



Original Article

A generalized model for longitudinal short- and long-term mortality data for commercial fishery discards and recreational fishery catch-and-releases

Hugues P. Benoit^{1,2*}, Connor W. Capizzano³, Ryan J. Knotek³, David B. Rudders⁴, James A. Sulikowski³, Micah J. Dean⁵, William Hoffman⁵, Douglas R. Zemeckis⁶, and John W. Mandelman⁷

¹Gulf Fisheries Centre, Fisheries and Oceans Canada, PO Box 5030, Moncton, NB, Canada E1C 9B6

²Department of Biology, Dalhousie University, Halifax, NS, Canada B3H 4J1

³Marine Science Center, University of New England, Biddeford, ME 04005, USA

⁴College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, VA 23062, USA

⁵Massachusetts Division of Marine Fisheries, Gloucester, MA 01930, USA

⁶School for Marine Science and Technology, University of Massachusetts Dartmouth, 200 Mill Road, Suite 325, Fairhaven, MA 02719, USA

⁷New England Aquarium, John H. Prescott Marine Laboratory, Boston, MA 02110, USA

*Corresponding author: tel: +1 506 851 3146; fax: +1 506 851 2620; e-mail: hugues.benoit@dfo-mpo.gc.ca

Benoit, H. P., Capizzano, C. W., Knotek, R. J., Rudders, D. B., Sulikowski, J. A., Dean, M. J., Hoffman, W., Zemeckis, D. R., and Mandelman, J. W. A generalized model for longitudinal short- and long-term mortality data for commercial fishery discards and recreational fishery catch-and-releases. – ICES Journal of Marine Science, 72: 1834–1847.

Received 4 January 2015; revised 15 February 2015; accepted 18 February 2015; advance access publication 11 March 2015.

Conservation concerns and new management policies such as the implementation of ecosystem-based approaches to fisheries management are motivating an increasing need for estimates of mortality associated with commercial fishery discards and released fish from recreational fisheries. Traditional containment studies and emerging techniques using electronic tags on fish released to the wild are producing longitudinal mortality-time data from which discard or release mortalities can be estimated, but where there may also be a need to account analytically for other sources of mortality. In this study, we present theoretical and empirical arguments for a parametric mixture-distribution model for discard mortality data. We show, analytically and using case studies for Atlantic cod (*Gadus morhua*), American plaice (*Hippoglossoides platessoides*), and winter skate (*Leucoraja ocellata*), how this model can easily be generalized to incorporate different characteristics of discard mortality data such as distinct capture, post-release and natural mortalities, and delayed mortality onset. In simulations over a range of conditions, the model provided reliable parameter estimates for cases involving both discard and natural mortality. These results support this modelling approach, indicating that it is well suited for data from studies in which fish are released to their natural environment. The model was found to be less reliable in simulations when there was a delay in discard mortality onset, though such an effect appears only in a minority of existing discard mortality studies. Overall, the model provides a flexible framework in which to analyse discard mortality data and to produce reliable scientific advice on discard mortality rates and possibilities for mitigation.

Keywords: discard mortality, natural mortality, parametric survival analysis, post-release mortality simulation study.

Introduction

A large proportion of worldwide commercial fishery catches are discarded for economic or regulatory reasons, with rates varying by region, species, and gear type (Alverson, 1997; Harrington *et al.*, 2005). Discarding is typically a wasteful practice that may have far reaching consequences on populations and ecosystems

(e.g. Kappel, 2005; Bellido *et al.*, 2011). Meanwhile, catch-and-release in recreational marine and freshwater fisheries is becoming a more common practice given an increasing conservation ethic among anglers and the implementation of management measures that require such behaviour; however, mortality rates and thus the resulting conservation benefits from such practices can vary

greatly by region and species (e.g. [Cooke and Schramm, 2007](#); [Cowx et al., 2010](#)).

Many fisheries management agencies are trying to limit discarding by improving gear selectivity to reduce incidental catch, or by instituting regulations that minimize discarding. In some instances, the amount of bycatch in a fishery has been capped either overall or as a percentage of directed species catch. Additionally, some fisheries management bodies have instituted mandatory landing of fish that would otherwise be discarded, as will occur under the revised European Union Common Fisheries Policy (CFP; [European Union, 2013](#)). Such landing obligations provide a strong incentive for harvesters to reduce incidental catch; however, they can also have the unintended consequence of increasing fishing mortality if the survival rate of otherwise discarded fish is high. In recognition of this, the CFP has provisions that allow for discarding in instances where there is a demonstrated high likelihood of survival. Consequently, additional studies on discard mortality will be required to this end. The need for such studies is also being motivated elsewhere by the desire to establish management measures that can improve the likelihood of successful live release, such as for protected or depleted species (e.g. [Grant and Hiscock, 2014](#)) or in recreational fisheries (e.g. [Cooke and Schramm, 2007](#)), as well as the need to account for discard-related losses of incidentally captured fish in population assessments (e.g. [Benoît, 2013](#)).

Many experimental approaches have been used to estimate discard or post-release mortality rates. These methods typically involve fish that are obtained on-board commercial or recreational fishing vessels, during scientific research trips that are designed to approximate typical fishing operations, or from simulated fishing activities in the laboratory ([Pollock and Pine, 2007](#); [Gilman et al., 2013](#); [ICES, 2014](#)). The fate of these fish is then observed by keeping them in captivity (aquaria or sea cages; e.g. [Mandelman et al., 2013](#)), inferred via recaptures of conventionally tagged fish (e.g. [Wilson and Burns, 1996](#); [Kaimmer and Trumble, 1998](#)), or from the inferred activity of fish tagged with acoustic transmitters (e.g. [Yergey et al., 2012](#); [Baktoft et al., 2013](#)) or pop-up satellite archival tags (PSATs; e.g. [Campana et al., 2009](#)). While varied in their experimental design, all approaches generate one of the two types of mortality data. “Cross sectional” data take the form of the numbers of dead and live animals at one or more fixed points in time. In contrast, “longitudinal” mortality data are made up of the times at which individuals died or at which they were last observed alive. Ongoing tracking of the fate of individuals is required to obtain these event times. Individuals that were alive when last observed at time t provide right-censored observations in that their time of death is only known to occur after t . In fact, cross sectional data are merely a special case of longitudinal data, in that individuals that are alive at time t are right-censored observations, while dead ones are left-censored observations, that is, observations for which the time of death is only known to have occurred before t [e.g. see application in [Benoît et al. \(2013\)](#)]. Compared with cross sectional data, longitudinal data have the advantage that they describe survivorship over time (the survivor function), providing information on the mechanisms affecting mortality and potentially helping to distinguish different sources of mortality. Furthermore, some form of longitudinal data is required to ensure full accounting of discard mortality ([Davis, 2002](#)).

Traditionally used methods for the analysis of longitudinal data generally fall under the class of survival or event analysis. They model survival as a function of time using non-parametric [e.g. Kaplan–Meier (KM) method], semi-parametric (e.g. Cox proportional-

hazards regression), or parametric forms ([Cox and Oakes, 1984](#)). Non-parametric models have the advantage of making very few assumptions about the survivor function, but cannot make predictions beyond the range of the data and inferences on the mechanisms underlying the shape of the survivor function are necessarily subjective. In contrast, parametric models allow predictions beyond the range of the observations and models can be built based on assumed forms of survivorship, including forms with mechanistic interpretations for survival patterns over time. Models making different assumptions about mechanisms can then be compared objectively using data. This is a particularly useful feature for the analysis of discard mortality data, where researchers are often ultimately interested, for example, in parsing out the effects of discard and background (or natural) mortality, in distinguishing capture and post-release mortality, and in objectively determining how long after release fish in a sample will continue to die as a direct result of capture and release events.

In this study, we elaborate on a parametric survival analysis model that appears particularly well suited for the analysis of discard and release mortality data (hereafter termed discard mortality data). This model, which comprises a latent mixture of survivor functions, was first applied to this field of study by [Benoît et al. \(2012\)](#). We begin by briefly describing this basic mixture model and by presenting supporting arguments and examples. We then show, analytically and by three brief case studies, how this model can be generalized to incorporate different characteristics of discard mortality data such as distinct capture, post-release and natural mortalities, and delayed mortality onset. We also use simulations to evaluate whether and under what conditions the model can reliably estimate the parameters for two challenging cases: separating fishing-related and natural mortalities and survival functions that include a delay in the onset of mortality.

The model

Basic structure

The cornerstone for the generalized model is a basic parametric survivor function. Here, we have chosen the commonly used Weibull-type survival function ([Cox and Oakes 1984](#), chapter 2):

$$S(t) = \exp[-(\alpha \cdot t)^\gamma], \quad (1)$$

where $S(t)$ is the survival probability to time t , and α and γ are, respectively, the scale and shape parameters of the underlying Weibull distribution. This simple function is particularly attractive due to its flexibility, whereby different values of α and γ can produce a range of survival function shapes commonly encountered in ecological data such as [Deevey's \(1947\)](#) Type I, II, and III survival functions (Figure 1). Notably, exponential mortality, typically assumed in stock assessments, is a special case of Equation (1) for $\gamma = 1$. The Weibull model has been successfully applied to discard survival data in many studies (e.g. [Neilson et al., 1989](#); [Campana et al., 2009](#); [Depestele et al., 2014](#)).

