Results of evaluating the performance of empirical estimators of natural mortality rate

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Introduction

  This document has been issued as VIMS Data Report 62 and provides additional results and analyses for Then et al. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES Journal of Marine Science 72(1): 82-92.

  Natural mortality rate, M, of fish is a highly influential stock assessment parameter. The M parameter is also difficult to estimate directly and reliably. Various empirical estimators have been developed to estimate M indirectly, based on relationships established between M and predictor variables such as growth parameters, lifespan and water temperature (e.g., Beverton and Holt, 1959; Alverson and Carney, 1975; Pauly, 1980; Hoenig, 1983). Despite the importance of these estimators, there is no consensus in the literature on how well they work in terms of prediction error or how their performance may be ranked. Then et al. (in press) evaluated estimators based on various combinations of maximum age (t_{max}), von Bertalanffy growth parameters (K) and asymptotic length (L_∞), and water temperature (T), by seeing how well they reproduce independent, direct estimates of M for more than 200 unique fish species. They also considered the possibility of combining different estimators using a weighting scheme to improve estimation of M. This report documents additional analyses and results to supplement the results in the journal article. The estimators, evaluation criteria, and other important details are given in the journal article.

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Table 1. The full list of estimation approaches for predicting natural mortality, *M,* investigated in this study. lm = log-log model; ls = least squares; gm = geometric mean or functional regression, as described by Ricker (1975); nls = non-linear least squares; bc = bias-corrected; quad = quadratic model; NA = not applicable. SE = residual standard error from the Hoenig$_{lm}$ model. NP = non-parametric. Parameters for the locally weighted scatterplot smoothing regression (loess): degree of smoothing (α) = 0.75; degree of polynomials = 2. The "~" notation is used to indicate that a loess model was fitted with the response variable given on the left and predictor given on the right.

Table 2. Ten-fold cross-validation prediction error (CVPE) of empirical estimators of natural mortality, *M*, evaluated using the common dataset (n = 215). The parameter estimates, coefficient of determination (unadjusted r^2), mean absolute difference (MAD) and root mean square error (RMSE) between predicted and literature *M* estimates are presented as well for the updated estimators. See Table 1 for definition of models. Combinations of estimators for the weighted estimator were not surveyed exhaustively. The "~" notation is used to indicate that a loess model was fitted with the response variable given on the left and predictor given on the right. The weights for the composite models were chosen to minimize the variance.

Table 3. Updated equations and cross-validation prediction error (CVPE) of empirical estimators of natural mortality, *M*, evaluated using the fullest dataset. The parameter estimates, mean absolute difference (MAD) and the coefficient of determination (unadjusted r^2) between predicted and literature *M* estimates are presented as well for the updated estimators. n denotes sample size for the full dataset. See Table 1 for definition of models. Combinations of estimators for the weighted estimator were not surveyed exhaustively. The "~" notation is used to indicate that a loess model was fitted with the response variable given on the left and predictor given on the right.

Table 4. Selected updated estimators based on the fullest dataset (sample size n). Model and bootstrap-based estimates of standard error (SE) are presented. Two types of non-parametric bootstrap 95% confidence intervals (CI) using the normal approximation and the bias-corrected and accelerated (BCa) methods for the model parameter estimates are also given. coef. = coefficient; exp. = exponent. All length measurements are in mm.

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Figure 11. Effect of sample size on the accuracy and precision of the parameter estimates of select empirical estimators. Specifically, 1000 bootstrap samples were drawn with replacement from the complete dataset (n=215) with sample sizes of 50, 75, 100, 125, 150 and 200. The empirical models were fitted to each bootstrap sample and the coefficient of variation (CV) of the parameter estimates was calculated. Boxplots of the 1000 parameter estimates (left) and the corresponding CV (right) shown as a function of sample size. The parameters are the (a) t_{max} coefficient for one-parameter t_{max}, (b1) scaling and (b2) t_{max} exponent for Hoenig$_{nls}$. Dashed horizontal lines in the left column indicate the updated parameter coefficients for each model based on the common dataset (n = 215).

Figure 12. Effect of sample size on the accuracy and precision of the parameter estimates of select empirical estimators. Specifically, 1000 bootstrap samples were drawn with replacement from the complete dataset (n=215) with sample sizes of 50, 75, 100, 125, 150 and 200. The empirical models were fitted to each bootstrap sample and the coefficient of variation (CV) of the parameter estimates was calculated. Boxplots of the 1000 parameter estimates (left) and the corresponding CV (right) shown as a function of sample size. The parameters are the (c1) scaling, (c2) K exponent, (c3) L_∞ exponent for Pauly$_{nls-T}$ and (d) K coefficient for one-parameter K. Dashed horizontal lines in the left column indicate the updated parameter estimates for each model based on the common dataset (n = 215).

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Table 1. The full list of estimation approaches for predicting natural mortality, *M,* investigated in this study. lm = log-log model; ls = least squares; gm = geometric mean or functional regression, as described by Ricker (1975); nls = non-linear least squares; bc = bias-corrected; quad = quadratic model; NA = not applicable. SE = residual standard error from the Hoenig$_{lm}$ model. NP = non-parametric. Parameters for the locally weighted scatterplot smoothing regression (loess): degree of smoothing (α) = 0.75; degree of polynomials = 2. The "~" notation is used to indicate that a loess model was fitted with the response variable given on the left and predictor given on the right.

Model name	Formula	Fitting Method	Model used empirically by
t_{max}			
one-parameter t_{max}	$M = a/\, t_{max}$	nls	Tauchi (1956); Tanaka (1960); Bayliff (1967); Ohsumi (1973)
Hoenig$_{lm}$	$\log(M) = a + b\log(t_{max})$	ls	Hoenig (1983)
Hoenig$_{gm}$	$\log(M) = a + b\log(t_{max})$	ls	Hoenig (1983)
Hoenig$_{bc}$	$M = \exp(a + b\log(t_{max}) + SE^2/2)$	ls	this study
Hoenig$_{quad}$	$\log(M) = a + b\log(t_{max}) + c\log(t_{max}^2)$	ls	this study
Hoenig$_{nls}$	$M = at_{max}^{b}$	nls	this study
Hoenig$_{nls(weighted)}$	$M = at_{max}^{b}$	nls	this study
NP regression 1	$M \sim t_{max}$	loess	this study
NP regression 2	$\log(M) \sim \log(t_{max})$	loess	this study
K			
one-parameter K	$M = aK$	ls	Beverton & Holt (1959); Beverton (1963); Charnov (1993); Jensen (1996)
two-parameter K	$M = a + bK$	ls	Ralston (1987); Jensen (2001)
log(one-parameter K)	$\log(M) = a\log(K)$	ls	this study
log(two-parameter K)	$\log(M) = a + b\log(K)$	ls	this study
K, L_∞, T			
Pauly$_{lm}$	$\log(M) = a + b\log(K) + c\log(L_\infty) + d\log(T)$	ls	Pauly (1980); Djabali *et al.*(1993); Pauly & Binohlan (1996)
Pauly$_{lm-T}$	$\log(M) = a + b\log(K) + c\log(L_\infty)$	ls	this study
Pauly$_{nls}$	$M = aK^b L_\infty^{c} T^d$	nls	this study
Pauly$_{nls-T}$	$M = aK^b L_\infty^{c}$	nls	this study
Pauly$_{nlsK}$	$M = aK^b$	nls	this study
K, t_{max}			
Alverson-Carney	$M = 3K/\, (e^{aKtmax} - 1)$	nls	Alverson & Carney (1975)
Composites			
Weighted M	$M = pM_{Estimator1} + (1 - p)\, M_{Estimator2}$	NA	this study

Table 2. Ten-fold cross-validation prediction error (CVPE) of empirical estimators of natural mortality, M, evaluated using the common dataset (n = 215). The parameter estimates, coefficient of determination (unadjusted r^2), mean absolute difference (MAD) and root mean square error (RMSE) between predicted and literature M estimates are presented as well for the updated estimators. See Table 1 for definition of models. Combinations of estimators for the weighted estimator were not surveyed exhaustively. The "~" notation is used to indicate that a loess model was fitted with the response variable given on the left and predictor given on the right. The weights for the composite models were chosen to minimize the variance.

