release rates (based on numbers) varied between 37 (2010) and 60% (2009) in the German Baltic recreational cod fishery (Strehlow *et al*., 2012). In contrast, discards by the German

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commercial cod fishery in the western Baltic Sea were estimated to be 423 t in 2009 and 390 t in 2010 (U. Berth, pers. comm.). High release rates similar to those in Germany have also been observed in Danish (61% in 2010) and Swedish (48% in 2010) waters (ICES, 2012; Sparrevohn *et al.*, 2011).

In view of the major impact of the recreational fishery on the western Baltic cod stock, it has been recommended to incorporate recreational cod catches (harvest and release/discards) in future stock assessments to increase accuracy and to improve management (Sparrevohn and Storr-Paulsen, 2012; Strehlow *et al.*, 2012). Only recently have recreational catches been integrated into the stock assessment of western Baltic cod, and this may act as a precedent for other cases. Therefore, in addition to regular catch estimations, studies investigating mortality rates of cod released by anglers are needed to provide accurate recreational fishing mortality estimates.

Many mortality studies have indicated that the average post-release mortality is rather low (<20%), but highly variable (ranging from 0–95%) between and within species, fisheries, and habitats, with multiple factors (e.g. gear type, anatomical hooking location, capture depth, and water temperature) influencing the survival of released fish (reviewed in Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005, Cooke and Wilde, 2007).

Despite the high release rates, no literature exists exploring the post-release mortality of cod or other gadoids in recreational fisheries. A few studies have investigated discard mortality rates of cod by commercial fishing methods such as handline, longline, or jigging, which are more comparable to the angling process. These studies have revealed mortality rates for cod between 0 and 69% (Milliken *et al.*, 1999, 2009; Pálsson *et al.*, 2003; Brattey and Cadigan, 2004). However, concerning the high variation in the results and the different characteristics of these studies, the mortality rates should not be generalized and applied to recreational cod fisheries.

The goals of this pilot study were to (i) estimate the immediate and delayed post-release mortality rate of undersized cod, (ii) examine factors affecting mortality, and (iii) investigate the effects of catch-and-release (physical condition and behaviour in the cages) on cod.

Material and methods

Experimental design and data collection

A containment study design with treatment (angling) and control (trapping) groups of fish was conducted to evaluate the effects of the catch-and-release process on cod. Fieldwork was carried out in the waters off Warnemünde (ICES Subdivision 24) bordering the south coast of the western Baltic Sea located in the German federal state of Mecklenburg–Western Pomerania. Four experiments were conducted between April and July 2012.

A local charter vessel offering regular cod angling tours was hired to mimic realistic fishing conditions. A charter vessel trip was conducted once a month per trial to catch the treatment groups. Fishing trips began early in the morning and lasted until noon, resulting in fishing times between 2 and 5 h depending on catch and weather conditions. Due to low abundance of undersized cod (minimum landing size in the Baltic Sea is 38 cm), all fish ≤45 cm were included. Since many Baltic Sea cod anglers have higher voluntary minimum landing sizes (between 40 and 45 cm), this adjustment appears to be justified (MSW, pers. obs.). Between 12 and 17 volunteer anglers, with different skill levels and experience, were recruited for each angling session. On-site interviews were conducted with the anglers to assess their individual skill levels. Participants were introduced to the study design, but no specific handling or fishing instructions were provided to best mimic real angling practice and to avoid bias. Anglers used their own fishing tackle, especially small jigs (5–7 cm) and shads (7–12 cm) with single hooks or pilks (30–125 g) with treble hooks. Water depths in the study area were between 8.5 and 14 m. During fishing operations, water temperature, salinity, and dissolved oxygen were measured with hand-held probes (WTW TA 197-Oxi and TA 197-LF) at surface and bottom. Holding-water temperatures (onboard and netpen holding) on the day of capture were similar within trials and ranged between 6.5 (April) and 16.3°C (July). Differences in bottom and surface water temperatures (onboard and netpen holding temperatures) ranged between 0.4 and 4.1°C during the experiments. Unfortunately, bottom-water temperatures were not recorded accurately in May due to technical problems of the probe; therefore, temperature differences were excluded from the analysis.

Fish of suitable size were landed by the anglers, and hooks were removed by hand or with pliers. Data were recorded for: time of capture, capture depth, lure type, hook type (single or treble hook), hooking location, total length, bleeding, barotrauma, and time of air exposure. Anatomical hooking locations were categorized in five classes: (i) shallow hooking (lip and jaw), (ii) medium hooking (oral cavity, vomer, and tongue), (iii) deep hooking (gills, oesophagus, and stomach), (iv) foul hooking 1 (outside, frontal head area in front of a vertical line behind the eyes), and (v) foul hooking 2 (outside, remaining body) (see Figure 1). Cod were tagged with individually numbered t-bar anchor tags (type TBA-2, Hallprint Pty Ltd) inserted at the base of the first dorsal fin.

