NRC Research Press

ARTICLE

Catch-and-release of Atlantic cod (*Gadus morhua*): post-release behaviour of acoustically pretagged fish in a natural marine environment

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Abstract: Studying the sublethal effects of catch-and-release (C&R) is challenging, as there are several potential sources of bias. For example, if behavioural alterations immediately after the release event are to be studied, separation of tagging effects from actual C&R effects is required, which is a challenge in the wild, particularly in marine environments. To investigate the effects of C&R on Atlantic cod (*Gadus morhua*) in their natural environment, 80 cod were caught in fyke nets, fitted with acoustic transmitters, and released. After recovery from tagging and handling for at least 14 days, nine individuals were recaptured and released at least once during experimental angling, following best release practice. All cod survived the C&R event and did not show any large-scale behavioural changes (i.e., changes in diel vertical migrations). However, analysis of small-scale vertical movements showed that three individuals underwent short-term alterations (e.g., reduced or increased swimming activity). This study showed that pretagging fish with acoustic transmitters before experimental angling is an option when investigating fish behaviour immediately after the release event in marine environments. Moreover, release guidelines for cod should be developed, as cod can recover quickly if caught in shallow waters (<20 m) and properly handled and released.

Résumé : L'étude des effets sublétaux de la pêche avec remise à l'eau (PRE) pose un défi de taille étant donné différentes sources possibles de biais. Par exemple, l'étude des modifications comportementales immédiatement après la remise à l'eau nécessite de distinguer les effets du marquage de ceux de la PRE, un exercice difficile en milieu naturel, particulièrement en milieu marin. Afin d'étudier les effets de la PRE sur la morue (*Gadus morhua*) dans son milieu naturel, 80 morues ont été capturées dans des verveux, équipées d'émetteurs acoustiques, puis remises à l'eau. Après une période de récupération d'au moins 14 jours suivant le marquage et la manipulation, neuf individus ont été repris et relâchés au moins une fois durant une pêche expérimentale à la ligne, en respectant les meilleures pratiques de remise à l'eau. Toutes les morues ont survécu à l'évènement de PRE et ne présentaient aucun changement de comportement à grande échelle (c.-à-d. modifications des migrations verticales nycthémérales). L'analyse des déplacements verticaux à petite échelle a toutefois révélé que trois individus présentaient des changements de courte durée (p. ex. activité natatoire réduite ou accrue). L'étude démontre que le marquage de poissons avec des émetteurs acoustiques préalablement à la pêche expérimentale à la ligne est une option envisageable pour l'étude du comportement des poissons immédiatement après la remise à l'eau en milieu marin. En outre, des directives relatives à la remise à l'eau des morues devraient être élaborées puisque ces poissons peuvent récupérer rapidement s'ils sont capturés en eau peu profonde (<20 m) et manipulés et remis à l'eau convenablement. [Traduit par la Rédaction]

Introduction

During the last two decades, recreational fisheries have been increasingly recognized both as an important contributor to fishing mortalities of marine fish stocks (Coleman et al. 2004; Cooke and Cowx 2004; Lewin et al. 2006; McPhee et al. 2002) and as a socioeconomically important activity (e.g., Arlinghaus and Cooke 2009). In parallel with this, the introduction of harvest regulations like daily bag limits and minimum landing sizes, as well as changes in angler attitudes, have led to an increased practice of regulatory and voluntary catch-and-release (C&R) in freshwater and marine recreational fisheries (Arlinghaus et al. 2007; Ferter et al. 2013*a*). C&R can potentially reduce fishing mortalities (Arlinghaus et al. 2007) and, at the same time, maintain angling opportunities (Policansky 2002). However, the practice has also led to controversies and public debates, particularly in Europe (Aas et al. 2002; Arlinghaus 2007; Arlinghaus et al. 2012; Salmi and Ratamäki 2011). Apart from ethical challenges connected to C&R (Arlinghaus 2008), the hooking, fighting, and handling of fish can lead to unintended post-release mortalities (for reviews see Bartholomew and Bohnsack 2005; Hühn and Arlinghaus 2011; Muoneke and Childress 1994) or sublethal effects like behavioural alterations or physiological stress responses (Cooke et al. 2013; Cooke and Sneddon 2007). As post-release mortalities and sublethal impacts can vary substantially between species, it is important to conduct species-specific C&R studies that can aid in the development of best practice guidelines to minimize negative impacts (Cooke and Suski 2005).

Received 23 June 2014. Accepted 5 October 2014.

Paper handled by Associate Editor Josef Michael Jech.

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To study the potentially negative effects of C&R on the fish, different study approaches, including containment, tag-return, and telemetry studies, can be chosen (Pollock and Pine 2007). Containment studies are widely used to study post-release mortalities, as they are relatively cost-effective, but they are conducted in unnatural conditions (e.g., in absence of natural predators; Pollock and Pine 2007). In contrast, tag-return studies make it possible to study the long-term fate of released fish in their natural environment, but they are dependent on a large number of tagged individuals and may be biased by tag loss and nonreporting of recaptures (Arnason and Mills 1981; Pollock et al. 2001). Telemetry studies have become increasingly popular for studying C&R impacts in recent years (Donaldson et al. 2008), as they allow for the study of released fish in their natural environment and deliver high-resolution data on the post-release behaviour (Pollock and Pine 2007). Potential challenges when using telemetry to study C&R impacts are that the deployed tags are generally relatively large and often require anaesthesia and surgical implantation, all of which can have an impact on the post-release behaviour of the fish (Bridger and Booth 2003; Donaldson et al. 2008; Jepsen et al. 2002), even though theses impacts may be short-lasting (Moore et al. 1990). In particular, when short-lasting, sublethal effects immediately after the release event are to be studied, these cannot be easily separated from impacts caused by the tagging procedure (Baktoft et al. 2013; Bettoli and Osborne 1998). Thus, to avoid such interactions, a separation of the tagging event from the actual release event is needed. Apart from laboratory or seminatural experimental settings (e.g., Anderson et al. 1998; Cooke et al. 2004), this has, to the best of our knowledge, only been done in a few freshwater studies (e.g., for largemouth bass (*Micropterus salmoides*) (Cooke et al. 2000), European pike (*Esox lucius*) (Baktoft et al. 2013; Klefoth et al. 2008), and Atlantic salmon (*Salmo salar*) (Halttunen et al. 2010)). Since the fish need to be recaptured, they have to be available during the experimental angling, which may be a challenge for marine species in particular because fish can easily disperse (Cooke et al. 2002). However, if the species to be studied is relatively stationary, such a study design may also work in marine environments and thus be an option to obtain unbiased data on behaviour immediately after the release event.