Model name	Updated Estimator (n = 215)	r^2	MAD	RMSE	CVPE
t_{max}					
one-parameter t_{max}	$M = 4.934/ t_{max}$	0.87	0.18	0.30	0.305
Hoenig$_{lm}$	$\log(M) = 1.717 - 1.01\log(t_{max})$	0.87	0.19	0.32	0.328
Hoenig$_{gm}$	$\log(M) = 1.966 - 1.1\log(t_{max})$	0.86	0.23	0.50	0.510
Hoenig$_{bc}$	$M = \exp(1.717 - 1.01\log(t_{max}) + 0.096)$	0.87	0.21	0.38	1.266
Hoenig$_{quad}$	$\log(M) = 1.46 - 0.789\log(t_{max}) - 0.042 \log(t_{max})^2$	0.88	0.17	0.28	0.286
Hoenig$_{nls}$	$M = 4.504t_{max}^{-0.863}$	0.88	0.18	0.27	0.281
Hoenig$_{nls(weighted)}$	$M = 4.81t_{max}^{-0.908}$	0.88	0.18	0.28	0.285
Hoenig$_{loess}$	$M \sim t_{max}$	0.74	0.23	0.40	0.387
Hoenig$_{loess(log)}$	$\log(M) \sim \log(t_{max})$	0.88	0.17	0.27	0.284
K					
one-parameter K	$M = 1.68K$	0.47	0.37	0.58	0.582
two-parameter K	$M = 0.096 + 1.54K$	0.47	0.37	0.57	0.580
log(one-parameter K)	$\log(M) = 0.713\log(K)$	0.44	0.37	0.66	0.658
log(two-parameter K)	$\log(M) = 0.051 + 0.739\log(K)$	0.44	0.36	0.65	0.649
K, L_∞, T					
Pauly$_{lm}$	$\log(M) = 0.606 + 0.488\log(K) - 0.394\log(L_\infty) + 0.196\log(T)$	0.51	0.34	0.60	0.605
Pauly$_{lm-T}$	$\log(M) = 1.091 + 0.545\log(K) - 0.361\log(L_\infty)$	0.50	0.35	0.60	0.610
Pauly$_{nls}$	$M = 2.338K^{0.619}L_\infty^{-0.435}T^{0.277}$	0.53	0.35	0.54	0.577
Pauly$_{nls-T}$	$M = 4.313K^{0.726}L_\infty^{-0.354}$	0.51	0.36	0.55	0.578
Pauly$_{nlsK}$	$M = 1.673K^{0.954}$	0.46	0.37	0.58	0.586
K, t_{max}					
Alverson-Carney	$M = 3K/ (e^{0.41Kt_{max}} - 1)$	0.81	0.26	0.40	0.414
Composites					
Weighted M	$M = 0.8M_{Hoenignls} + 0.2M_{Paulynls}$	0.86	0.19	0.29	0.302
	$M = 0.8M_{Hoenignls} + 0.2M_{Paulynls-T}$	0.87	0.19	0.29	0.301
	$M = 0.77M_{onetmax} + 0.23M_{Paulynls}$	0.86	0.19	0.30	0.307
	$M = 0.77M_{onetmax} + 0.23M_{Paulynls-T}$	0.86	0.19	0.30	0.303
	$M = 0.79M_{onetmax} + 0.21M_{oneK}$	0.86	0.19	0.30	0.304
	$M = 0.77M_{Hoeniglm} + 0.23M_{Paulylm}$	0.87	0.19	0.29	0.298

Table 3. Updated equations and cross-validation prediction error (CVPE) of empirical estimators of natural mortality, M, evaluated using the fullest dataset. The parameter estimates, mean absolute difference (MAD) and the coefficient of determination (unadjusted r^2) between predicted and literature M estimates are presented as well for the updated estimators. n denotes sample size for the full dataset. See Table 1 for definition of models. Combinations of estimators for the weighted estimator were not surveyed exhaustively. The "~" notation is used to indicate that a loess model was fitted with the response variable given on the left and predictor given on the right.

Model name	Updated Estimator	r^2	MAD	RMSE	n	CVPE
t_{max}						
one-parameter t_{max}	$M = 5.109/\,t_{max}$	0.89	0.19	0.31	226	0.317
Hoenig$_{lm}$	$\log(M) = 1.72 - 1.01\log(t_{max})$	0.89	0.19	0.33	226	0.329
Hoenig$_{gm}$	$\log(M) = 1.952 - 1.099\log(t_{max})$	0.88	0.24	0.50	226	0.519
Hoenig$_{bc}$	$M = \exp(1.72 - 1.01\log(tmax) + 0.094)$	0.89	0.21	0.38	226	1.402
Hoenig$_{quad}$	$\log(M) = 1.516 - 0.828\log(t_{max}) - 0.035\,\log(t_{max})^2$	0.89	0.18	0.31	226	0.339
Hoenig$_{nls}$	$M = 4.899 t_{max}^{-0.916}$	0.89	0.19	0.30	226	0.323
Hoenig$_{nls(weighted)}$	$M = 4.992 t_{max}^{-0.925}$	0.89	0.19	0.30	226	0.309
Hoenig$_{loess}$	$M \sim t_{max}$	0.70	0.25	0.50	226	0.420
Hoenig$_{loess(log)}$	$\log(M) \sim \log(t_{max})$	0.90	0.18	0.30	226	0.287
K						
one-parameter K	$M = 1.692K$	0.46	0.37	0.58	218	0.593
two-parameter K	$M = 0.098 + 1.55K$	0.46	0.38	0.58	218	0.591
$\log$(one-parameter K)	$\log(M) = 0.71\log(K)$	0.44	0.37	0.67	218	0.667
$\log$(two-parameter K)	$\log(M) = 0.06 + 0.74\log(K)$	0.44	0.37	0.65	218	0.659
K, L_∞, T						
Pauly$_{lm}$	$\log(M) = 0.606 + 0.488\log(K) - 0.394\log(L_\infty) + 0.196\log(T)$	0.51	0.34	0.60	215	0.605
Pauly$_{lm\text{-}T}$	$\log(M) = 1.07 + 0.557\log(K) - 0.348\log(L_\infty)$	0.49	0.35	0.61	218	0.627
Pauly$_{nls}$	$M = 2.338 K^{0.619} L_\infty^{-0.435} T^{0.277}$	0.53	0.35	0.54	215	0.577
Pauly$_{nls\text{-}T}$	$M = 4.118 K^{0.73} L_\infty^{-0.333}$	0.50	0.36	0.56	218	0.597
Pauly$_{nlsK}$	$M = 1.683 K^{0.946}$	0.46	0.37	0.58	218	0.597
K, t_{max}						
Alverson-Carney	$M = 3K/\,(e^{0.41 K tmax} - 1)$	0.81	0.26	0.40	215	0.414

Table 4. Selected updated estimators based on the fullest dataset (sample size n). Model and bootstrap-based estimates of standard error (SE) are presented. Two types of non-parametric bootstrap 95% confidence intervals (CI) using the normal approximation and the bias-corrected and accelerated (BCa) methods for the model parameter estimates are also given. coef. = coefficient; exp. = exponent. All length measurements are in mm.