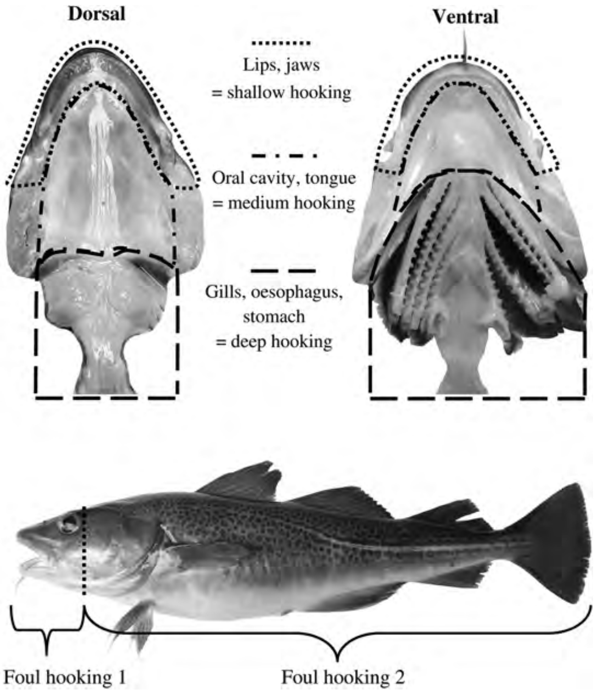

Figure 1. Dorsal, ventral (horizontal cuts of the area inside the head), and lateral view of cod, with anatomical hooking locations.

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For each experiment, a control group of cod was caught with pots to account for additional mortality caused by handling, tagging, and holding processes (Pollock and Pine, 2007). In total, 20 bottom-set, two-chamber pots (150 × 100 × 120 cm, 25-mm mesh size; Refa Frøystad Group AS) were set near an artificial reef west of Warnemünde (54°10.50′N 11°56.60′E). Pots were baited with chopped herring (*Clupea harengus* L.), and half of them were additionally equipped with a green LED lure light for visual stimulation. Pot fishing depths varied from 11–12 m, and soak-time of the pots ranged from 5–8 d. After being caught, fish in the control group underwent the same treatment (handling, onboard holding, transportation, netpen holding) as angled fish, and hydrographic conditions were measured the same way as during the angling sessions.

Immediately after tagging and data collection, fish were sorted by size ($\leq$30 and $>$30 cm) and placed into two 1200-l holding tanks to prevent cannibalism. The holding tanks were aerated and supplied with flow-through surface seawater. Holding-water temperature, salinity, and dissolved oxygen were continuously monitored with hand-held probes, and condition of the fish was frequently checked to monitor immediate mortality. Maximum stocking density was 30 cod for each tank, and tank holding times ranged from 1–7 h, depending on time of capture. At the end of each sampling day, fish were transported to two netpens located at the port entrance of Warnemünde. Fish were transferred from the holding tanks into the netpens (again sorted by size to minimize cannibalism) with a rubberized dipnet to prevent abrasions. Each netpen consisted of a square floating V4A stainless steel frame with a polyamide net (3 × 3 × 3 m, 20-mm mesh size). The net could be lifted to facilitate control of the fish, and a 100-mm predator net covered the netpens. Water depth was 6 m at the cage site, and natural water movement ensured adequate water exchange. Cod were held in the netpens for at least 10 d to account for delayed post-release mortality, which might have occurred from hooking injuries, diseases, or physiological dysfunctions. Each pen was limited to 50 fish per experiment. Fish condition and behaviour as well as occurrence of dead fish were checked using an underwater viewing scope every 12 h during the first three days and then daily the following seven days. After 72 h, feeding was begun with chopped sandeel (*Ammodytes marinus* L.) at a daily rate of approximately 1% of the cod biomass. Weather conditions, salinity, and dissolved oxygen (at a depth of 3 m) were recorded at least once a day. Holding-water temperature (at 3 m depth) was measured hourly by an automated data logger (Onset Optic StowAway Temp WTA32).

Dead fish were removed, measured, and identified by their tag number. A comprehensive visual examination was performed on all mortalities to determine probable causes of death. Hooking location, progress of wound healing, nutritional state, occurrence of wound infections, and haemorrhages were recorded and photo documented. The same examination procedure was applied to all fish that survived the 10-d observation period. Surviving fish were released at the cage site after final examination.

Data analysis

Total and adjusted mortality rates as well as their standard errors (s.e.) and 95% confidence intervals (*CI*) were calculated using the methods for catch-and-release experiments developed by Wilde (2002). However, the formula used to calculate sampling variance estimates (VAR), which was needed to calculate standard errors, was slightly modified to provide an unbiased estimate of the unknown population variance:

$$\mathrm{VAR} = \frac{[MT*(1-\mathrm{MT})]}{(n-1)} \tag{1}$$

where MT is the calculated mortality rate and n the sample size.

