Brief Communication

Is bigger really better? Towards improved models for testing how Atlantic salmon *Salmo salar* smolt size impacts marine survival

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Running head Smolt size and marine survival

Abstract

A general framework is presented that should enhance our understanding of how intrinsic factors, such as body size, and extrinsic factors, such as climate, affect the dynamics and demographics of fish populations. Effects of intrinsic factors, notably studies relating juvenile Atlantic salmon *Salmo salar* body size to their probability to return as an adult, are often context-dependent and anecdotal, due to data constraints. By merit of its flexible specification, this framework should admit datasets with a range of situation-specific nuances, collected using different approaches, and thereby deliver more general and robust findings for more effective population management.

Key words: smolt body size, migration, lifecycle, state-space model, Bayesian

There are few wild populations unaffected by human-induced environmental changes, such as climate change, overexploitation, invasive species and their synergies (Brook, Sodhi & Bradshaw, 2008). For example, the abundance of Atlantic salmon *Salmo salar* (taken as their nominal catches) has declined precipitously across their range since the 1970s (ICES, 2017; Fig. 1), probably due to a range of interacting factors (Limburg & Waldman, 2009; Mills *et al*., 2013), with populations now often augmented by hatchery-reared fish (Aprahamian *et al*., 2003; Molony *et al*. 2003).

To manage populations effectively generally requires understandings of how intrinsic and extrinsic factors, and their interactive and legacy effects, affect individual traits and behaviours (Clutton-Brock & Sheldon, 2010). Extrinsic factors potentially implicated in *S. salar* population declines include climate-driven changes in sea conditions and planktonic communities (Beaugrand & Reid, 2012), predation (e.g., Riley *et al*., 2011) and the timing of seaward emigrating juvenile salmon (known as *smolt*) migration associated with climate (e.g., Otero *et al*., 2014). However, there is growing evidence that intrinsic factors carried over from their freshwater stages are important in marine mortality, such as their body size and/ or condition at smolting (Russell *et al*., 2012). Should the effects of their freshwater life-phase strongly influence their marine survival, then this would have fundamental implications for smolt management because it would promote strategies that maximise not just the number of smolts but also their quality (Russell *et al*., 2012). Furthermore, it is important to account for such legacy effects in modelling the respective contributions of different factors to overall change in population strength. Correspondingly, the aim of this study was to explore, through literature review, the potential influences of *S. salar* body size at smolting on their subsequent marine survival, and consider how this can be tested more robustly, for example, by accounting for imperfect detection.

At a general level, theory suggests that smolt mortality might be inversely related to their body size, i.e., the inverse-weight hypothesis (Ricker, 1976). Many studies have provided some empirical evidence testing this 'bigger is better' paradigm (*sensu* Sogard, 1997). Koenings *et al*. (1993) suggested a positive influence of smolt length on marine survival in 12 populations, although the pattern was non-linear across age groups and exacerbated by latitudinal variation. Several studies, including Henderson & Cass (1991) and Holtby *et al*. (1990), revealed surviving *S. salar* smolts were generally of greater length (as estimated by scale back-calculations) than the mean length of their corresponding cohort. While the bigger is better paradigm could reflect the consequences of general processes, such as avoiding gape-limited predators and increasing prey options, it might not be universal. For example, medium-sized smolts had the highest marine survival rates in the River Imsa, Norway, although the relatively low survival of larger smolts could not be disentangled from the influence of their emigration timing (Jonsson *et al*. 2017). Armstrong *et al*. (2017) and Saloniemi *et al*. (2004) both provided strong arguments that larger smolt body sizes increased marine survival, where both utilised individual-level data and considered covariates and their interactions (Fig. 2). However, when assessed across a larger number of studies assessing the influence of smolt length on subsequent marine survival, support for the bigger is better paradigm seems equivocal (Table 1).