A basic assumption of Equation (1) and of other basic parametric survivor functions is that they represent a mortality process that begins at time $t = 0$ and for which $S(t)$ is continuously decreasing as a function of t . To the extent that discard mortality data conform to a basic parametric survivor function, and that the mortality is believed to result solely from the capture, handling, and release (CHR) process, the analyst must conclude that discard-related mortality is complete and survival is nil. While this may be

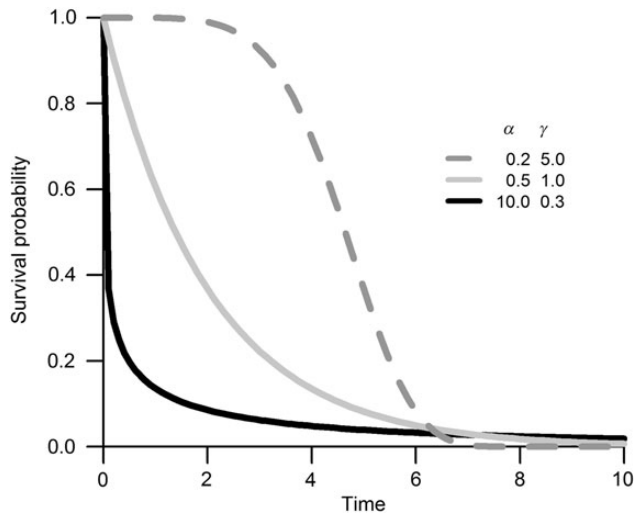


Figure 1. Examples of the form of the Weibull survival function as a function of its rate (α) and shape (γ) parameters, illustrating patterns comparable to [Deevey's \(1947\)](#) Type I (dashed grey line), Type II (solid grey), and Type III (black) survivorship curves.

the case in some instances, it is not the norm [see review presented in Figure 4 of [Benoît et al. \(2012\)](#)]. Instead, many longitudinal discard mortality studies have revealed a pattern of initial loss of individuals during the first hours or days of the study, followed by little or no losses of the remaining survivors.

To account for these patterns, [Benoît et al. \(2012\)](#) relaxed the assumption that $S(t)$ is the same for all individuals in a sample of discarded animals, instead assuming that the sample was composed of a latent mixture of two groups of individuals; those that were adversely affected by the CHR process and which will die as a result, and those that were unaffected (i.e. immune individuals). Mathematically, this can be written as

$$S(t) = \pi \cdot S_A(t) + (1 - \pi) \cdot S_I(t), \quad (2)$$

where $S(t)$ is the overall survival function for the sample, π is the probability that an individual is adversely affected, and $S_A(t)$ and $S_I(t)$ are the survival functions for the affected and immune groups, respectively. [Benoît et al. \(2012\)](#) were interested in the short-term (scale of days) mortality of fish held for observation in captivity following capture and handling under commercial fishery-like conditions. At such a short time-scale relative to natural longevity, and given the exclusion of predators, the authors assumed $S_I(t) = 1$; that is the likelihood of death during the experiment for individuals that were not adversely affected by CHR was essentially nil. This assumption enhances model identifiability when fitting to data. Clearly, the validity of this assumption declines if experimental subjects are exposed to predators and as the duration of the observation period increases, thereby increasing the likelihood of mortality from natural causes during the span of the experiment. Below we show how this assumption can be relaxed.

Using Equation (2), modelling $S_A(t)$ using the Weibull survival function as in Equation (1) and setting $S_I(t) = 1$, we obtain

$$S(t) = \pi \cdot \exp[-(\alpha \cdot t)^\gamma] + (1 - \pi). \quad (3)$$

From which it is easy to see that as $t \rightarrow \infty$, $S(t) \rightarrow 1 - \pi$, where π is the discard mortality rate. When $\pi = 1$, all individuals are said to be

adversely affected by the fishing event, such that $S(t) = S_A(t)$ and the ultimate CHR survival rate is 0. With Equation (3), there is no need to arbitrarily define a time at which to evaluate $S(t)$ such as to provide an estimate of discard mortality (e.g. [Neilson et al., 1989](#)). In fact, Equation (3) can be re-arranged to solve for t and therefore provide an estimate of the time when essentially all (e.g. 99.9%) of the CHR-related mortality has occurred

$$t_{S(t) \approx 1 - \pi} = -(\alpha \cdot \gamma)^{-1} \log(0.001). \quad (4)$$

The influence of covariates believed to influence discard mortality can be incorporated in $S_A(t)$, typically by including them in the α term, in π , or both ([Benoît et al., 2012](#); [Depestele et al., 2014](#)). An exponential function is typically used for covariate effects on α , $\alpha = \exp(\mathbf{X}'_1 \boldsymbol{\beta}_1)$, whereas a logistic function is used for π , $\pi = [1 + \exp(-\mathbf{X}'_2 \boldsymbol{\beta}_2)]^{-1}$, where \mathbf{X}_1 and \mathbf{X}_2 are design matrices for the covariates and $\boldsymbol{\beta}_1$ and $\boldsymbol{\beta}_2$ are vectors of parameters for the effect of the covariates. The same set of covariates need not be used for the effects on α and on π , as indicated by the different subscripts for the two generic design matrices above.

Researchers are increasingly modelling discard mortality as a function of semi-quantitative status indicators that summarize the degree of injury of individuals just before release, the degree of impairment of movement and response to stimuli, or a combination of the two which is often termed vitality or condition (e.g. [Richards et al., 1995](#); [Campana et al., 2009](#); [Benoît et al., 2012](#); [Depestele et al., 2014](#)). These measures (hereafter, status indicators) are known to be good predictors of eventual mortality ([Davis and Ottmar, 2006](#); [Humborstad et al., 2009](#); [Davis, 2010](#)), and are particularly useful in scaling up the results of small-scale CHR experiments to the fishery-wide level ([Richards et al., 1995](#); [Benoît et al., 2012](#); [ICES, 2014](#)).

[Benoît et al. \(2012\)](#) found strong support for the model in Equation (3) with status indicator effects on π for four of the five species they studied (e.g. Figure 2c and d), which included Atlantic cod (*Gadus morhua*), two flatfish species, and skates (*Rajidae* spp.). Similarly, [Depestele et al. \(2014\)](#) also found support for four species captured in a North Sea commercial fishery (cod, skates, and two flatfish). Further support for this model is also evident in the data for discarded blue sharks (*Prionace glauca*), whose fate was inferred using data from PSATs (Figure 2a; [Campana et al., 2009](#)), and in recent data for scallops (*Placopecten magellanicus*) captured in a commercial dredge fishery and held for observation in ship-board refrigerated seawater tanks (Figure 2b; [Knotek et al., pers. comm.](#)). In all of these cases, patterns in survivorship are characterized by initial loss of individuals during the first few hours or days after release to the water, followed by the absence of mortality thereafter (Figure 2). Furthermore, in each case, the level at which survivorship asymptotes, $1 - \pi$ (the discard survival rate), is inversely related to an individual's semi-quantitative pre-release status.

Generalization of the basic model

While the mixture-distribution model in Equation (3) appears appropriate for discard mortality data across a diversity of taxa, the contexts to which it applies are limited to cases where all individuals are alive at time $t = 0$, some individuals begin dying soon after $t = 0$ and there is no additional mortality [i.e. $S_I(t) = 1$]. However, simple modifications to the model can be made to relax these assumptions.

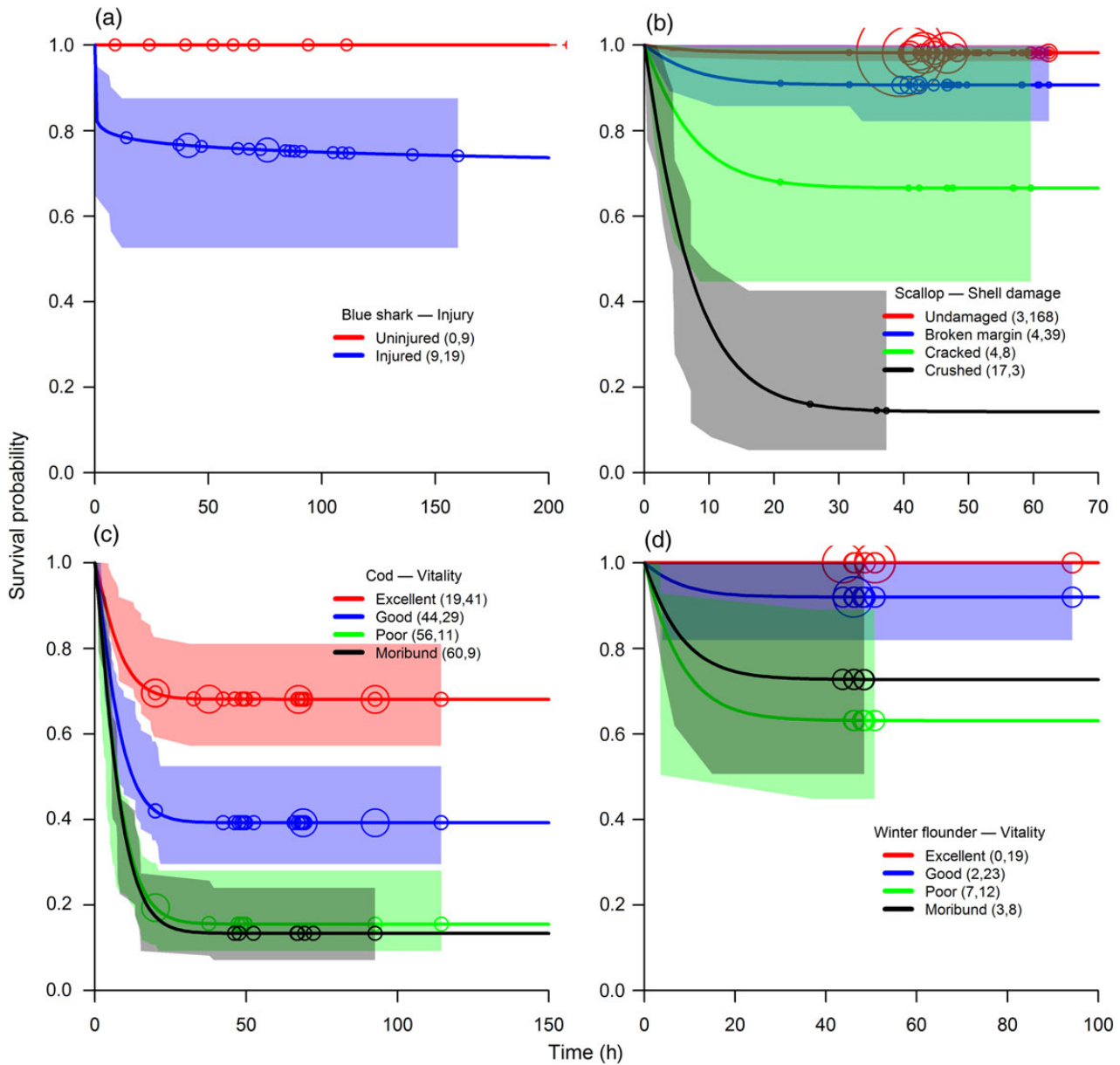


Figure 2. Examples of longitudinal discard survival functions for a diversity of taxa, as a function of the degree of injury, shell damage, or pre-release vitality: (a) blue sharks released from commercial longlines and tagged with PSATs [redrawn from [Campana et al. \(2009\)](#)], (b) scallops captured in a commercial dredge fishery and released into on-board refrigerated seawater tanks for monitoring ([Knotek et al.](#), unpublished results), and (c) Atlantic cod and (d) winter flounder captured in bottom-trawls and held for monitoring [redrawn from [Benoît et al. \(2012\)](#)]. In each plot, the shaded areas are the 95% confidence band for estimated injury/vitality-specific non-parametric KM survivor functions, the solid lines are estimates from the survival mixture model [Equation (3)], and the circles indicate the occurrence and relative frequency (circle size) of censored observations (plotted along the estimated survival curves for ease of presentation). The KM estimates are presented as a means of demonstrating model fit, given that the KM estimates are non-parametric representations of the patterns in the data. The horizontal span of the KM bands indicates the span of the data. The numbers in parentheses in the legend indicate the number of (dead, censored) observations for each injury or vitality class.