| Models	Updated equations	n	Parameter	Model SE	Bootstrap SE	Normal 95% CI	BCa 95% CI
t_{max}							
one-parameter t_{max}	$M = 5.109/\,t_{max}$	226	Scaling	0.10	0.22	(4.676, 5.528)	(4.716, 5.568)
Hoenig$_{lm}$	$\log(M) = 1.717 - 1.01\log(t_{max})$	226	Intercept	0.08	0.08	(1.561, 1.871)	(1.568, 1.882)
			$\log(t_{max})$ coef.	0.03	0.03	(-1.066, -0.956)	(-1.071, -0.959)
Hoenig$_{nls}$	$M = 4.899\,t_{max}^{-0.916}$	226	Scaling	0.11	0.33	(4.311, 5.597)	(4.365, 5.653)
			t_{max} exp.	0.02	0.04	(-1.009, -0.838)	(-1.009, -0.844)
K							
one-parameter K	$M = 1.692K$	218	K coef.	0.08	0.16	(1.365, 2.001)	(1.366, 2.006)
two-parameter K	$M = 0.098 + 1.55K$	218	Intercept	0.06	0.06	(-0.028, 0.212)	(-0.019, 0.223)
			K coef.	0.11	0.24	(1.104, 2.033)	(1.082, 2.011)
K, t_{max}							
Pauly$_{nls-T}$	$M = 4.118\,K^{0.73}L_{\infty}^{-0.33}$	218	Scaling	0.80	2.11	(-0.570, 7.689)	(1.886, 9.285)
			K exp.	0.08	0.18	(0.417, 1.124)	(0.323, 1.001)
			L_{∞} exp.	0.08	0.15	(-0.595, -0.014)	(-0.603, -0.040)
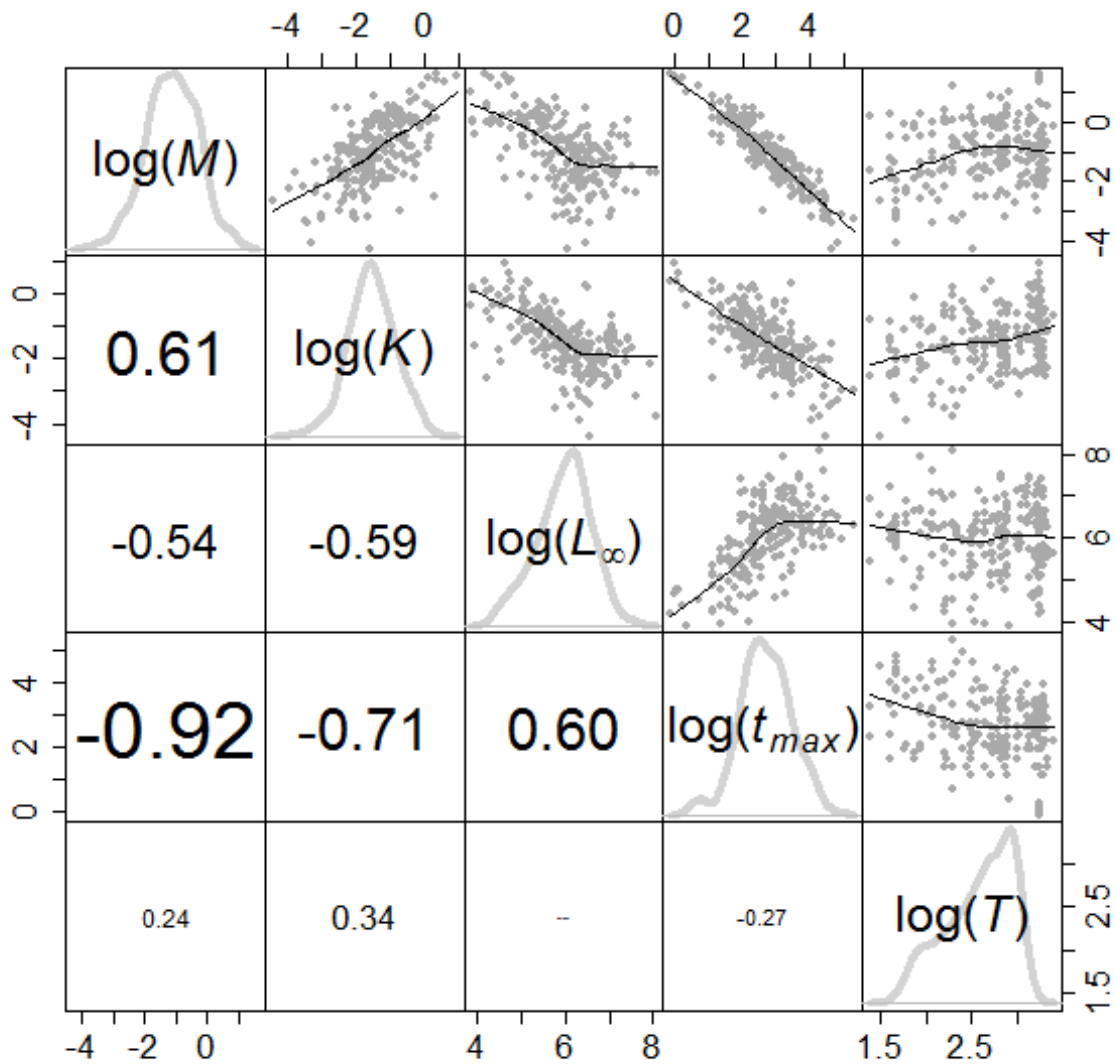
Figure 1. Scatterplot of pairs of log-transformed variables in the upper half of the panel, with locally weighted scatterplot smoothing (LOWESS) lines added (smoothing parameter $f = 2/3$). Variables: Natural mortality rate M, maximum