There are some patterns evident in Table 1 that can be used for formulating future studies and model development. Most of the studies regress a time series of mean lengths on a time series of marine survival (usually expressed as "adult return rate", which measures individual probability to return as an adult irrespective of time spent at sea) for a single river or stock (Type 1 in Table 1). There are two exceptions to this approach that regress the same variables but for 6 stocks (Dempson *et al*., 2003) and 12 stocks (Koenings *et al*., 1993), although the latter does not account for stock in the statistical model, risking possible pseudo-

replication. Another group of studies use back-calculated lengths from scales (Type 2 in Table 1), which introduces a non-quantified uncertainty due to measurement and model choice. Another group of studies examine the fate of tracked individuals (via telemetry) and examines the influence of length class on their survival (Type 3 in Table 1). The final group of studies presents plots of patterns but with no formal statistical analyses to quantify length effects (Type 4 in Table 1). Most studies also tend to use time series data on *S. salar* and consider year as the unit of variance. This is not surprising, since most of knowledge on *S. salar* marine survival comes from long-term monitoring programmes (ICES, 2017). This is, at least in part, due to difficulties associated with studying individuals and populations at sea, although telemetry studies are now able to provide movement data from estuarine and even near-shore coastal environments (e.g., Newton *et al*., 2016).

Statistically, only 4 of the studies considered covariates to either represent the variance fairly, i.e., to avoid pseudo-replication, or as potential competing hypotheses. In each case, the covariates were important to the study findings and thus there is a strong case for using covariates in future models. A good example is provided by Armstrong *et al*. (2017), who used individual-level covariates to generalise their findings beyond the years sampled (by using a random year effect) and to examine evidence for competing hypotheses (body condition and migration timing). Among the studies of Table 1, all but one considered linear terms only, despite acknowledging their inadequacy for some of the datasets (e.g., Holtby *et al*., 1990).

Most of the studies in Table 1 benefitted from monitoring programmes that provided long time series and large numbers of smolts. Such large numbers, even when stratified by year, afford a good representation of the sample mean – the response variable most commonly used. However, using the individual data, where available, could provide greater insight, especially for individuals at the limits of the population length range and where using

population means is not meaningful. For example, Saloniemi *et al*. (2004) used logistic regression to examine the effect of individual smolt length, relevant covariates and their interactions to reveal a positive effect of length on marine survival. Moreover, their use of individual-level data meant they required only two years of data and a moderate sample size (Table 1; Fig. 2). While a rich source of individual length data could be sourced from scale analyses and back-calculation (as per the Type 2 studies in Table 1), this requires careful consideration as: (i) lengths back-calculated from scales are subject to uncertainty in the model used and its parameters (Francis, 1990); (ii) scale collection protocol could be biased towards individuals of common characteristics, e.g., larger individuals sought by anglers; and (iii) if comparing the back-calculated lengths to the pool of observed lengths (e.g., Henderson & Cass, 1991), it should be considered that the denominator (the pool of observed lengths) might include the numerator (the back-calculated lengths).

If individual-level information is lacking from 'data-rich' long-term monitoring programmes, then an alternative might be to use abundant short and noisy datasets from 'data-poor' fisheries (Bentley, 2015). For example, Koenings *et al*. (1993) used short time series (1 to 9 years) from 12 stocks to suggest a positive effect of length on subsequent marine survival, albeit that they used annual mean data and omitted factors to allow for baseline differences between rivers and years (*c.f.* Armstrong *et al*., 2017). Methods exist that can integrate small and noisy datasets to tease out common signals, and these methods can also admit missing data, which is often a feature of these datasets (Bentley, 2015).

As most of the datasets in Table 1 utilise mark-recapture methods, then their data also present a potential confound to marine survival estimates, as not all individuals are re-detected, i.e., detection is imperfect. Detection efficiency is a measure of the probability (p) that a device (or array of devices) detects a tag moving within the area that the device was installed to monitor, which under perfect conditions will be $p = 1$. Many factors will cause

$p < 1$, including animal behaviour, which might relate to size, and environmental conditions. Imperfect detection is the term used to describe the effect of these factors on perfect detection. There is a large and growing literature highlighting the importance of imperfect detection, factors affecting it and methods that can account for it (e.g., Guillera-Arroita, 2017), including a class of models that separate observation and process errors, commonly called state-space models (e.g., Gimenez *et al*., 2007). Failure to account for imperfect detection, particularly when the probability of detecting an individual is low to moderate (e.g., < 90%) or the sample size is low, can result in imprecise inferences that are biased and inaccurate (e.g., Gimenez *et al*., 2007). This is particularly concerning when interpreting data from telemetry studies that usually have low to moderate detection rates and low sample sizes. For example, Newton *et al*. (2016) studied the effect of tagging on survival of smolts migrating through Lough Foyle, Ireland, and found no evidence that smaller smolts were less likely to survive to be detected exiting the lough to sea, although they could not disregard the possibility that the 8 of 33 unsuccessful lough migrants (or indeed the 27 smolts not detected entering the lough) were simply not detected. Imperfect detection is likely to affect most studies in Table 1, and its effect should not be neglected.