Chi-squared tests were conducted to investigate the independence of (i) total mortality rates (for each group) and trials, and (ii) total mortality rates and groups (control and angling). In cases where the number of observations per cell was < 5, a two-tailed Fisher's exact test was used. Furthermore, Fisher's exact tests were applied to determine the existence of associations between hooking locations and lure types, bleeding and hooking location, and bleeding and lure type. In cases of significant results, follow-up comparisons were conducted using multiple pairwise Fisher's exact tests, and the Dunn–Šidák correction was applied to account for alpha inflation. The two-sample Kolmogorov–Smirnov test was utilized to compare size frequency distributions of the control and the treatment group (data from all trials were pooled for each group). Additionally, total lengths and air exposure times of both groups were compared using the Mann–Whitney–U–Test.

A generalized linear model (GLM) with a binomial probability distribution was fitted to the data using maximum likelihood estimation. The model describes the relationships between total mortality (after 10 d) as a binary response variable and nine potential explanatory variables. The explanatory variables (main effects) were: mean water temperature during the holding period in the cages (temp), total length (*TL*), duration of air exposure (air), holding time onboard (time), which were treated as continuous variables; angler experience (angler) based on the individual interview answers; and a score-based rating system, occurrence of bleeding (bleeding), lure type (lure), hooking location (hooking), and hook type (hook) treated as categorical variables. The explanatory variables were analysed for interactions by using conditioning plots, scatterplots of matrices (SPLOM) and contingency table analysis. Model selection was achieved by using a stepwise backward elimination ("step" procedure of R$^{©}$) based on the Akaike information criterion (AIC). Additionally, a manual forward selection was conducted, and results were checked for consistency. Initially, a model with all variables and biologically plausible interaction terms was fitted and tested, but no interaction was found that explained a significant amount of variation in the data. As a result, a simpler model with only the main effects and a logit link function linking the random and the systematic component was developed (Crawley, 2005).

The full model was:

$$\begin{aligned}\log[\mu(1-\mu)] = {} & \beta_0 + \beta_1(TL_i) + \beta_2(\mathrm{temp}_i) + \beta_3(\mathrm{air}_i) \\ & + \beta_4(\mathrm{time}_i) + \beta_5(\mathrm{angler}_i) + \beta_6(\mathrm{bleeding}_i) \\ & + \beta_7(\mathrm{lure}_i) + \beta_8(\mathrm{hooking}_i) + \beta_9(\mathrm{hook}_i) + \varepsilon_i,\end{aligned} \tag{2}$$

where β_i is the coefficient of the ith explanatory variable and ϵ_i is the binomial error term. A comparison between the saturated (full) model and the optimal (reduced) model was accomplished by using a likelihood ratio χ^2 statistic (G-test). Variance inflation factors (VIF), examination of conditioning plots, Cook's distance

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Table 1. Capture characteristics of the angling and control groups, including number of cod (n), total length (TL), incidence of bleeding (Bleeding), air exposure duration (Air), capture depth (Depth), and water temperature during holding (Temp.).

	Control				Angling			
	April	May	June	July	April	May	June	July
Fish (n)	12	33	20	36	9	32	52	44
TL (cm)	29.9	31.2	30.5	31.1	36.1	37.7	37.4	37.5
± s.d.	7.7	6.0	6.4	5.3	1.6	2.8	3.5	3.9
Bleeding (%)	0.0	0.0	0.0	0.0	0.0	15.6	13.5	31.8
Air (s)	34.3	30.4	42.5	33.5	84.9	61.2	66.3	75.8
± s.d.	7.9	5.4	24.7	6.7	33.5	11.9	19.7	30.6
Depth (m)	11.0	11.0	11.0	12.0	10.7	10.4	11.3	13.0
± s.d.	0.0	0.0	0.0	0.0	0.5	1.4	0.5	1.1
Temp. (°C)	7.9	11.9	15.6	17.1	7.0	11.9	15.6	16.5
± s.d.	0.5	0.7	0.8	0.9	0.4	0.7	0.8	0.3

Mean ± standard deviation (s.d.) for continuous variables.

measures, and analysis of Pearson residuals were used to detect violations of the multiple logistic regression assumptions (Quinn and Keough, 2002).

All statistical analysis and model fittings were performed using the software R version 2.15.0 and basic packages were complemented by the packages "AED" and "car" (Zuur, 2010; Fox and Weisberg, 2011; R Development Core Team, 2012).

Results

Capture characteristics

A total of 137 angled and 101 trapped cod were caught during the four experimental trials and included in the analysis (Table 1). Total lengths of cod ranged from 22–45 cm and size frequency distributions between the angling and the control group were significantly different (Kolmogorov–Smirnov test: $D = 0.560$; $p \leq 0.001$; $n = 238$) with a significantly higher median of total length for the angled fish (38.0 cm) compared to the control fish (29.0 cm) (Mann–Whitney–U–Test: $W = 11\,148.5$; $p \leq 0.001$; $n = 238$).

