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

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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: Bayesian; lifecycle; migration; smolt body size; state-space model.

There are few wild populations unaffected by human-induced environmental changes, such as climate change, overexploitation, invasive species and their synergies (Brook *et al.,* 2008). For example, the abundance of Atlantic salmon *Salmo salar* L. 1758 (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 (Riley *et al.,* 2011) and the timing of seaward emigrating juvenile *S. salar* (known as smolts) migration associated with climate (Otero *et al.,* 2014). There is growing evidence, however, that intrinsic factors carried over from their freshwater stages are important in marine mortality, such as their body size and condition at smolting (Russell *et al.,* 2012). Should

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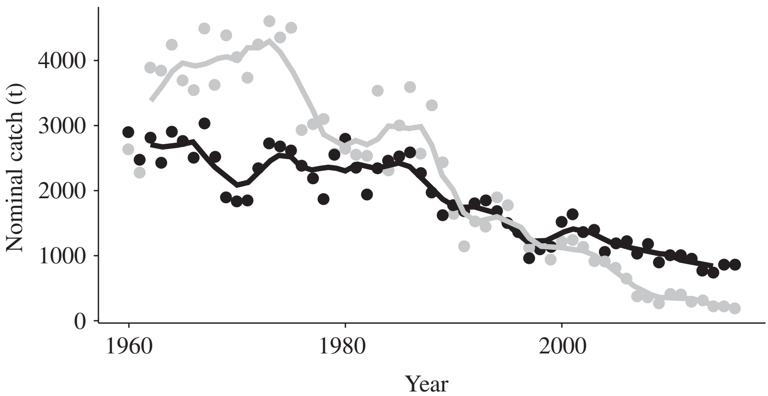


FIG. 1. *Salmo salar* populations are declining, as indicated by the 5-year rolling mean reported nominal catch (ICES, 2017). —●—, Northern and —○—, Southern countries within the North East Atlantic Commission (www.nasco.int/neac.html).

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 maximize 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 of tagged fish.

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.* (2018) and Saloniemi *et al.* (2004) both provided strong arguments that larger smolt body sizes increased marine survival, where both utilized 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 appears equivocal (Table I).

There are some patterns evident (Table I) that can be used for formulating future studies and model development. Most of the studies regress a time series of mean

