







Original Article

Post-release survival and prolonged sublethal effects of capture and barotrauma on deep-dwelling rockfishes (genus *Sebastes*): implications for fish management and conservation

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Barotrauma—injury induced by changes in pressure—is a widespread challenge for successfully releasing fishes following capture. We used acoustic telemetry to examine the long-term post-release survival and behaviour of four rockfish species (genus *Sebastes*) suffering from barotrauma following capture using recreational fishing techniques. We placed particular emphasis on examining Cowcod (*Sebastes levis*) and Bocaccio (*Sebastes paucispinis*), two historically overfished species along the United States West Coast that serve as good model species representing different ecological lifestyles. We show that fish survival was species specific and that 40% of observed mortality occurred more than 48 h post release—a typical time period used in many short-term survivorship studies. Cowcod survival was correlated with fish length, sea surface temperature, and dissolved oxygen concentration at the mean depth of capture. Generalized additive mixed models of Cowcod and Bocaccio behaviour showed that surviving individuals were negatively affected by capture and barotrauma for at least 30 d post-release. Our findings demonstrate the need for extended observations to accurately quantify the mortality of fishes suffering from barotrauma and show how such data can be successfully implemented into fisheries management through engagement between managers, scientists, and the fishing community.

Keywords: Bocaccio, catch and release, Cowcod, descending device, fisheries management, oxygen, post-release mortality, recreational fisheries.

Introduction

Recreational fisheries can heavily impact fish species, populations, and communities when not properly managed (Schroeder and Love, 2002; Coleman *et al.*, 2004; Cooke and Cowx, 2004; Lewin *et al.*, 2006). Accurate quantification of fishery-induced mortality for both targeted and bycaught fish species is critical for effective fisheries management (Davis, 2002; Arlinghaus *et al.*, 2007; Arlinghaus and Cooke, 2009). For fisheries in which all catch is retained, estimates of total fish mortality can be easily quantified. However, catch and release has become an increasingly popular practice worldwide, with an estimated 60% of all recreationally-caught fish being released (Cooke and Cowx, 2004; Bartholomew and Bohnsack, 2005). This is often done voluntarily by anglers in an effort to conserve the resource. In addition, many fisheries management agencies often use release (no retention) mandates for undersized or protected species as one of the main management tools to control fishing mortality and promote the rebuilding of overfished stocks. While this management strategy may drastically reduce fishery-induced mortality, it also increases uncertainty around post-release mortality estimates (Davis, 2002; Coggins Jr *et al.*, 2007). Underestimation of post-release mortality can lead to inaccurate projections of fish stock health, while overestimation can place undue restrictions on anglers.

While a global synthesis of catch-and-release research across recreational fisheries suggests the mean survival rate of released fishes is greater than 80%, mortality rates vary widely between species, fisheries, and habitats, with some fisheries approaching 100% mortality (Bartholomew and Bohnsack, 2005). Post-release mortality rates are often particularly high for physoclistous fishes—species with a “closed” gas bladder that lack a pneumatic duct connecting the gas bladder to the digestive tract. Reef-associated physoclists including sea basses (Serranidae), groupers (Epinephelidae), snappers (Lutjanidae), and rockfishes (Sebastidae) comprise some of the most heavily targeted marine fish groups. These fishes cannot “off gas” their gas bladder during rapid changes in depth experienced during capture. This results in the expansion and leakage of gas from the gas bladder into the visceral and cranial cavities which causes bloating and excessive buoyancy, displaced and crushed organs, and emphysema and emboli in various tissues (Rummer and Bennett, 2005; Hannah *et al.*, 2008b; Pribyl *et al.*, 2011). This capture-induced barotrauma can drastically increase post-release mortality through failure of the fish to overcome buoyancy issues and return to its depth of capture and through both acutely lethal (e.g. organ rupture and severe internal bleeding) or chronically lethal (e.g. internal haemorrhaging and secondary infection) injury (Rummer and Bennett, 2005; Jarvis and Lowe, 2008; Hannah *et al.*, 2008a). In addition, fish that ultimately survive may suffer sublethal effects post-release (e.g. if injuries affect swimming ability, behaviour, or energetic requirements) that can reduce individual fish growth and reproductive output, and if occurring in a significant portion of the population, can potentially impact fish stock health (Cooke and Schramm, 2007).

Research examining the effects of barotrauma on physoclistous fishes has primarily focused on short-term mortality rates, with some of the first mortality estimates derived from the ability of fish to overcome barotrauma-induced buoyancy and successfully submerge following release (Gitschlag and Renaud, 1994; Hannah *et al.*, 2008a; Hochhalter, 2012). As the inability of fish to submerge is a major determining factor of post-release survival, numerous

studies have examined the process of venting excess gas from the gas bladder and visceral cavity (using a hypodermic needle or other mechanism) to reduce buoyancy. While this technique has been shown to be beneficial in some cases, the general effectiveness of venting has had mixing results (Wilde, 2009; Brownscombe *et al.*, 2017). The recent advent of commercially available descending devices now allows anglers to release fish back to their depth of capture without venting (Hochhalter and Reed, 2011; Runde and Buckel, 2018; Bellquist *et al.*, 2019) and emphasizes the study of fish survival rates following recompression when barotrauma symptoms (e.g. bloating, organ displacement, and emphysemas) are largely reversed, but tissue damage caused by these symptoms may still be severe. Laboratory-based studies using hyperbaric chambers to simulate catch-and-release and invoke barotrauma have provided useful estimates of fish survival following recompression (Rummer and Bennett, 2005; Parker *et al.*, 2006; Pribyl *et al.*, 2012), but generally cannot reproduce many factors that affect mortality, including environmental conditions, predation, or fish handling practices. Field studies on short-term mortality in which captured fish suffering from barotrauma are held in cages at depth more accurately simulate fish handling practices and environmental stressors and are useful complements to hyperbaric chamber studies (Jarvis and Lowe, 2008; Hannah *et al.*, 2012, 2014). However, such studies are often limited in duration (48–72 h), precluding examination of delayed mortality and sublethal effects in the natural environment, and can have potentially confounding “cage effects” that can positively or negatively affect mortality estimates (Pollock and Pine, 2007).

Data-transmitting (acoustic telemetry) tagging methods provide useful information on post-release fish behaviour that can inform both short-term and long-term survival rates in the natural environment. Here, we build upon previous acoustic tagging work (Curtis *et al.*, 2015; Capizzano *et al.*, 2016; Runde *et al.*, 2020) to examine the post-release survival and behaviour of four species of rockfish (genus *Sebastes*), the most heavily targeted and captured group of fishes by recreational anglers along the West Coast of the United States. Particular emphasis was placed on Cowcod (*Sebastes levis*) and Bocaccio (*Sebastes paucispinis*), species that have heavily influenced regional groundfish management decisions since their original designation as “overfished” in 2000 and 1999, respectively. In an effort to conserve these species and allow their populations to rebuild, a number of regulations including forced release mandates (zero or limited retention) have been enacted and adjusted over the past 20 years (He and Field, 2017; Dick and He, 2019). Understanding the long-term survival of these species following capture and release is thus critical to their proper conservation and management. These two rockfish species are also excellent models for examining the effects of catch and release and barotrauma on species with contrasting movement patterns and habitat use—Cowcod are largely sedentary and benthic oriented, while Bocaccio, although still reef dependent, are more pelagic and conduct relatively large vertical movements above the reef (Love *et al.*, 2002; Starr *et al.*, 2002). Using depth and acceleration time series to monitor both short-term and delayed mortality, we quantify rockfish survivorship following capture and release with respect to environmental conditions, fish size, and barotrauma severity. We also provide the first descriptions of prolonged sublethal effects of barotrauma on rockfish behaviour in the months following release with a descending device and discuss our results in the context of local fisheries management and conservation measures.