Mean incidence of bleeding was 23.4% for fish caught with rod and line. Comparison of the overall medians of air exposure duration revealed a significantly higher air exposure duration for the angled cod (Mann–Whitney–U–Test: $W = 13\,361.5$; $p \leq 0.001$; $n = 237$). Mean capture depths and holding-water temperatures were approximately the same for both groups (Table 1). Overall, 38% of the cod were shallow-hooked, 40% medium-hooked, 4% deep-hooked, 12% foul-hooked 1 (frontal head area), and 6% foul-hooked 2 (remaining parts of the body). Incidences of deep hooking and foul hooking were highest for fishing with jigs and pilks (Figure 2). However, lure type did not significantly affect hooking location (Fisher's exact test: $p = 0.060$). Depth of capture ranged from 9–14 m, and no clear evidence of barotrauma was observed during this study. Therefore, capture depth and barotrauma were not further considered in the analysis. On-site interviews revealed that 55.6% ($n = 35$) of the participating anglers were categorized as inexperienced and 44.4% ($n = 28$) as experienced.

Post-release mortality

The overall adjusted mortality rate for the angling group was 11.2% (s.e. ± 22.0). The average total post-release mortality was 14.5% (s.e. ± 10.6) for control fish and 25.7% (s.e. ± 19.3) for angled cod. Comparison of overall total mortality rates between both groups indicated a significantly higher mortality rate for the angled cod ($\chi^2 = 7.34$; d.f. = 1, $p = 0.007$). Total mortality rates of the angling groups increased until June and decreased slightly in July (Table 2).

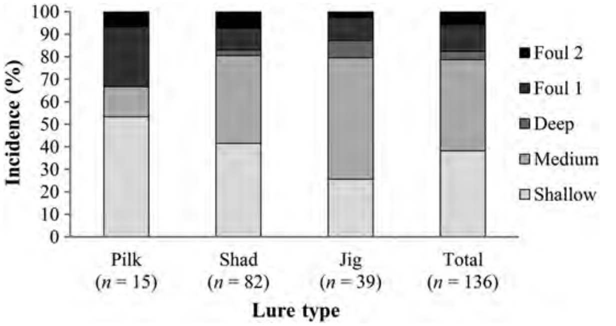

Figure 2. Incidence of hooking locations (%) for different lure types and total catch (one fish caught on natural bait was excluded).

Fisher's exact test showed that total mortality rates of the angled cod were significantly different between trials ($p = 0.026$). However, follow-up (*post hoc*) pairwise comparisons failed to detect significant associations between trials. In contrast, no clear mortality pattern was observed in the control groups, and the total mortality rates of the different trials were independent (Fisher's exact test: $p = 0.278$).

Most post-release deaths of the angled fish occurred during the onboard holding period (47.8%) and within 24 h of capture (84.8%), respectively. In total, 92.9% of the cod that survived the first 24 h survived the 10-day holding period. However, delayed mortality was observed in June and July (Figure 3). Control-group fish showed a similar temporal mortality trend as fish caught with hook and line.

Factors affecting mortality

The multiple logistic regression analysis revealed that a model including bleeding, holding-water temperature, hooking location, and air exposure duration provided the best fit to the data ($AIC_{\text{full model}} = 162.9$; $AIC_{\text{optimal model}} = 154.3$). However, only bleeding and holding-water temperature were significant predictors of mortality (Table 3). The odds of dying were 4.8-fold ($CI = 1.6–15.8$) higher for bleeding cod. Furthermore, each degree increase in holding-water temperature increased the likelihood of dying by a factor of 1.3 ($CI = 1.1–1.6$).

The incidence of bleeding was significantly associated with the hooking location (Fisher's exact test: $p < 0.001$). Multiple pairwise comparisons showed that the likelihood of bleeding was significantly higher for deep-hooked or foul-2-hooked fish. In addition, deep hooking and foul 2 hooking caused the highest mortality rates (Figure 4). Nevertheless, overall hooking location proved to be an insignificant predictor of mortality in the logistic model ($\chi^2 = 8.666$, d.f. = 4, $p = 0.070$).

Post-mortem examination showed that mortality was highest when the throat or gill region or the oesophagus/stomach sustained serious injuries, which were mostly associated with severe bleeding. However, some of the fish died without noticeable hook-related physical trauma.

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Table 2. Number of cod caught, absolute, total, (± s.e.) and adjusted (± s.e.) post-release mortality (after 10 d) of the angling and control groups.