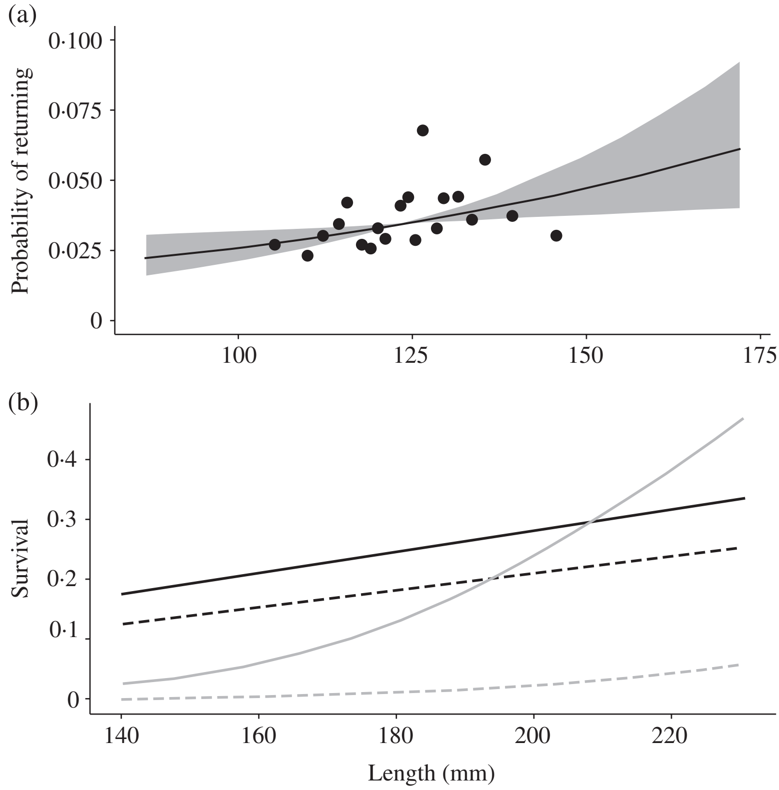


FIG. 2. Fitted effect of *Salmo salar* smolt length on their subsequent marine survival. (a) Effect measured using a cumulative link mixed model including covariates condition and day and a random year effect. ●, Observed proportions of returning individuals per length class, calculated by splitting smolt length (conditioned by other explanatory variables) into 20 bins with equal numbers of individuals and calculating the proportion of returning individuals in each. ——, The overall probability of returning and spans the observed range of smolt length. ▭, The 95% pointwise confidence band about the solid line (redrawn from Armstrong *et al.,* 2018). (b) Effect measured using a logistic regression including covariates origin and year and using just 2 years of data: ——, 1991 and ——, 1993 wild smolts; - - - -, 1991 and - - - -, 1993 reared smolts (redrawn from Saloniemi *et al.,* 2004). N.B. Similarity in intercept and slopes of the fits.

lengths on a time series of marine survival (usually expressed as the 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 I). 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 I), 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 I). The final group of studies presents plots of patterns but with no formal statistical analyses to quantify length effects (type 4 in Table I). 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 knowledge on

TABLE I. Some studies testing the effect of salmonid (*Oncorhynchus kisutch*, *Oncorhynchus nerka*, *Salmo salar* and *Salmo trutta*) smolt length on their subsequent marine survival, with a focus on *Salmo salar*

| Type | Method | Study | Species | Origin | Evidence | Number smolts | Number of years | Number of 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.* (2018) | *Salmo salar* | Hw | Positive effect of length on 1SW and 2 + SW adult return rate | > 12 500 | 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 | > 262 000 | 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 | > 1 300 000 | 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 | 12 849–404 667 | 9–16 | 1 | Year | Medium sample size, long time series, perfect adult detection | Linear only, no covariates |

TABLE I. Continued

| Type | Method | Study | Species | Origin | Evidence | Number smolts | Number of years | Number of rivers | Unit of variance | Data characteristics | Model characteristics |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 | Retrospective classification of radio-tagged individual fates during their early (estuarine) seaward migration | Dieperink *et al.* (2001) | *Salmo trutta* | W H | Weak positive effect of length on probability to be predated by bird | 37 | 1 | 1 | Binomial error | Small sample size, imperfect smolt detection | No covariates, unaccounted classification uncertainty, 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) | *Oncorhynchus 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) | *Oncorhynchus 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 |

TABLE I. Continued

| Type | Method | Study | Species | Origin | Evidence | Number smolts | Number of years | Number of rivers | Unit of variance | Data characteristics | Model characteristics |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | Relating annual lengths back-calculated from returned adult scales to annual lengths | Holtby *et al.* (1990) | *Oncorhynchus 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 | 36 833 | 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 | >15 000 | 21 | 1 | Year | Large sample size, long time series | Linear only, unaccounted tag mortality, unknown reporting effort, no covariates |

TABLE I. Continued

| Type | Method | Study | Species | Origin | Evidence | Number smolts | Number of years | Number of rivers | Unit of variance | Data characteristics | Model characteristics |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 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 | 35 000–505 000 & 11 000–577 000 | 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 |

Type 1, time series of marine survival for a single river or stock; type 2, studies using back-calculated lengths from scales; type 3, examination of the fate of tracked individuals (*via* telemetry) and the influence of length class on their survival; type 4, no formal statistical analyses to quantify length effects.
SW, Sea winter; W, wild; H, hatchery; Hw, hatchery from wild stock; NR, not reported.

*S. salar* marine survival comes from long-term monitoring programmes (ICES, 2017). This is due, at least in part, 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 (Newton *et al.,* 2016).

Statistically, only four of the studies considered covariates to either represent the variance fairly, *i.e.* to avoid pseudo-replication, or to explore as potential competing hypotheses. In each case, the covariates were important to the study findings; thus, there is a strong case for using covariates in future models. A good example is provided by Armstrong *et al.* (2018), who used individual-level covariates to generalize 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 I, 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 listed in Table I 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, which is the response variable most commonly used. Using the individual data, where available, however, 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 2 years of data and a moderate sample size (Table I; 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 I), this requires careful consideration as: lengths back calculated from scales are subject to uncertainty in the model used and its parameters (Francis, 1990); scale collection protocol could be biased towards individuals of common characteristics, *e.g.* larger individuals sought by anglers; if comparing the back-calculated lengths to the pool of observed lengths (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.,* 2018). 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 I utilize mark–recapture methods, then their data also present the potential to confound 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 (Guillera-Arroita, 2017), including a class of models that separate observation and process errors, commonly called state–space models (SSM; 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 (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 of the studies listed in Table I and its effect should not be neglected.