age t_{max}, von Bertalanffy growth parameters K and L_∞, mean temperature T. Kernel density plots of the log-transformed variables are shown in the diagonal panels. Correlation coefficients (r) for variable pairs are shown in the lower half of the panel, where the font size corresponds to the magnitude of the r values.
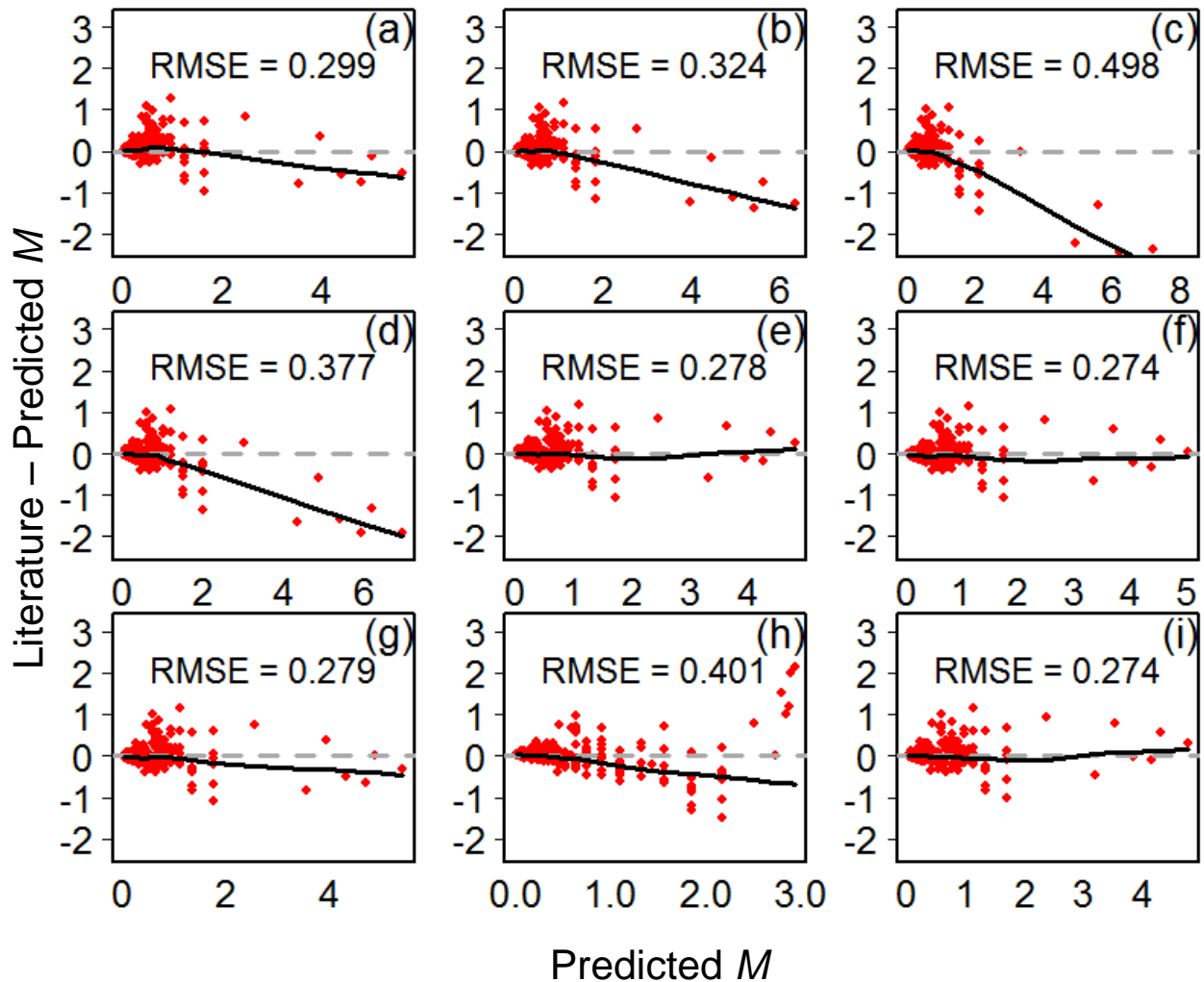
Figure 2. Model residuals for the updated t_{max}–based estimators of (a) one-parameter t_{max}, (b) Hoenig$_{lm}$, (c) Hoenig$_{gm}$, (d) Hoenig$_{bc}$, (e) Hoenig$_{quad}$, (f) Hoenig$_{nls}$, (g) Hoenig$_{nls(weighted)}$, (h) non-parametric regressions of M as a function of t_{max}, and (i) non-parametric regressions of $log(M)$ as a function of $log(t_{max})$ based on the common dataset (n = 215). Residuals are defined as literature – predicted M and are plotted on the same y-axis scale. Locally weighted scatterplot smoothing (LOWESS) lines shown in each panel (smoothing parameter f = 2/3). Root mean square error (RMSE) for each model is given. See Figure 5 for the same residual plots but restricted to literature M values < 0.5.
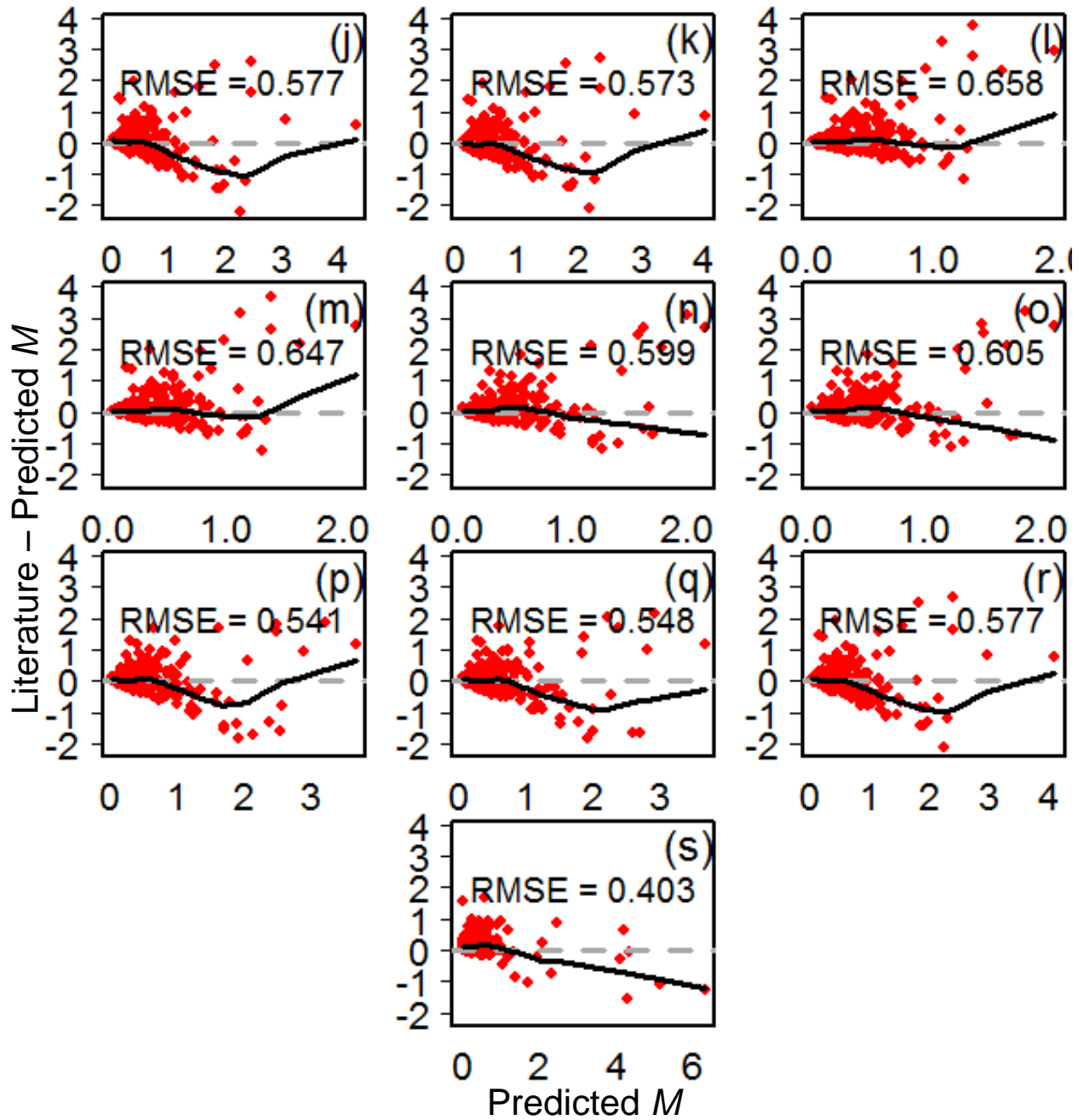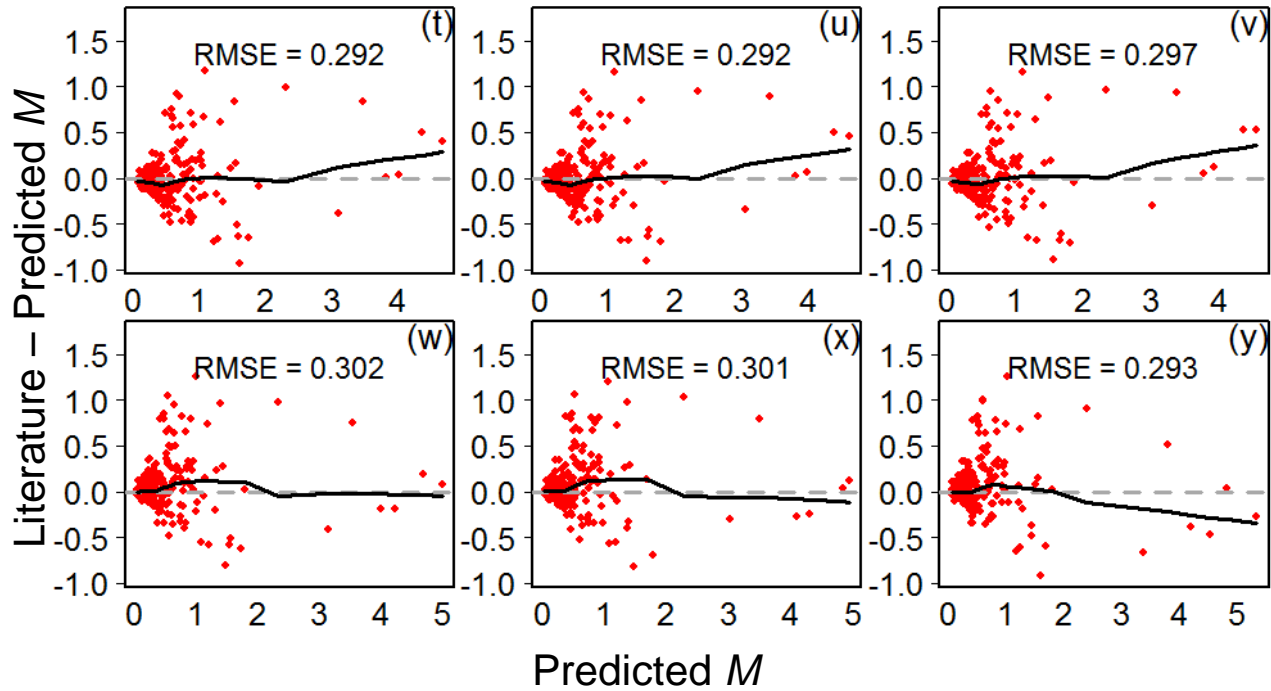