First, a parameter τ can be added to account for mortality occurring before release:

$$S(t) = \tau \cdot (\pi \cdot \exp[-(\alpha \cdot t)^\gamma]) + (1 - \pi), \quad (5)$$

where $1 - \tau$ is the probability that an individual died during capture or handling. While this mortality could be estimated separately, with the post-release mortality estimated using Equation (3) only for those individuals that were alive at release (e.g. [Benoît et al., 2012](#)), joint estimation of τ with the other parameters provides an

estimate of covariance among all parameters. Under this formulation, $1 - \tau + \tau\pi$ is the total CHR (discard) mortality probability.

Second, a delay in the onset of the post-release mortality can be incorporated by subtracting the time delay, t_0 , from t in Equation (5):

$$S(t) = \tau \cdot (\pi \cdot \exp[-(\alpha \cdot (t - t_0))^\gamma]) + (1 - \pi). \quad (6)$$

This delay reflects the time interval following discarding before any mortality occurs, and is not part of the among-individual variability in times of death that occurs normally due to attrition. Such a delay

may occur, for example, if initial capture-induced metabolic perturbations progress and/or are not resolved (Wood *et al.*, 1983), or, if captivity represents an additive stressor that eventually induces mortality in the sample (e.g. Mandelman and Farrington 2007).

Third, it may be important to model not only discard-related mortality but also natural or background mortality, for instance if individuals are released back into their natural environment which contains predators, pathogens, and other sources that might lead to mortality in the absence of CHR. Assuming an exponential function for the natural mortality, M , as is common in stock assessments and population modelling, we obtain

$$S(t) = \tau \cdot (\pi \cdot \exp[-(\alpha \cdot (t - t_0))^2] + (1 - \pi)) \cdot \exp(-M \cdot t). \quad (7)$$

The influence of the natural mortality function differs from that of τ with respect to its time dependence. In this formulation, M is assumed to act equally on both the affected and unaffected components and is therefore an independent additional mortality source. Any increase in predation risk that results from being affected by the CHR process, a component of discard mortality, is subsumed in the mortality modelled by the Weibull function.

As with other parameters of the model, it is possible to model these additional parameters as a function of status indicators or other covariates. The parameters t_0 or M can be written as a linear function of the covariates with a log-link to ensure that these parameters take on strictly positive values. For the τ parameter, a linear predictor with a logit link could be used to ensure that the parameter is bounded in the interval $[0, 1]$. Of course, it is unlikely that all three of these additional parameters t_0 , M , or τ will be pertinent for a given study. They are shown together in Equation (7) to illustrate the basic flexibility of the model, which of course could be modified in other ways to accommodate the particularities of a study, species, or context.

Material and methods

Special cases of Equation (7) were fit to three case studies to illustrate the use and relevance of the model. The goal is illustration and not to draw specific conclusions about the results of each study in the context in which they were conducted. Consequently, the methods for each study are presented with only enough detail for the reader to understand the application of the model. The first case study uses data from published research and further details on the study and its conclusions can be found in Benoît *et al.* (2012). The other two case studies are from yet to be published experiments. Further methodological details and more fulsome analysis will be available in forthcoming papers.

Model fitting via maximum-likelihood and simulations were all undertaken using the R statistical computing software (R Core Team, 2014). Optimization of the log-likelihood functions for the models (Appendix) was undertaken using the R *optim* function.

Case study I: distinguishing capture and handling mortality from post-release mortality

Benoît *et al.* (2012) examined the mortality of American plaice, *H. platessoides*, caught using a bottom-trawl in the southern Gulf of St Lawrence (Canada, NW Atlantic) under conditions similar to those in the local commercial fisheries. Fish were caught in hauls lasting 1–2 h, dumped on deck and handled in a manner comparable to that used by harvesters. They were then individually measured, scored with respect to vitality class, tagged using streamer tags, and placed in on-board refrigerated seawater tanks. The vitality classes used by the authors were: 1—excellent (lively fish with minor

injuries only), 2—good (injured and with weak body movements), 3—poor (injured and unresponsive but ventilating), and 4—moribund (unresponsive and apparently not ventilating). Tanks were monitored regularly, and dead animals were removed from the tanks and their time of mortality was recorded. Fish were held for holding periods of up to 110 h, and the holding times for individuals that were still alive at the end of a given holding period were treated as right-censored observations. All event times were in hours.

The authors undertook the analysis of their data in two parts. First, capture and handling mortality was modelled using a binomial model. Individuals that were dead when the tanks were first monitored after an initial 30- to 60-min holding period were assumed to have been dead before being placed in the tanks. These were all fish that had been classified as moribund. Second, the authors modelled the conditional in-tank mortality of individuals considered to have been alive when they were placed in tanks (i.e. post-release survival) using Equation (3), with vitality scores as covariates.

Here, we modelled the data for American plaice using a variant of Equation (7) that includes capture and handling mortality and a vitality effect on π :

$$S(t) = \tau \cdot (\pi \cdot \exp[-(\alpha \cdot t)^2] + (1 - \pi))$$

with $\pi = [1 + \exp(-\mathbf{X}'\boldsymbol{\beta})]^{-1}$ and

$$\tau = \begin{pmatrix} 1, & \text{vitality} \in (1, 2, 3) \\ \tau_0, & \text{vitality} = 4 \end{pmatrix}, \quad (8)$$

where \mathbf{X} is a design matrix for the injury scores, τ_0 is a parameter to estimate and the other parameters are as defined above. Capture and handling mortality applies only to moribund individuals (vitality = 4) by definition. Furthermore, natural mortality was not included in the model because the fish were held in tanks sheltered from predators and the duration of the study was too short for other mortality risks to be of importance. To fit the model, individuals that were dead when first monitored in the tanks were treated as left-censored observations, consistent with the fact that their time of mortality is only known to have occurred before the first observation period. This approach remains closer to the true nature of the data, compared with Benoît *et al.*'s (2012) assumption that the fish were necessarily dead before release to the tanks. For all other individuals, the mortality or censoring times used by Benoît *et al.* (2012) were used.

Case study II: distinguishing discard mortality from natural mortality

In 2013, Capizzano *et al.* (C. Capizzano, pers. comm.) studied the post-release mortality of Atlantic cod captured in the recreational rod-and-reel fishery that occurs on Jeffreys Ledge in the Gulf of Maine (USA, NW Atlantic). One hundred and thirty captured fish were brought to the surface, measured, tagged with an external acoustic transmitter with a depth-sensor (Vemco© V9P-1H), assessed for their degree of injury on an ordinal four-level scale (none, minor, moderate, and severe), and released alive. The release area was monitored by an array of 31 acoustic receivers (Vemco VR2W) that were spaced ~1.1 km apart, covering ca. 35 km². Acoustic transmitters emitted a unique, coded signal and depth measurement every 2 min for the first 7 d, every 5 min for the next 23 d, and then every 15 min until transmissions terminated at 365 d. Fish that exhibited minor vertical and horizontal movements, such as those observed for known dead fish that were

tagged as a reference, were considered dead. The time of onset of those limited movement patterns was taken as the time of death. The other fish were monitored until they left the array, at which point they were considered right-censored observations. In a few instances, fish were detected by receivers in the surrounding area or were captured in fisheries. The times of these later observations were considered as the censoring times. All event times were in days.

Here we modelled these data using

$$S(t) = (\pi \cdot \exp[-(\alpha \cdot t)^\gamma] + (1 - \pi)) \cdot \exp\left(\frac{-M \cdot t}{365}\right) \text{ with} \quad (9)$$

$$\pi = [1 + \exp(-\mathbf{X}'\boldsymbol{\beta})]^{-1},$$

where \mathbf{X} is a design matrix for the injury scores.

Delayed mortality onset was not included in the model because there was no evidence of this effect in the KM survivor functions for these data. Furthermore, the KM survival functions for fish classified as being uninjured or having minor injuries only before release were statistically indistinguishable (log-rank test: $\chi^2_{df=1} = 0.01, p = 0.859$) and therefore those two categories were combined. The natural mortality rate M was scaled by 365 in Equation (9) to estimate an annual instantaneous rate that could then be compared with values used in stock assessments or predicted from meta-analyses, as a means of validating the model estimates.

Case study III: delayed onset of discard mortality

Knotek *et al.* (R. Knotek, pers. comm.) undertook a study similar to that of Benoît *et al.* (2012). The discard mortality rate for three skate species captured in scallop dredge fisheries on Georges Bank (USA, NW Atlantic) was assessed by placing individuals in on-board refrigerated seawater tanks. Here, we consider only the results for winter skate (*L. ocellata*). Individuals were captured and handled under conditions typical of the fishery, with dredge hauls that varied in duration between 10 and 90 min. Individuals were measured, tagged, and attributed a semi-quantitative physical injury score (none/minor, moderate, and severe) before being placed in the tanks for a target holding period of 72 h. Event times were in hours.