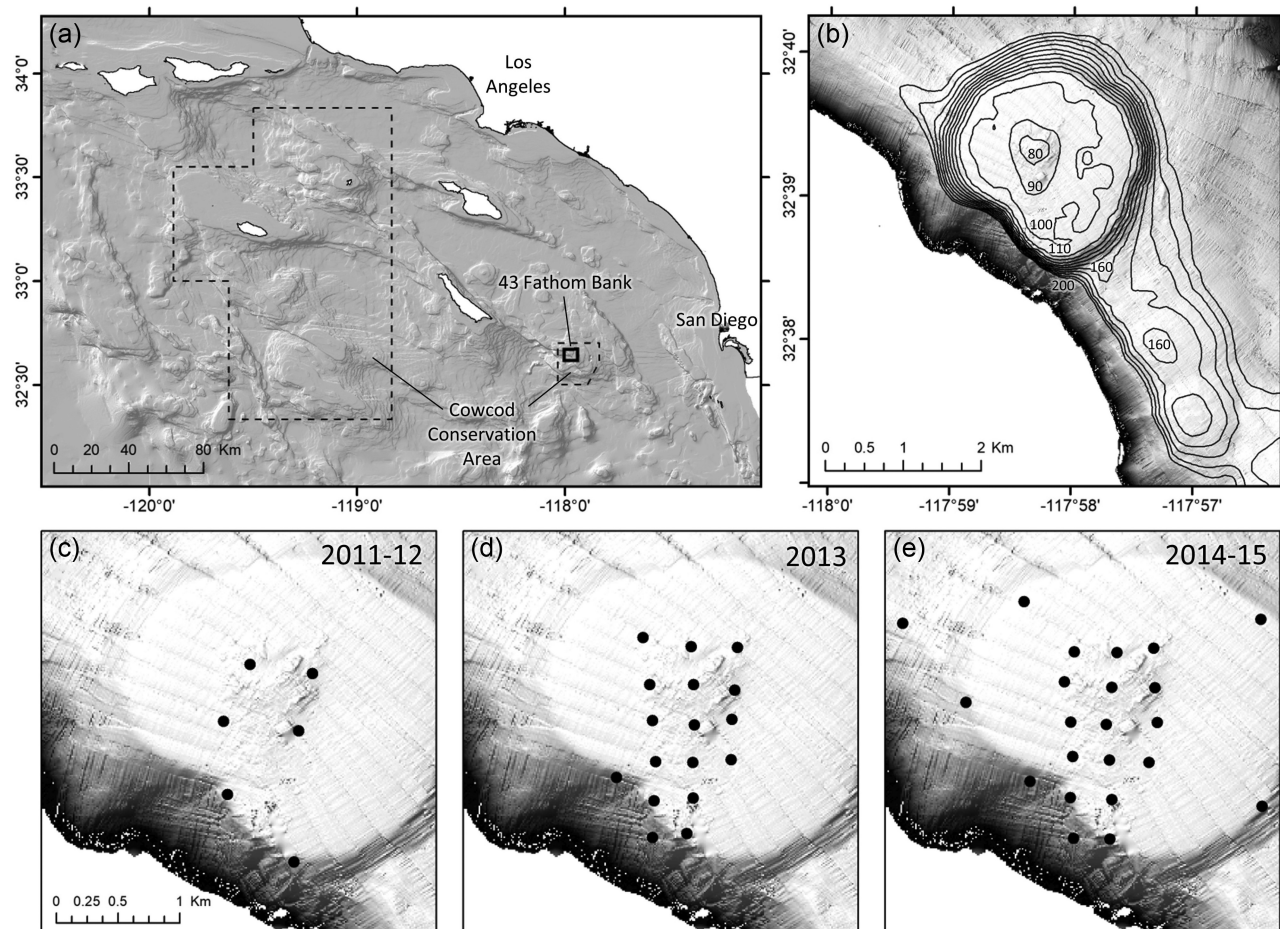


Figure 1. 43 Fathom Bank study site containing acoustic receivers (location indicated by black dots) used to assess the post-release survival and behaviour of 113 tagged rockfishes from four species. (a) The Southern California Bight showing the 43 Fathom Bank (black square) located approximately 80 km west of San Diego, CA within the Cowcod Conservation Area (dashed lines). (b) Enlarged view of the black box in (a) showing the bathymetry of the 43 Fathom Bank with contour lines depicted from 80 to 200 m depth. The location of receivers on the upper plateau and slope of the bank are shown for the study period: (c) 2011–12, (d) 2013, and (e) 2014–15.

Methods

Fish capture, tagging, and release

A total of 113 rockfish [47 Cowcod, 41 Bocaccio, 13 Sunset Rockfish (*Sebastes crocotulus*), and 12 Bank Rockfish (*Sebastes rufus*)] were captured and tagged between December 2011 and March 2015 on the 43 Fathom Bank, an underwater plateau approximately 80 km west of San Diego, CA within the Cowcod Conservation Area (Figure 1). This small, isolated bank (plateau area ~ 4.0 km²) was chosen to maximize post-release monitoring by minimizing potential fish emigration and limiting the potential recapture of tagged fish by recreational or commercial fishers. All fishing was conducted aboard the commercial passenger fishing vessel *M/V Outer Limits* using standard recreational fishing practices and gear: rod and reel with spectra-braided fishing line and a monofilament leader containing two baited J-hooks. Fish were captured at depths of 75–183 m (Table 1).

Upon capture, fish were measured (fork length; Table 1) and assessed for five external indicators showing the progression of barotrauma severity (Hannah *et al.*, 2008a, b; Pribyl *et al.*, 2009): (1) a stiff and bloated body from an expanded gas bladder, (2) accumulation of gas under the pharyngo–cleithral membrane confirming

the escape of gas from the gas bladder into the visceral cavity, (3) oesophageal eversion (protrusion of the oesophagus and or stomach) into the buccal cavity due to excessive gas expansion in the visceral cavity, (4) exophthalmia (bulging of the eyes) indicating the intrusion of gas into the orbital spaces, and finally, (5) ocular emphysema (recorded if present in at least one eye) showing the intrusion of gas into the eye under the cornea (Figure 2). The presence of each indicator was equally weighted and combined to determine a barotrauma score (Table 1). Fish were then tagged externally with either a V9AP or a V13AP acceleration and pressure-sensing acoustic transmitter (VEMCO, Innovasea, Bedford, NS, Canada) using FLOY TAG (Seattle, WA) intramuscular nylon darts (FIM-96, single anchor for V9, double anchor for V13) pushed between the pterygiophores near the front of the first dorsal fin (Figure 2). Although external attachment led to some tag shedding, surgical embedment of the tag within the visceral cavity would have been more invasive, prolonged the surface interval, and potentially enhanced a fish's ability to descend upon release by allowing gas to escape from the body. External tagging was thus considered to minimize the effects of tagging on fish survival and post-release behaviour, and to most closely match recreational fish release practices (Johnson *et al.*,

Table 1. Summary of rockfish size, capture, barotrauma, and tagging data (means \pm standard deviation).

Species	<i>n</i>	Fork length (cm)	Depth of capture (m)	Barotrauma score	Ocular emphysema (%)	Deck time (min)
Cowcod	47	61.4 \pm 7.5	123.1 \pm 22.7	4.68 \pm 0.47	70.2	2.3 \pm 0.8
Bocaccio	41	53.5 \pm 4.0	117.9 \pm 27.2	4.66 \pm 0.75	82.9	2.3 \pm 1.4
Sunset	13	51.0 \pm 2.0	141.5 \pm 10.9	4.08 \pm 0.83	38.5	4.2 \pm 1.0
Bank	12	40.7 \pm 2.0	141.0 \pm 20.1	3.75 \pm 1.30	75.0	4.1 \pm 0.8
Total/mean	113	55.1 \pm 8.4	125.3 \pm 24.8	4.50 \pm 0.81	71.7	2.7 \pm 1.3

Barotrauma score derived as the total number of external barotrauma indicators recorded out of: (1) Stiff and bloated body, (2) Expanded pharyngo–cleithral membrane, (3) Oesophageal eversion, (4) Exophthalmia, and (5) Ocular emphysema. Ocular emphysema (the most progressed barotrauma indicator) is presented as a percentage of fish exhibiting the injury.

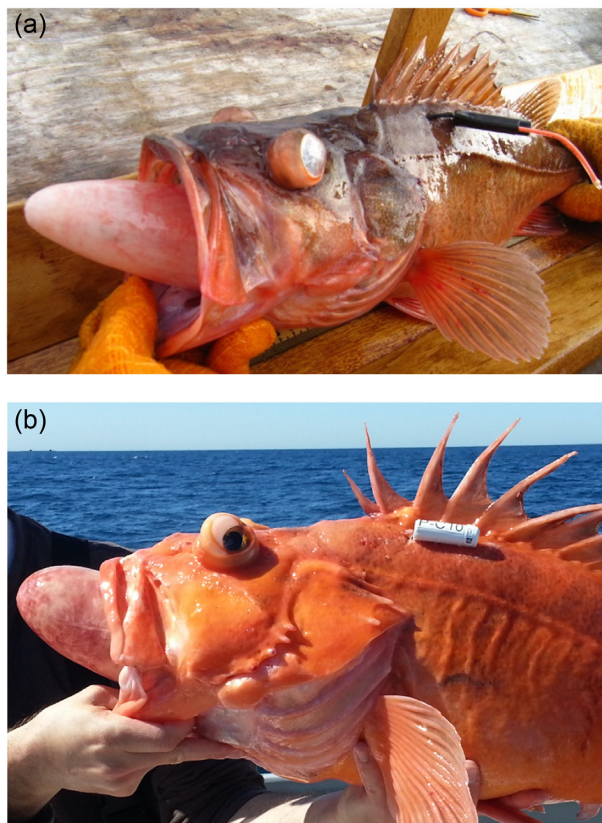


Figure 2. Acoustic transmitter attachment and external barotrauma indicators for (a) a 47.5 cm FL Bocaccio (*S. paucispinis*) tagged with a V9 single-anchored transmitter displaying a bloated body, everted oesophagus, exophthalmia, and ocular emphysema and (b) a 64.0 cm Cowcod (*S. levis*) tagged with a double-anchored V13 transmitter showing a bloated body, everted oesophagus, exophthalmia, and the first onset of ocular emphysema (anterior–dorsal portion of eye). Not visible in these images is the expansion of the pharyngo–cleithral membrane under the gill operculum.

