

APPENDIX B: BOOTSTRAPPING MORTALITY PARAMETERS

B1 INTRODUCTION

This appendix explains the bootstrapping methods used to estimate the annual variability of the early life-history parameters: production at the time of hatching (P_h), the coefficient of larval mortality (β), egg instantaneous mortality (IMR) (α) and the daily egg production (P_0). Mortality curves estimated in the main manuscript (section 2.2.1), used a Pareto type mortality curve (this regression will be referred to as MC^0). The iterative procedure used to identify the egg IMR (α) (equation 2) and the calculation of P_0 (equation 3) yields only point estimates for α and P_0 . Lo (1985a) approached the problem of estimating variability for these point estimates using an approximation based on the delta method. When applied to our data the standard errors produced were too large to be meaningful, frequently displaying a coefficient of variation greater than 1.

The bootstrap is used to provide more precise estimates of the variability using confidence intervals of the bootstrapped distributions. An advantage of this approach is that it characterizes confidence intervals for a general class of true underlying distributions, in particular accurate interval construction is more robust to fat tails and extreme tail events. The residual bootstrap method (MacKinnon 2006) is used, which samples from the residual empirical cumulative distribution function (cdf) of MC^0 and applies the resampled residuals to the fitted daily larval production estimates \widehat{dlp} to for bootstrapped \widehat{dlp}^* , on which new mortality curves with new parameters were estimated. Normalization is required to stabilize the heteroskedasticity in the residual distribution. When applied to equations 1–3 annual bootstrap distribution of β , P_h , α , and P_0 are created from which we take the 0.025 and 0.975 quantiles as the 95% confidence interval of the associated statistics.

The results of methods used in this appendix are 95% confidence intervals for β , P_h , α , and P_0 . In addition, the residual analysis necessary for the heteroskedasticity stabilization is discussed in the results and discussion section.

The next section describes the bootstrapping methods in detail. Section three reports some of the intermediate estimation results and section four discusses the methods used and the residual distribution. Confidence intervals were referenced in the text of the main manuscript and can be found in table 1, and figure 4.

B2 METHODS

The residual bootstrap uses the empirical cdf of the residuals from the initial estimation of the mortality

curve MC^0 (section 2.2.1) as a measure of the true error term associated with larval mortality estimation. Residuals are given by

$$\widehat{\varepsilon}_{c,s} = dl_{p_{c,s}} - \widehat{dl}_{p_{c,s}}, \text{ where } \widehat{dl}_{p_{c,s}} = \widehat{P}_{h,s} \left(\frac{t_{c,s}}{t_s^I} \right)^{-\widehat{\beta}_s} \quad (\text{B1})$$

and $\widehat{\beta}_s$ and $\widehat{P}_{h,s}$ are the annual ($s = 1981, 1982, \dots, 2009$) estimated parameter values relating daily larval production ($dl_{p_{c,s}}$) to larval ages ($t_{c,s}$) over the incubation time (t_s^I) for larval size class ($c \in \{\text{larval class } 2.5 \text{ mm}, 3.75 \text{ mm}, \dots, 9.75 \text{ mm}\}$) (appendix A1 and table A1).

There were eight larval size classes in a year and simply resampling from the eight residuals on that year would not provide a sufficiently rich set of residuals to characterize the true residual distribution. Furthermore, size class dependent heteroskedasticity precluded resampling from this small set of residual. To overcome this residuals from all 29 years of mortality estimation normalized by exploiting the longitudinal structure were of the residual data. Linear approaches to bootstrap normalization are not applicable for nonlinear regression (MacKinnon 2006)¹. We use a linear regression with ages and years as independent variables to model the heteroskedasticity and purge the residuals of class and temporal dependence. Higher-order polynomial terms and other categorical variables were tried, and a first-order linear regression minimized the AIC criterion. The heteroskedasticity stabilizing regression is:

$$\omega_{c,s} = |\widehat{\varepsilon}_{c,s}|, \quad \gamma_s = \frac{s - \text{mean}(s)}{\text{stdev}(s)}$$

$$\omega_{c,s} = \theta_0 + \theta_1 t_{c,s} + \theta_2 \gamma_s + \theta_3 D2_s + \nu_{c,s} \quad (\text{B2})$$

where $\omega_{c,s}$ is the absolute deviation of the residual, γ_s is the normalized year, $t_{c,s}$ is the larval size class age, $D2_s$ is a categorical 0–1 variable capturing the anomalous years 2005 and 2006 ($D2_s = 1$) (section 2.3) and $\nu_{c,s}$ is the error term. Outliers exerted excessive leverage and led to a poor fit. Outliers were determined from a preliminary regression of B2 as observations associated with a preliminary residual z-score greater than six, $6 \leq \widehat{\nu}_{c,s} - \text{mean}_{0.01}(\widehat{\nu}) / \text{stdev}_{0.01}(\widehat{\nu})$ (where the 0.01 subscript indicates a trimmed mean/standard deviation). This identified three observations as outliers. Equation B2 was then fit with outliers removed to determine the final fit. The fitted root-squared residuals were then used to normalize the residuals distribution.

¹E.g. using the diagonal element of the hat data matrix $X(X'X)^{-1}X'$ where X is the data matrix used in linear regression.