Preliminary analyses using the non-parametric KM method revealed a delay in the onset of mortality. The magnitude of this delay appeared to be inversely related to the severity of injury. Skates were placed in the tanks alive (i.e. no capture and handling mortality) and given the experimental conditions it appeared reasonable to assume $M = 0$. Therefore, the post-release survival of winter skate from the experiment was modelled as

$$S(t) = \pi \cdot \exp[-(\alpha \cdot (t - t_0))^\gamma] + (1 - \pi) \quad (10)$$

with $\pi = [1 + \exp(-\mathbf{X}'\boldsymbol{\beta}_1)]^{-1}$ and $t_0 = \exp(\mathbf{X}'\boldsymbol{\beta}_2)$,

where the notation $\boldsymbol{\beta}_1$ and $\boldsymbol{\beta}_2$ is used to distinguish two distinct vectors of parameters, and \mathbf{X} is the design matrix for the injury scores.

To ensure that all calculations remained defined in light of logarithms used during the fitting process, we removed five right-censored observations that were made before the first mortality observations. Assuming there truly is a delay in mortality onset, fish removed from the experiment before any mortality is observed contribute no information to define the shape of the survivor function.

Simulations

Simulations were undertaken to evaluate whether and under what conditions it is possible to reliably estimate the parameters for a model involving discard mortality and natural mortality [Equation (9)], or for a model with delayed mortality onset [Equation (10)]. These two special cases of Equation (7) present the greatest potential model fitting challenges given possible confounding among the parameters that determine discard mortality and parameters for either natural mortality or mortality delay. Limiting the simulations to these two special cases kept the number of simulations tractable. The model fitting associated with the simulations was always done assuming the correct model structure. The goal was to establish whether correct parameter estimates could be recovered. Exploring the extent to which the model is robust to misspecification is a separate issue and is beyond the scope of this paper.

Two sets of simulations were undertaken: one aimed at replicating the conditions for case studies II and III, and a second generic set to consider the effects for a diversity of conditions. For the first set of simulations, injury group-specific sample sizes and study durations were matched to those of the case studies, and the parameter estimates obtained from the analyses of the case studies were used as the “true” parameter values for the simulation.

For the generic simulations, three status classes of fish were simulated, each defined by a discard mortality rate that was common across the simulations: $\pi_1 = 0.75$, $\pi_2 = 0.50$, or $\pi_3 = 0.25$. Three groups of generic simulations were undertaken. In the first, discard mortality with additional natural mortality was modelled using Equation (9).

Table 1. Parameters used for each generic simulation (case).

Case	N_{sim}	T_{max}	α	γ	M_{All}	M_1	M_2	M_3	$T_{0,1}$	$T_{0,2}$	$T_{0,3}$
1	100	200	0.10	1.99	0.25	—	—	—	—	—	—
2	30	200	0.10	1.99	0.25	—	—	—	—	—	—
3	10	200	0.10	1.99	0.25	—	—	—	—	—	—
4	100	25	0.10	1.99	0.25	—	—	—	—	—	—
5	100	18	0.10	1.99	0.25	—	—	—	—	—	—
6	100	12	0.10	1.99	0.25	—	—	—	—	—	—
7	30	25	0.10	1.99	0.25	—	—	—	—	—	—
8	30	18	0.10	1.99	0.25	—	—	—	—	—	—
9	30	12	0.10	1.99	0.25	—	—	—	—	—	—
10	100	200	0.03	1.99	0.82	—	—	—	—	—	—
11	100	200	0.03	1.99	2.71	—	—	—	—	—	—
12	100	200	0.10	1.99	—	0.25	0.15	0.09	—	—	—
13	30	200	0.10	1.99	—	0.25	0.15	0.09	—	—	—
14	100	200	0.10	1.99	—	0.61	0.37	0.08	—	—	—
15	30	200	0.10	1.99	—	0.61	0.37	0.08	—	—	—
16	100	200	0.10	1.99	—	2.71	1.65	0.05	—	—	—
17	30	200	0.10	1.99	—	2.71	1.65	0.05	—	—	—
18	100	200	0.03	1.99	—	—	—	—	1	8	15
19	100	200	0.02	7.39	—	—	—	—	1	8	15
20	100	60	0.03	1.99	—	—	—	—	1	8	15
21	100	200	0.03	1.99	—	—	—	—	1	25	50
22	100	200	0.02	7.39	—	—	—	—	1	25	50
23	100	60	0.03	1.99	—	—	—	—	1	25	50

In each case, three status classes of fish were simulated, each containing N_{sim} fish and each defined by a discard mortality rate that was common to all simulations $\pi_1 = 0.75$, $\pi_2 = 0.50$, and $\pi_3 = 0.25$. The duration of the study period (T_{max}) was varied between cases, as were the parameters of the Weibull survival function for the affected fish (α and γ). Cases 1–11 are simulations with additional natural mortality common to all status classes (M_{All}), cases 12–17 are simulations with status-dependent natural mortality (M_1 , M_2 , and M_3), and cases 18–23 are simulations with status-dependent delays in mortality onset ($T_{0,1}$, $T_{0,2}$, and $T_{0,3}$).

In the second, discard and natural mortalities were also modelled, but with status class-dependent natural mortalities [i.e. assuming $M = \exp(\mathbf{X}'\boldsymbol{\beta})$ in Equation (9)]. This was done to evaluate model robustness for cases where the assumption of a common natural mortality for affected and immune individuals is not met (refer to “Generalization of the basic model”). This would occur if there are long-term survivorship differences between status classes that are not subsumed in the rapidly depleting survivor function for affected individuals. For these two groups of generic simulations, we looked at the effect on estimation robustness of differences in sample size, study duration, and the relative magnitude of discard and natural mortality (cases 1–17 in Table 1 and Figure 3a and b). In the third group of generic simulations, discard mortality with delayed onset was modelled using Equation (10), assuming an inverse relationship between class-dependent discard mortality and delay. For this third group of simulations, we looked at the effect on estimation robustness of differences in study duration, the shape of the discard mortality function, and the magnitude of delays (cases 18–22 in Table 1 and Figure 3c).

A modification of the method of Bender *et al.* (2005) was used for the simulations. For each simulated individual, i , a value of $S(t)_i$ was drawn from a uniform distribution:

$$S(t)_i \sim U(0, 1).$$

The associated survival time t_i was then obtained by solving the simulated survival function equation using the Newton–Raphson algorithm. For each individual, a censoring time was also simulated, and the lesser of the survival and censoring times was used as the simulated observation for that individual. For simulations of case study II and for all the generic simulations, censoring times were drawn from a modified Beta distribution ($\alpha = 0.7$, $\beta = 1.4$ and with support rescaled to 185 days), chosen to broadly reflect the observed distribution of censoring times in case study II (Figure 4, black line). We used this single distribution to keep the number of simulations tractable and because the preliminary results obtained using other reasonable censoring functions produced very comparable results. A separate case-specific modified Beta distribution ($\alpha = 1.8$, $\beta = 0.2$ and with support rescaled to 75 h) was used to simulate censoring times for the simulations of case study III (Figure 4, grey lines).

Once the observations for all individuals were simulated, the relevant survival model was fit to the data to estimate parameter values. Each simulation comprised 1000 iterations, from which the mean, median, 2.5th, and 97.5th percentiles of estimated parameter values were calculated. For the case study-specific simulations, relative bias (RB) for each parameter was also calculated as

$$RB = \frac{100}{n} \sum_{i=1}^n \frac{\hat{\theta}_i - \theta_{\text{true}}}{\theta_{\text{true}}},$$

where n is the number of iterations, $\hat{\theta}_i$ is the estimate of the parameter for iteration i , and θ_{true} is the simulated “true” value for the parameter. RB was not calculated for the results of the generic simulations because those results were summarized only in a graphical form and bias can be inferred from those graphs.

Results

Case study I: distinguishing capture and handling mortality from post-release mortality

The model in Equation (8) fits the estimated KM survivor functions for the American plaice data very well (Figure 5a), suggesting that the

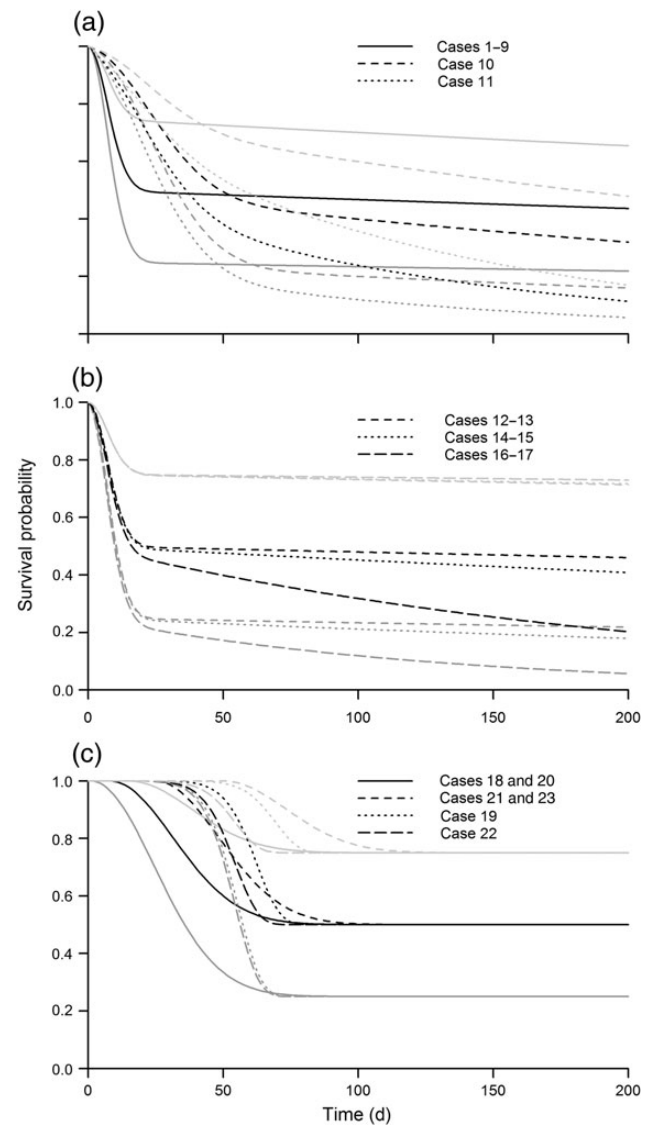


Figure 3. Survival functions used in the generic simulations, as defined by the parameters in Table 1. Status-specific functions are distinguished by shading for all simulated cases with discard mortality and (a) a single overall natural mortality, (b) status-specific natural mortalities, or (c) delays in discard mortality onset.

model provides an adequate description of those data. Relatively large samples sizes in each vitality class resulted in narrow confidence intervals for the KM estimates and the parameters of the parametric model. Discard mortality was lowest for fish with excellent vitality, increasing with worsening vitality across classes (Table 2). The total mortality probability for moribund plaice was very high at 0.962. Most of the observed mortality in this vitality class occurred during the capture and handling process.