Given the issues outlined above, it is suggested that 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:

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

$$z_{i,t+1} \mid z_{i,t} \sim \text{Bernoulli}\left(z_{i,t}\phi_i\right), \tag{2}$$

where $t > 0$, $z$ is a latent variable describing the state of smolt $i$ at time $t$, $\phi_i$ 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 $\phi_i$ 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, $\phi_i$ is specified as a deterministic function of logistic regression parameters:

$$\text{logit}\left(\phi_i\right) = \alpha + \beta_1 l_i, \tag{3}$$

where $\alpha$ is the estimated marine survival of any smolt returning to our river and $\beta_1$ is the effect of smolt $i$ length on $\alpha$, 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–recapture data collected on the European dipper *Cinclus cinclus*. Holbrook *et al.* (2014) uses SSM to estimate sea lamprey *Petromyzon marinus* L. 1758 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, …, $R$ (where $R$ is the number of rivers) and is therefore indexed with $r$ as $l_{i,r}$. Note, by leaving $\beta_1$ 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 $\beta_3$ as a single coefficient, it is specified it as a vector of coefficient $\beta_3$, 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.,* 2018).

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 I. 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 (*c.* 0·1 g in air), are considered negligible while the effects of larger tags, *e.g.* acoustic telemetry transmitters (> 1·0 g in air), 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 Markov chain Monte-Carlo (MCMC) methods 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 an 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 (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 maximize not just the number but also the body size and condition of emigrating smolts, perhaps by improving overwintering habitat. (It is acknowledged that a management strategy designed to maximize 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 (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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## References

Aprahamian, M. W., Martin Smith, K., McGinnity, P., McKelvey, S. & Taylor, J. (2003). Restocking of salmonids – opportunities and limitations. *Fisheries Research* **62,** 211–227. https://doi.org/10.1016/S0165-7836(02)00163-7

Armstrong, J. D., Mckelvy, S., Smith, G. W., Rycroft, P. & Fryer, R. J. (2018). Effects of individual variation in length, condition and run-time on return rates of wild-reared Atlantic salmon smolts. *Journal of Fish Biology* (this issue).

Auger-Méthé, M., Field, C., Albertsen, C. M., Derocher, A. E., Lewis, M. A., Jonsen, I. D. & Flemming, J. M. (2016). State-space models' dirty little secrets: even simple linear Gaussian models can have estimation problems. *Scientific Reports* **6,** 26677. dx.doi.org, https://doi.org/10.1038/srep26677

Beaugrand, G. & Reid, P. C. (2012). Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science* **69,** 1549–1562. https://doi.org/10.1093/icesjms/fss153

Bentley, N. (2015). Data and time poverty in fisheries estimation: potential approaches and solutions. *ICES Journal of Marine Science* **72,** 186–193. https://doi.org/10.1093/icesjms/fsu023

Brook, B. W., Sodhi, N. S. & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23,** 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Clutton-Brock, T. & Sheldon, B. C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* **25,** 562–573. https://doi.org/10.1016/j.tree.2010.08.002

Dieperink, C., Pedersen, S. & Pedersen, M. I. (2001). Estuarine predation on radiotagged wild and domesticated sea trout (*Salmo trutta* L.) smolts. *Ecology of Freshwater Fish* **10,** 177–183. https://doi.org/10.1034/j.1600-0633.2001.100307.x

Dieperink, C., Bak, B. D., Pedersen, L.-F., Pedersen, M. I. & Pedersen, S. (2002). Predation on Atlantic salmon and sea trout during their first days as postsmolts. *Journal of Fish Biology* **61,** 848–852. https://doi.org/10.1111/j.1095-8649.2002.tb00917.x

Francis, R. I. C. C. (1990). Back-calculation of fish length: a critical review. *Journal of Fish Biology* **36,** 883–902. https://doi.org/10.1111/j.1095-8649.1990.tb05636.x

Gimenez, O., Rossi, V., Choquet, R., Dehais, C., Doris, B., Varella, H., Vila, J.-P. & Pradel, R. (2007). State-space modelling of data on marked individuals. *Ecological Modelling* **206,** 431–438. https://doi.org/10.1016/j.ecolmodel.2007.03.040