Atlantic cod (*Gadus morhua*, hereinafter cod) along the inshore coast of Norway is known to exhibit distinct home range behaviour (Olsen et al. 2012), and the species is one of the most popular marine target species in several European recreational fisheries (Kleiven et al., in review; Sparrevohn and Storr-Paulsen 2012; Strehlow et al. 2012; Vølstad et al. 2011). C&R rates for this species range from 1% (in Poland) to over 50% in several other European countries (Ferter et al. 2013*a*), with more than one million cod released annually by recreational anglers in both Denmark (Sparrevohn and Storr-Paulsen 2012) and Germany (Strehlow et al. 2012), as well as by marine angling tourists in Norway (Ferter et al. 2013*b*). Weltersbach and Strehlow (2013) estimated a mean mortality of 11.2% for cod released by charter boat anglers in the Baltic Sea, which is in the lower range of post-release mortality estimates compared with other species (Bartholomew and Bohnsack 2005). However, cod have a closed physoclistous swim bladder, and when brought up from deeper water, they can develop serious barotrauma symptoms. Barotrauma occurs when the swim bladder expands because of the rapid decompression (e.g., Midling et al. 2012; Nichol and Chilton 2006; Rummer and Bennett 2005) and has been shown to increase post-release mortalities in some species (e.g., Alós 2008). Barotrauma issues were not observed in the German Baltic Sea study, as the majority of cod in the German recreational Baltic Sea fishery are caught in less than 20 m depth (Weltersbach and Strehlow 2013). Cod catches in shallow waters are also the case in the Danish recreational Baltic Sea fishery, except for cod caught in the Sound during winter (Hans Jakob Olesen, personal communication). A randomized roving creel survey that was conducted along the coast of southern Norway (from Kristiansand to Risør) covering all potential angling areas from inshore to offshore between April and August 2012 showed that recreational boat anglers released 55% of their cod catches. Based on the depths where the boats were intercepted during angling, 49% of the released cod were caught between 4 and 20 m depth (A.R. Kleiven, K. Ferter, and J.H. Vølstad, unpublished data). In the UK, 100 000 cod (57% of recreational cod catches from shore) were released by recreational shore anglers in 2012 (Armstrong and Hyder 2013), who mainly fish in depths less than 20 m (Kieran Hyder, personal communication). As shown by Weltersbach and Strehlow (2013), these cod have a high survival potential if hooking damage is minimized and the fish are carefully handled and released. However, while their study yielded information on the overall proportion of mortality caused by C&R (though potentially biased because of seminatural holding conditions), it did not deliver information on possible individual behavioural alterations (e.g., changes in feeding and movement patterns), which may have been caused by the C&R event.

Considering the high release rates for cod and the lack of knowledge on potential sublethal C&R effects, there is a need to investigate consequences of C&R for this species in depth. Therefore, in the present study, we investigated whether cod showed any behavioural changes after being caught and released into their natural environment under best release practice conditions using acoustic telemetry. As the cod were tagged and released several weeks prior to the experimental C&R event, it was possible to separate tagging effects from C&R effects.