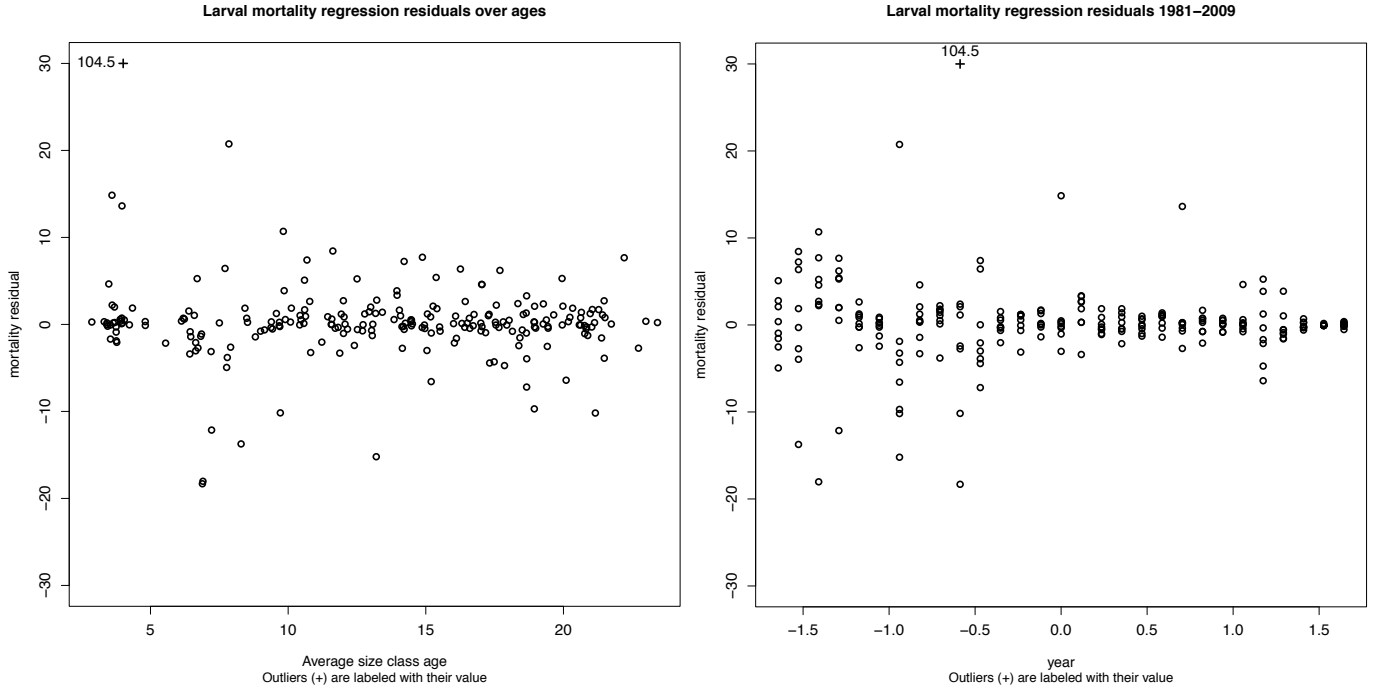


Figure B1. Larval mortality residuals (from equation 1) over the average size-class ages ($t_{c,s}$) (left panel), and normalized years (y_s) (right panel) 1981–2009.

$$\tilde{\varepsilon}_{c,s} = \varepsilon_{c,s} / |\hat{\omega}_{c,s}| \quad (\text{B3})$$

where

$$\hat{\omega}_{c,s} = \hat{\theta}_0 + \hat{\theta}_1 t_{c,s} + \hat{\theta}_2 y_s + \hat{\theta}_3 D2_s \quad (\text{B4})$$

This procedure produces a set (29 years x 8 classes = 232) of temporally and class “independent” residuals forming a distribution that was used to perform the bootstrapped. For each year s , eight residuals (one for each size class) were randomly sampled with replacement from the set of residual, $\varepsilon^{BS} \in \{\tilde{\varepsilon}_{c,s}\}$. Residuals were centered and rescaled to have the size class and temporal variance as determined by equation B4. The new resampled residuals were added to the fitted daily larval production from the initial estimation stage (equation 1 and B1) to obtain bootstrapped DLP estimates.

$$\varepsilon^{BS^t} = \varepsilon^{BS} - \frac{1}{8} \sum_{i=1}^8 \varepsilon_i^{BS}, \quad \varepsilon_{c,s}^* = \varepsilon^{BS^t} * |\hat{\omega}_{c,s}|,$$

and $dlp_{c,s}^* = \hat{d}lp_{c,s} + \varepsilon_{c,s}^* \quad (\text{B5})$

The bootstrapped DLP $dlp_{c,s}^*$ estimates were then used to fit a new mortality curve.

$$dlp_{c,s}^* = \hat{P}_{h,s}^* \left(t_{c,s} / t_s^I \right)^{-\hat{\beta}_s^*} \quad (\text{B6})$$

The estimated production at the time of hatching $\hat{P}_{h,s}^*$ was then used with the standing stock of eggs (m_s)

and the incubation time (t_s^I) to determine the egg IMR ($\hat{\alpha}_s^*$) by iterative method (section 2.2.1, equation 2).

$$\hat{\alpha}_s^* \text{ is the } \alpha_s \text{ such that } \frac{m_s}{\hat{P}_{h,s}^*} = \frac{e^{\alpha_s^* t_s^I} - 1}{\alpha_s} \quad (\text{B7})$$

Bootstrapped $\hat{P}_{0,s}^*$ was obtained by the calculation (section 2.2.1, equation 3):

$$\hat{P}_{0,s}^* = \hat{P}_{h,s}^* e^{\hat{\alpha}_s^* t_s^I} \quad (\text{B8})$$

The preceding bootstrap algorithm (equations B1–B6) was repeated 1000 times. On occasion, some of the bootstrap residuals ($\varepsilon_{c,s}^*$) would be sufficiently negative to produce a daily larval production value less than zero ($dlp_{c,s}^* < 0$) which was treated as if no larvae were observed for that class. If this happened for more than two size classes during an iteration then that iteration was discarded and repeated. If NLS failed to converge or β_s was estimated to be positive (illogical curvature of the mortality curve) or $\beta_s < -3$ (suggesting convergence in a bad area of the parameter space) then a log linearization was performed and parameters were estimated using OLS. Final estimates of $P_{h,s}$ were then calculated assuming normality of $\log(P_{h,s})$ (i.e. $P_{h,s}$ is log normally distributed).