2015). Fish were released at depths of 32.2–91.4 m using a weighted cage (Hannah and Matteson, 2007) or a SeaQualizer descending device (Davie, FL). The mean (\pm SD) surface interval for tagged fishes (including dehooking, tagging, and attachment to the descending device) was 2.7 \pm 1.3 min (Table 1). All rockfish capture and tagging was conducted in accordance with the NOAA Southwest Fisheries Science Center and University of California, San Diego Institutional Animal Care and Use Committee protocols SW1901 and S00080.

Estimating rockfish survival rates

Each acoustic transmitter was programmed to report an alternating pressure or acceleration measurement approximately every 240 s (randomized between 170 and 310 s to avoid acoustic signal collisions among nearby tags). Each acceleration measurement (m s^{-2}) was derived from the root mean square of acceleration on three axes (*x*, *y*, and *z*) averaged over the sampling period (90 s at 5 Hz). Fish depth and acceleration data were transmitted for up to 330 d at 69 kHz and recorded by VEMCO receivers (VR2, VR2W) positioned in an array across the main rocky-reef habitat on the 43 Fathom Bank (Figure 1).

Depth and acceleration data were used to determine survival status for each tagged individual. When both depth and acceleration varied over time, the fish was considered alive. If tag depth permanently stopped changing more than \pm 2.0 m from the mean (approximate cyclic pressure change observed due to the tidal cycle at the site), the dataset was further assessed to determine if mortality occurred or if the tag was shed from the animal. Such occurrences were compared to control tags attached to seven sacrificed (dead) fish (three Bocaccio and four Sunset Rockfish) that were placed directly on the seafloor in the middle of the receiver array using a Blacktip Catch and Release Recompression Tool (dead control fish were not tethered to the bottom and were allowed to drift in order to provide unaltered depth and acceleration profiles of known fish mortalities). Each negative control tag showed a stable depth profile (\pm 2 m) with 1–8 d of variable acceleration attributed to a scavenging period on the rockfish carcass. In five of the seven controls, the acceleration profile had a strong diel pattern, showing higher acceleration (scavenging) during the night (Figure 3a). Tagged experimental fish that displayed a similar diel pattern in acceleration following a permanent cessation of changes in depth were considered mortalities, while tags that showed little to no change in acceleration (all acceleration measures \leq 0.07 m s^{-2}) were considered to have been shed from the animal (Figure 3b and c). For tagged fish that stopped changing depth but showed an acceleration profile without a distinct diel pattern, the fish was considered to have died if there were significant differences in either mean or variance of acceleration pre- and post-cessation of depth change (T-test and F-test, respectively). In rare cases, there was significant background noise in acceleration (acceleration measures $>$ 0.07 m s^{-2}) long after scavenging would have occurred, which likely represented slight movement of a free tag on the seafloor possibly associated with large numbers of crinoids (Crinoidea) that have been observed on the reef. In such instances, mean acceleration and variance in acceleration were compared immediately following cessation of depth change and far removed from the event (fish death/tag shed). If these did not differ, the tag was considered shed.

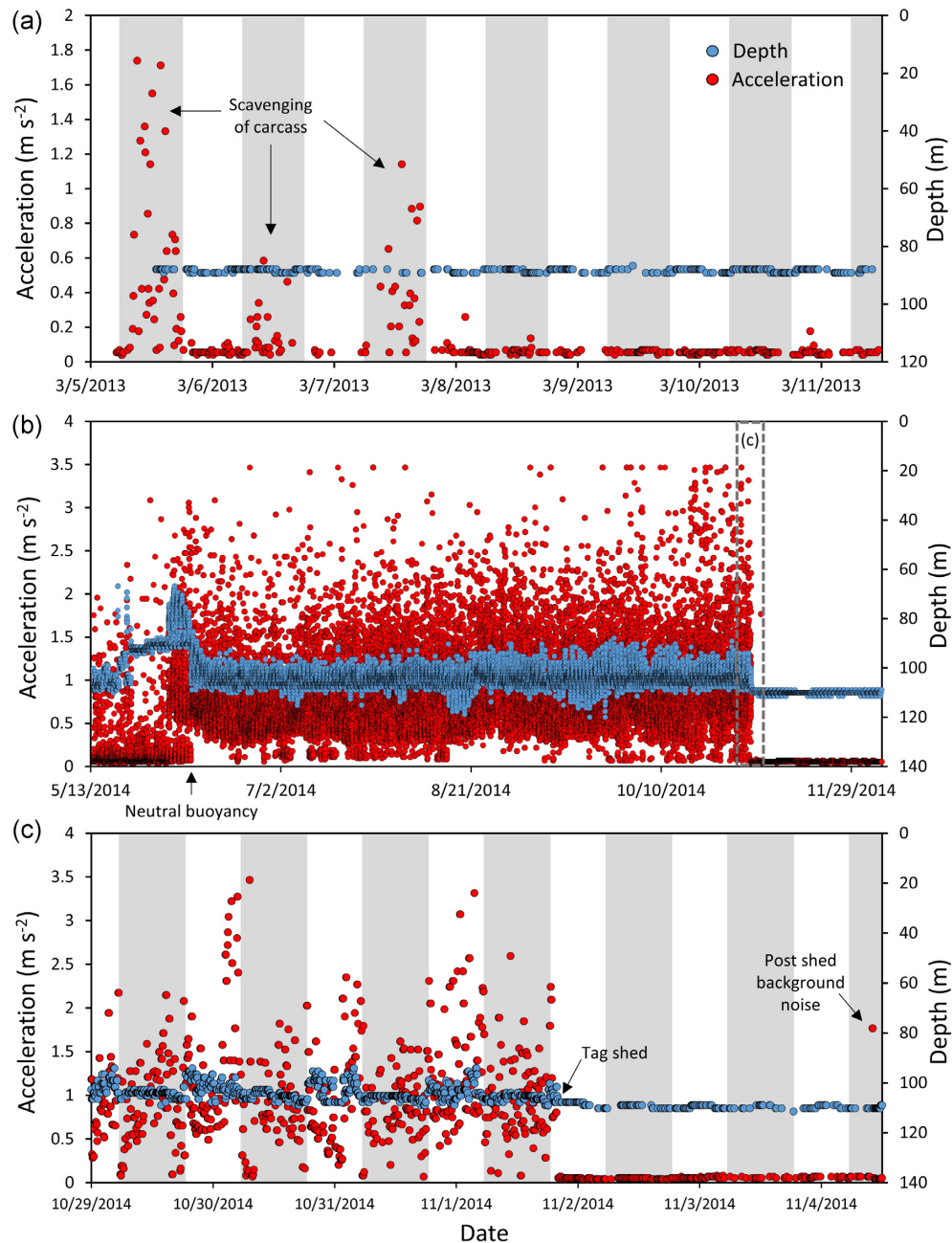


Figure 3. Depth (blue) and acceleration (red) profiles of (a) a sacrificed 45.5 cm Sunset Rockfish (*S. crocotulus*) control tag showing the typical diurnal scavenging period observed following fish mortality in comparison to (b) a live 54.0 cm Cowcod (*S. levis*) showing changes in depth and acceleration for 173 d at which point the tag was shed from the fish. Note point at which fish regains neutral buoyancy (26 d post-capture) (c) Enlarged view of dashed box in (b) showing the cessation in changes in tag depth and acceleration (with no scavenging period) indicating the tag was shed and resting on the bottom. White and grey bars designate daylight and nighttime hours based on sunrise and sunset. Note acceleration background noise/erroneous point post tag shedding in (b and c).

Using these criteria, survival status was determined for 110 of 113 tagged fish (46 Cowcod, 41 Bocaccio, 13 Sunset Rockfish, and 10 Bank Rockfish) until either their observed mortality, emigration from the system, battery failure of the tag, or shedding of the tag. The three fish for which survival status could not be determined (one tag accelerometer failure, two fish with insufficient data to distinguish between a dead fish or a shed tag) were not used in subsequent analyses. In five cases, the fate of the fish was opportunistically

informed through recapture events or by multiple detections on another acoustic array not on the 43 Fathom Bank (Supplementary Table S1). Because of the limited number of tagged Sunset and Bank Rockfish, our analyses, results, and discussion focus on Cowcod and Bocaccio.