Materials and methods

Study area

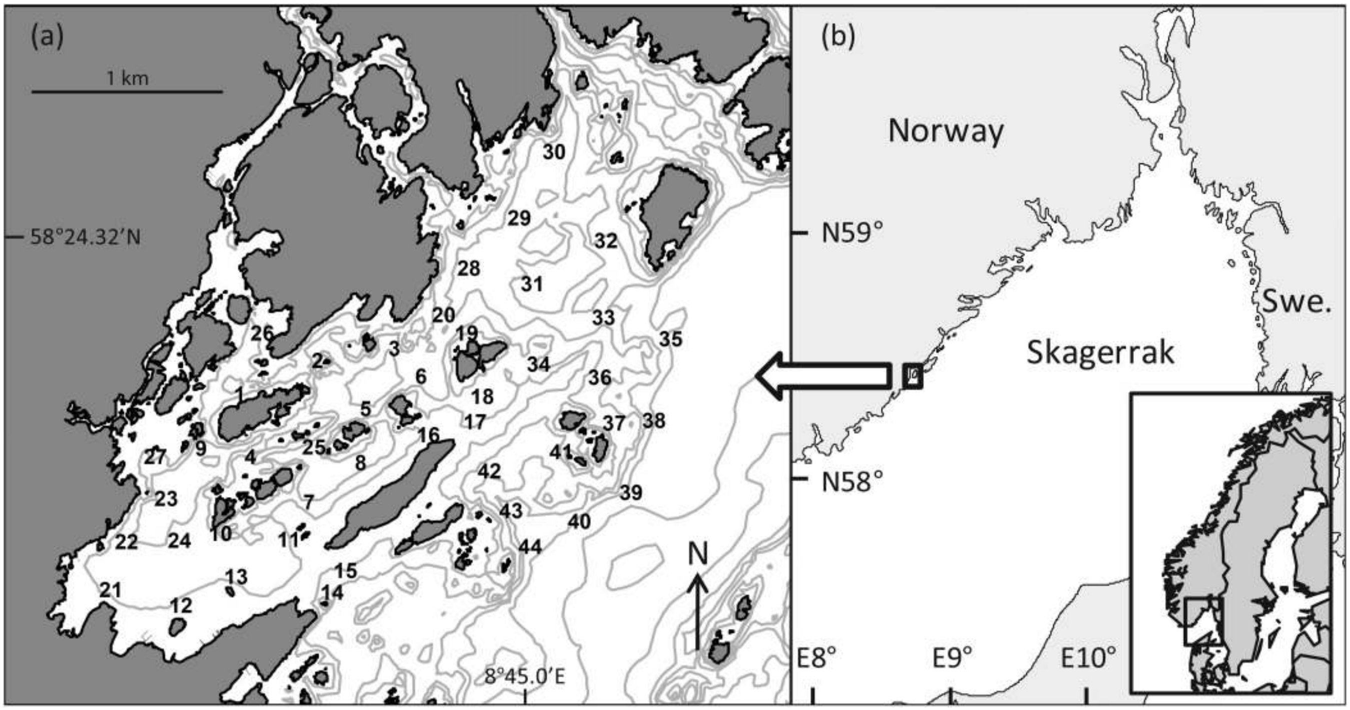
This study was conducted within a semisheltered coastal archipelago on the Norwegian Skagerrak coast (58°24′N, 8°45′E; Fig. 1). Maximum depth is 40 m and the habitat is diverse, including exposed and submerged islands, boulder fields, flats consisting of soft sediment, eel grass beds, and kelp forest (Olsen and Moland 2011). A partly submerged glacial moraine cuts through the area, forming a rock reef consisting of variable-sized cobble. Because of its vicinity to human population centers and its multitude of sheltered locations, this part of the coastline is popular for both commercial and recreational fishers.

Tagging procedure and acoustic monitoring

During May 2012, 302 cod (11–80 cm) were captured using fyke nets, measured to the nearest centimetre, and weighed. Eighty of the 302 cod were selected for acoustic tagging with the aim to cover all size groups evenly. These cod were equipped with V9P-2L acoustic transmitters with a built-in pressure (depth) sensor (9 mm × 38 mm, Vemco Division, Amirix Systems Inc., Halifax, Canada), which were surgically implanted into the body cavity. The tags were programmed to send a signal randomly every 110 to 250 s (mean 180 s) to avoid signal collision. Before surgical implantation, the cod were anaesthetized in a clove oil bath for about 2 min. Afterwards, the cod were taken out of the bath, and the acoustic transmitters were inserted into the body cavity through a 10–12 mm long cut posterior to the pelvic fins. The wound was closed using synthetic absorbable surgical suture material (Dexon II, Tyco Healthcare Group, Mansfield, Massachusetts, USA), and after completed surgery, the fish were placed in an aerated container for recovery. In addition to the acoustic transmitters, each cod was tagged with an individually numbered external T-bar anchor tag (TBA-1, 30 mm × 2 mm, Hallprint Pty. Ltd, Holden Hill, South Australia) below the anterior dorsal fin for identification. After tagging, the cod were released at the capture location.

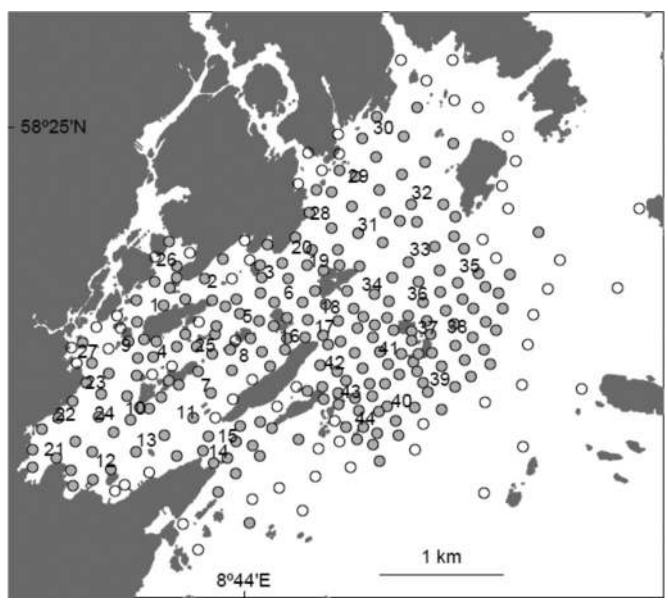
To monitor cod behaviour and fate, 44 ultrasonic receivers (VR2W, Vemco Division, Amirix Systems Inc.) were moored throughout the study area (geographic coverage ≈ 3 km^2) and attached at 3 m depth using subsurface trawl floats or surface buoys (Fig. 1) (Olsen and Moland 2011; Wiig et al. 2013). The detection range of the receivers was evaluated using a V9-tag with a fixed 5 s interval between signals, transmitting with the same signal strength as the tags used in the cod study. The range test tag was lowered to the sea floor at global

Fig. 1. Study area: the Sømskilen basin and nearby islands (*a*) on the Norwegian Skagerrak coast and (*b*) overview of the Scandinavian Peninsula (Norway and Sweden (Swe)), Denmark, and the location of the Skagerrak Sea (figure taken from Wiig et al. 2013). Isobaths shown are the 5, 10, 20, 30, 50, 100, and 150 m depth contours. Numbers denote the GPS positions of 44 Vemco VR2W acoustic receivers deployed to receive signals sent by acoustic transmitters. The cod studied (*n* = 9) were caught and released near receivers No. 3 (IDs 7293, 7308, 7351a, and 7351b), No. 6 (IDs 7303 and 7364), No. 19 (ID 7356), and No. 25 (IDs 7313, 7344, and 7359).



positioning system (GPS) positions (*n* = 452) 150–200 m apart throughout the study area. At each position, the range test tag was given a bottom time of 1 min. Range testing resulted in 62 of 452 positions (13.7%) not being detected by any of the receivers. Most of these undetected positions were outside the receiver network or in shallow water near shore (Fig. 2). After approximately 3 months (10–13 September 2012), data were downloaded from the acoustic receivers and processed in a VUE database (Vemco Division, Amirix Systems Inc.).