Figure 3. Model residuals for the updated growth-based and composite estimators of (j) one-parameter K, (k) two-parameter K, (l) log(one-parameter K), (m) log(two-parameter K), (n) Pauly$_{lm}$, (o) Pauly$_{lm-T}$, (p) Pauly$_{nls}$, (q) Pauly$_{nls-T}$, (r) Pauly$_{nlsK}$, and (s) Alverson-Carney, based on the common dataset (n = 215). Residuals are defined as literature – predicted M. Locally weighted scatterplot smoothing (LOWESS) lines shown in each panel (smoothing parameter f = 2/3). Root mean square error (RMSE) for each model is given. See Figure 6 for the same residual plots but restricted to literature M values < 0.5.
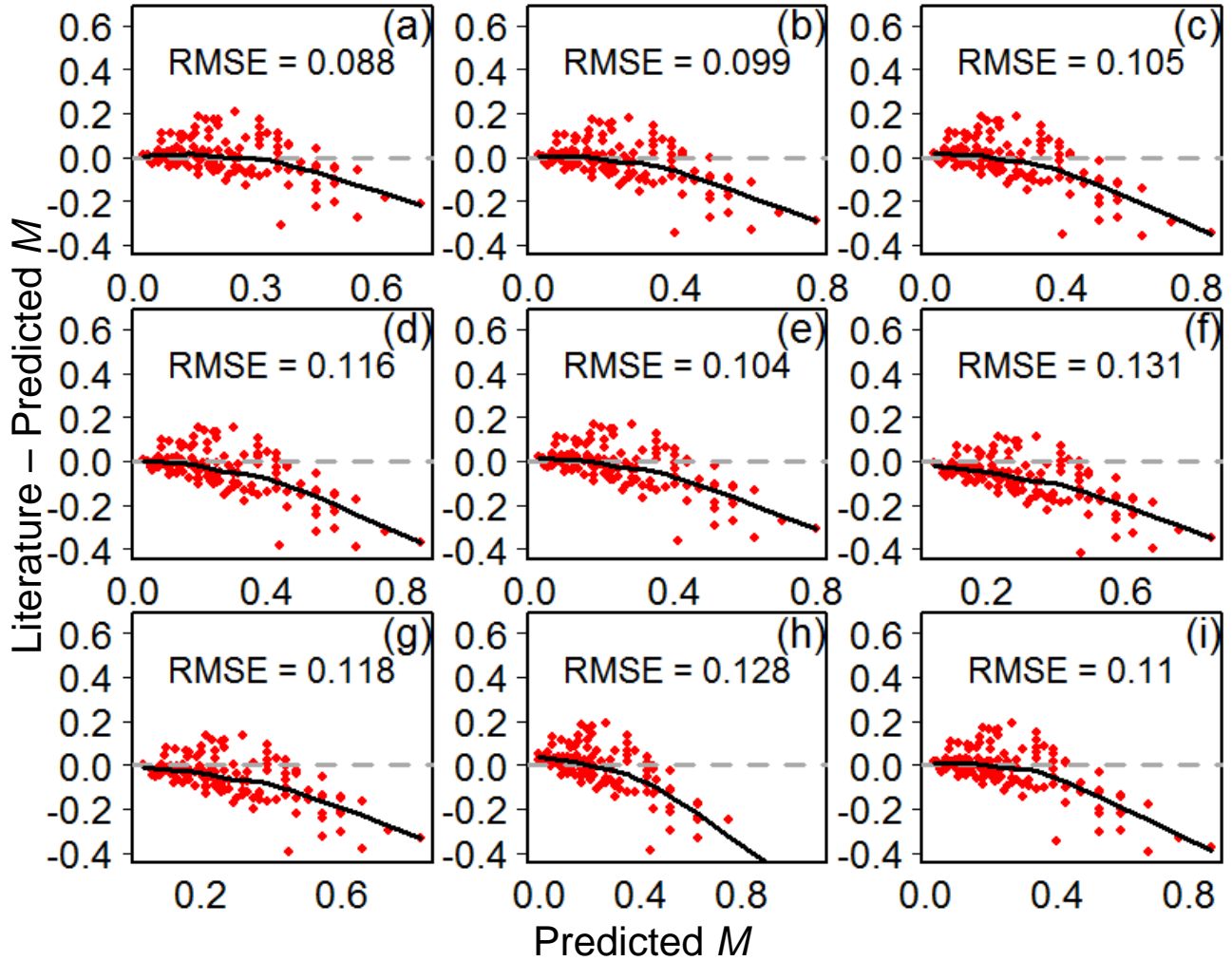
Figure 4. Model residuals for the updated weighted (composite) estimators of (t) Hoenig$_{nls}$ and Pauly$_{nls}$, (u) Hoenig$_{nls}$ and Pauly$_{nls-T}$, (v) one-parameter t_{max} and Pauly$_{nls}$, (w) one-parameter t_{max} and Pauly$_{nls-T}$, (x) one-parameter t_{max} and one-parameter K, and (y) Hoenig$_{lm}$ and Pauly$_{lm}$, based on the common dataset (n = 215). Residuals are defined as literature − predicted M. Locally weighted scatterplot smoothing (LOWESS) lines shown in each panel (smoothing parameter $f = 2/3$). Root mean square error (RMSE) for each model is given. See Figure 7 for the same residual plots but restricted to literature M values < 0.5.