Given the issues outlined above, it is suggested that state-space models (SSM) are well suited to future testing of the bigger is better paradigm for migrating *S. salar* smolts. These explicitly model the underlying ecological or state process (Equation 1), e.g., the effect of smolt size on its marine survival, and the observational process (Equation 2), e.g., the probability of detecting a surviving smolt. When formulated in a Bayesian language (e.g., Just Another Gibbs Sampler [JAGS]: http://mcmc-jags.sourceforge.net/), they amount to a set of deterministic and stochastic equations. In the simple case of estimating the effect of length on the survival probability of smolt i in a single river, then:

$$y_{i,t}|z_{i,t} \sim \text{Bernoulli}(z_{i,t}p) \tag{1}$$

$$z_{i,t+1}|z_{i,t} \sim \text{Bernoulli}(z_{i,t}\phi_i) \qquad (2)$$

where $t > 0$, z is a latent variable describing the state of smolt i at time t, ϕ_i is the survival rate of smolt i from state $z_{i,t}$ to state $z_{i,t+1}$ and y is the observation of that smolt given the probability p of detecting it. From these equations, it can be noted that ϕ_i and p are time-invariant and p does not vary for individuals. To estimate the effect of smolt i length l_i on its survival, ϕ_i is specified as a deterministic function of logistic regression parameters:

$$\text{logit}(\phi_i) = \alpha + \beta_1 l_i \qquad (3)$$

where α is the estimated marine survival of any smolt returning to our river and β_1 is the effect of smolt i length on α, while accounting for imperfect detection, i.e., $1 - p$.

The ecological applications of SSM have increased due, at least in part, to their flexibility (Royle & Dorazio, 2008). For example, Gimenez *et al.* (2007) provide an instructive overview of SSM theory and an accompanying illustration using individual mark and recapture data collected on the European dipper *Cinclus cinclus*. Holbrook *et al.* (2014) uses SSM to estimate sea lamprey *Petromyzon marinus* passage through a dam using individual acoustic tagging data. A few SSM extensions are also worth noting. Equation 3 can be modified through additional covariates that are measured at the level of individual, group, or stock and are included by specifying coefficients for their (fixed) effects. For example, an effect of fat content of smolt i could be estimated by including the term $\beta_2 w_i$ in Equation 3. Care should be taken to ensure the effects are indexed at the correct level. For example, a fixed effect of river is included with the term $\beta_3 r$ that adds another stratum to all other effects, i.e., length is measured for smolts emigrating from river r in $1, 2, \ldots, R$ (where R is the number of rivers) and is therefore indexed with r as $l_{i,r}$. Note, by leaving β_1 unindexed, the effect of smolt length is estimated assuming that it is identical across rivers. It is a small step to specifying river as a random effect, i.e., acknowledging differences between rivers but treating rivers as a sample of a larger "population" of rivers: rather than specifying β_3 as a

single coefficient, it is specified it as a vector of coefficients $\boldsymbol{\beta_3}$, with effects drawn from a distribution defined by a common mean effect and variance (see Kéry & Schaub [2011] for a more complete description). With these extensions, it is straightforward to include fixed effects (e.g., latitude; Koenings *et al*., 1993) or random effects (e.g., year; Armstrong *et al*., 2017).

A further strength of SSM, and hierarchical models more generally, is the idea that information contained in short and noisy datasets can use information from larger, longer and less noisy datasets (Parent & Rivot, 2012). Assuming a single stock dataset per river (although this could be relaxed), then this is achieved by including a random effect of river. Although both datasets provide information to update the common mean effect estimate (and its variance), presumably the longer and less noisy dataset is providing more information, which is transferred to the shorter and noisier dataset.