Fig. 2. Acoustic range testing in the ≈3 km² study area used for monitoring behaviour and movement of cod (see also Fig. 1), showing positions where a range test tag was deployed and detected (filled circles) or not detected (open circles) by at least one of the acoustic receivers (Nos. 1–44).



Experimental C&R angling

Ten days after the last cod had been tagged and released, experimental angling from a small boat was initiated in the study area during June 2012. Only lures (i.e., soft plastic lures or metal jigs) with single or small triple hooks were used to minimize the risk of hooking damage. During this angling, a total of 698 cod were caught, of which nine cod were recaptures with acoustic transmitters (after a recovery period of at least 14 days after being tagged and released; Table 1). The recaptured cod were landed with a landing net and carefully released after de-hooking and length measurement. Capture depth was monitored using a conventional echo sounder (Humminbird Inc., Eufaula, Alabama, USA).

Data analysis

Out of the 80 individuals equipped with acoustic tags in the study area, data were poor or missing for nine cod (most likely due to harvesting and dispersal out of the study area), and these fish were excluded from further analyses. The remaining 71 cod ranged from 30 to 80 cm body length (mean = 48 cm).

To test whether the experimental angling was selective with regard to fish life history or behavioural traits, individual fish behaviour during the week from 28 May to 3 June was quantified. This time interval was chosen for generating "before data" because the last fish was tagged and released on 24 May, and the first fish was subsequently recaptured on 4 June. Diel vertical migration (DVM) was quantified as the range of depths (maximum – minimum observed depth) logged by the acoustic receivers for each individual at each date (24 h period). Similarly, the mean daily depth occupied by each fish during this period was quantified. In addition to these two behavioural traits, fish length was

Table 1. Summary details for the acoustically pretagged cod that were recaptured during the experimental angling.

ID	Tag date	Length (cm)	Mass (g)	Recapture date	Time	Depth (m)	Hook	Hooking location	Bleeding
7351*	18 May 2012	58	2105	4 June 2012	1153	14	Triple	Lips	No
7351*	18 May 2012	58	2105	4 June 2012	1831	14	Single	Lips	No
7308	9 May 2012	46	820	4 June 2012	2009	15	Single	Lips	No
7359	22 May 2012	60	2130	5 June 2012	1955	13	Single	Mouth	No
7344	18 May 2012	56	1580	6 June 2012	1043	13	Single	Lips	No
7313	11 May 2012	41	630	8 June 2012	1149	13	Single	Lips	No
7293	7 May 2012	39	615	10 June 2012	1542	14	Triple	Lips	No
7364	24 May 2012	41	645	12 June 2012	2051	7	Single	Lips	No
7303	9 May 2012	40	625	13 June 2012	1332	14	Single	Lips	No
7356	22 May 2012	56	1850	15 June 2012	1146	17	Triple	Lips	No

Note: ID, tag ID; Time, recapture time (UTC); Hook, type of hook used; Bleeding, continued bleeding after hook removal (Yes or No).

*Fish 7351 was recaptured twice during the experimental angling.

included as a life history variable in the analyses. The selectivity of the experimental angling (4–15 June) was analysed using a generalized linear model (GLM) (McCullagh 1984) with cod fate (recaptured or not recaptured) as a binary response variable (i.e., logistic regression), in which mean depth and DVM during the week before the experimental angling were included as explanatory variables. Fish length was added as a life history covariate in the model.

To explore whether the experimental C&R event influenced the large-scale movements (i.e., DVM behaviour over a 24 h period) of the cod, the recaptured cod (n = 9) were compared with the fish that were not recaptured (control group; n = 62). The analysis was somewhat complicated by the fact that for a given date, usually only one fish was recaptured (i.e., n = 1 observation on fish behaviour at this factor level). This was dealt with by comparing the mean of DVMs of the recaptured fish 1 day after recapture with the mean behaviour of the control fish during the corresponding 12-day "recovery" period (5–16 June). A GLM was used to explore if and how the experimental C&R event affected the DVM (response variable) of the cod. In this model, the fate of each fish was included as a factor with two levels (recaptured or not recaptured). For the recaptured fish, the response variable was the mean of DVMs on the day after capture, while for the nonrecaptured fish it was the mean of DVMs during the period from 5 to 16 June. To correct for (and quantify) individual "personality" differences in fish behaviour, the DVM during the week before fishing (28 May – 3 June) was added as a covariate in the model. A positive effect of this "before" variable meant that there were consistent individual differences in behaviour where, for instance, a fish that was among the more active individuals during the "before" period also tended to be among the more active individuals during the experimental angling period. Adding this variable allowed to directly quantify an additive effect of fish fate on post-release behaviour. For the statistical modelling, all variables were standardized to a mean of 0 and a standard deviation of 1.

To test if the C&R event had an impact on the short-term behaviour (i.e., 2 h intervals) of the cod, a GLM was used to compare the levels of activity before and after the C&R event. The depth measurements for each fish were aggregated into 20 min windows in each of which the mean and standard deviation of the depth were calculated. The standard deviation of the depth during each 20 min window was used as a proxy of the level of activity. Intermediate midwater depths in the short period during capture and following release were omitted where present.