Survivorship curves were developed for each species using a standard Kaplan–Meier (KM) non-parametric estimate of survival (Kaplan and Meier, 1958) as well as a parametric survival model

from Benoit *et al.* (2012, 2015) in the form of:

$$S(t) = \tau (\pi e^{-(\alpha t)^\gamma} + (1 - \pi)), \quad (1)$$

where survival probability (S) as a function of time (t) is dependent on the probability the fish survives initial capture at time zero (τ), and the probability of delayed mortality (π). Should the fish survive initial capture, π accounts for adverse effects of the fishing event on survivorship through prolonged injury (e.g. barotrauma) and stress. $\alpha \geq 0$ and $\gamma \geq 0$ are shape parameters for an underlying Weibull distribution that determines delayed mortality associated with injury and stress (Benoit *et al.*, 2012, 2015). This parametric model follows the KM survival estimate closely and as $t \rightarrow \infty$, $S(t)$ approaches the long-term survival rate (S_{lt}):

$$S_{lt} = \tau(1 - \pi). \quad (2)$$

The model can further be used to estimate the time at which essentially all catch-related mortality has occurred ($t_{s_{99}}$, set here as 99.9% per Benoit *et al.*, 2015):

$$t_{s_{99}} = -(\alpha \cdot \gamma)^{-1} \log(0.001). \quad (3)$$

Examining covariate effects on survival

Following initial model development, model variants of Equation (1) for both Cowcod and Bocaccio were fit by allowing π and τ to depend on the following covariates that potentially affect survival (Benoit *et al.*, 2015; Capizzano *et al.*, 2016): (1) trip ID, (2) capture depth, (3) barotrauma score (Table 1), (4) ocular emphysema (presence or absence of the most progressed barotrauma indicator), (5) fish fork length, (6) fish surface interval, (7) percent oxygen saturation at 125 m (mean depth of capture for all fish), (8) temperature at 125 m, (9) an interaction term of oxygen saturation and temperature at 125 m, (10) sea surface temperature, and (11) tag size (V9 vs. V13). Oxygen saturation and temperature at depth were measured directly on the bank via oxygen sensors (RBRsolo or RBRconcerto, RBR, Ottawa, ON, Canada) and temperature/depth sensors (LAT1400, Lotek Wireless, St. John's, NL, Canada) attached to various receiver moorings. Based on exploratory visualization (most distinct single-variable models and plotted trends) and data availability, we limited our model covariates to barotrauma score, presence of ocular emphysema, fish length, oxygen saturation level, and sea surface temperature as too many potential models would dilute inferential power of our relatively small dataset, which included 38 Cowcod and 39 Bocaccio. With these selected covariates, all possible models were fit using maximum likelihood and compared using the corrected Akaike's information criterion (AICc). We fit partial dependence plots for each covariate in the final selected model to visually assess the effects of each covariate on survival (Hastie *et al.*, 2009).

Quantifying sublethal effects of capture and barotrauma

We used generalized additive mixed models (GAMMs) (Hastie *et al.*, 2009) to examine the sublethal effects of capture and barotrauma on behaviour in surviving Cowcod and Bocaccio. Depth and acceleration data were used to define four behavioural proxies per day of sampling: (1) mean depth, (2) amplitude of vertical movement, quantified as the difference between the daily 10th-percentile ($P_{10\%}$) and 90th-percentile ($P_{90\%}$) depths, (3) mean acceleration, and (4) the proportion of time resting on the bottom, defined as the number of acceleration readings less than 0.1 m s^{-2} divided by the to-

tal number of acceleration readings in a given day (the 0.1 m s^{-2} cutoff was determined based on captive tagged animals in which hovering and swimming individuals always had acceleration readings $> 0.1 \text{ m s}^{-2}$). To prevent the inclusion of potentially moribund fish that emigrated outside the range of the acoustic receiver array, all individuals having fewer days of data than the species-specific time to 99.9% mortality thresholds (as determined by the parametric mortality model, Equation 3) were excluded from the GAMMs. All behavioural proxies were calculated per fish, per day (24 h period from 00:00 through 23:59). To increase the chances that daily variability in behaviour was captured, we excluded days represented by fewer than 50 data points and with less than 50% of the expected proportion of nighttime data points based on local dawn and dusk in the package *sunalc* (version 0.5.0; Thieurmel and Elmarhraoui, 2019) in R (version 3.6.0, R Core Team 2019). To account for tidal effects on measured depth, tidal predictions at 1-minute intervals from the nearest NOAA tide station were subtracted from the depth data (Station 9410032, Wilson Cove, San Clemente Island, ~65 km northwest of the study area). A summary of the average number of days of data per fish used to calculate behavioural proxies is given in Supplementary Table S2. To account for individual variability in capture and release conditions, barotrauma severity, and behavioural baselines, fish individual (Fish ID) was included in each of our GAMMs as a random effect. GAMMs of each behavioural proxy were run separately for each species.

To better elucidate sublethal effects of capture and barotrauma, other covariates expected to affect the behavioural proxies were also included in the GAMMs. For all behavioural proxies, average daily %O₂ saturation at 125 m depth (mean depth of capture for all fish) was included to account for changes in behaviour that may reflect responses to oxygen availability on the 43 Fathom Bank, which could be particularly important following capture stress. Although temperature is also an important determinant of fish metabolism, temperature at 125 m exhibited a much smaller range (9.2–10.7 °C) than O₂ saturation at 125 m (25.0–59.7% saturation) and the covariates were strongly positively correlated (Pearson's $R = 0.67$, $p < 0.001$). Thus, oxygen was considered a more useful proxy for the range of physiological conditions on the bank and temperature at the depth of capture was not considered as a covariate. Moon phase was included as a covariate in the models of mean depth and amplitude to account for potential associated changes in fish vertical habitat selection. $P_{10\%}$ depth was included in GAMMs of amplitude to account for the reduction in maximum possible amplitude with shoaling $P_{10\%}$ depth. Finally, because increased vertical habitat use might require periods of increased acceleration, amplitude of vertical movement was included in GAMMs of mean acceleration and proportion of acceleration data lower than 0.1 m s^{-2} . For each behavioural proxy, GAMMs with all possible combinations of covariates included in the full model were fit using restricted maximum likelihood using the *mgcv* package (version 1.8–28; Wood, 2011; Supplementary Table S3). Residuals of all models were normally distributed, thus Gaussian distributions with identity link functions were used for smoothing parameter estimations. Model selection was performed by comparing AICc among all candidate models in the *AICcmodavg* package (Mazerolle, 2020).

Finally, for fish that remained in the system for greater than the calculated time to 99.9% mortality, acceleration profiles allowed for estimation of the time (days post-release) at which fish regained neutral buoyancy, thus indicating the repair of gas bladder function. This time was defined when acceleration measurements < 0.1

Table 2. Summary of Kaplan–Meier (KM) and parametric (Benoît *et al.*, 2012, 2015) post-release survivorship curves and associated parameters for four rockfish species following capture and barotrauma.

Species	<i>n</i>	Observed mortalities	KM survival rate (%)	Parametric survival rate (%)	Prob. of surviving capture (τ) (%)	Prob. of delayed mortality (π) (%)	Last observed mortality (dpc)	Time to 99.9% mortality (dpc)
Cowcod (<i>S. levis</i>)	46	19	50.0 (35.7–70.5)	50.0 (34.5–64.4)	91.3 (84.8–97.8)	45.2 (29.9–61.8)	17.1	47.5 (25.2–73.2)
Bocaccio (<i>S. paucispinis</i>)	41	4	89.5 (80.2–99.8)	89.4 (80.1–97.6)	95.1 (88.5–100.0)	6.0 (0.0–13.7)	9.1	22.7 (0–26.4)
Sunset Rockfish (<i>S. crocotulus</i>)	13	3	76.9 (57.1–100.0)	76.9 (53.8–92.3)	76.9 (53.8–92.3)	0.0 (0.0–0.0)	0.0	0.0 (0.0–0.0)
Bank Rockfish (<i>S. rufus</i>)	12	4	45.0 (19.7–100.0)	45.4 (14.4–78.8)	90 (70.0–100.0)	49.5 (14.9–83.3)	1.6	2.9 (0.8–3.2)

95% confidence intervals are shown in parentheses. Parametric survivorship model parameter confidence intervals were determined through 100 000 bootstrap replicates. Abbreviations: dpc, days post-capture; Prob., probability.