There are assumptions inherent in each approach in Table 1. For example, tagging studies generally use a constant tag size, which is a higher, albeit not necessarily significant, burden on smaller fish. For example, survival effects of some tags, e.g., passive integrated transponder tags (~0.1g), are considered negligible while the effects of larger tags, e.g., acoustic telemetry transmitters (>1.0g), deserve more consideration. To test for effects of a constant size tag on variable sized smolts requires a baseline understanding of how survival relates to smolt size in untagged fish. It is not valid to infer no effect of tags from an absence of a significant size-mortality effect in a group of tagged fish alone (Newton *et al*. 2016) because there is no control to inform on how mortality would relate to size in a particular study situation in the absence of tagging. Variation in tag effect with smolt size could, however, be quantified in an SSM by, for example, contrasting Type 1 (tagging) with Type 2 studies, in which fish handling and tagging is not a consideration. In this case, the Type 2 approach would provide the control situation.

Estimating SSM parameters by Monte Carlo Markov Chains (MCMC) allows for the natural expression and propagation of uncertainties in parameter estimates to model outputs. Correctly parameterised, uncertainties from other sources could also propagate through the model. For example, mark-recapture studies rely on detection devices that can fail, which would enter the model as missing data rather than removing them. Changes to the monitoring apparatus, e.g., loss or addition of a new acoustic receiver, could be accounted for in a similar manner. Another source of uncertainty is model choice. For example, uncertainty in the model used to estimate smolt length from scales through back-calculation could be captured in a SSM, either through prior information or by implementing the back-calculation within the SSM itself. Similarly, acoustic tracking data, which provide information about estuarine and near-shore coastal mortality, could be admitted directly or indirectly. SSM that accommodate information from different data sources are commonly referred to as Integrated Population Models, and their use in ecology is increasing (e.g., Robinson *et al*., 2014).

Although strongly advocating a move towards a general SSM to test the bigger is better paradigm for *S. salar* smolts, these models should not be considered as a panacea, as they too can have estimation problems when the process error is swamped by measurement error (Auger-Méthé *et al*., 2016). Consequently, this study can be considered as a call to population managers and researchers to contact the authors with details of datasets that they feel might contribute information to a general analysis to test the bigger is better paradigm for *S. salar* smolts in the manner described. This is important because a better understanding of how intrinsic and extrinsic factors affect the vital rates of the individuals that constitute a population could allow these populations to be better managed. In the case of *S. salar*, for example, evidence of a general positive effect of smolt size on their subsequent marine survival could support management strategies that maximise not just the number but also the

body size and condition of emigrating smolts, perhaps by improving overwintering habitat. (We acknowledge that a management strategy designed to maximise both number and size and condition of smolts would have to account for many complicating factors, such as any negative effect of density dependence on body size.) This could be a particularly pertinent message at present given evidence that body sizes of juvenile *S. salar* are decreasing in countries such as England and France (e.g., Gregory *et al.*, 2017). In summary, determining the role of smolt body size in marine survival could provide considerable conservation and fishery benefits for *S. salar* and could be incorporated into methods currently used to set conservation limits and fishing quotas (MacLean *et al.*, 2003).

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Tables

Table 1: Studies (non-exhaustive) testing the effect of salmonid smolt length on the subsequent marine survival, with a focus on *Salmo salar*. Origin: W = wild, H = hatchery, Hw = hatchery from wild stock; Number of smolts: NR = not reported.

Type	Method	Study	Species	Origin	Evidence	Number smolts	Number years	Number rivers	Unit of variance	Data characteristics	Model characteristics
1	Relating annual mean length to annual overall adult return rate	Amiro (2003)	*Salmo salar*	W Hw	No effect of length on adult return rate	NR	4	1	Year	Small sample size, Imperfect adult detection	Linear only, No covariates
1	Relating annual mean length to 1SW and 2+SW adult return rates	Armstrong *et al.* (2017)	*Salmo salar*	Hw	Positive effect of length on 1SW and 2+SW adult return rate	>12500	15	1	Individual	Medium sample size, Long time series, Perfect adult detection	Linear only, Individual-level covariates
2	Relating annual lengths back-calculated from 1SW and 2SW returned adult scales to annual lengths	Caron & Dodson (2003)	*Salmo salar*	W	Positive effect of length on 1SW and 2SW adult return rate	> 262000	4	1	Individual	Large sample size, Short time series	No covariates, Unaccounted back-calculation uncertainty
1	Relating mean length and adult return rate	Dempson, *et al.* (2003)	*Salmo salar*	W	Weak positive effect of length on adult return rate	>1300000	10	6	River	Multiple rivers for generality, Small sample size, Perfect adult detection	Linear only, No covariates
1	Relating annual mean length and annual adult return rate	Dempson, *et al.* (2003)	*Salmo salar*	W	Weak positive and negative river-specific effects of length on adult return rate	12849-404667	9-16	1	Year	Medium sample size, Long time series, Perfect adult detection	Linear only, No covariates
3	Retrospective classification of radio-tagged individual	Dieperink, *et al.* (2001)	*Salmo trutta*	W H	Weak positive effect of length on probability to be predated	37	1	1	Binomial error	Small sample size, Imperfect smolt	No covariates, Unaccounted classification uncertainty,