Tags were analysed separately using a GLM relating activity to an independent variable corresponding to capture phase and another corresponding to the time of day. Analysing fish separately made no assumptions about shared behavioural traits, effectively allowing for complete "personality" differences. The capture phase was categorical containing three levels — (*i*) "pre-capture" during the 2 h prior to capture, (*ii*) "post-capture" during the 2 h after release, and (*iii*) "normal" for the period prior to the pre-capture period. The normal category was used to estimate diurnal activity patterns prior to the C&R event. The pre-capture category was used to establish activity patterns just prior to the C&R event, which allowed correcting for any deviations from regular pre-capture behaviour the fish was exhibiting shortly before the C&R event. The time of day was categorical with eight bins of 3 h each (i.e., 0000–0300, 0300–0600, etc.). The time of day was included to de-trend the data from diurnal patterns in the level of activity. This was suspected to be of particular importance when captures occurred near dusk or dawn, so that the pre- and post-capture periods may have corresponded to different behavioural periods.

The recovery period was examined for those fish that exhibited a significant difference in post-release behaviour. This was determined by dividing the day following capture into 2 h periods, which were compared with the 2 h pre-capture period.

Results

During the week prior to the experimental angling (28 May – 3 June), DVMs ranged from 5 to 25 m among individual cod, while the mean depth occupied ranged from 5 to 28 m. During the experimental angling, nine acoustically tagged cod were recaptured and released. Based on the before data, there was no statistical support for our experimental angling being selective on fish length (recaptured cod: mean length = 48.56 cm, SE = 2.93 cm; noncaptured cod: mean length = 47.37 cm, SE = 1.50 cm), DVM, or mean depth occupied by the fish ($p > 0.3$; Fig. 3; Table 2). All cod survived the release event, and there was no statistical support for an effect of C&R on large-scale movements (i.e., DVMs) during the day following recapture and release ($p = 0.31$; Table 2; recaptured cod: mean DVM = 14.7 m, SE = 1.7 m; noncaptured cod: mean DVM = 12.5 m, SE = 0.6 m). There was a strongly positive association between DVM during the week before fishing and DVM during the experimental angling period (regression slope = 0.74, $p < 0.001$).

While there were no significant changes in large-scale behaviour, three individuals (i.e., IDs 7344, 7356, and 7359) showed significantly altered small-scale behaviour ($p < 0.05$); two of these (7356 and 7359) exhibited decreased activity and one (7344) had increased activity during the first 2 h after the release event (Fig. 4). However, once diurnal patterns in activity were considered, only one (7356) of these individuals showed a significant change in activity ($p < 0.001$), and this change was a decrease in activity.

The recovery period for the three cod with altered behaviour after the C&R event ranged from 10 to 15 h (Fig. 5, left panel), when diurnal changes in activity were not considered. After this period,

Fig. 3. Life history (*a*) and behaviour (*b* and *c*) of coastal Atlantic cod during the week (28 May – 3 June 2012) before the experimental angling in the Sømskilen basin on the Norwegian Skagerrak coast, showing the individuals that were recaptured and released (filled bars, n = 9) and the individuals that were not recaptured (open bars, n = 62).

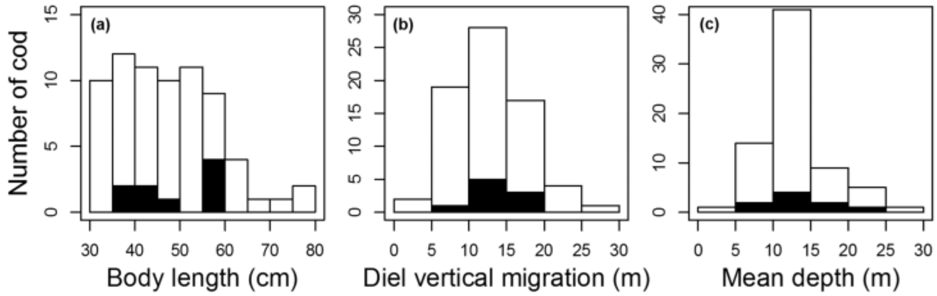


Table 2. Model estimates for the binomial fishing selectivity model and the large-scale DVM GLM.

	Binomial fishing selectivity model			Large-scale DVM changes		
	Estimate	SE	*p* value	Estimate	SE	*p* value
Intercept	2.02	0.39	0.00	0.22	0.22	0.34
DVM before	–0.42	0.43	0.33	0.74	0.08	0.00
Depth before	–0.28	0.39	0.46	—	—	—
Size	–0.43	0.45	0.34	—	—	—
Not recaptured	—	—	—	–0.25	0.24	0.31

Note: The binomial fishing selectivity model considered whether fish captured (response variable) was related to fish behaviour or size, which would have indicated fishing selectivity. The large-scale DVM model considered whether the DVM after the recapture period (response variable) differed between fish that were recaptured and those that were not recaptured.

all three cod returned to their normal behaviour patterns. Even when diurnal changes in activity were considered, a similar recovery period was observed for the cod (7356) that showed a significant change in activity after the C&R event (Fig. 5, right panel).

Discussion

To the best of our knowledge, this study is the first to investigate potential behavioural changes of cod after being caught and released by recreational anglers. While no significant effects of C&R on large-scale movements could be observed, the study revealed that some cod undergo short-lasting, small-scale alterations in their vertical movements after being released. Since the cod were fitted with acoustic tags several weeks prior to the C&R experiment, it was possible to study even small behavioural alterations immediately after the C&R event without bias caused by additional handling (Bridger and Booth 2003; Donaldson et al. 2008). While this study design has been used for some freshwater species in natural settings (e.g., Baktoft et al. 2013; Cooke et al. 2000; Halttunen et al. 2010; Klefoth et al. 2008), it has not been used for marine species in their natural environment. The most important reasons for this may be that the acoustic transmitters are relatively expensive and that the risk of losing tagged fish from the study area is generally higher in marine environments than in freshwater systems (Cooke et al. 2002). However, the present study showed that if the species to be studied is relatively stationary and (or) the study area is confined by natural barriers, such an approach can also work in marine environments.