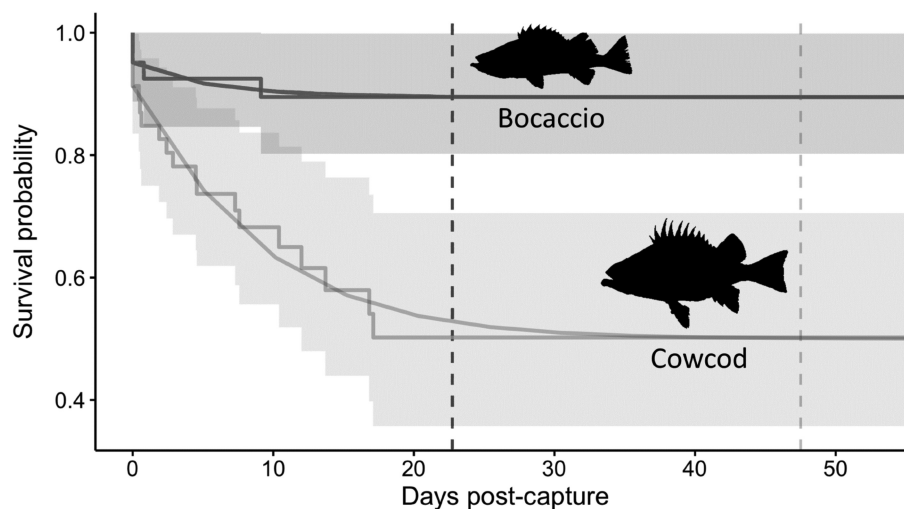


Figure 4. Parametric (smooth, Benoît *et al.*, 2012, 2015) and non-parametric (stepped, Kaplan–Meier) survivorship curves for Cowcod (*S. levis*) and Bocaccio (*S. paucispinis*). Shaded areas denote 95% confidence intervals for the Kaplan–Meier survivorship functions. Dashed lines represent the time at which 99.9% of catch-related mortality has occurred (22.7 d post-capture for Bocaccio, 47.5 d post-capture for Cowcod).

$m \cdot s^{-2}$ (representative of fish laying on the bottom) comprised less than 5% of the daily readings (see Figure 3b).

Results

Rockfish post-release mortality

Post-release survival status was determined for 110 rockfish, of which mortality was observed for 19/46 Cowcod, 4/41 Bocaccio, 3/13 Sunset Rockfish, and 4/10 Bank Rockfish. Of the observed mortality events, 33.3% (10/30) occurred immediately (four Cowcod, two Bocaccio, three Sunset Rockfish, and one Bank Rockfish), which was observed as fish either returning to the surface upon release (4 of the 10 immediate mortalities) or as no change in depth upon arriving on the seafloor (6/10). An additional 26.7% (8/30, all species combined) of mortality occurred within the first 48 h, with the remaining 40.0% of observed mortality occurring thereafter. The median time (Q1 and Q3) to observed mortality in all fish was 0.7 (0.0 and 7.4) d, 2.9 (0.4 and 10.4) d for Cowcod, 0.4 (0.0 and 7.0) d for Bocaccio, 0.4 (0.1 and 1.3) d for Bank Rockfish, and 0.0 d for Sunset Rockfish (all three Sunset Rockfish mortality

events were immediate), with the longest observed mortality occurring 17.1 d post-release in a Cowcod. Tags were determined to have been shed from 13 individuals from between 2.0 and 173.0 d post-release with a median (Q1 and Q3) shed time of 35.0 (12.0 and 86.7) d post-capture.

Modelled survival rates for each species using the non-parametric Kaplan–Meier (KM) as well as the parametric survival model (Equation 1) are given in Table 2, and survival rate versus time post release is shown for Cowcod and Bocaccio in Figure 4. The survival rate for Cowcod (KM survival 50.0%, CI: 35.7–70.5%) was much lower than for Bocaccio (89.5%, CI: 80.2–99.8%), while the more data-limited Sunset (76.9%, CI: 57.1–100.0%) and Bank Rockfish (45.0% CI: 19.7–100.0%) fell within a similar range (Table 2, Figure 4). The probability of surviving initial capture (τ) was generally similar among species, but Cowcod had a much higher probability of delayed mortality ($\pi = 45.2\%$, CI: 29.9–61.8%) than Bocaccio ($\pi = 6.0\%$, CI: 0.0–13.7%). Modelled time to 99.9% mortality based on Equation 3 was 47.5 d for Cowcod and 22.7 d for Bocaccio.

When including covariates considered to affect survival, the top performing parametric model for Cowcod included fish length,

sea surface temperature, and dissolved oxygen at 125 m, but did not include barotrauma score, or the presence or absence of ocular emphysema (Supplementary Table S4). Cowcod survival was negatively associated with fish fork length and positively associated with sea surface temperature and dissolved oxygen concentration at depth (Figure 5). Fish length had the greatest impact on survival rate (Figure 5a), followed by sea surface temperature (Figure 5b), and dissolved oxygen (Figure 5c). None of the covariates considered to affect survival were found to enhance model fit for Bocaccio (Supplementary Table S4), likely due to the small number of observed mortalities for this species.

Sublethal effects of capture and barotrauma on rockfish behaviour

Sublethal effects models showed that capture and barotrauma significantly impacted mean depth, amplitude of vertical movement, mean acceleration, and proportion of acceleration $< 0.1 \text{ m s}^{-2}$ in both species (Figures 6 and 7; Supplementary Tables S5–S7). Models were based on five Cowcod and 16 Bocaccio that remained within the range of the receiver array for longer than the 99.9% time-to-mortality thresholds (47.5 and 22.7 d, respectively; Supplementary Table S2). In all but one case, selected models explained over 50% of the variance in mean depth, amplitude, mean acceleration, and proportion of acceleration $< 0.1 \text{ m s}^{-2}$ (Supplementary Table S5). Days post-capture was the most important covariate explaining variance in mean depth and proportion of acceleration $< 0.1 \text{ m s}^{-2}$ for both species, as well as mean acceleration in Cowcod (F-statistics, Supplementary Tables S6 and S7). In the GAMMs describing Cowcod and Bocaccio amplitude, days post-capture was the second most important covariate following $P_{10\%}$ depth, which was used as a proxy for the “minimum depth” of daily vertical movement. Across all models, capture and barotrauma affected both species similarly. Immediately after release, both Cowcod and Bocaccio utilized shallower depths (Figures 6a and 7a) and showed increased amplitude of vertical movement (Figure 6d and 7c). In addition, mean acceleration was significantly depressed (Figures 6g and 7f), and both species exhibited higher proportions of time spent resting on the bottom (acceleration $< 0.1 \text{ m s}^{-2}$) in the weeks following release (Figures 6i and 7i). For all behavioural proxies, initial impacts of capture and barotrauma decreased in severity over ~30–60 d after release before the relationships became uninformative. Fish individual (Fish ID) was a significant predictor of all behavioural proxies, and there was substantial variability in behavioural proxy baselines among individuals of both species (Supplementary Figure S1).

Even though Cowcod and Bocaccio exhibited similar responses to capture and barotrauma, the magnitude of response often differed. The change in mean depth, acceleration, and proportion of acceleration $< 0.1 \text{ m s}^{-2}$ following capture and barotrauma was larger in Cowcod than Bocaccio (Figures 6a, g, and i and 7a, f, and i). Conversely, the change in amplitude of vertical movement of Bocaccio following barotrauma was approximately twice as large as in Cowcod (Figures 7c and 6d). Cowcod exhibited a significant negative relationship between mean depth of occurrence and % oxygen saturation at 125 m (Figure 6b), but oxygen was not a useful predictor of other Cowcod behavioural proxies. For Bocaccio, oxygen saturation was a significant predictor of all behavioural proxies (Figure 7d, g, and j), with the exception of mean depth, which showed a negative trend similar to Cowcod, but was not significant (Figure 7b).

Mean acceleration tended to increase with increasing oxygen saturation (Figure 7d), while amplitude and proportion of acceleration $< 0.1 \text{ m s}^{-2}$ decreased (Figure 7g and j).

Based on acceleration profiles (e.g. Figure 3b), neutral buoyancy was re-established $21.5 \pm 5.9 \text{ d}$ (range 13–26 d) post release for Cowcod ($n = 4$) and $25.7 \pm 19.7 \text{ d}$ (range 10–87 d) for Bocaccio ($n = 14$). These means do not include three individuals surviving past the time to 99.9% mortality threshold that emigrated from the system before the gas bladder was healed (one Cowcod emigrated 53 d post release and two Bocaccio at 28 and 31 d).

Discussion

The conservation and management of fisheries requires an accurate accounting of post-release and discard mortality, particularly when release (no retention) mandates are part of the active management strategy. Here, we show that rockfishes experiencing extreme barotrauma during capture can be successfully released, but survival and recovery rates are largely species specific. Differences in survival rates are likely linked to susceptibility to internal barotrauma injury associated with gas bladder morphology and the extent to which fish regularly move up and down in the water column (Parker *et al.*, 2006; Jarvis and Lowe, 2008), with more benthicly-oriented species such as Cowcod, generally showing lower survival rates (50.0%) than more pelagic species such as Bocaccio (89.5%). Due to the high rates of delayed mortality observed, our results suggest that short-term field and laboratory-based studies can overestimate fish post-release survival, and that external barotrauma symptoms (e.g. oesophageal eversion, exophthalmia, and ocular emphysema) are not necessarily useful predictors of fish mortality. Our findings thus emphasize the importance of quantifying long-term survival in the wild with respect to fishing and environmental conditions and monitoring post-release behaviour to fully gauge the effects of capture and release following barotrauma.