	Control				Angling		
	Caught	**Dead**	**Total mortality (%)**	**Caught**	**Dead**	**Total mortality (%)**	**Adjusted mortality (%)**
April	12	0	0.0 (0.0)	9	0	0.0 (0.0)	0.0 (0.0)
May	33	6	18.2 (6.8)	32	7	21.9 (7.4)	3.7 (10.1)
June	20	3	15.0 (8.2)	52	22	42.3 (6.9)	27.3 (10.7)
July	36	9	25.0 (7.3)	44	17	38.6 (7.4)	13.6 (10.4)

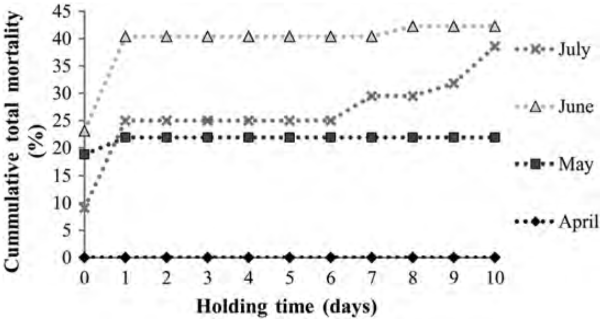

Figure 3. Cumulative total mortality rates (%) of angled cod in relation to holding time.

Table 3. Summary of the final logistic regression model that describes the relationships between absolute mortality of angled cod and holding temperature, bleeding, hooking location, and air exposure duration, based on stepwise GLM analysis.

Parameter	Estimate	s.e.	*CI* (95%)	*z*-value	Pr(<|z|)
Intercept	−6.150	1.826	−10.035, −2.806	−3.367	***
Bleeding (presence)	1.577	0.576	0.479, 2.761	2.740	**
Temperature	0.238	0.098	0.061, 0.451	2.429	*
Hooking location					
Shallow	−0.308	0.767	−1.753, 1.342	−0.402	0.688
Medium	0.987	0.723	−0.339, 2.579	1.365	0.172
Deep	0.333	1.535	−2.544, 3.832	0.217	0.828
Foul 2	1.120	1.058	−0.921, 3.316	1.058	0.290
Air exposure	0.018	0.012	−0.006, 0.042	1.446	0.148

Estimates, standard errors (s.e.) and 95% confidence intervals (*CI*) are on a logit scale.
$^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

The multiple logistic regression analysis revealed that higher water temperatures during holding negatively affected survival of angled cod (Figure 5). Adjusted mortality increased with rising holding-water temperatures between April and June and remained on a relatively high level during July.

Post-release physical condition and behaviour

After release, the majority of cod swam steadily near the bottom of the onboard holding tanks. Cod with serious hooking injuries or showing signs of bleeding were unable to reach equilibrium, and frequently died during the onboard holding period. However, some fish that initially seemed to be in good condition lost equilibrium and floated near the surface within a few minutes of release. Most of these fish recovered and achieved neutral buoyancy immediately after being placed in netpens, even if equilibrium was lost for several hours.

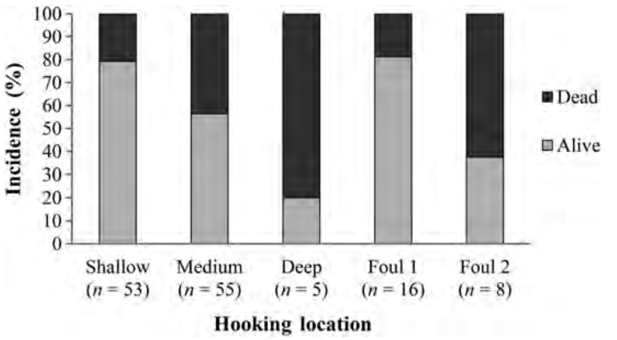

Figure 4. Total mortality (%) of angled cod in relation to hooking locations.

A substantial fraction of cod began to feed within a couple of days after feeding had begun. Visual observations showed that cod actively preyed on stickleback (*Gasterosteus* sp.) and sandeel (Ammodytidae) that entered the net pens naturally. The time of first feeding was delayed depending on the intensity of hooking injuries. Furthermore, the observed proportion of angled fish that had definitely fed was lower than that of control fish.

Final visual examination of the surviving fish revealed that overall healing of hooking injuries was relative slow (>10 d), but varied between individuals and trials. Some fish that were foul-hooked in the frontal belly survived, although essential organs such as liver or gut could have been punctured. About 26% of the surviving cod showed bacterial infections of their hooking injuries, which led to the development of skin ulcerations in the affected region in a few cases (8%). Extensive physical irritations of the skin or mucosa due to handling were not observed after 10 d of retention.

Discussion

Mortality

The post-release mortality rate (adjusted for handling and caging effects) for angled cod ranged from 0.0–27.3% (overall mean 11.2%). This overall mean mortality rate was close to the average release mortality rate of 18% calculated by Bartholomew and Bohnsack (2005), who carried out a meta-analysis of 274 catch-and-release mortality studies.