Effects of C&R on cod behaviour

All nine recaptured cod survived the release event, but even though the cod were caught in depths less than 20 m and released as carefully as possible (i.e., following best practice), three of them showed temporary (up to 15 h) changes in their vertical swimming movements following C&R. These changes included resting periods or more active movements directly after the release. However, for two of these fish these changes in activity appeared to be attributable to diurnal changes in activity rather than the C&R event. A previous telemetry study in the same study area by Olsen et al. (2012) found that cod performed distinct DVMs, with smaller cod showing higher magnitudes in their migration patterns than larger cod. DVMs are explained as an evolutionary (adaptive) trade-off between food availability and predation risk, where the profitable shallow-water environments are exploited only in the shelter of darkness (Clark and Levy 1988). Alternative explanations may also involve adaptive thermoregulation during summer, since deeper waters are typically cooler than shallower habitats (Sims et al. 2006). The overall DVM patterns were not influenced by the C&R event in the present study. However, the fact that three cod in the present study showed short-lasting, small-scale activity changes after C&R indicates that these fish were temporarily less bold and displayed short-lasting increased antipredator behaviour. A variety of behavioural responses following C&R have been shown in other studies both for freshwater and marine species. Like two of the impacted cod in this study, European pike reduce swimming activity shortly after the C&R event, but resumed pre-capture behaviour within a short period of time (Baktoft et al. 2013; Klefoth et al. 2008). Similarly, Cooke and Philipp (2004) reported short-lasting lower post-release swimming activity of bonefish (*Albula* spp.) that were angled to exhaustion. For other species (e.g., large cichlids (*Serranochromis robustus* and *Oreochromis andersonii*) (Thorstad et al. 2004) and Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) (Gurshin and Szedlmayer 2004)), short-term hyperactivity has been shown as a response to C&R, which also was the case for one cod in the present study. Although none of these studies, including the present, showed long-lasting, large-scale impacts on the fish species studied, one has to keep in mind that even temporary small-scale behavioural alterations may have considerable consequences. For example, the released fish could be an easy target for predators during their resting periods (e.g., Cooke and Philipp 2004). Moreover, if the species shows parental care behaviour (e.g., smallmouth bass (*Micropterus dolomieu*)), the temporary removal from the nest and short-term behavioural changes due to C&R could eventually lead to nest abandonment and thus loss of reproductive success (Suski et al. 2003). Similarly, a temporary removal from lekking behaviour or ongoing spawning activities followed by a period of altered behaviour could result in lost mating opportunities for cod.

Although all cod were treated similarly during the experimental angling (i.e., similar fighting times, hooking damages, and air exposure), they responded differently, with some of them not impacted at all by the C&R event. One possible explanation for this could be differing physiological status among the individual cod (Nelson et al. 1994), although physiological parameters were not tested in the present study, as blood sampling could have influenced the results (Cooke et al. 2013). Many studies have shown that C&R can lead to physiological disturbances in released fish, for example, elevations in stress hormone levels (e.g., cortisol) (e.g., Donaldson et al. 2011; Gustaveson et al. 1991; Meka and McCormick 2005) and blood

Fig. 4. Vertical movements (as recorded by the ultrasonic receivers) of the nine recaptured cod 24 h before and 48 h after the C&R event sorted in the order of recapture. The vertical dotted line indicates the C&R event (i.e., fish ID 7351 was caught and released twice on the same day).