Gregory, S. D., Nevoux, M., Riley, W. D., Beaumont, W. R. C., Jeannot, N., Lauridsen, R. B., Marchand, F., Scott, L. J. & Roussel, J.-M. (2017). Patterns on a parr: drivers of long-term salmon parr length in U.K. and French rivers depend on geographical scale. *Freshwater Biology* **62,** 1117–1129. https://doi.org/10.1111/fwb.12929

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. *Ecography* **40,** 281–295. https://doi.org/10.1111/ecog.02445

Henderson, M. A. & Cass, A. J. (1991). Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **48,** 988–994. https://doi.org/10.1139/f91-115

Holbrook, C. M., Johnson, N. S., Steibel, J. P., Twohey, M. B., Binder, T. R., Krueger, C. C. & Jones, M. L. (2014). Estimating reach-specific fish movement probabilities in rivers with a Bayesian state-space model: application to sea lamprey passage and capture at dams. *Canadian Journal of Fisheries and Aquatic Sciences* **71**, 1713–1729. https://doi.org/10.1139/cjfas-2013-0581

Holtby, L. B., Andersen, B. C. & Kadowaki, R. K. (1990). Importance of smolt size and early ocean growth to interannual variability in marine survival of Coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **47,** 2181–2194. https://doi.org/10.1139/f90-243

Jonsson, B., Jonsson, M. & Jonsson, N. (2017). Influences of migration phenology on survival are size dependent in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology* **95,** 581–587. https://doi.org/10.1139/cjz-2016-0136

Jutila, E., Jokikokko, E. & Julkunen, M. (2006). Long-term changes in the smolt size and age of Atlantic salmon, *Salmo salar* L., in a northern Baltic river related to parr density, growth opportunity and postsmolt survival. *Ecology of Freshwater Fish* **15,** 321–330. https://doi.org/10.1111/j.1600-0633.2006.00171.x

Kallio-Nyberg, I., Jutila, E., Saloniemi, I. & Jokikokko, E. (2004). Association between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simojoki River in the Baltic Sea. *Journal of Fish Biology* **65,** 122–134. https://doi.org/10.1111/j.0022-1112.2004.00435.x

Kéry, M. & Schaub, M. (2011). *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*. New York, NY: Academic Press.

Koenings, J. P., Geiger, H. J. & Hasbrouck, J. J. (1993). Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effects of smolt length and geographic latitude when entering the sea. *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 600–611. https://doi.org/10.1139/f93-069

Limburg, K. E. & Waldman, J. R. (2009). Dramatic declines in North Atlantic diadromous fishes. *Bioscience* **59,** 955–965. https://doi.org/10.1525/bio.2009.59.11.7

Mills, K. E., Pershing, A. J., Sheehan, T. F. & Mountain, D. (2013). Climate and ecosystem linkages explain widespread declines in north American Atlantic salmon populations. *Global Change Biology* **19,** 3046–3061. https://doi.org/10.1111/gcb.12298

Molony, B. W., Lenanton, R., Jackson, G. & Norriss, J. (2003). Stock enhancement as a fisheries management tool. *Reviews in Fish Biology and Fisheries* **13,** 409–432. https://doi.org/10.1007/s11160-004-1886-z

Newton, M., Barry, J., Dodd, J. A., Lucas, M. C., Boylan, P. & Adams, C. E. (2016). Does size matter? A test of size-specific mortality in Atlantic salmon *Salmo salar* smolts tagged with acoustic transmitters. *Journal of Fish Biology* **89,** 1641–1650. https://doi.org/10.1111/jfb.13066

Otero, J., L'Ábee-Lund, J. H., Castro-Santos, T., Leonardsson, K., Storvik, G. O., Jonsson, B., Dempson, D., et al. (2014). Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Global Change Biology* **20,** 61–75. https://doi.org/10.1111/gcb.12363

Parent, E. & Rivot, E. (2012). *Introduction to Hierarchical Bayesian Modeling for Ecological Data*. New York, NY: CRC Press.