Figure 5. Model residuals shown for the subset of literature M values < 0.5 (n = 132) for the updated t_{max}–based estimators of (a) one-parameter t_{max}, (b) Hoenig$_{lm}$, (c) Hoenig$_{gm}$, (d) Hoenig$_{bc}$, (e) Hoenig$_{quad}$, (f) Hoenig$_{nls}$, (g) Hoenig$_{nls(weighted)}$, (h) non-parametric regressions of M as a function of t_{max}, and (i) non-parametric regressions of log(M) as a function of log(t_{max}). Estimators were updated based on the common dataset (n = 215). Residuals are defined as literature – predicted M and are plotted on the same y-axis scale. Locally weighted scatterplot smoothing (LOWESS) lines shown in each panel (smoothing parameter $f = 2/3$). Root mean square error (RMSE) for each model is given, calculated based on the data subset.
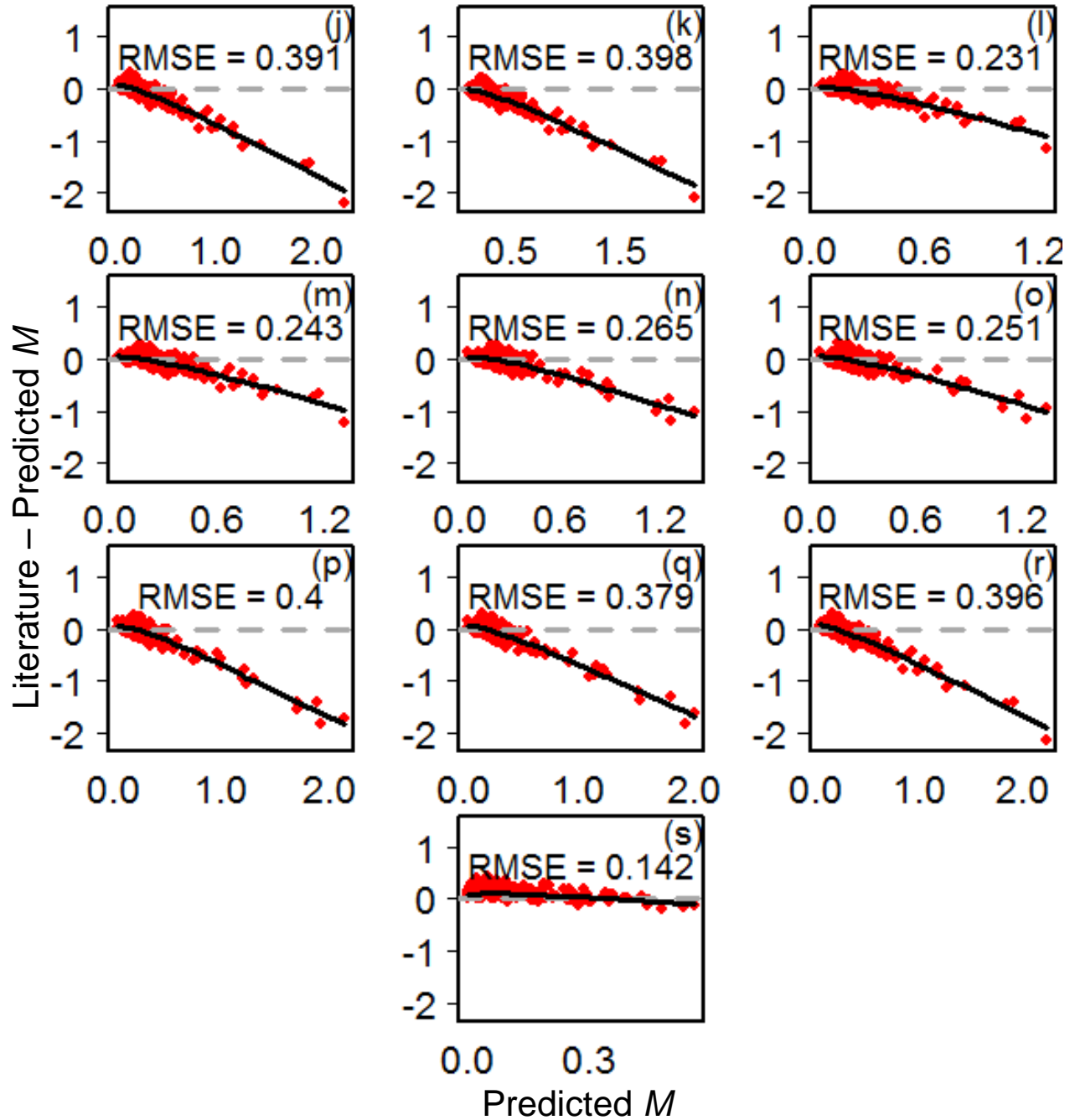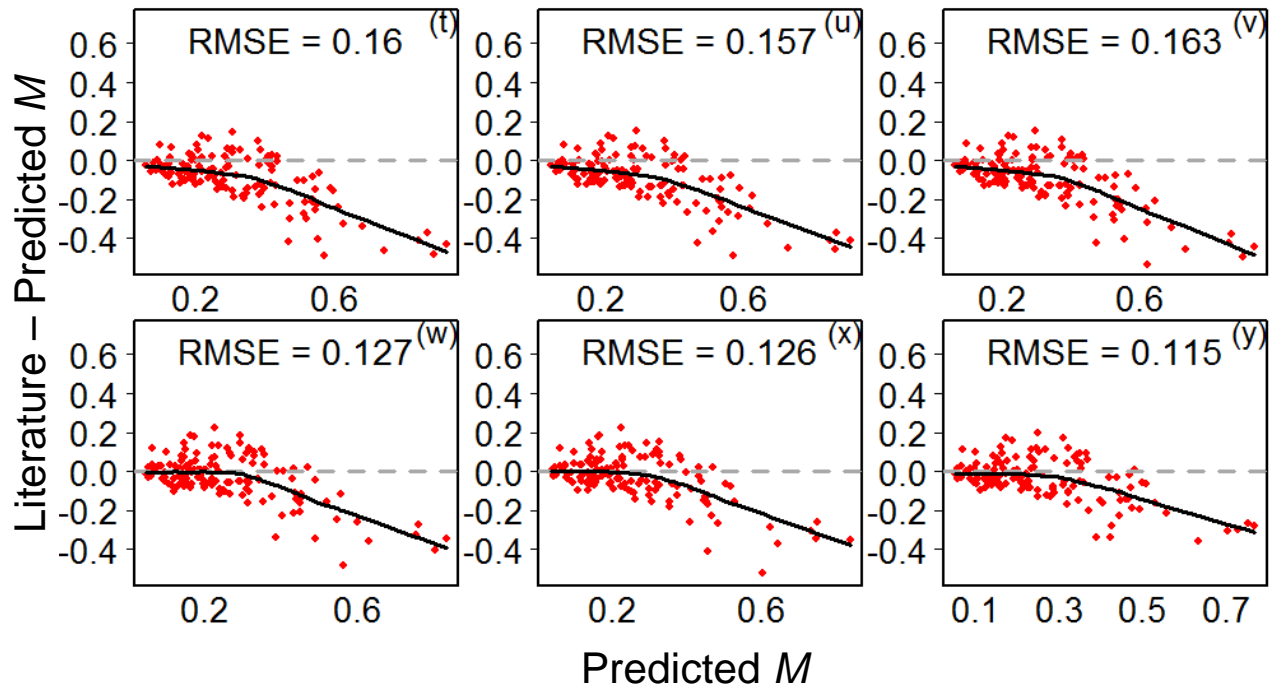
Figure 6. Model residuals shown for the subset of literature M values < 0.5 ($n = 132$) for the updated growth-based estimators of (j) one-parameter K, (k) two-parameter K, (l) log(one-parameter K), (m) log(two-parameter K), (n) Pauly$_{lm}$, (o) Pauly$_{lm-T}$, (p) Pauly$_{nls}$, (q) Pauly$_{nls-T}$, (r) Pauly$_{nlsK}$, and (s) Alverson-Carney, based on the common dataset ($n = 215$). Residuals are defined as literature $-$ predicted M and are plotted on the same y-axis scale. Locally weighted scatterplot smoothing (LOWESS) lines shown in each panel (smoothing parameter $f = 2/3$). Root mean square error (RMSE) for each model is given, calculated based on the data subset.
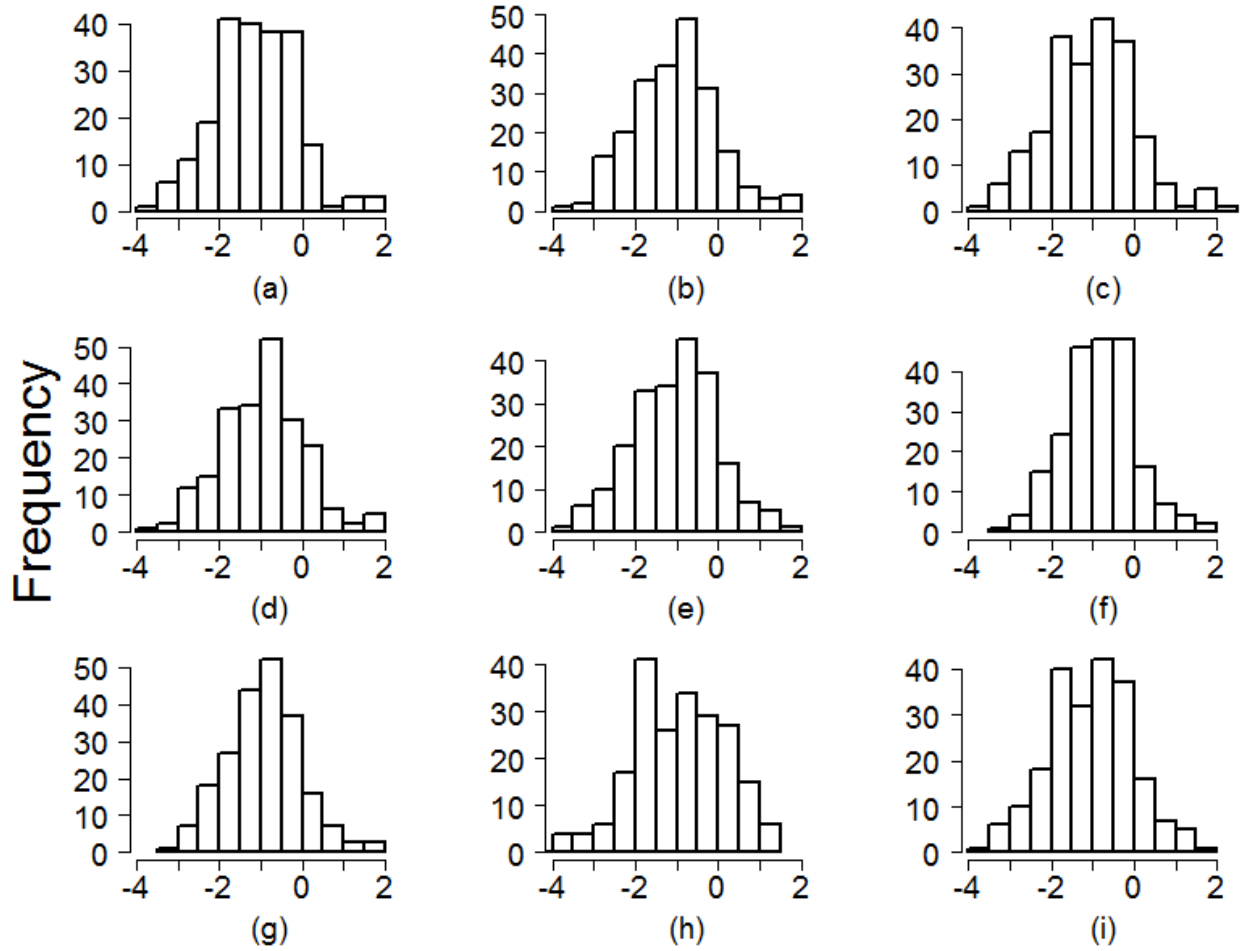
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Figure 7. Model residuals shown for the subset of literature M values < 0.5 (n = 132) for the updated weighted (composite) estimators of (t) Hoenig$_{nls}$ and Pauly$_{nls}$, (u) Hoenig$_{nls}$ and Pauly$_{nls-T}$, (v) one-parameter t_{max} and Pauly$_{nls}$, (w) one-parameter t_{max} and Pauly$_{nls-T}$, (x) one-parameter t_{max} and one-parameter K, and (y) Hoenig$_{lm}$ and Pauly$_{lm}$, based on the common dataset (n = 215). Residuals are defined as literature – predicted M and are plotted on the same y-axis scale. Locally weighted scatterplot smoothing (LOWESS) lines shown in each panel (smoothing parameter $f = 2/3$). Root mean square error (RMSE) for each model is given, calculated based on the data subset.