Case study II: distinguishing discard mortality from natural mortality

The mixture-distribution model that included M [Equation (9)] provided a substantially better fit to the cod data compared with the model that excluded M [Equation (3)], with a reduction in the value of the Akaike Information Criterion corrected for small

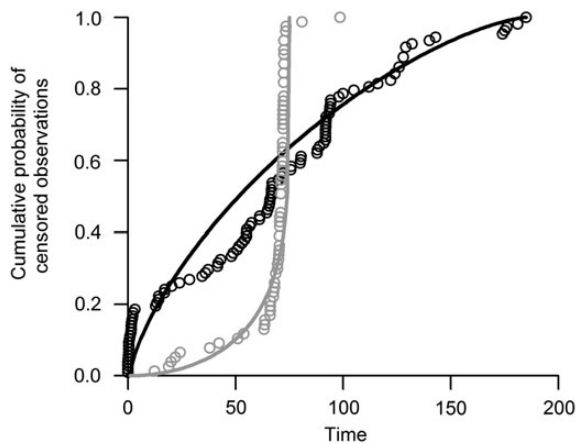


Figure 4. Cumulative distributions of observed censoring times in the cod case study (time in days; black circles) and the winter skate case study (time in hours; grey circles), and the modified Beta distributions used to generate censoring times in the simulations for each (solid black and grey lines, respectively). The distribution described by the black line was used for the generic simulations.

sample size, ΔAIC_c , of 18.9. The favoured model fit the estimated KM survivor functions well (Figure 5b), suggesting that the model provides an adequate description of the data. The estimates of CHR mortality increased with the severity of injury among classes (Table 3). The precision of the estimates was low for the moderate and severely injured classes, as a function of low sample sizes. The estimate of M from the favoured model was similar to the values assumed in a recent assessment of Gulf of Maine cod (0.2 or 0.4; NEFSC, 2013), as well as with the values predicted from empirical life history approaches: assuming von Bertalanffy parameters for cod of $k = 0.15$ and $L_\infty = 110$ (Froese and Pauly, 2014), $M = 0.30$ using Jensen's (1996) estimator, and $M = 0.46$ using Gislason *et al.*'s (2010) estimator for a mean length of 47 cm.

Case study III: delayed onset of discard mortality

Fitting the model with injury-specific mortality delays to data was a little less straightforward than for the other case studies. Achieving model convergence and obtaining an invertible Hessian required that initial parameter values for the mortality delay parameters be close to the first observed mortality times, and that a range of values be examined. There were strong correlations ($r \geq 0.93$) among the estimates of the Weibull shape parameter ($\hat{\gamma}$) and the three parameters that define the t_0 's, as well as among the three parameters that define the π 's. The former set of correlations can be explained by the fact that delays are constrained to occur before the first observed mortalities. Estimates of the delay are therefore derived from a backwards projection of the shape of the subsequent survivor function, leading to a strong confounding between the magnitude of delay and the parameters that shape the post-delay survivorship function.

The model fits the KM estimates of the survivor function well (Figure 5c). The estimated magnitude of the delay was inversely related to the severity of injury, though the estimates did not differ statistically (Table 4). A lack of mortality observations soon after the initial onset of mortality may largely explain the wide confidence intervals for the estimates of t_0 . As with the other examples presented here, estimates of discard mortality varied inversely with the severity of injury (Table 4). Confidence intervals on those

estimates were wide given that mortality had yet to level off over the time span in which the data were collected.

Simulations

The simulated survival functions for the cod case study (Figure 6a) produced patterns comparable to the original observations (Figure 5b). The means and medians of parameters obtained from the simulations were essentially identical with the simulated values with a very little estimation bias (Table 3). Furthermore, the 2.5th and 97.5th quantiles for the estimated parameters from the simulations were comparable to estimated 95% confidence intervals for the original parameter estimates. Taken together, this suggests that the properties of the empirical dataset for case study II were simulated reasonably well, and that the model could reliably estimate the parameters.

The simulated survival functions for the winter skate case study (Figure 6b) produced patterns that also were comparable to the original observations (Figure 5c), again suggesting that the simulations were reasonably accurate. The simulations indicated that there were estimation biases particularly for the delay parameters for all three injury classes and the discard mortality parameter for the moderately injured class (π_{Moderate} ; Table 4). Among the simulations, there were high densities of estimated delay parameters with values near zero (Supplementary Figure 1). Likewise, there were high densities of extreme values for the CHR parameters for the uninjured and severely injured classes ($\pi_{\text{None/Minor}}$ and π_{Severe}). These results occurred even when initial parameter values were set in a manner similar to what was done in the analysis of the winter skate case study. However, while careful attention was paid to model fitting for the case study (e.g. visual assessment of the fits and examination of a range of initial values), this degree of rigour was not replicated in the simulation study. Had this degree of rigour been implemented, it is likely that estimation problems would have been flagged for most simulation iterations for which the delay parameter estimates were close to zero (indicative of poor fits to the data).

In the generic simulations that included natural mortality, the discard mortality parameters were estimated accurately in almost all cases examined and even when the estimates were biased, the magnitude of RB was no more than 20% (Figure 7). The estimates were slightly biased when the study duration (T_{max}) was less than the time it took for the survival functions to level off (cases 5, 6, 8, and 9). A moderate bias was present when the rates of loss for discard and natural mortality were of similar magnitude (cases 10 and 11), or when there were large absolute differences in natural mortality rates between status classes and sample sizes were small (case 17). Reductions in sample size resulted in predictable increases in the dispersion of simulated estimates (e.g. compare cases 1, 2, and 3). Simulated estimates of the natural mortality parameter were also generally accurate and always had a skewed distribution. Bias in parameter estimates was greater when the simulated discard and natural mortality rates were of similar magnitude (cases 10 and 11). Parameter estimates were also biased when there were large differences in class-specific natural mortality rates (cases 16 and 17), particularly when sample sizes were smaller (case 17).

In the generic simulations that included a delay in discard mortality onset, the discard mortality parameters were accurately estimated when the study duration included the asymptote of the survival functions and when there was moderate variation among classes in the magnitude of the delay (cases 18 and 19; Figure 8). Estimates were biased when variation in the delay was greater (cases 21–23), especially when T_{max} occurred before the survival functions reached their

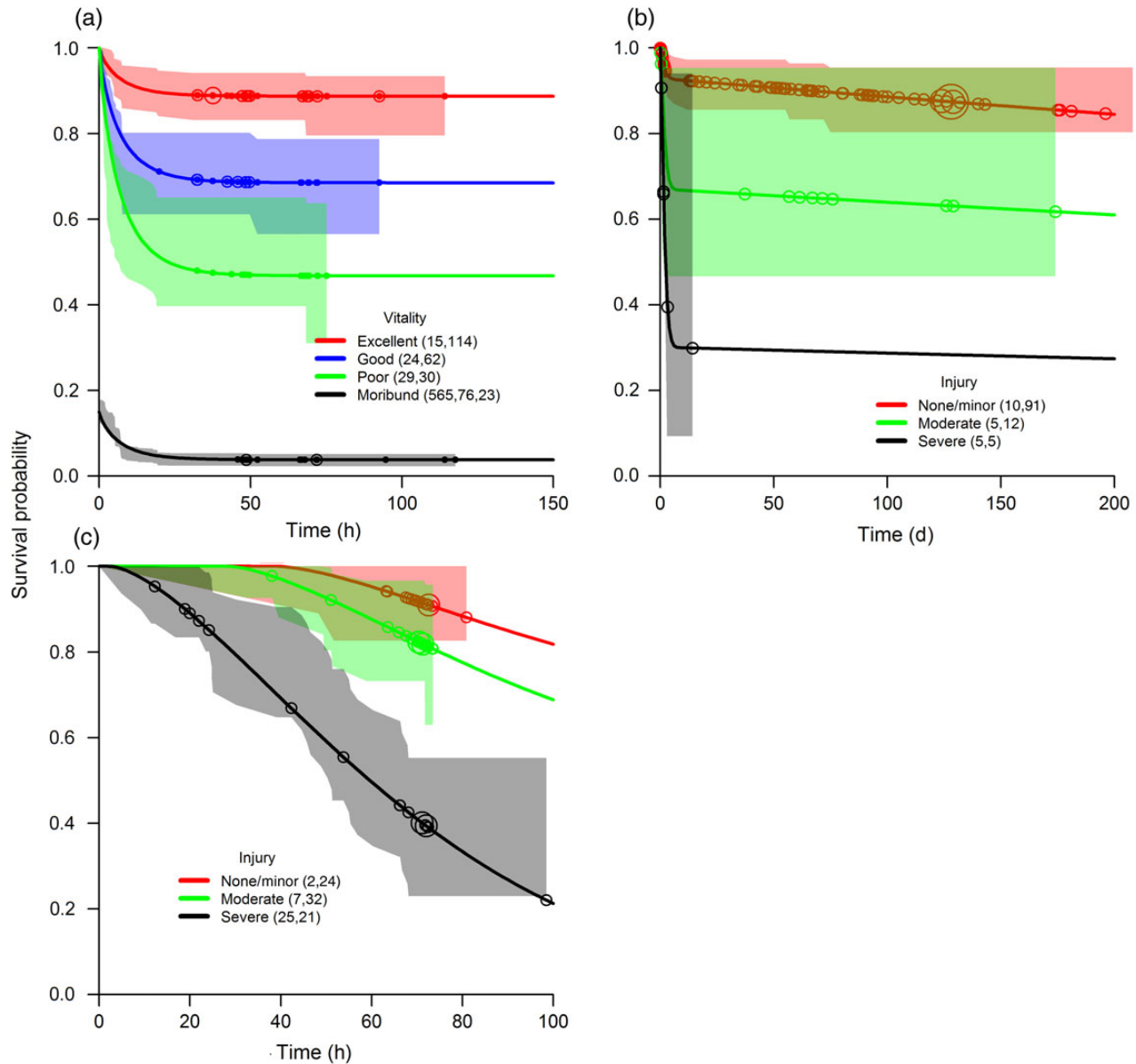


Figure 5. Non-parametric (KM; shaded areas) and estimated parametric survival functions for the three case studies: (a) American plaice captured by bottom-trawls and monitored in refrigerated seawater tanks (model with distinct capture/handling mortality and post-release mortality; Benoît *et al.*, 2012), (b) Atlantic cod captured in a recreational fishery and released with acoustic tags (model with distinct discard and natural mortalities; Capizzano *et al.*, pers. comm.), and (c) winter skate captured in a commercial scallop dredge fishery and held for monitoring (model with delayed mortality onset; Knotek *et al.*, pers. comm.). The interpretation of the contents of the plots is described in Figure 2.