Long-term survival

Many fish mortality estimates used in fisheries conservation and management are based on short-term field studies (e.g. behavioural observation, temporary cage studies). However, our work suggests that such methods can underestimate fish mortality rates. Particularly, we found that Cowcod experienced much higher rates of delayed mortality than the other rockfish species examined, with 11 of 19 observed mortalities occurring more than 48 h post release, a common short-term holding time in many cage survivorship studies. We observed Cowcod mortality up to 17 d post release and modelled estimates suggest fishing-induced mortality could occur for up to 47.5 d (time to 99.9% mortality). Similarly, we have observed delayed mortality up to 22 d after capture when bringing Cowcod into captivity using hyperbaric chambers (Wegner, unpublished data). Such high rates of delayed mortality suggest at least for some species, short-term survivorship estimates using cages or other means underestimate total mortality. Conversely, for more robust species, such as Bocaccio, which show both limited short-term and delayed mortality, determination of long-term survival rate may only minimally increase resolution. Bocaccio long-term survival (89.5%, *CI*: 80.2–99.8%) determined in this study at capture depths of 74.7–182.9 m was similar to the short-term survivorship rate (~82%, *CI*: 79–89%) at depths of 57–89 m determined by Jarvis and Lowe (2008) using cages; the slightly lower survival rate

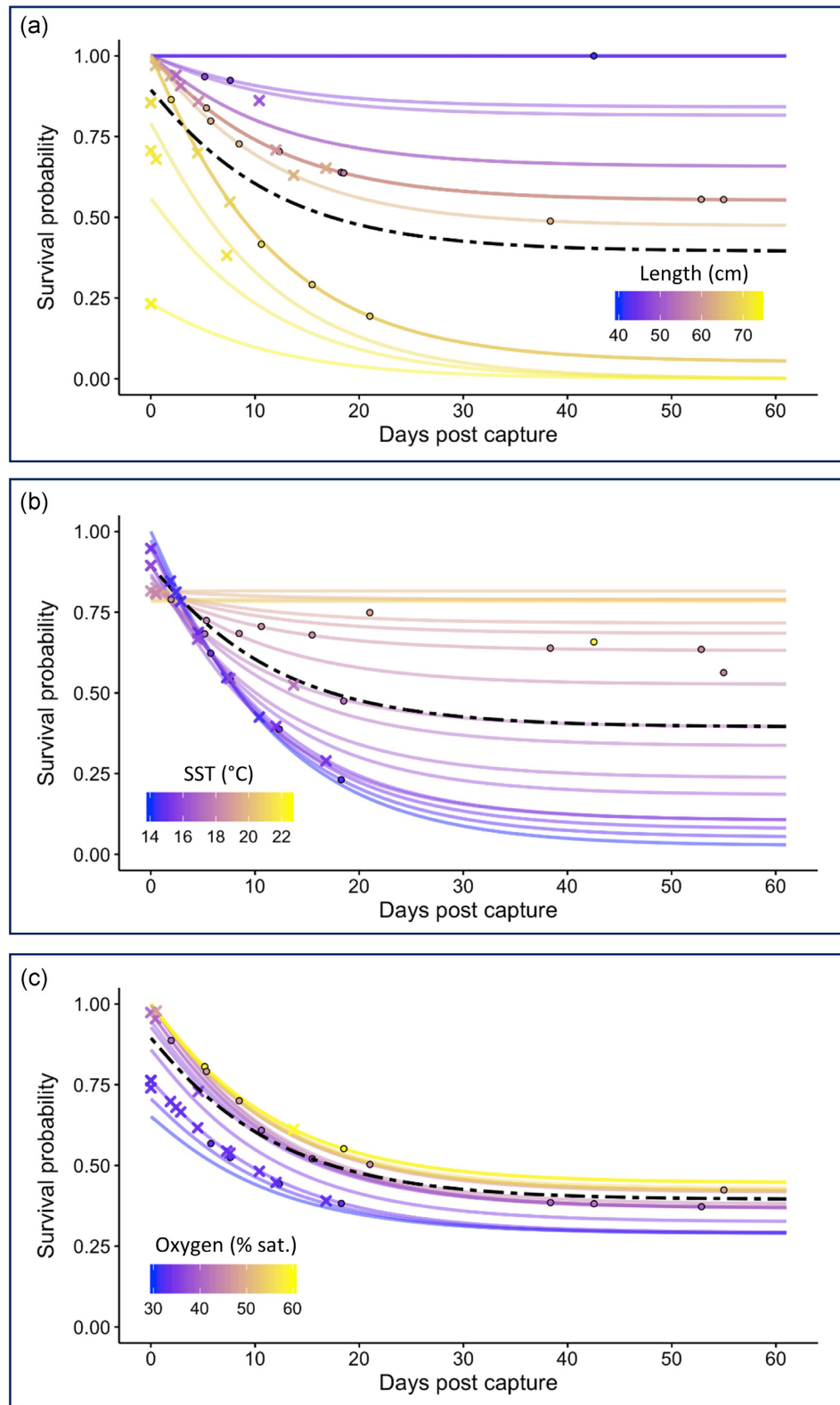


Figure 5. Partial dependence plots of modelled survival rates for Cowcod as a function of individual covariates: (a) fish fork length (cm) (b) sea surface temperature (SST), and (c) dissolved oxygen (% saturation) at 125 m, averaged over the other covariates. Individual fish data used for model fitting are shown as open circles (live fish at the time post capture they were last detected) or x's (fish that died shown at the time of mortality) as the estimated probability they would survive until that point. The dashed black line represents the mean modelled survival rate with all covariates included.

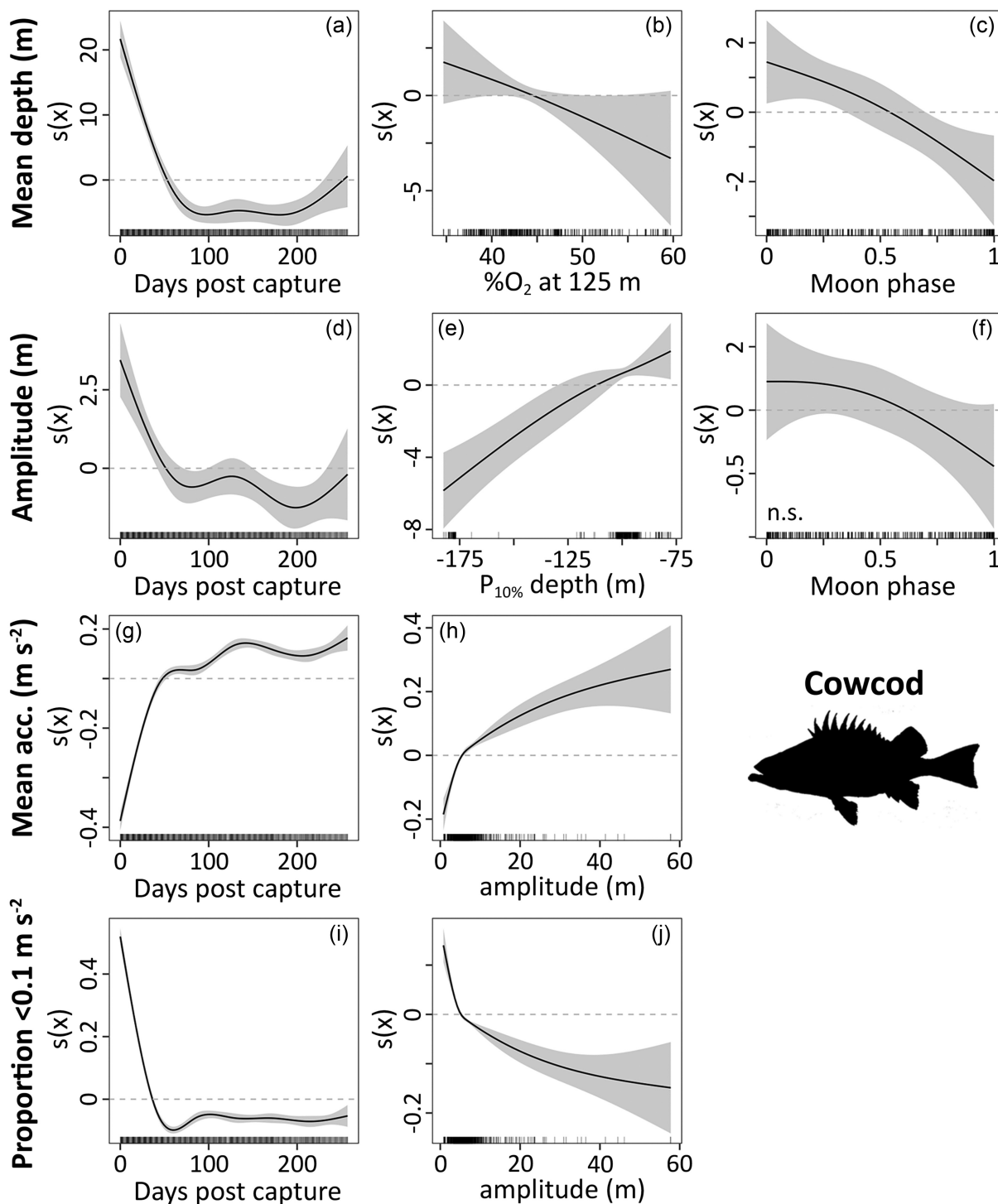


Figure 6. Partial effects plots from generalized additive mixed models showing the influence of days post-capture and other covariates on Cowcod (*S. levis*) mean daily depth (a–c), amplitude of daily vertical movement (d–f), mean daily acceleration (g and h), and daily proportion of acceleration < 0.1 m s⁻² (i and j). Each panel shows the response of the behavioural proxy (y-axis) across the observed range of a single covariate (x-axis). Responses are shown as deviations from the behavioural proxy’s mean value (0 = dashed line) while accounting for the effects of all other covariates in the model. Covariates = days post-capture, % oxygen saturation at 125 m (%O₂ at 125 m), moon phase (0 = new moon, 1 = full moon), daily 10th-percentile depth (P_{10%} depth), and amplitude of daily vertical movement. Rug plots at the base of each panel show the distribution of observations for each model. Shaded grey regions represent the 95% confidence intervals for each curve. Depths are negative, so positive partial effects reflect a shoaling response and negative partial effects reflect deepening. $s(x)$ = spline smoother of each covariate describing the behavioural response. Panels with “n.s.” in the lower left corner (f) indicate that the covariate in the selected model was not significant (see Supplementary Table S6).