Figure 8. Histograms of model predicted M estimates (log-scale) for the updated t_{max}–based estimators of (a) one-parameter t_{max} (b) Hoenig$_{lm}$ (c) Hoenig$_{gm}$ (d) Hoenig$_{bc}$ (e) Hoenig$_{quad}$ (f) Hoenig$_{nls}$ (g) Hoenig$_{nls(weighted)}$ (h) non-parametric regressions of M as a function of t_{max} and (i) non-parametric regressions of $\log(M)$ as a function of $\log(t_{max})$. Estimators were updated based on the common dataset (n = 215).
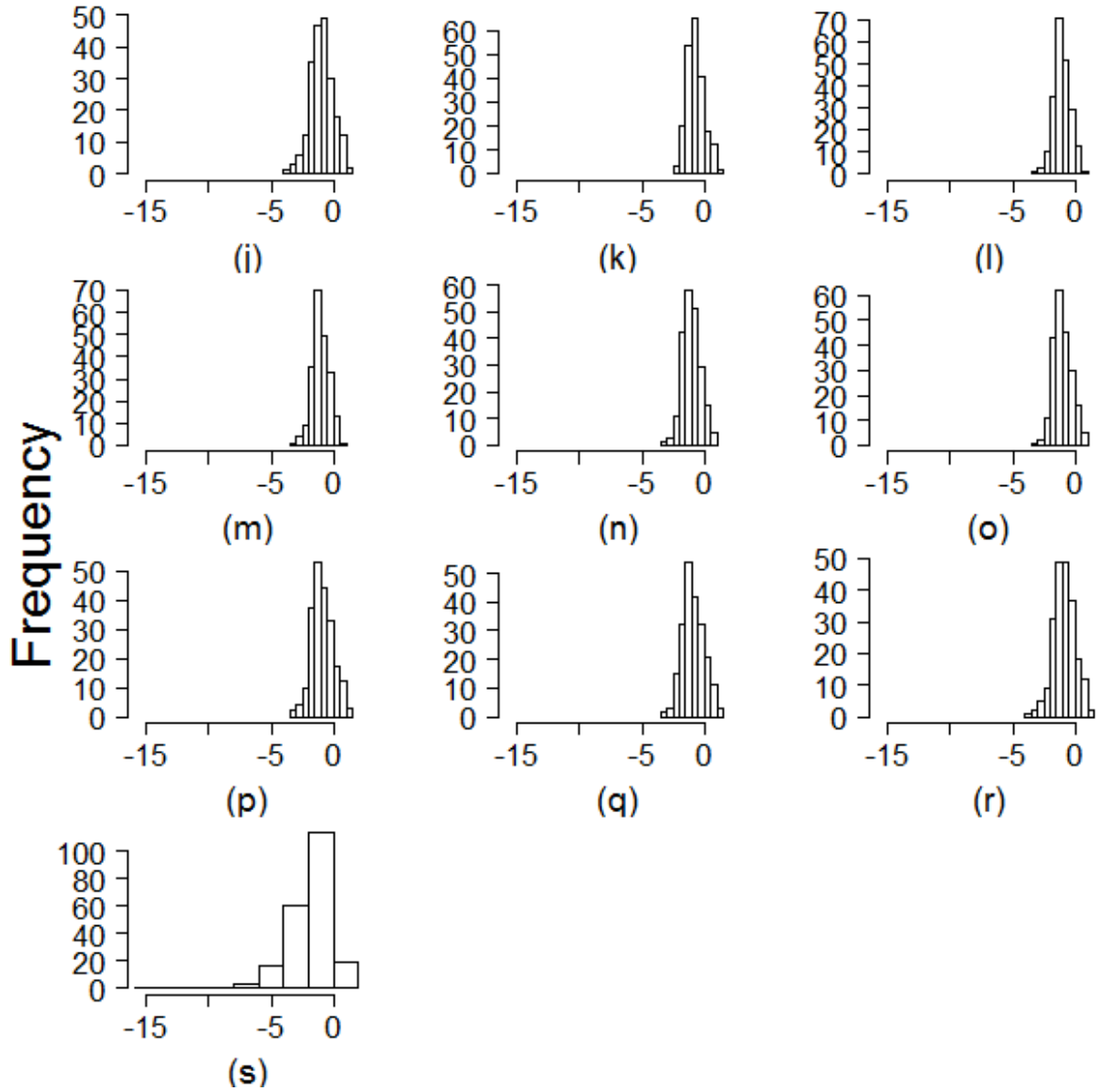
Figure 9. Histograms of model predicted M estimates (log-scale) for the updated t_{max}–based estimators of of (j) one-parameter K, (k) two-parameter K, (l) log(one-parameter K), (m) log(two-parameter K), (n) Pauly$_{lm}$, (o) Pauly$_{lm-T}$, (p) Pauly$_{nls}$, (q) Pauly$_{nls-T}$, (r) Pauly$_{nlsK}$, and (s) Alverson-Carney. Estimators were updated based on the common dataset (n = 215).
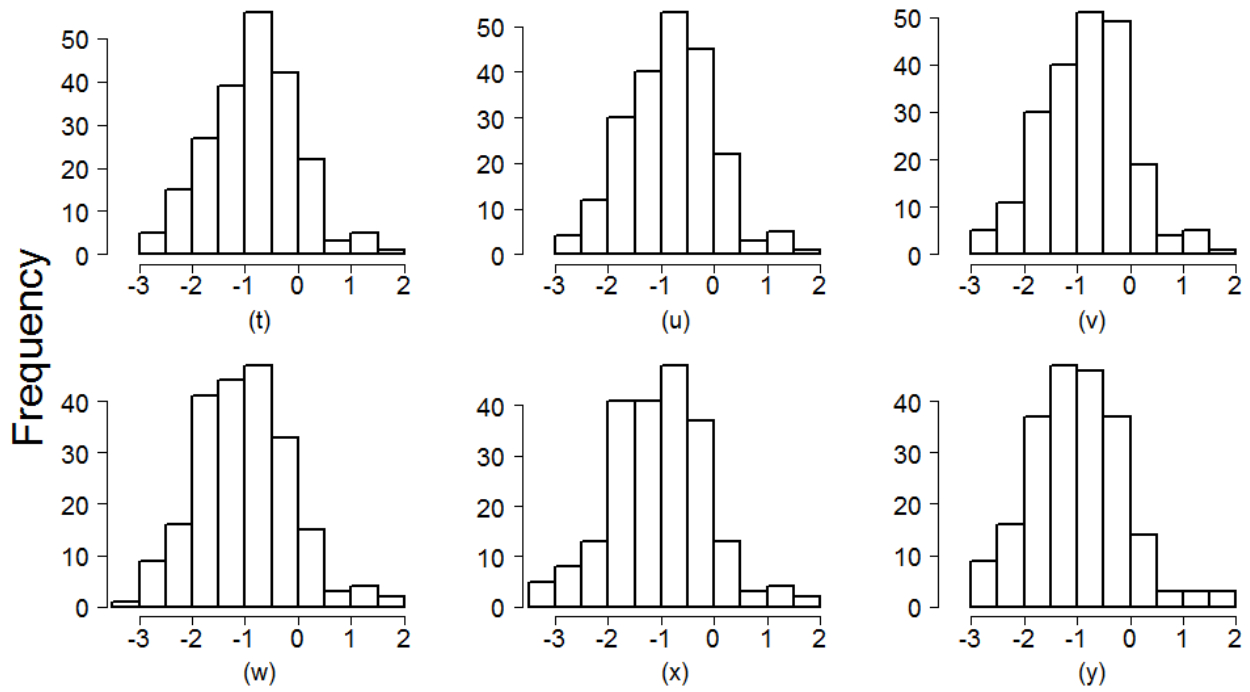
Figure 10. Histograms of model predicted M estimates (log-scale) for the updated weighted (composite) estimators of (t) Hoenig$_{nls}$ and Pauly$_{nls}$, (u) Hoenig$_{nls}$ and Pauly$_{nls-T}$, (v) one-parameter t_{max} and Pauly$_{nls}$, (w) one-parameter t_{max} and Pauly$_{nls-T}$, (x) one-parameter t_{max} and one-parameter K, and (y) Hoenig$_{lm}$ and Pauly$_{lm}$. Estimators were updated based on the common dataset (n = 215).
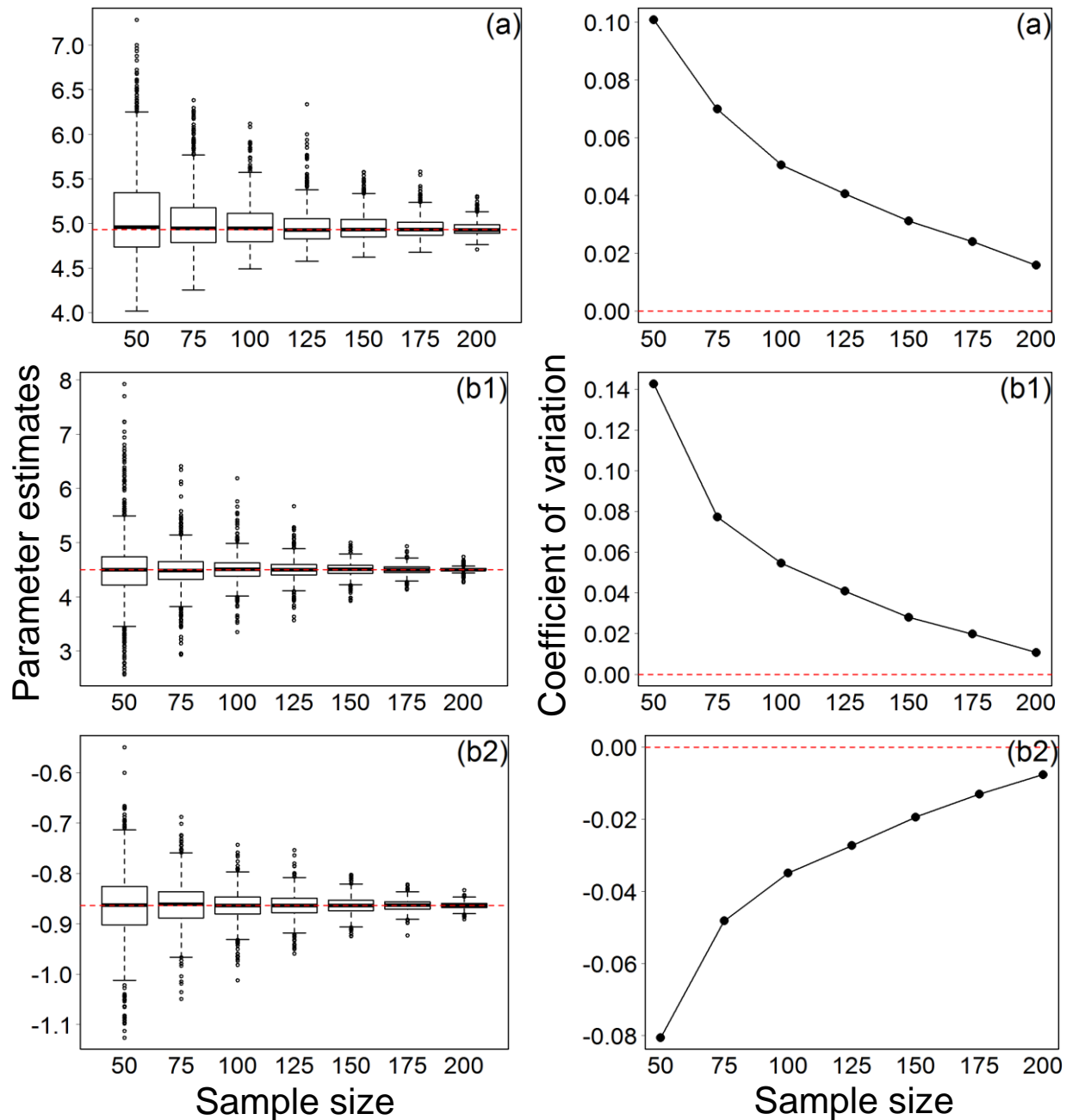