Table 2. Parameter estimates and associated confidence intervals for Case study I, American plaice captured using a bottom-trawl.

Parameter	N	Estimate	95% CI
$\pi_{\text{Excellent}}$	129	0.113	0.067–0.177
π_{Good}	86	0.315	0.232–0.413
π_{Poor}	59	0.532	0.405–0.649
$\text{CH}_{\text{Moribund}}$	664	0.851	0.819–0.877
$\text{CHR}_{\text{Moribund}}$		0.962	0.945–0.975

Results are presented for the vitality class-specific discard mortality probability estimates (π 's for excellent, good, and poor vitality classes; $\text{CHR}_{\text{Moribund}} = 1 - \tau + \tau\pi_{\text{Moribund}}$ for the moribund vitality class), the capture and handling mortality rate for moribund individuals ($\text{CH}_{\text{Moribund}}$), and the number of fish in each injury class (N).

asymptote (case 23). Biases were of similar magnitude whether the simulated Weibull function for affected individuals followed a Deevey type II curve (e.g. case 18) or a Deevey type I curve (e.g. case 19). Estimates of the delay terms were highly biased in all simulated cases (Figure 7). These problematic results are like those obtained in the simulations mimicking the winter skate case study (Table 4), probably also as a reflection of poor data fits in many iterations, likely resulting from sensitivity to initial parameter values.

Discussion

In this study, we present theoretical arguments and empirical support for parametric mixture-distribution models for the analysis

Table 3. Parameter estimates and associated confidence intervals for Case study II, cod released from a recreational rod-and-reel fishery, and a summary of results from a simulation based on those estimated parameter values (mean, median, 2.5th, and 97.5th percentiles [95% interval], and RB).

Parameter	N	Study results		Simulation results			
		Estimate	95% C.I.	Mean	Median	95% Interval	RB
$\pi_{\text{None/Minor}}$	101	0.071	0.031–0.150	0.070	0.070	0.031–0.150	–0.83
π_{Moderate}	17	0.329	0.144–0.597	0.325	0.311	0.086–0.617	1.91
π_{Severe}	10	0.699	0.293–0.938	0.696	0.700	0.257–0.999	1.61
M		0.173	0.056–0.564	0.197	0.171	0.001–0.616	–1.80

The injury class-specific discard mortality parameters (π 's) and the natural mortality parameter (M) are presented, along with the number of fish in each injury class (N).

Table 4. Parameter estimates and associated confidence intervals for Case study III, winter skate captured in a scallop dredge, and a summary of results from a simulation based on those estimated parameter values (mean, median, 2.5th, and 97.5th percentiles [95% interval], and RB).

Parameter	N	Study results		Simulation results			
		Estimate	95% CI	Mean	Median	95% interval	RB
$\pi_{\text{None/Minor}}$	26	0.341	0.042–0.870	0.362	0.250	0.011–0.999	19.2
π_{Moderate}	39	0.500	0.169–0.831	0.393	0.303	0.105–0.952	–31.4
π_{Severe}	46	0.998	0.048–1.000	0.924	0.998	0.586–0.999	–5.5
$t_{0,\text{None/Minor}}$		39.4	12.8–115.6	20.9	7.0	0.0–63.0	–48.3
$t_{0,\text{Moderate}}$		28.6	11.7–69.9	8.6	$2.6e^{-4}$	0.0–46.2	–71.3
$t_{0,\text{Severe}}$		2.7	0.0–51.7	1.8	$1.3e^{-2}$	0.0–11.2	–48.8

The injury class-specific discard mortality parameters (π 's) and mortality onset delay parameters (t_0 's) are presented, along with the number of fish in each injury class (N)

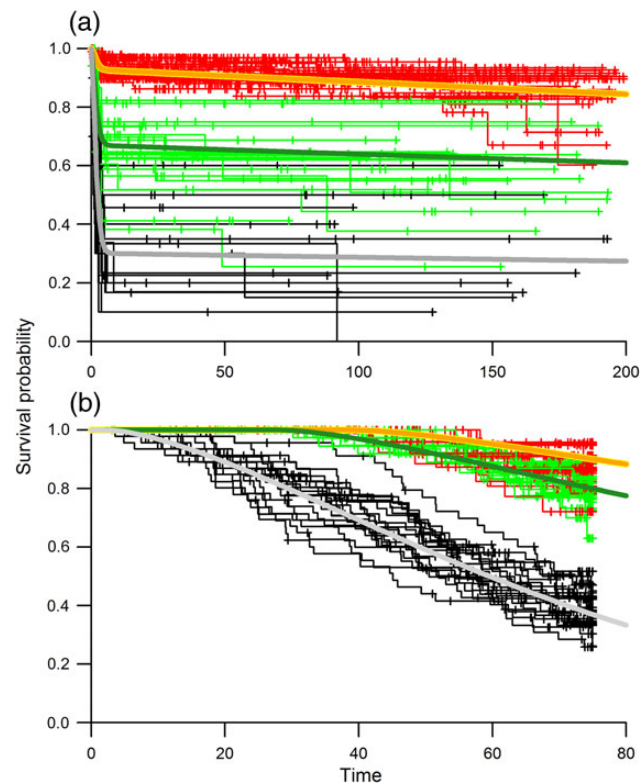


Figure 6. Injury class-specific underlying survival functions (thick lines) and examples of KM estimates for 20 simulation iterations (thin lines with crosses to indicate censored observations) for (a) the cod case study and (b) the winter skate case study. Injury classes are distinguished using colours: red/orange = none/minor, green = moderate, and black/grey = severe. Note how the variability among KM curves scales with sample size, for example by comparing the results for the simulated none/minor ($N = 101$) and severely injured ($N = 10$) classes in (a).

of longitudinal discard mortality data. A common feature of these data is an eventual asymptote in mortality in the absence of other mortality sources. We are aware of few current alternative modelling approaches that can satisfactorily deal with this property in light of the need to provide scientific advice on discard mortality. While non-parametric and semi-parametric (e.g. Cox proportional-hazards) models can adequately fit the data, these models cannot be used to parse out different mortality sources (capture/handling, post-release, and M), nor do they provide mechanistic interpretation for the shape of the survival function. Multiphase or change-point models, in which survivorship is modelled with different survival functions (and therefore different underlying mechanisms) over time (e.g. Arani *et al.*, 2001), are a possible alternative; however, the underlying assumption of these models seems unlikely for post-release mortality. Rather, the impacts of CHR should be manifested continuously, and not involve distinct interventions over time unless there are plausible external or physiological reasons to expect them. Of course, our model with a mortality onset delay is a type of multiphase model; however, reasonable biological explanations are possible for the two phases as noted earlier in this paper.

We have also shown how the mixture model can be generalized to accommodate key aspects common to survival data, as illustrated by the case studies. Using simulations, we demonstrated that special cases of the generalized model can provide robust estimates of discard mortality rates with little or no bias when there is additional low-to-moderate natural mortality. Moderate estimation bias occurred when the natural mortality rate was large ($M > 1.5$), with values representative of short-lived species, not of the species considered in our case studies. Furthermore, under many conditions M was also reliably estimated, with biases occurring mainly when M was large, in which case some natural mortality was incorrectly attributed to discard mortality. Surprisingly, discard mortality and M parameters were reasonably well estimated even when observations were terminated before the survival functions showed signs of levelling-off.