High rates of short-term mortality have been observed for jigged sublegal-sized cod held in submerged cages during mortality experiments in the Northwest Atlantic longline fishery (0–56%

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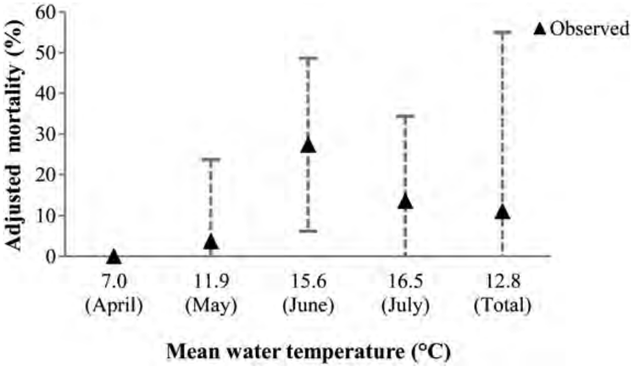

Figure 5. Relationship between adjusted mortality rates (dashed lines indicating the 95% confidence intervals) of angled cod and mean holding-water temperatures during the 10-d holding periods.

after 72 h, Milliken *et al.*, 1999, 2009). Another study by Pálsson *et al.* (2003) showed that mortality rates of undersized cod caught with automatic jigging machines north of Iceland ranged from 32–54% (overall average mortality rate 43%). In contrast, no mortality was observed in the control experiments carried out with cod captured by sportfishing gear in shallow waters (5–15 m). Brattey and Cadigan (2004) reported short-term (5–10 d) mortality rates of 0–15.6% (average mortality rate 3.2%) for adult cod (>45 cm) captured with handlines and held in submersible cages during a tagging mortality experiment.

However, in all these studies, individuals were very carefully handled and only fish in excellent condition were considered for the experiments, thus not allowing direct comparisons with the present study (Milliken *et al.*, 1999, 2009; Pálsson *et al.*, 2003; Brattey and Cadigan, 2004). The high variation in mortality rates observed in previous studies demonstrates that even within one species, habitat- and fishery-specific investigations of post-release mortality rates are needed (Cooke and Suski, 2005).

The majority of deaths (~85%) occurred within 24 h, potentially caused by acute stress reactions (Figure 3). This result is consistent with survival observations of discarded undersized cod in the handline fishery (Pálsson *et al.*, 2003), and with results of other catch-and-release mortality studies in general (reviewed in Muoneke and Childress, 1994). Nevertheless, considerable delayed mortality was observed for the angling (13.6%) and the control group (11.1%) in July, which might have been caused by acute thermal stress due to a rapid rise in holding-water temperature from about 16 to 18°C (peak value 19.8°C) rather than by delayed lethal effects of the catch-and-release process. The critical thermal maximum for cod has been identified at between 16 and 24°C, and some fish may have reached it under the given holding conditions (reviewed in Pérez-Casanova *et al.*, 2008).

Mortality factors

The logistic regression analysis revealed that bleeding and holding-water temperature were the only significant predictors of mortality (Table 3). Bleeding significantly increased the likelihood of mortality, but not all cod that suffered bleeding died. It has been widely accepted that intense bleeding decreases the chance of survival (Muoneke and Childress, 1994; Arlinghaus *et al.*, 2007). Pálsson *et al.* (2003) and Milliken *et al.*, (1999, 2009) revealed that mortality was higher for cod with multiple or severe hooking injuries, which are most likely associated with bleeding as well. Prospective studies should investigate whether the use of barbless hooks could help to minimize hooking injuries and bleeding. Barbless hooks are easier to remove, resulting in less tissue damage and reduced air exposure duration. However, the use of barbless hooks is very uncommon in the Baltic Sea recreational cod fishery (MSW, pers. obs.), and catch efficiency may decrease (Cooke and Wilde, 2007). In addition, the potential benefits of barbless hooks on post-release mortality have generated controversy in the literature and appear to be species-specific (reviewed in Muoneke and Childress, 1994; Cooke and Suski, 2005; Cooke and Sneddon, 2007; Cooke and Wilde, 2007).