This algorithm produced bootstrap distributions ($\{\hat{\beta}_s^*\}$, $\{\hat{P}_{h,s}^*\}$, $\{\hat{\alpha}_s^*\}$, $\{\hat{P}_{0,s}^*\}$) each with 1000 observations. The 0.025 and 0.975 quantiles of these distri-

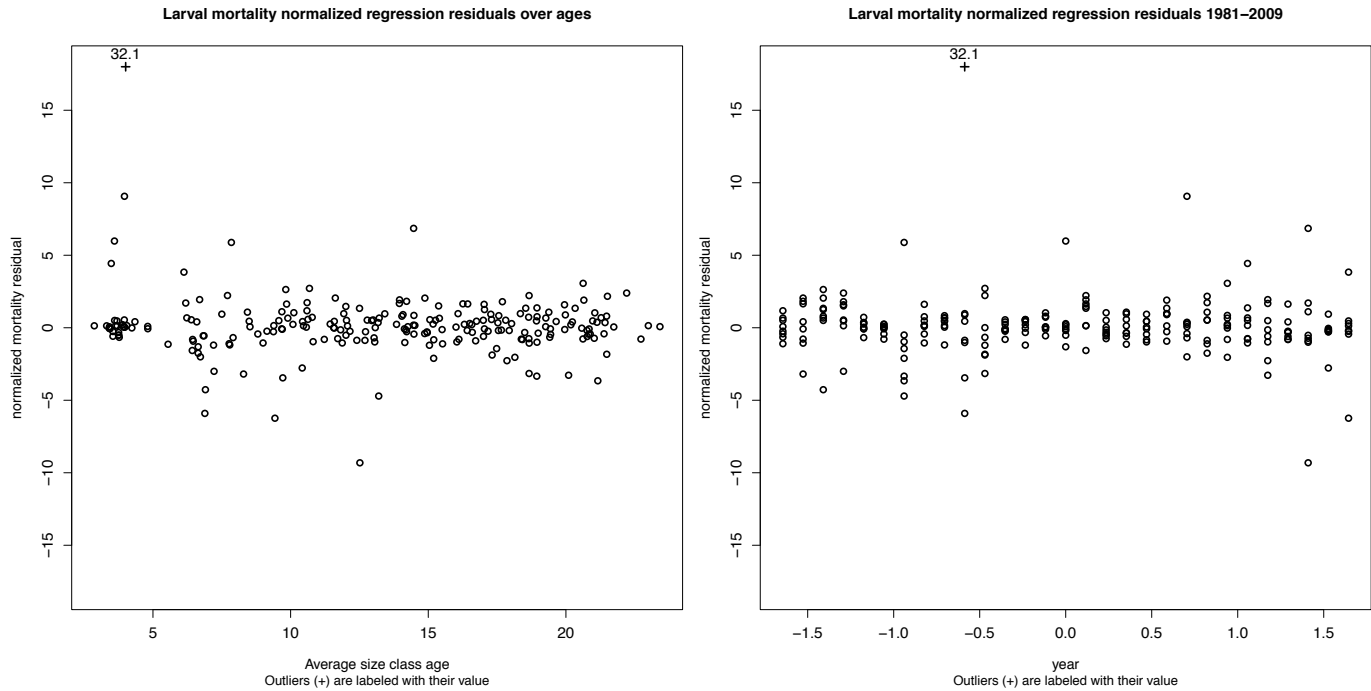


Figure B2. Larval mortality residuals over average size-class ages from hatching ($t_{c,s}$) (left panel), and normalized years (y_s) (right panel) after normalization.

butions were taken as a nonparametric estimate of their respective 95% confidence intervals.

B3 RESULTS

The residuals from MC^0 (section 2.2.1, equation 1) displayed heteroskedasticity across both ages and years (fig. B1). Coefficient estimates for the heteroskedasticity stabilizing regression support the visual observation of a decreasing volatility with both age and time (table B1).