										detection	Potential confounding by origin
	fates during their early (estuarine) seaward migration				by bird					detection	Potential confounding by origin
3	Retrospective classification of radio-tagged individual fates during their early (estuarine) seaward migration	Dieperink, et al. (2002)	*Salmo salar & Salmo trutta*	W	Weak positive effect of length on probability to be predated by bird	24 (*S. salar*) & 15 (*S. trutta*)	1	1	Binomial error	Small sample size, Imperfect smolt detection	No covariates, Unaccounted classification uncertainty
1	Relating annual mean length to annual overall adult return rate	Henderson & Cass (1991)	*Oncsrhynchus nerka*	W	No effect of length on adult return rate	NR	34	1	Year	Medium sample size, Long time series, Imperfect adult detection	Linear only, No covariates
2	Relating annual mean length back-calculated from returned adult scales to annual mean lengths	Henderson & Cass (1991)	*Oncsrhynchus nerka*	W	Significantly higher mean length back-calculated from returned adult scales for 2 years	585, 474, 484	3	1	Individual	Imperfect detection	Separate years, Unaccounted back-calculation uncertainty, No covariates
2	Relating annual lengths back-calculated from returned adult scales to annual lengths	Holtby, et al. (1990)	*Oncsrhynchus kisutch*	W	Significantly higher(lower) mean length back-calculated from returned adult scales for 7(2) years; equal in 5 years	NR	14	1	Individual	Imperfect detection	Separate years, Unaccounted back-calculation uncertainty, No covariates
4	Comparing mean marine survival among length classes migrating in different time periods	Jonsson, et al. (2017)	*Salmo salar*	W	Higher survival among longer individuals migrating during middle emigration period	36833	37	1	Group	Large sample size, Long time series, Perfect adult detection	Unaccounted tag mortality, No formal statistical test, Group-level covariates
1	Relating annual mean length to annual tag recovery rate	Jutila, et al. (2006)	*Salmo salar*	Hw	Positive effect of length on post-smolt tag recovery rate	NR	23	1	Year	Large sample size, Long time series	Linear only, Unaccounted tag mortality, Unknown reporting effort, No covariates
1	Relating annual mean length to annual tag recovery rate	Kallio-Nyberg, et al (2004)	*Salmo salar*	Hw	No evidence of size-dependent mortality	>15000	21	1	Year	Large sample size, Long time series	Linear only, Unaccounted tag mortality, Unknown

											reporting effort, No covariates
1	Relating annual mean length to annual overall adult return rate	Koenings, *et al.* (1993)	*Oncorhynchus nerka*	W H	Positive effect of length on adult return rate, with possible quadratic effect	NR	1-9	12	Year	Multiple rivers for generality, Medium sample size, Imperfect adult detection	Linear and non-linear, Unaccounted river effect, River-level covariates
3	Acoustic-tagged individual lengths compared to their fates during early (estuarine) seaward migration	Newton, *et al.* (2016)	*Salmo salar*	W	No evidence of size-dependent mortality	68	2	1	Individual	Imperfect detection	Separate years, No covariates
4	Early (estuarine) marine tag recovery rate calculated and plotted for different smolt size classes	Salminen, *et al.* (1995)	*Salmo salar*	H	Positive and no effects of length on tag recovery rate	35000-505000 & 11000-577000	12	2	Year	Large sample size, Long time series, Imperfect detection	Separate rivers, Unaccounted tag mortality, Unknown reporting effort, No formal statistical test
1	Relating individual length to early (estuarine) marine tag recovery rate	Saloniemi, *et al.* (2004)	*Salmo salar*	W H	Positive effect of length on tag recovery rate	>3740	2	1	Individual	Medium sample size, Short time series, Imperfect detection	Linear only, Unaccounted tag mortality, Unknown reporting effort, Group-level covariates

Figure Captions

Figure 1: Atlantic salmon populations are declining, as suggested by the 5-year rolling mean reported nominal catch (tonnes). Source: ICES2017.