Water temperature has been identified as an important factor influencing catch-and-release mortality in various studies. Most commonly, mortality increases at higher water temperatures as fish become more sensitive to physiological disturbances caused by increased metabolism (reviewed in Muoneke and Childress, 1994, Bartholomew and Bohnsack, 2005, Cooke and Suski, 2005; Arlinghaus *et al.*, 2007; Cooke and Sneddon, 2007; Cooke and Wilde, 2007). The GLM model revealed that a 1°C increase in holding-water temperature increased the odds of dying by a factor of 1.3. This result is consistent with findings by Brattey and Cadigan (2004) as well as by Milliken *et al.* (2009), who also observed significantly higher mortality rates of jigged cod at higher water temperatures. Other seasonal changes such as reproductive status and nutritional condition or synergistic effects, which cannot be separated from temperature effects, may also play an important role (reviewed in Muoneke and Childress, 1994; Cooke and Wilde, 2007). Several studies showed that great differences between bottom and surface (holding) water temperature, or the presence of thermoclines can negatively affect mortality rates (Brattey and Cadigan, 2004; Diamond and Campbell, 2009; Campbell *et al.*, 2010). Surface temperatures (onboard and netpen holding temperatures) and bottom temperatures (temperatures at capture depth) recorded at the capture sites showed that the water column was mixed in April and July (temperature differences <1°C). In contrast, a thermocline was present during the experiments in May (difference >1.5°C) and June (difference 4.1°C). Even though temperature differences were excluded from the GLM, our results showed that the mortality rates were strongly coupled to higher water temperatures in general rather than to the observed bottom and surface temperature differences (at least for differences <4.1°C). However, potential effects of surface (holding) and bottom temperature differences need to be considered when interpreting the results. Using submersible cages directly at the fishing spots could help minimize effects in temperature differences and in addition, reduce onboard holding times in future experiments.

Post-release mortality rates were lowest when cod were shallow-hooked (Figure 4), but the differences were not significant. Hooking location as a mortality factor has to be viewed in connection with bleeding, because both are frequently correlated (Muoneke and Childress, 1994; Cooke and Suski, 2004). Although air exposure duration remained in the final logistic regression model, it had no significant effect on mortality for the range of exposure studied (maximum air exposure duration 210 s). This is consistent with results from Humborstad *et al.* (2009), who demonstrated that no immediate or delayed mortality occurred in Atlantic cod after 300 s of air exposure at 9°C. Our results suggest that the vulnerability to longer air exposure periods (<5 min) is relatively low in comparison to other species, at least at low and medium temperatures (reviewed in

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Muoneke and Childress, 1994, Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005; Arlinghaus *et al.*, 2007; Cooke and Wilde, 2007).

Capture depth was excluded from the analysis as it only ranged from 9–14 m and, therefore, is unlikely to influence mortality. Typically, the German recreational cod fishery in the Baltic Sea occurs in water depths < 20 m (MSW, pers. obs.). This has led to the assumption that capture depth has a relative low impact on post-release mortality in German waters. However, studies from other ecosystems showed that the mortality of jigged cod was lower in shallow waters (<50 m) compared to deep-water (>50 m) experiments (Pálsson *et al.*, 2003; Milliken *et al.*, 2009), which is in agreement with findings for many other species (e.g. Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005). As a result, the potential consequences of capture depth on catch-and-release mortality due to hydrostatic effects should be taken into account in deep-water recreational cod fisheries.

Total length, holding time onboard, angler experience, lure type, and hook type had no statistically verifiable effect on cod mortality. Several reviews have revealed that the impact of these factors on post-release mortality is the subject of controversy in the literature (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Cooke and Wilde, 2007).

However, some fish died for no apparent reason. Several studies indicate that differences in the responsiveness to stress exist between species, populations, and even individuals (e.g. Barton, 2002; Hori *et al.*, 2012). Hori *et al.* (2012) suggested that there is a genetic component in cod that has an effect on stress resistance. Additionally, differences in resilience have been linked to a fish's individual nutritional condition (Olsen *et al.*, 2008). Overall, our observations during the onboard and cage-holding processes indicated that cod seem to possess high stress resistance against handling and holding stress, particularly in conjunction with low holding-water temperatures. This assumption is consistent with low physiological stress responses to acute stressors observed in handling and transportation experiments involving cod (Hemre *et al.*, 1991; Staurnes *et al.*, 1994).

Fish condition and behaviour in captivity

Hooking injuries appeared to be relatively slow to heal for surviving cod as hooking wounds were frequently still visible after 10 d. Individuals might have suffered sublethal consequences, such as temporary impaired feeding ability or higher vulnerability to diseases and parasites, which could have negatively influenced their overall fitness (Arlinghaus *et al.*, 2007; Cooke and Sneddon, 2007). This assumption was supported by the lower proportion of feeding fish in the angling group and the development of bacterial wound infections in some cases. However, to date, it has not been investigated whether recreationally released cod develop similar bacterial infections after release into the wild. Furthermore, it is unknown if observed wound infections potentially lead to skin ulcers, which are frequently observed in Baltic Sea cod. Those ulcers are usually associated with a bacterial infection caused by *Vibrio anguillarum*, which, in some cases, has been considered to be fishing-gear induced (Mellergaard and Bagge, 1998). Observed wound infections might also have been induced by caging effects or lower water quality and higher concentration of bacteria in the harbour area of Warnemünde.