Based on the observed heteroskedasticity in the residuals, failing to stabilize the class and temporally dependent variation would introduce spurious nonstationarity into the residuals upon resampling for the bootstrap. The heteroskedasticity stabilizing regression (equation B2) does an acceptable job of modeling the heteroskedasticity in MC^0 (table B1). Graphical analysis shows that dispersion around the mean is more evenly distributed (fig. B2) after the variance stabilization. Outliers are still outliers in the normalized residuals as they were intentionally removed during the regression. The normalized residual distribution is still highly leptokurtotic even with the outliers removed with a kurtosis of 12.08 (a standard normal distribution has a kurtosis of 3). Thus, heavy tails and extreme tail events are still a feature of the residual distribution used for resampling.

The grid search algorithm over initial condition during the NLS estimation (section 2.2.3) made more iterations computationally prohibitive in R. Furthermore, it was verified through histograms of 1000 iterations per-year that the number of iterations was sufficient. Mar-

ginal increases in the number of iterations to 1500 and 2000 iteration failed to noticeably change the distribution or confidence intervals from it.

Bootstrapped confidence intervals were referenced in the text of the main manuscript and can be found in table 1, and figure 4.

B4 DISCUSSION

Residual bootstrapping treats the empirical distribution formed by the set of residuals as sufficient for the true distribution. Resampling randomly reassigns residual from other classes and times to the fitted dI_p estimates. Failing to account for the class and temporal differences in the residual distribution would introduce spurious variation into the residuals upon resampling for the bootstrap. The linear model for the heteroskedasticity is based on a Breusch-Pagan test for heteroskedasticity (Breusch-Pagan 1979), except it uses the absolute deviation. The normalization is identical to the normalization performed in a feasible weighted least squares heteroskedasticity correction (Cameron and Trivedi 2005). The heteroskedasticity stabilizing regression appears to have stabilized the variation as indicated by the more homogeneous variance (fig. B2). The heavy tails or extreme tail events of the normalized residual distribution is quite likely a feature of the true mortality error distribution which should be retained during resampling.

An implied assumption in this approach of the estimation variability for P_0 and α is that all variability comes from random error at the larval stage, $\epsilon_{c,s}$ (equation 1).

Other potential sources of variation in P_0 and α were explored. The calculation of P_0 and the iterative method for α are simple definitional relationships and any error in the methods for the point estimates calculated after mortality estimation is negligible. The standing stock of eggs (m) and incubation time (t^I) are also used in HEP estimation and can potentially have a stochastic component. Reduced form attempts to model this stochasticity, that attempted to exploit the spatial variation over station within a year, were explored. A residual bootstrap method was again used with residual taken as deviation from a reduced form spatial model such as a spatial moving average process, spatial autoregressive process or a spatial distributed lag process. The results were that some additional variation was introduced but did not widen the confidence intervals for the parameters of interest significantly. The ad-hoc nature of this approach coupled within its marginal contribution led us to abandon this approach. Furthermore, aggregation over samples, cruises, and stations is likely to smooth the stochastic components of m and t^I . Thus, we assume that the calculated values of m and t^I are accurate annual statistics for the region in the sense that randomness in sampling or other sources is minimized by the aggregation. Alterna-

tively, our bootstrapped distributions can be interpreted as conditional on the observed m and t^I .

Calculations of higher order moments (such as the variance) of the data can be particularly sensitive to extreme tail events. Thus, confidence intervals for parameter estimates can have poor coverage when constructed using standard errors based on a distribution prone to extreme tail events. The large standard error estimates for α_s and P_0 based on the delta method were likely the result of the heavy-tailed distributions. Furthermore, extreme events can also result in uncentered distributions. We obtain accurate coverage for parameter confidence intervals by reporting bootstrapped confidence intervals in place of the regression standard errors for the NLS estimation of MC^0 (equation 1).

APPENDIX B LITERATURE CITED

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