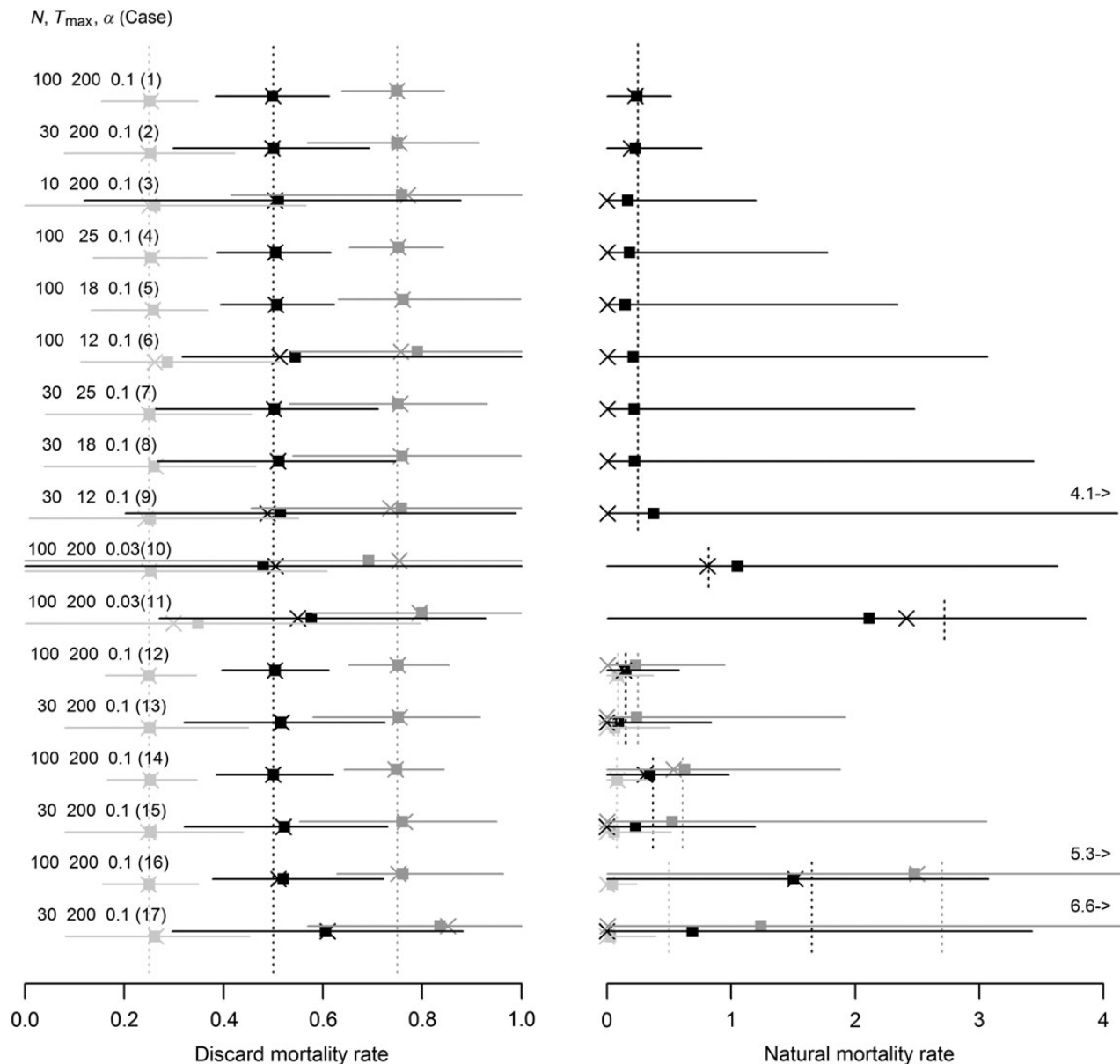


Figure 7. Summary of the results of the generic simulations with discard and natural mortalities [based on Equation (9)]. Results for the different simulated cases are presented along the y-axis. The mean (square), median (x), and 95 percentile interval (horizontal line) are presented for the estimated discard mortality rate parameter for each of the three status classes (distinguished by shading) in the left panel and for the global (cases 1–11) or class-specific (cases 12–17) natural mortality rates (M) in the right panel. In each panel, the vertical dashed lines indicate the simulated value of the parameter. The numbers on the left indicate the value of the simulated parameters other than M that were varied among cases. Details on the parameters used in the simulations can be found in Table 1, and the shapes of the simulated survival functions that generated these results are in Figure 3a and b.

The model presented here is therefore likely to be highly useful given the move towards a greater ecological realism in discard and post-release mortality studies (Raby *et al.*, 2014).

The model that incorporated a delay in mortality presented some challenges. Fitting the model required attention to starting parameter values, in contrast to the model with M , which was largely insensitive to starting values. The simulations for the “delay model” indicated that the discard mortality rates were only accurately estimated when mortality delays were at most moderate. However, the delay parameters were generally underestimated, as the estimation procedure tended towards delays close to nil for many simulation

iterations. In effect, the estimations tended towards implied very low probability of mortalities during the early part of the experiments, rather than consistently estimating a nil probability of mortality as was simulated. Unfortunately, there will be very little information in the data during the initial part of an experiment to distinguish between these two possibilities. However, using information from past studies or knowledge of physiological processes to derive informative priors for the delay parameters would certainly improve estimation for models fit under the Bayesian paradigm. More generally, our results suggest that diligence is required when fitting models with mortality delays, and we recommend the use of case-specific

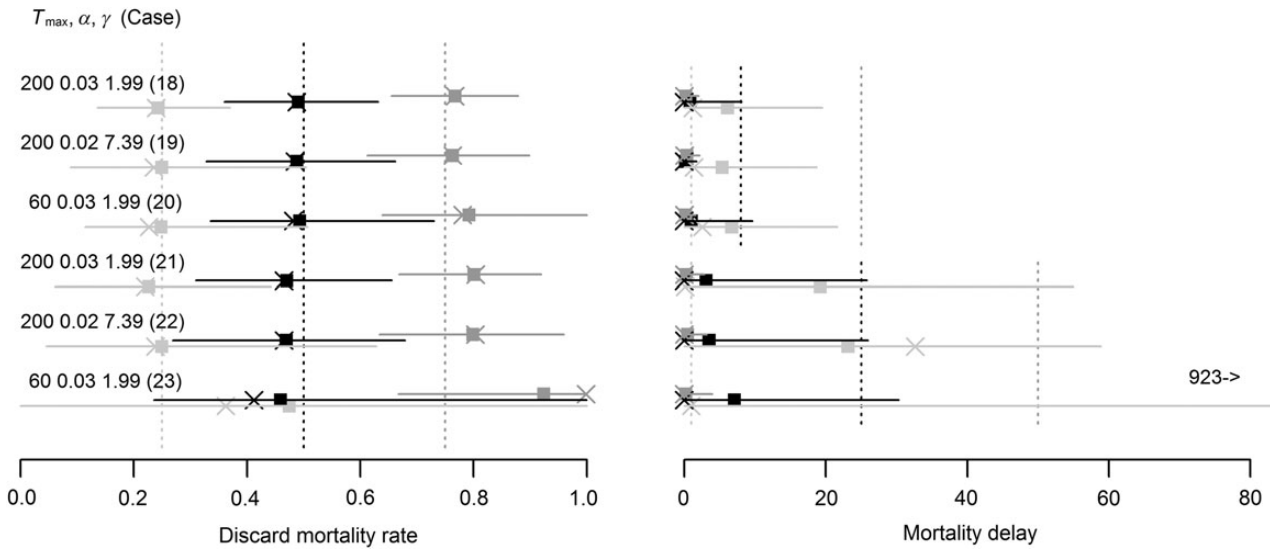


Figure 8. Summary of the results of the generic simulations with discard mortality and status-dependent mortality delays [based on Equation (10)]. Results for the different simulated cases are presented along the y-axis. The mean (square), median (x), and 95 percentile interval (horizontal line) are presented for the estimated discard mortality rate parameter for each of the three status classes (distinguished by shading) in the left panel and for the class-specific delay parameters in the right panel. In each panel, the vertical dashed lines indicate the simulated value of the parameter and the numbers on the left indicate the value of the simulated parameters other than the delay parameters that were varied among cases. Details on the parameters used in the simulations can be found in Table 1, and the shapes of the simulated survival functions that generated these results are in Figure 3c.

simulations to explore the robustness of the model for the situation at hand. Despite the preceding, it must be noted that delays in mortality onset appear rare in the available literature on discard mortality, with no cases identified in the review of longitudinal studies undertaken by Benoit *et al.* (2012). The above considerations may therefore only apply to a limited number of cases.

Here, we paid little attention to multi-model comparison; that is, comparing the evidence for a suite of models based on the data. Multi-model comparisons can guide the selection of the most probable model(s) to have generated the observed data, in light of data variability, and are considered good practice (Hilborn and Mangel, 1997; Burnham and Anderson, 2002). We have reserved this type of analysis for the detailed examinations of the case studies (Benoit *et al.* 2012; C. Capizzano in prep; R. Knotek in prep). Additionally, we did not consider the consequences of model misspecification. A logical next step for longitudinal discard mortality modelling research would be to use simulations to study the consequences for discard mortality estimates of assuming an incorrect model. Identifying the most robust models would help ensure that scientific advice on discard mortality is as reliable as possible.

Though the generalized model presented here can provide estimates of natural mortality, given appropriate data, these estimates may not accurately reflect actual rates. For example, for acoustic transmitters, if a predator consumes a tagged fish and carries the tag outside of the array, the individual will be assumed to provide a censored observation and predation mortality (part of the discard mortality for ‘affected’ individuals or part of M for “immune” individuals) will be underestimated. Such an effect, combined with the estimation variability, means that the present approach may not be suitable for providing reliable independent estimates of M for stock assessments. However, the approach does appear to provide an estimate that is of the correct scale. It is also worth noting that if tags are shed before fish die or become censored observations, mortality (discard or natural) is likely to be overestimated, and scientists may

need to account for such effects in their study design or perhaps during analysis to ensure accurate estimation of mortality terms.

In summary, we have provided theoretical arguments, and empirical support via simulations and case studies for the generalized mixture model to estimate discard mortality from longitudinal data. This model appears particularly well suited for this field of study and performed well for the cases most likely to be encountered: CHR-mortality only, CHR-mortality with additional natural mortality, and distinct CH and post-release mortalities. As the case studies illustrate, this model approach—assuming satisfaction of assumptions—is conducive to both shorter term enclosure studies or more temporally extended electronic tagging and telemetry studies where animals are at liberty. Because this model is founded on a basic parametric survival function, it can easily be adapted to include other effects not modelled here, and can be fit using maximum-likelihood or Bayesian methodologies. Furthermore, model fitting can readily incorporate both left- and right-censored data thereby allowing data from cross sectional studies to be readily combined with longitudinal data to improve estimation of key parameters (e.g. Benoit *et al.*, 2013). We believe that these properties, taken together, result in a powerful framework in which to analyse discard mortality data and to produce reliable scientific advice on discard mortality rates and possibilities for mitigation.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Acknowledgements

We thank Steve Campana for providing his data on blue shark discard mortality and Ken Goldman for his contributions to the scallop mortality experiments and for reviewing an earlier draft of this paper. Suggestions from two anonymous reviewers improved the paper. We are also grateful to the captains, crew, and participants

of the trips that provided the data for our three case studies. Funding for the cod and skate case studies was provided by the NOAA National Marine Fisheries Service Bycatch Reduction Engineering Program (Award #NA12NMF4720256) and NOAA National Marine Fisheries Service Sea Scallop Research Set Aside Program (Award #NA12NMF4540030). Portions of this study were sanctioned by the New England Aquarium Animal Care and Use Committee (protocol #2013-02), and College of William and Mary IACUC (Protocol-2012-06-27-8018).