Limitations of the study

Next to the advantages of containment studies, such as low costs and effort, easy access, direct visual observation in short time-intervals, and general acceptance of the methodology in the literature, several potential disadvantages have been pointed out (Muoneke and Childress, 1994; Pollock and Pine, 2007). Drawbacks entail semi-natural conditions (e.g. disrupted behaviour, non-natural forage, artificial environment, and temporary exclusion of post-release predation risk), no information about long-term and sublethal effects of the catch-and-release process, and potential additive stress, as well as physical damage imposed by confinement and transportation. In contrast, the inclusion of control groups helps to deal with some of these limitations (Cooke and Schramm, 2007; Pollock and Pine, 2007; Donaldson *et al.*, 2008). Furthermore, cod were held at low stocking densities during onboard holding (maximum 25.0 kg m^{-3}) and in the netpens (maximum 1.5 kg m^{-3}) compared to holding and transportation situations in the aquaculture industry to minimize negative effects of transportation and containment (Hemre *et al.*, 1991; Staurnes *et al.*, 1994). However, the inclusion of control groups and holding at low densities cannot clearly separate the potentially lethal effects of handling and containment on fish from the mortality caused by the catch-and-release process because these effects may interact or act cumulatively.

A main shortcoming of our study was unnatural holding conditions. This is particularly relevant in terms of the observed holding-temperature effects. Cod living in thermally stratified waters are known to migrate to areas and depths of preferred water temperatures (Claireaux *et al.*, 1995). In contrast, caged cod were limited in their movements and had to remain in relatively warm surface water. Therefore, mortality rates might have been overestimated due to thermal stress, at least during summer months (Figure 5). In addition, the experiments did not cover an entire year, and seasons with cooler holding-water temperatures were underrepresented, which might have led to further overestimation of the overall mortality. Onboard holding periods were sometimes longer for angled cod due to logistical and cost constraints, which might also have biased mortality rates. However, the logistic regression model did not identify the onboard holding time as a significant predictor of mortality.

The temporary exclusion of post-release predation is an important issue, which can bias the results. However, the post-release predation risk of Baltic cod is limited due to low cannibalism rates (low abundance of big cod >60 cm) for the usual size range of released cod, the absence of other large piscivore fish species, and small populations of marine mammals (reviewed in Hüssy, 2011). It, therefore, seems unlikely that the estimated mortality rates are strongly biased in this way.

A further limitation of the present study is the potential bias due to non-representative experimental angling trips, with respect to factors such as angler experience and behaviour, tackle used, and variation in angling methods applied. Furthermore, the presence of scientists onboard might have influenced anglers' behaviour and individual fish handling. However, angling conditions were kept as realistic as possible. In addition, the logistic regression analysis revealed that angler experience, lure, and hook type did not significantly affect post-release mortality.

Previous studies have shown that most undersized cod were either caught from small boats or charter vessels in the western Baltic Sea (Strehlow *et al.*, 2012). Thus, our study design focused on releases from sea-based fishing methods. However, release

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rates of undersized cod are also high for land-based fishing methods (mostly shore angling with natural baits) along the German Baltic coast (Strehlow *et al*., 2012). Therefore, caution should be exercised when applying the present mortality rates to land-based cod releases, because post-release mortality is probably higher due to rougher fishing conditions (e.g. surf, abrasion risk, longer fighting time) and the use of natural baits (deep hooking).

Conclusions and implications

This study can be considered a first step in closing the existing scientific gap in investigating possible post-release mortalities and the consequences of catch-and-release on cod in the recreational fishery. Our findings suggest that a substantial amount of recreationally released cod survive and thus cannot be classified as removals from the western Baltic cod stock. However, the present post-release mortality rates should only serve as first estimations. The results have to be viewed with great caution on a population/stock level, as post-release mortality estimates derived from containment experiments cannot accurately predict recreational fishing mortality of a population in its natural environment. Although bleeding and high holding-water temperatures were the most crucial mortality factors, it is most likely that post-release mortality of cod depends on multiple factors, including possible interactions. We suggest that the use of barbless hooks can help to reduce tissue damage, bleeding, and mortality and may generally increase fish welfare and fitness after catch-and-release.

Further research on post-release mortality and the potential long-term sublethal effects of catch-and-release (e.g. predation risk, reduction of growth and reproductive success, behavioural effects, and vulnerability to diseases or parasites) is needed for this commercially and recreationally important species. Containment studies could be extended and complemented by mark–recapture as well as biotelemetry studies (Cooke *et al*., 2002; Block, 2005; Cooke and Schramm, 2007; Pollock and Pine, 2007; Donaldson *et al*., 2008). Furthermore, studies need to be conducted for other European cod stocks and ecosystems to account for differences in population levels, angling methods, and environmental conditions (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005).

Finally, prospective research should aim to provide fishery managers and anglers with accurate information about the effects of the recreational fishery on cod stocks and, if necessary, about ways to reduce catch-and-release mortality such as species- and fishery-specific guidelines, ultimately promoting a sustainable recreational cod fishery.

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