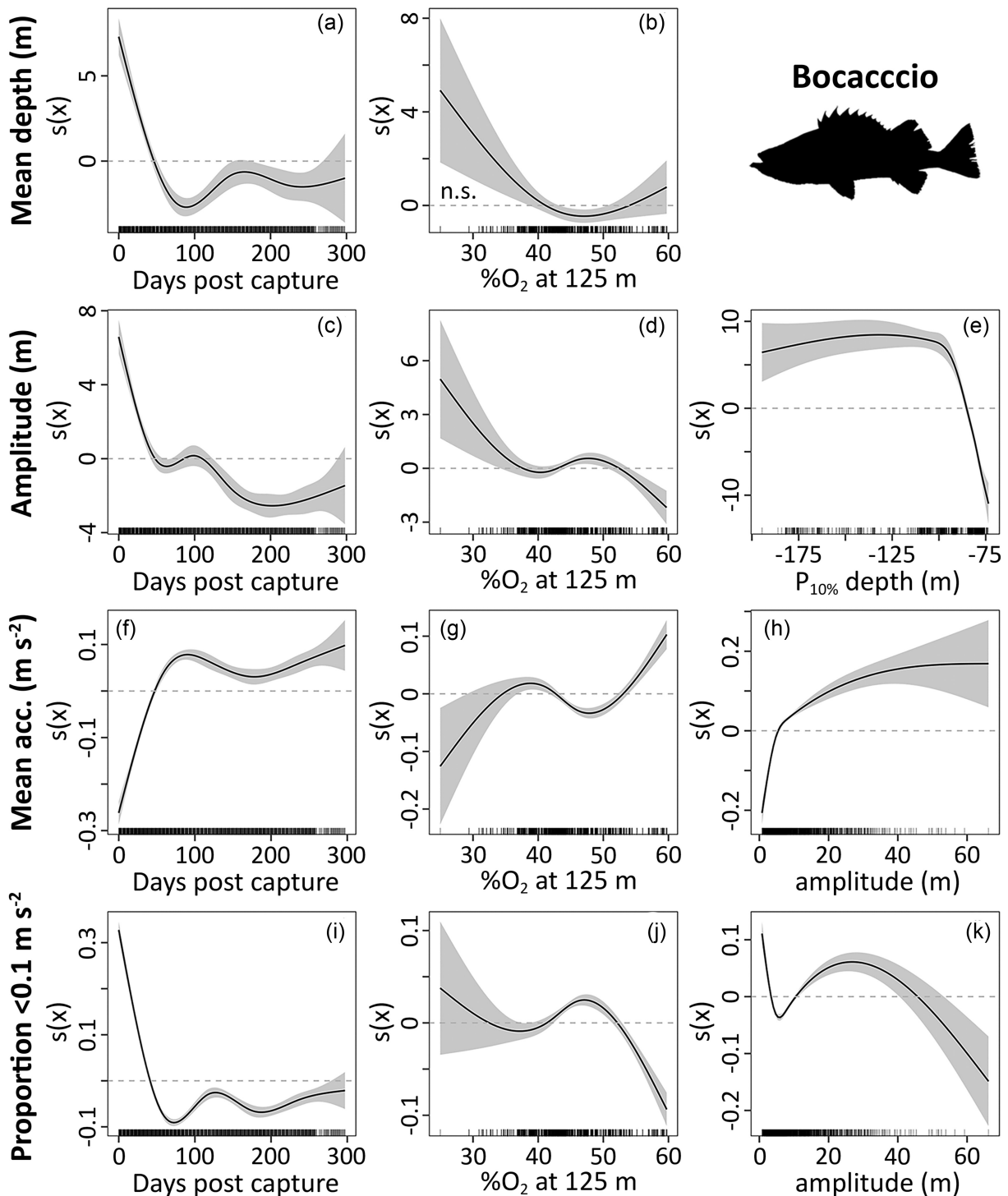


Figure 7. Partial effects plots from generalized additive mixed models showing the influence of days post-capture and other covariates on Bocaccio (*S. paucispinis*) mean daily depth (a and b), amplitude of daily vertical movement (c–e), mean daily acceleration (f–h), and daily proportion of acceleration $< 0.1 \text{ m s}^{-2}$ (i–k). Each panel shows the response of the behavioural proxy (y-axis) across the observed range of a single covariate (x-axis). Responses are shown as deviations from the behavioural proxy's mean value (0 = dashed line) while accounting for the effects of all other covariates in the model. Covariates = days post-capture, % oxygen saturation at 125 m (%O₂ at 125 m), daily 10th-percentile depth ($P_{10\%}$ depth), and amplitude of daily vertical movement. Rug plots at the base of each panel show the distribution of observations for each model. Shaded grey regions represent the 95% confidence intervals for each curve. Depths are negative, so positive partial effects reflect a shoaling response and negative partial effects reflect deepening. $S(x)$ = spline smoother of each covariate describing the behavioural response. Panels with “n.s.” in the lower left corner (b) indicate that the covariate in the selected model was not significant (see Supplementary Table S7).

from Jarvis and Lowe (2008) likely reflects the much longer surface interval experienced (14.4 ± 6.7 vs. 2.3 ± 0.8 min in this study).

While laboratory-based studies using hyperbaric chambers can invoke barotrauma and simulate catch and release in order to examine long-term survival and recovery (Parker *et al.*, 2006; Pribyl *et al.*, 2009, 2011), these studies are generally unable to capture many of the fishing and environmental variables that can impact survival. We show that Cowcod survival was impacted by both sea surface temperature and the dissolved oxygen level at the depth of capture (Figure 5b and c). Unlike previous studies in which mortality typically increased with warmer sea surface temperature due to thermal shock and increased fish metabolic demand (Davis, 2002; Jarvis and Lowe, 2008; Diamond and Campbell, 2009), we found that Cowcod survival was lowest at colder sea surface temperatures. This is likely associated with poor water conditions including low levels of dissolved oxygen (Figure 5c) associated with cold, deep-water upwelling, which is common along the U.S. West Coast (McClatchie *et al.*, 2010). Thus, when capturing fish from greater depths in which dissolved oxygen and other water conditions are likely sub-optimal, the physiological oxygen debt incurred during capture associated with exercise, stress, and barotrauma injury may result in increased post-release mortality. This likely explains why survival rates of Cowcod captured and brought into captivity using hyperbaric chambers [69% (11/16) Smiley and Drawbridge (2007), 75% (12/16) Wegner *et al.* (unpublished data)], in which oxygen saturation was kept near 100%, are higher than those determined herein for fish released in the wild (50% survival). This emphasizes that laboratory-based studies conducted under more ideal environmental conditions also likely underestimate fish post-release mortality.

Despite the importance of dissolved oxygen and temperature, fish length was the strongest predictor of Cowcod mortality with survival rates decreasing precipitously with size (Figure 5a). The six largest Cowcod tagged (70.5–74.0 cm) all succumbed to post-release mortality, while four of the five smallest Cowcod (41.4–50.5 cm) survived. This has particularly important ramifications for conserving historically overfished Cowcod populations, for which management efforts have established large offshore Cowcod Conservation Areas which prohibit groundfish fishing (Figure 1) as well as depth restrictions [bottom fishing is prohibited outside the 100 fathom contour (182.9 m) in any location in southern California as of Jan 2021] in order to minimize Cowcod interactions. Because Cowcod segregate spatially and by depth, with larger, mature individuals tending to inhabit offshore banks and deeper water (Love *et al.*, 2002; Butler *et al.*, 2003), these restrictions are particularly effective at avoiding the catch of large Cowcod, which based on our results, are less likely to survive capture, even when properly released with a descending device. The continuation of such measures to avoid fishing interactions with large Cowcod are particularly important as larger females disproportionately contribute to recruitment through larger clutch sizes and multiple broods (Love *et al.*, 1990). Conversely, interactions with smaller Cowcod are likely less concerning as our data suggest they can be released with much higher survival rates, although data on smaller juvenile Cowcod less than 41 cm FL (= 50% maturity according to Love *et al.*, 1990) are still needed.