Ricker, W. E. (1976). Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. *Journal of the Fisheries Research Board of Canada* **33,** 1483–1524. https://doi.org/10.1139/f76-191

Riley, W. D., Ibbotson, A. T., Beaumont, W. R. C., Pawson, M. G., Cook, A. C. & Davison, P. I. (2011). Predation of the juvenile stages of diadromous fish by sea bass (*Dicentrarchus labrax*) in the tidal reaches of an English chalk stream. *Aquatic Conservation Marine and Freshwater Ecosystems* **21,** 307–312. https://doi.org/10.1002/aqc.1184

Robinson, R. A., Morrison, C. A. & Baillie, S. R. (2014). Integrating demographic data: towards a framework for monitoring wildlife populations at large spatial scales. *Methods in Ecology and Evolution* **5,** 1361–1372. https://doi.org/10.1111/2041-210X.12204

Royle, J. A. & Dorazio, R. M. (2008). *Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities*. New York, NY: Academic Press.

Russell, I. C., Aprahamian, M. W., Barry, J., Davidson, I. C., Fiske, P., Ibbotson, A. T., Kennedy, R. J., Maclean, J. C., Moore, A. & Otero, J. (2012). The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES Journal of Marine Science* **69,** 1563–1573. https://doi.org/10.1093/icesjms/fsr208

Salminen, M., Kuikka, S. & Erkamo, E. (1995). Annual variability in survival of sea-ranched Baltic salmon, *Salmo salar* L: significance of smolt size and marine conditions. *Fisheries Management and Ecology* **2,** 171–184. https://doi.org/10.1111/j.1365-2400.1995.tb00110.x

Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E. & Pasanen, P. (2004). Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. *ICES Journal of Marine Science* **61,** 782–787. https://doi.org/10.1016/j.icesjms.2004.03.032

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60,** 1129–1157.

## Electronic References

Amiro, P. G. (2003). Trends in marine survival of hatchery-origin Atlantic salmon (*Salmo salar* L.) to four maritime rivers with comparisons to indices of wild-origin smolt survival to the LaHave river, Nova Scotia, Canada. In *Marine Mortality of Atlantic Salmon, Salmo salar L: Methods and Measures* (Potter, E. C. E., O'Maoileidigh, N. & Chaput, G., eds), pp. 44–58. Canadian Science Advisory Secretariat Research Document 2003/101. Ottawa: Department of Fisheries and Oceans Available at http://waves-vagues.dfo-mpo.gc.ca/Library/281668.pdf

Caron, F. & Dodson, J. (2003). Change in size selective mortality in Atlantic salmon (*Salmo salar* L.), de la Trinité river, Québec, Canada. In Marine Mortality of Atlantic Salmon, *Salmo Salar* L: Methods and Measures (Potter, E. C. E., O'Maoileidigh, N. & Chaput, G., eds), pp. 118–123. *Canadian Science Advisory Secretariat Research Document* **2003/101**. Department of Fisheries and Oceans: Ottawa Available at http://waves-vagues.dfo-mpo.gc.ca/Library/281668.pdf

Dempson, J., Mullins, C., Bourgeois, C., O'Connell, M. & Reddin, D. (2003). Perspectives on smolt production and marine survival of Newfoundland Atlantic salmon (*Salmo salar* L.) related to smolt size and run timing. In *Marine Mortality of Atlantic Salmon, Salmo salar L: Methods and Measures* (Potter, E. C. E., O'Maoileidigh, N. & Chaput, G., eds), pp. 27–43. *Canadian Science Advisory Secretariat Research Document* **2003/101**. Ottawa:

Department of Fisheries and Oceans Available at http://waves-vagues.dfo-mpo.gc.ca/Library/281668.pdf

ICES. (2017). *Report of the Working Group on North Atlantic Salmon (WGNAS) 29 March–7 April 2017,* Copenhagen*,* Denmark. Available at http://ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2017/WGNAS/wgnas_2017.pdf (last accessed 6 August 2017).

MacLean, J., Hansen, L. & Friedland, K. (2003). Links between environment, growth and survival in Atlantic salmon (*Salmo salar* L.) and the implications for modelling prefishery abundance. In *Marine Mortality of Atlantic Salmon, Salmo salar L: Methods and Measures* (Potter, E. C. E., O'Maoileidigh, N. & Chaput, G., eds), pp. 137–149. Canadian Science Advisory Secretariat Research Document 2003/101. Ottawa: Department of Fisheries and Oceans Available at http://waves-vagues.dfo-mpo.gc.ca/Library/281668.pdf