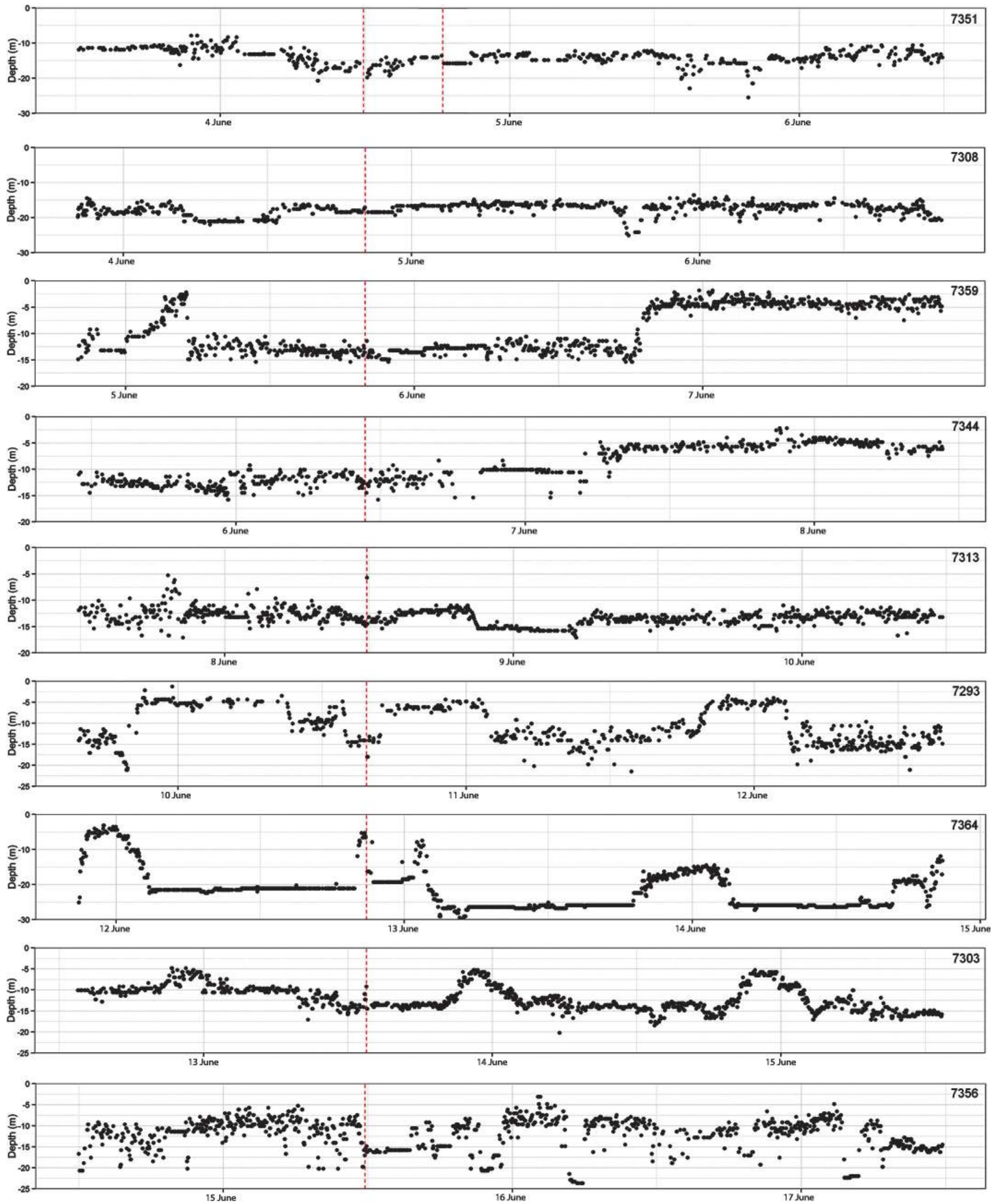
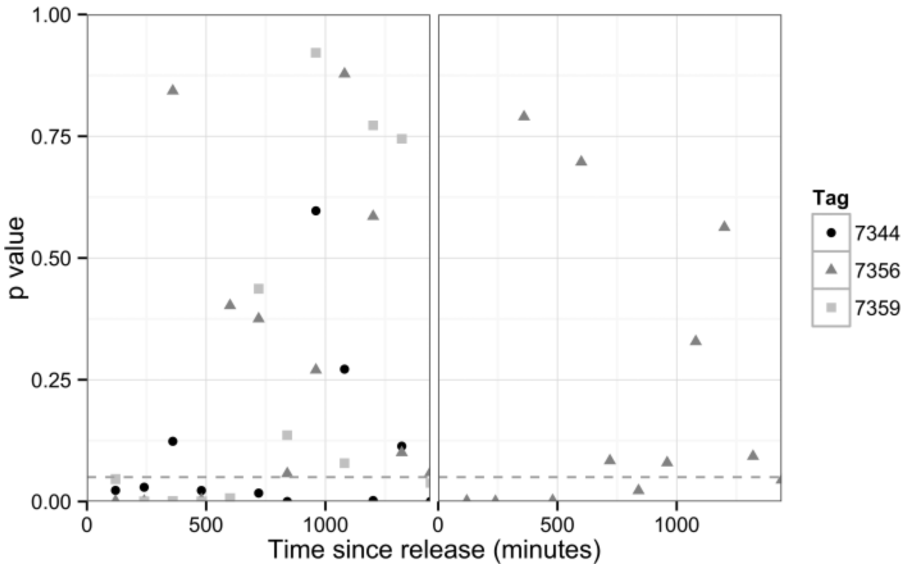


Fig. 5. Recovery periods of the cod that showed significantly different vertical movements during the 2 h before (–2 h – 0 h) and 2 h after (0 h – 2 h) the C&R event (left panel) when diurnal changes in activity were not considered in the analysis and (right panel) when diurnal changes in activity were considered. The *p* value for each comparison of time intervals (i.e., –2 h – 0 h versus 0 h – 2 h; –2 h – 0 h versus 2 h – 4 h, –2 h – 0 h versus 4 h – 6 h, etc.) is plotted for 24 h post-release. The broken line indicates the 0.05 significance level.



lactate concentrations (Ferguson and Tufts 1992; Roth and Rotabakk 2012), as well as changes in hematological parameters (Heberer et al. 2010). For cod, changes in physiological parameters such as decreased blood pH, and increased blood glucose and blood lactate levels after physical exhaustion during trawling have been described by Olsen et al. (2013) and thus have most likely also occurred to some degree in the present study.

Physiological disturbances have been suggested as one of the main reasons for reduced swimming activity in European pike after the release event (Klefoth et al. 2008). Hence, it is likely that the temporary behavioural alterations observed in the present study are also due to changes in physiological parameters and that the impacted cod returned to normal behaviour once their physiological balance had recovered to pre-capture conditions. Olsen et al. (2013) observed an increase in blood and muscle pH accompanied with a significant decrease in blood lactate already after 6 h compared with 3 h of recovery from the trawling event. This coincides with the relatively short recovery periods observed in the present study. Moreover, fighting times were very short as cod are relatively poor fighters on angling gear and can be brought to the boat quickly. Therefore, it is likely that cod are usually not completely exhausted during normal angling procedures. Similarly, Currey et al. (2013) found that the blood lactate levels of angled red throat emperor (*Lethrinus miniatus*) (fighting time <30 s) were significantly lower than those of maximally exhausted individuals. Neat et al. (2009) were able to follow the behaviour of one cod that was fitted with a data storage tag, recaptured by trawling, discarded, and recaptured again. This cod survived the discard event, although it was in the trawl for about 150 min, brought up from 110 m depth, and kept at the surface for about 15 to 20 min before it was discarded. However, in contrast with the impacted cod in the present study, this cod had a recovery period of at least 4 days, which is considerably longer than the recovery phase for the cod in the present study and is another indication that normal angling procedures do not exhaust cod to their maximum limits.