Other factors such as depth, barotrauma score, and the presence of ocular emphysema (the most progressed symptom of barotrauma measured) did not improve survivorship model fit for either Cowcod or Bocaccio. While some previous studies have shown external barotrauma indicators can be useful predictors of post-release mortality (Diamond and Campbell, 2009; Hannah *et al.*, 2012; Runde

et al. 2019), for many species these indicators are not representative of internal injury or survival when releasing fish at depth (Rummer and Bennett, 2005; Jarvis and Lowe, 2008). Depth of capture has often been shown to be a strong predictor of barotrauma injury and post-release survival in other physoclistous species, and for some species “critical depths” have been estimated below which mortality drastically increases (Wilson and Burns, 1996; Rummer and Bennett, 2005; Hannah *et al.*, 2014). However, fish examined in this study were captured from deeper depths (75–183 m) than most previous studies and, in most cases, appear to have experienced a maximum effect of barotrauma as indicated by near maximum barotrauma scores (Table 1). Deep-dwelling species, like those studied here, may reach a point at which additive effects of depth are of less concern if expanded gas escapes the body and prevents further damage. While not specifically recorded for each fish captured, we noticed that most individuals were brought to the surface surrounded by numerous free gas bubbles that we assume escaped through rupture of the body wall. Such gas escape has been noted previously for certain rockfish species captured at shallower depths, and in many cases appears to drastically reduce barotrauma injury and likely increase survival (Hannah *et al.*, 2008a; Hochhalter, 2012; Pribyl *et al.*, 2012). For the species studied here, gas escape appears to usually occur only after severe barotrauma injury, but also appears to prevent further mortality with increased depth of capture. Thus, our findings show that physoclistous fishes captured at depths up to ~180 m and experiencing extreme barotrauma can survive if properly released using a descending device, and that increased capture depth for such deeper-dwelling species does not necessarily increase mortality.

Sublethal effects on swimming ability and habitat use

Key aspects of Cowcod and Bocaccio behaviour including depth preference, vertical movements, activity level, and the amount of time resting on the bottom were impacted by capture and barotrauma injury for 30–60 d. Immediately following release, both species exhibited lower than average activity (acceleration), largely explained by large amounts of time spent lying on the bottom (up to 50% more time by Cowcod, 30% more by Bocaccio immediately post release; Figures 6g and i and 7f and i). This behaviour was likely due to their negative buoyancy associated with a ruptured gas bladder in which some gas likely escaped the body during capture, while that retained within the peritoneal cavity would have been reabsorbed by the surrounding tissue (Rankin *et al.*, 2017). The acceleration profiles of Bocaccio and Cowcod showed that both species typically re-established neutral buoyancy—indicating the repair of the gas bladder—within 10–30 d post-release (e.g. Figure 3b). These gas bladder repair times are similar to those determined previously for other rockfishes (Parker *et al.*, 2006; Rankin *et al.*, 2017), but are shorter than the duration of behavioural impacts of capture and barotrauma on both Cowcod and Bocaccio (Figures 6 and 7), suggesting that re-establishing neutral buoyancy does not indicate complete recovery from capture. This is consistent with previous findings that rockfishes regaining neutral buoyancy may not have fully healed gas bladders and may still have compromised buoyancy control (Parker *et al.*, 2006; Rankin *et al.*, 2017). In one Bocaccio, neutral buoyancy was not re-established until 87 d post-capture, and three tagged animals did not regain neutral buoyancy before emigrating from the receiver array (up to 53 d post-release). Barotrauma injury may thus result in prolonged and perhaps permanent swim bladder injury, which is likely to have lasting impacts

on swimming energetics and prey capture efficiency, and may have ramifications for other behaviours such as courtship and spawning.

Both Cowcod and Bocaccio also showed altered habitat selection and vertical movements following capture and barotrauma. Immediately post release, both species occupied shallower than average habitat (Cowcod by ~ 20 m and Bocaccio by ~ 7 m) and made larger than average daily vertical movements (Cowcod amplitude increased by ~ 3 m, Bocaccio by ~ 7 m; Figures 6a and d and 7a and c). While such changes in behaviour could reflect disorientation and damage to depth-sensing mechanoreceptors in the gas bladder (Blaxter and Tytler, 1978; Rankin *et al.*, 2017), the scale and directionality of these movements suggest fish were actively selecting favourable habitat for recovery, possibly to avoid hypoxia, which increases with depth. With the effects of capture stress and barotrauma isolated, oxygen saturation on the bank was a significant predictor of mean daily depth for Cowcod (Figure 6b), which occupied shallower depths under lower oxygen concentrations. The more active and pelagic-oriented Bocaccio showed a decrease in activity (Figure 7g and j) and an increase in the amplitude of vertical movements (~ 5 m under lowest oxygen conditions, Figure 7d), likely rising off the bottom or moving up the slope of the bank to avoid hypoxia, which during upwelling or high tide is likely to shoal along the bottom (Gallo *et al.*, 2020). It thus seems likely that hypoxia-avoiding behaviour (selecting for shallower habitat and increasing vertical movements off the bottom, Figures 6a and d and 7a and c) as well as decreases in activity (Figures 6g and i and 7f and j) would be exacerbated by increased oxygen demand immediately following capture and injury, and that the more benthic-oriented Cowcod would show greater susceptibility to the impact of hypoxia on the rate of post-release mortality. These impacts of hypoxia on fish mortality rate and post-release behaviour suggest environmental conditions may be worth consideration in management decisions for species such as Cowcod when fishing on offshore banks where shallower habitat and more oxygenated waters are not available.

A case study for successful management—working together to promote sustainability and preserve future fishing opportunities

Rockfishes and related groundfish species comprise the largest species complex of recreationally caught fish on the U.S. West Coast. In 2019, nearly 1 750 metric tons were landed on over 800 000 angler trips in California alone (CDFW, 2019). While there are over 65 rockfish species that inhabit the shelf and slope habitat from California to Alaska (Love *et al.*, 2002), groundfish management decisions are based largely in response to the stock status of only a few key species. From 1999 to 2002 seven rockfish species were declared overfished by the Pacific Fisheries Management Council (PFMC), governing management body of U.S. West Coast fisheries), including Cowcod and Bocaccio (the two focal species of the current study), which led to large-scale rebuilding plans and sweeping regulations for both commercial and recreational fishers in an effort to reduce fishery-induced mortality. This included the establishment of distinct offshore Rockfish and Cowcod Conservation Areas (groundfish fishing prohibited at any depth) in federal waters (Figure 1), a network of coastal marine protected areas in state waters, regional fishing depth restrictions, fishing gear restrictions, seasonal closures, moratoriums on specific species such as Cowcod, and bag limits on species such as Bocaccio. Unfortu-

nately, fish moratoriums and bag limits were not necessarily effective in reducing fish mortality, as, if captured, prohibited species were typically discarded at the surface, where they would often be left floating (unable to submerge) to eventually succumb to their barotrauma injuries or predation. This led the PMFC to adopt an assumed 100% post-release mortality rate for most rockfish species caught at depths greater than 30 fathoms (54.9 m; PFMC, 2014).

In response, state and federal government, non-government organizations, and industry leaders in the recreational and commercial fishing communities came together in a massive education campaign to promote the release of rockfishes with descending devices to assist fish back to their depth of capture (Theberge and Parker, 2005; Bellquist *et al.*, 2019). This led to a flurry of hyperbaric chamber and cage studies to test the survival of rockfishes if properly recompressed following barotrauma. Data from such studies (Jarvis and Lowe, 2008; Hannah *et al.*, 2012), as well as preliminary long-term survivorship data from the present study were collated to update post-release mortality rates on the U.S. West Coast (PFMC, 2014). This, in conjunction with successful buy-in from the California recreational fleet to use descending devices for encounters with protected species such as Cowcod (mandates to use descending devices are used in other West Coast states), along with positive trends in the rebuilding of all seven overfished rockfish species, has led to relaxation of fishing depth restrictions (depth closures) for recreational fishing along the West Coast in recent years. The rebuilding of rockfish populations along the U.S. West Coast, including the adoption of descending devices by the recreational fishing community to increase rockfish release success and survival, is now touted as a major conservation success story fuelled by both effective management and the voluntary efforts of recreational anglers. Descending devices are now used (and in many cases required) along both coasts of the United States and Canada to successfully release fishes experiencing barotrauma, and although additional species-specific post-release survivorship studies are needed, the general adoption of descending devices represents a major step forward in managing fishery-induced mortality.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

Data availability

The data underlying this article are available in the article and in its online supplementary material. Individual fish behavioural data can be shared on reasonable request to the corresponding author.

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