Figure 2: Fitted effect of *S. salar* smolt length on their subsequent marine survival. (a) effect measured using a cumulative link mixed model including covariates condition and day and a random year effect. The dots show the observed proportions of returning fish; these are calculated by splitting the marginal distribution of the explanatory variable (length) into twenty bins with equal numbers of fish and calculating the proportion of returning fish in each. The position of the dots on the x-axis are the 2.5, 7.5, …, 97.5 percentiles of the explanatory variable so, 95% of fish had lengths between 104 and 143 mm. The solid lines span the observed range of each explanatory variable. The full range of lengths illustrated by the fitted line. Models with smooth relationships were also explored, but the nonlinear terms were never significant. Redrawn from Armstrong *et al*. (2017). (b) effect measured using a logistic regression including covariates origin and year and using just two years of data: black lines = 1991, grey lines = 1993, solid lines = wild smolts, dashed lines = reared smolts. Redrawn from Saloniemi *et al*. (2004). Note the similarity in intercept and slopes of the fits.
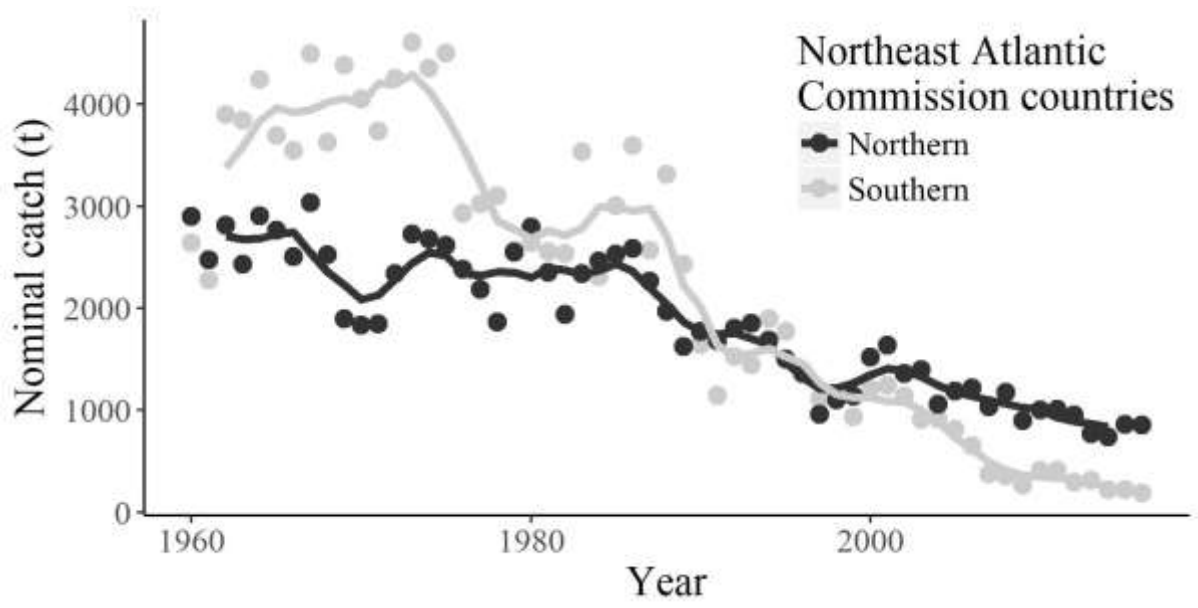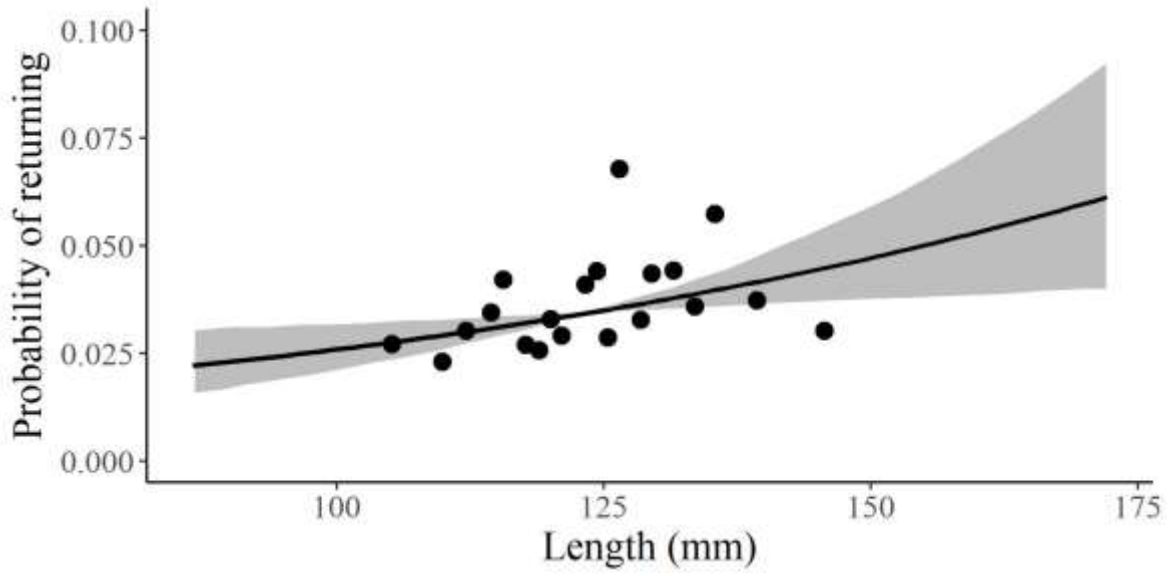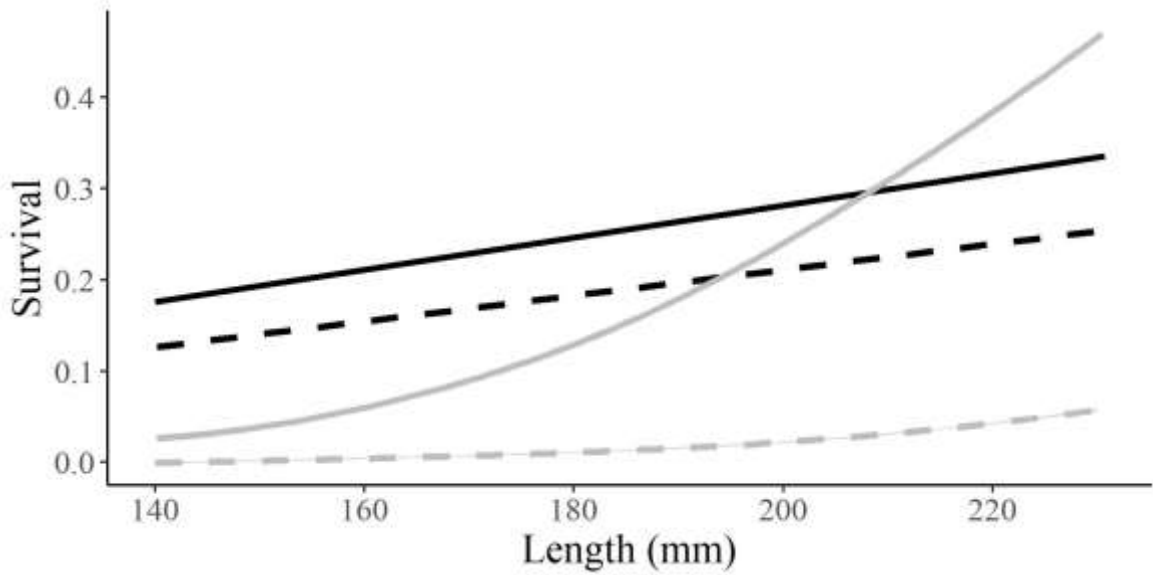
Figures

Fig. 1

(a)

(b)

Fig. 2