Implications for management

Although short-term effects of best practice C&R angling on the behaviour of cod are possible, this study revealed that C&R does not have significant lethal or long-lasting sublethal effects on cod if the fish are caught in shallow waters (<20 m), handled properly, and fishing gear that minimizes hooking damage is used. It is important to point out that these are necessary prerequisites for achieving minimal impacts on released cod, as for example bleeding due to hooking damage significantly decreases the likelihood for post-release survival of cod (Weltersbach and Strehlow 2013). As cod are protected by minimum landing sizes and bag limits in many European countries (Ferter et al. 2013*a*), fishery managers are encouraged to develop best practice guidelines and educate anglers on proper fish handling to reduce the negative impacts of C&R on this species (FAO 2012). Moreover, managers are encouraged to consider C&R practice in future management regulations, as the present study shows that C&R can work for cod if best practice guidelines are followed. Such guidelines should include the minimization of fighting time, reduction of air exposure, and the use of lures and hooks that do not cause major injury (Cooke and Suski 2005). In fact, the latter is of immediate importance because marine angling tourists in Norway reported that foul-hooking was an issue for smaller cod in particular (Ferter et al. 2013*b*). For fishing with natural bait, one recommendation could be to use circle hooks, as this hook type avoids foul- and deep-hooking and has been shown to reduce post-release mortalities without significantly reducing catch rates for other species (Alós et al. 2009).

Study limitations and future studies

The experimental angling in this study followed best release practice (e.g., Cooke and Suski 2005), and the results must therefore be seen as a best case scenario. Thus, an extrapolation to the general population of anglers targeting cod is not warranted because to date not all anglers release fish following best release practice. Long periods of air exposure as a result of slow de-hooking by inexperienced anglers, severe hooking damage, rough handling of the fish, and other factors, which could have a negative impact on the fish but generally can be avoided during normal angling, were not included in the present study.

Moreover, this study was conducted in rather shallow waters where barotrauma issues are negligible for cod (Weltersbach and Strehlow 2013). However, cod in the Dutch recreational fishery are often caught on wrecks that are located deeper than 20 m in the North Sea (T. van der Hammen, personal communication), and release rates of 24% have been shown (van der Hammen and de Graaf 2012). Similarly, in Norway, cod are often caught deeper than 20 m by recreational anglers, which can lead to increased mortality and behavioural changes in cod (van der Kooij et al. 2007).

In this study, the vertical movements of released cod were used as a measure of activity, and horizontal movements were not considered. Thus, changes in horizontal movements due to the C&R event may have been overlooked. The main reason for this was that the density of receivers in the study area was not high enough to receive the same acoustic signal by at least three hydrophones, which would have allowed calculation of the exact horizontal movements using triangulation (O'Dor et al. 1998). Some options would have been to estimate the mean horizontal position of each cod during intervals of 30 min (Simpfendorfer et al. 2002) or to estimate the kernel utilization distribution (McMahan et al. 2013; Simpfendorfer et al. 2012). However, considering the small impacts the C&R event had on the behaviour of the fish in this study, this method would not have picked up these behavioural alterations.

In future studies, the use of acoustic accelerometry may be a useful approach, as this method can quantify the energy use of aquatic animals based on body acceleration (compare Payne et al. 2011; Wright et al. 2014), which could be useful in post-release behaviour studies in particular. Moreover, it would be useful to include reflex testing before releasing the recaptured fish to obtain RAMP (reflex action mortality predictor) scores for each fish (Davis 2010). These scores could be linked to altered behaviour (e.g., a fish with one or more missing reflexes may be more likely to show certain behavioural alterations due to stress; e.g., Brownscombe et al. 2013). Once a relationship between altered behaviour and RAMP scores has been tested for a species in question, scientists and anglers can predict potential behavioural changes by testing a range of reflexes before they release their fish.

Olsen et al. (2012) showed that cod in the study area exhibit personality traits, as certain behaviours, such as DVM, were consistently more pronounced in some individuals than in others. The small-scale behaviour of cod in our study varied substantially on a day to day basis and between individuals, even in the absence of any C&R events. Consequently it was difficult to define "normal" behaviour and to determine whether a cod deviated from this behaviour after a C&R event. This formed a substantial statistical challenge as many of the assumptions underpinning traditional time-series analysis methods were violated. However, we were interested in changes of behaviour between the pre- and post-capture periods, and the approach we developed was able to identify small changes in behaviour between these two periods in an objective manner.

The present study showed that C&R does not have significant, long-lasting effects on the large-scale movement patterns of cod if the fish are caught in shallow waters and released following best practice guidelines. However, even if best practice is followed, short-lasting, small-scale behavioural alterations are possible. To minimize the negative impacts of C&R practice on cod, fisheries managers are encouraged to consider C&R practice in future management regulations, in conjunction with the development of best practice guidelines, and angler education on how to handle fish properly. Moreover, the present study highlights the importance of separating potential tagging effects from C&R effects when studying the sublethal consequences of C&R. The detection of small-scale behavioural changes as found in this study would most likely not have been possible if the tagging and C&R event were performed at the same time. This experimental approach has been used for freshwater species earlier, but as shown in this study, it can also work for marine fish if the species or stock to be studied is relatively stationary and (or) the study area is confined by natural barriers.

Acknowledgements

This research has been funded by the Institute of Marine Research and the University of Bergen. The acoustic telemetry work was funded by the Research Council of Norway through a grant to E.M.O. The authors thank Jon Helge Vølstad for input to the study design. Carla Freitas kindly analysed the range test data and created the graphics for these. Moreover, the authors are grateful to Martin Wiech, Enrique Blanco, Marine Dedeken, Florian Eggers, Arild Ring Pettersen, and Torbjørn Ertzeid Opsahl, who spent endless hours of angling during this study. The authors are also thankful to three anonymous reviewers, who provided constructive comments on an earlier version of the manuscript.

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