References

- Alverson, D. L. 1997. Global assessment of fisheries bycatch and discards: a summary overview. *In* Global Trends: Fisheries Management, pp. 115–125. Ed. by E. K. Pikitch, D. D. Huppert, and M. P. Sissenwine. American Fisheries Society Symposium Vol. 20. American Fisheries Society, Bethesda, MD.
- Arani, R., Seng-Jaw, S., Weiss, H., Wood, M., Fiddian, P., Gnnann, J., and Whitley, R. 2001. Phase specific analysis of herpes zoster associated pain data: a new statistical approach. *Statistics in Medicine*, 20: 2429–2439.
- Baktoft, H., Aarestrup, K., Berg, S., Boel, M., Jacobsen, L., Koed, A., Pedersen, M. W., et al. 2013. Effects of angling and manual handling on pike behaviour investigated by high-resolution positional telemetry. *Fisheries Management and Ecology*, 20: 518–525.
- Bellido, J. M., Santos, M. B., Pennino, M. G., Valeiras, X., and Pierce, G. J. 2011. Fishery discards and bycatch: solutions for an ecosystem approach to fisheries management? *Hydrobiologia*, 670: 317–333.
- Bender, R., Augustin, T., and Blettner, M. 2005. Generating survival times to simulate Cox proportional hazard models. *Statistics in Medicine*, 24: 1713–1723.
- Benoît, H. P. 2013. Twenty years of annual landed and discarded catches of three southern Gulf of St. Lawrence skate species estimated under multiple sources of uncertainty. *ICES Journal of Marine Science*, 70: 554–563.
- Benoît, H. P., Hurlbut, T., Chassé, J., and Jonsen, I. D. 2012. Estimating fishery-scale rates of discard mortality using conditional reasoning. *Fisheries Research*, 125–126: 318–330.
- Benoît, H. P., Plante, S., Kroiz, M., and Hurlbut, T. 2013. A comparative analysis of marine fish species susceptibilities to discard mortality: effects of environmental factors, individual traits, and phylogeny. *ICES Journal of Marine Science*, 70: 99–113.
- Burnham, K. P., and Anderson, D. R. 2002. *Model Selection and Multimodel Inference: A Practical Information Theoretic Approach*, 2nd ed. Springer-Verlag, New York.
- Campana, S. E., Joyce, W., and Manning, M. J. 2009. Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. *Marine Ecology Progress Series*, 387: 241–253.
- Cooke, S. J., and Schramm, H. L. 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. *Fisheries Management and Ecology*, 14: 73–79.
- Cowx, I. G., Arlinghaus, R., and Cooke, S. J. 2010. Harmonizing recreational fisheries and conservation objectives for aquatic biodiversity in inland waters. *Journal of Fish Biology*, 76: 2194–2215.
- Cox, D. R., and Oakes, D. 1984. *Analysis of Survival Data*. Chapman and Hall Ltd, London.
- Davis, M. W. 2002. Key principles for understanding fish bycatch discard mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 1834–1843.
- Davis, M. W. 2010. Fish stress and mortality can be predicted using reflex impairment. *Fish and Fisheries*, 11: 1–11.
- Davis, M. W., and Ottmar, M. L. 2006. Wounding and reflex impairment may be predictors for mortality in discarded or escaped fish. *Fisheries Research*, 82: 1–6.
- Deevey, E. S. 1947. Life tables for natural populations of animals. *Quarterly Review of Biology*, 22: 283–314.
- Depestele, J., Desender, M., Benoît, H. P., Polet, H., and Vincx, M. 2014. Short-term survival of discarded target fish and non-target invertebrate species in the “eurocutter” beam trawl fishery of the southern North Sea. *Fisheries Research*, 154: 82–92.
- European Union. 2013. Regulation (EU) No 1380/201308 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and (EC) No 639/2004 and Council Decision 2004/585/EC. *Official Journal of the European Union*, L 354: 22–61.
- Froese, R., and Pauly, D. (Ed.) 2014. *FishBase*. World Wide Web Electronic Publication. www.fishbase.org, version (08/2014).
- Gilman, E., Suuronen, P., Hall, M., and Kennelly, S. 2013. Causes and methods to estimate cryptic sources of fishing mortality. *Journal of Fish Biology*, 83: 766–803.
- Gislason, H., Daan, N., Rice, J. C., and Pope, J. G. 2010. Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries*, 11: 149–158.
- Grant, S. M., and Hiscock, W. 2014. Post-capture survival of Atlantic wolffish (*Anarhichas lupus*) captured by bottom otter trawl: Can live release programs contribute to the recovery of species at risk? *Fisheries Research*, 151: 169–176.
- Harrington, J. M., Myers, R. A., and Rosenberg, A. A. 2005. Wasted fishery resources: discarded by-catch in the USA. *Fish and Fisheries*, 6: 350–361.
- Hilborn, R., and Mangel, M. 1997. *The Ecological Detective: Confronting Models with Data*. Princeton Academic Press, Princeton, NJ.
- Humborstad, O. B., Davis, M. W., and Løkkeborg, S. 2009. Reflex impairment as a measure of vitality and survival potential of Atlantic cod (*Gadus morhua*). *Fishery Bulletin*, 107: 395–402.
- Ibrahim, J. G., Chen, M. -H., and Sinha, D. 2001. *Bayesian Survival Analysis*. Springer Science + Business Media, Inc., New York.
- ICES. 2014. Report of the Workshop on Methods for Estimating Discard Survival (WKMEDS), 17–21 February 2014, ICES HQ. ICES CM 2014/ACOM:51, Copenhagen, Denmark. 114 pp.
- Jensen, A. L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 820–822.
- Kaimmer, S. M., and Trumble, R. J. 1998. Injury, condition and mortality of Pacific halibut bycatch following careful release by Pacific cod and sablefish longline fisheries. *Fisheries Research*, 38: 131–144.
- Kappel, C. V. 2005. Losing pieces of the puzzle: threats to marine, estuarine, and diadromous species. *Frontiers in Ecology and the Environment*, 3: 275–282.
- Mandelman, J. W., Cicia, A. M., Ingram, G. W., Jr, Driggers, W. B., III, Coutre, K. M., and Sulikowski, J. A. 2013. Short-term post release mortality of skates (family Rajidae) discarded in a western North Atlantic commercial otter trawl fishery. *Fisheries Research*, 139: 76–84.
- Mandelman, J. W., and Farrington, M. A. 2007. The estimated short-term discard mortality of a trawled elasmobranch, the spiny dogfish (*Squalus acanthias*). *Fisheries Research*, 83: 238–245.
- NEFSC (Northeast Fisheries Science Center). 2013. 55th Northeast Regional Stock Assessment Workshop (55th SAW) Assessment Summary Report. US Department of Commerce, Northeast Fisheries Science Centre Reference Document 13-01. 41 p.
- Neilson, J. D., Waiwood, K. G., and Smith, S. J. 1989. Survival of Atlantic halibut (*Hippoglossus hippoglossus*) caught by longline and otter trawl gear. *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 887–897.
- Pollock, K. H., and Pine, W. E., III 2007. The design and analysis of field studies to estimate catch-and-release mortality. *Fisheries Management and Ecology*, 14: 1–8.

R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.

Raby, G. D., Packer, J. R., Danylchuk, A. J., and Cooke, S. J. 2014. The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. *Fish and Fisheries*, 15: 489–505.

Richards, L. J., Fargo, J., and Schnute, J. T. 1995. Factors influencing bycatch mortality of trawl-caught Pacific halibut. *North American Journal of Fisheries Management*, 15: 266–276.

Wilson, R. R., and Burns, K. M. 1996. Potential survival of released groupers caught deeper than 40 m based on shipboard and in-situ observations, and tag-recapture data. *Bulletin of Marine Science*, 58: 234–247.

Wood, C. M., Turner, J. D., and Graham, M. S. 1983. Why do fish die after severe exercise? *Journal of Fish Biology*, 22: 189–201.

Yergey, M. E., Grothues, T. M., Able, K. W., Crawford, C., and DeCristofer, K. 2012. Evaluating discard mortality of summer flounder (*Paralichthys dentatus*) in the commercial trawl fishery: Developing acoustic telemetry techniques. *Fisheries Research*, 115–116: 72–81.

Appendix

Description of the likelihood function used to fit the model

The log-likelihood function for the generalized mixture model is made up of three functions: the survival distribution function, the probability density function, and the mixture weight function [for the derivation, see Ibrahim *et al.* (2001)]. The survival distribution function, $S(t)$, is defined as the probability that an individual i survives to a time $T_i > t$. For the model in Equation (7), the survival distribution functions for affected and immune individuals are respectively given by

$$S_A(t) = \tau \exp(-Mt - [\alpha \cdot (t - t_0)]^\gamma), \quad (A1)$$

$$S_I(t) = \tau \exp(-Mt), \quad (A2)$$

where t is the survival time, τ models capture and handling mortality, and α and γ are, respectively, the scale and shape parameters of the Weibull distribution.

The probability density function, $f(t)$, is the probability of dying at t and is the first derivative of $1 - S(t)$. For affected and immune individuals, the density functions are respectively given by

$$f_A(t) = (\alpha \cdot \gamma (\alpha \cdot (t - t_0))^{\gamma-1} + M) \cdot S_A(t), \quad (A3)$$

$$f_I(t) = M \cdot S_I(t). \quad (A4)$$

The mixture density, $m(t)$, for uncensored observations is then given by

$$m(t) = \pi \cdot f_A(t) + (1 - \pi) \cdot f_I(t), \quad (A5)$$

where π is the probability that an individual is adversely affected.

The mixture probability for right-censored observations is

$$m_R(t) = \pi \cdot S_A(t) + (1 - \pi) \cdot S_I(t) \quad (A6)$$

and the mixture probability for left-censored observations is

$$m_L(t) = \pi \cdot (1 - S_A(t)) + (1 - \pi) \cdot (1 - S_I(t)). \quad (A7)$$

Now, let θ denote the vector of unknown parameters, y denote the set of b independent observed event times (mortality or censorship, as the case may be) indexed by i , d is the vector for a binary variable that denotes whether observations are left-censored ($d_i = 1$) or not ($d_i = 0$), and let e be a vector for a binary variable denoting whether observations are right-censored. The resulting full log-likelihood function to be minimized is then given by

$$\log L(\theta|y, d, e) = \sum_{i=1}^b -(1 - d_i) \cdot (1 - e_i) \cdot \log(m(t)_i) - e_i \log(m_R(t)_i) - d_i \log(m_L(t)_i) \quad (A8)$$

Handling editor: Shijie Zhou