Figure 11. Effect of sample size on the accuracy and precision of the parameter estimates of select empirical estimators. Specifically, 1000 bootstrap samples were drawn with replacement from the complete dataset (n=215) with sample sizes of 50, 75, 100, 125, 150 and 200. The empirical models were fitted to each bootstrap sample and the coefficient of variation (CV) of the parameter estimates was calculated. Boxplots of the 1000 parameter estimates (left) and the corresponding CV (right) shown as a function of sample size. The parameters are the (a) t_{max} coefficient for one-parameter t_{max}, (b1) scaling and (b2) t_{max} exponent for Hoenig$_{nls}$. Dashed horizontal lines in the left column indicate the updated parameter coefficients for each model based on the common dataset (n = 215).
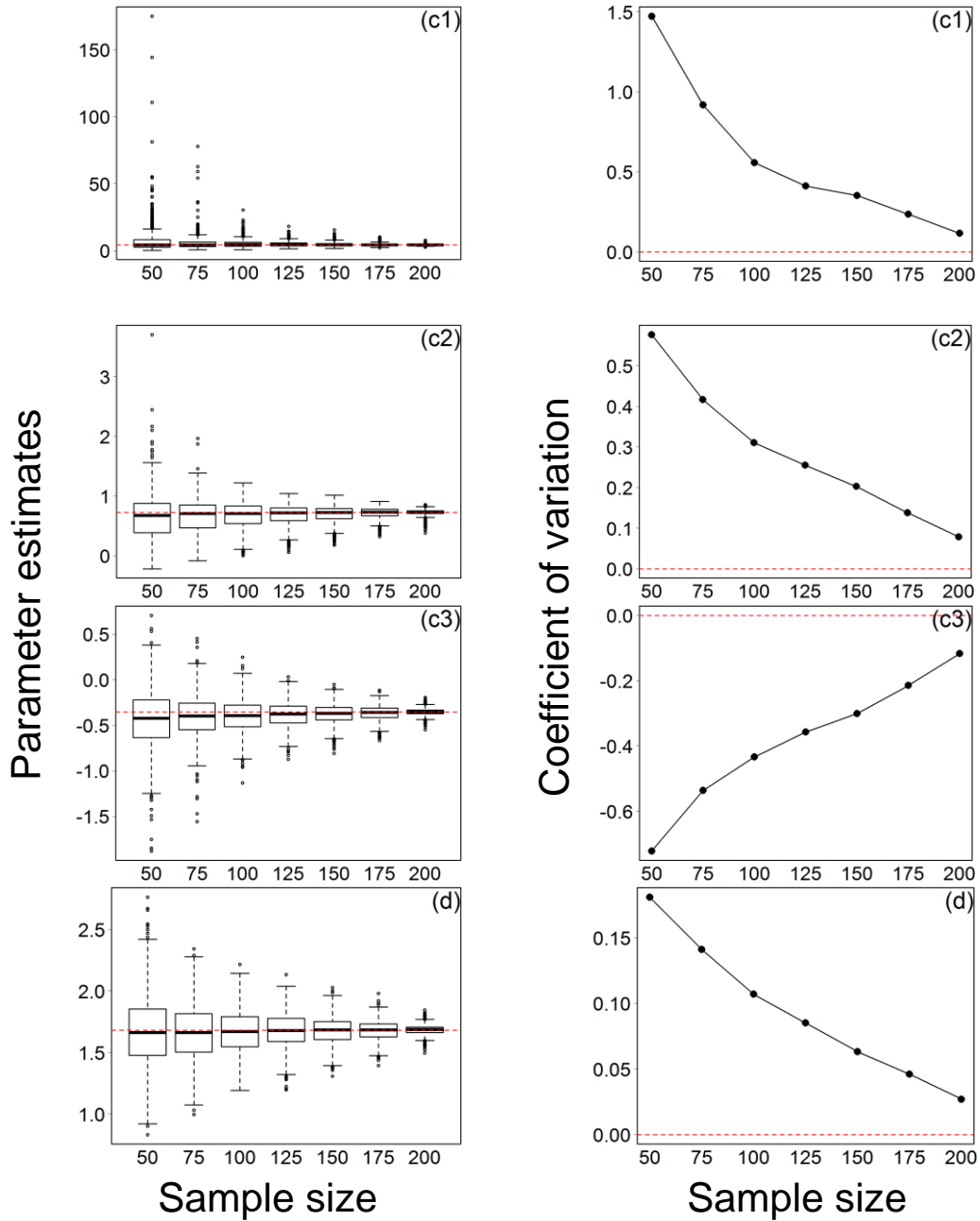
Figure 12. Effect of sample size on the accuracy and precision of the parameter estimates of select empirical estimators. Specifically, 1000 bootstrap samples were drawn with replacement from the complete dataset (n=215) with sample sizes of 50, 75, 100, 125, 150 and 200. The empirical models were fitted to each bootstrap sample and the coefficient of variation (CV) of the parameter estimates was calculated. Boxplots of the 1000 parameter estimates (left) and the corresponding CV (right) shown as a function of sample size. The parameters are the (c1) scaling, (c2) K exponent, (c3) L_∞ exponent for Pauly$_{nls\text{-}T}$ and (d) K coefficient for one-parameter K. Dashed horizontal lines in the left column indicate the updated parameter estimates for each model based on the common dataset (n = 215).
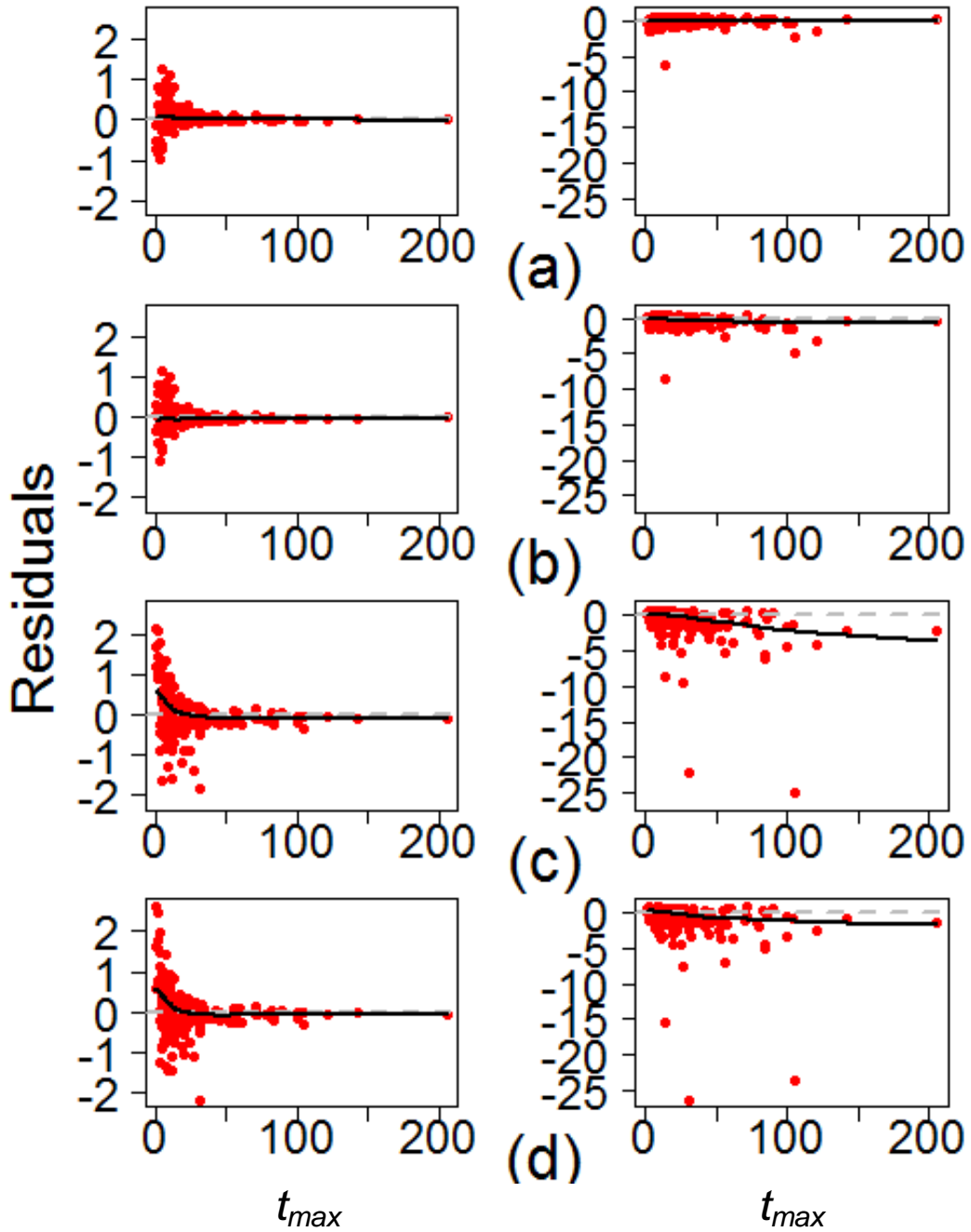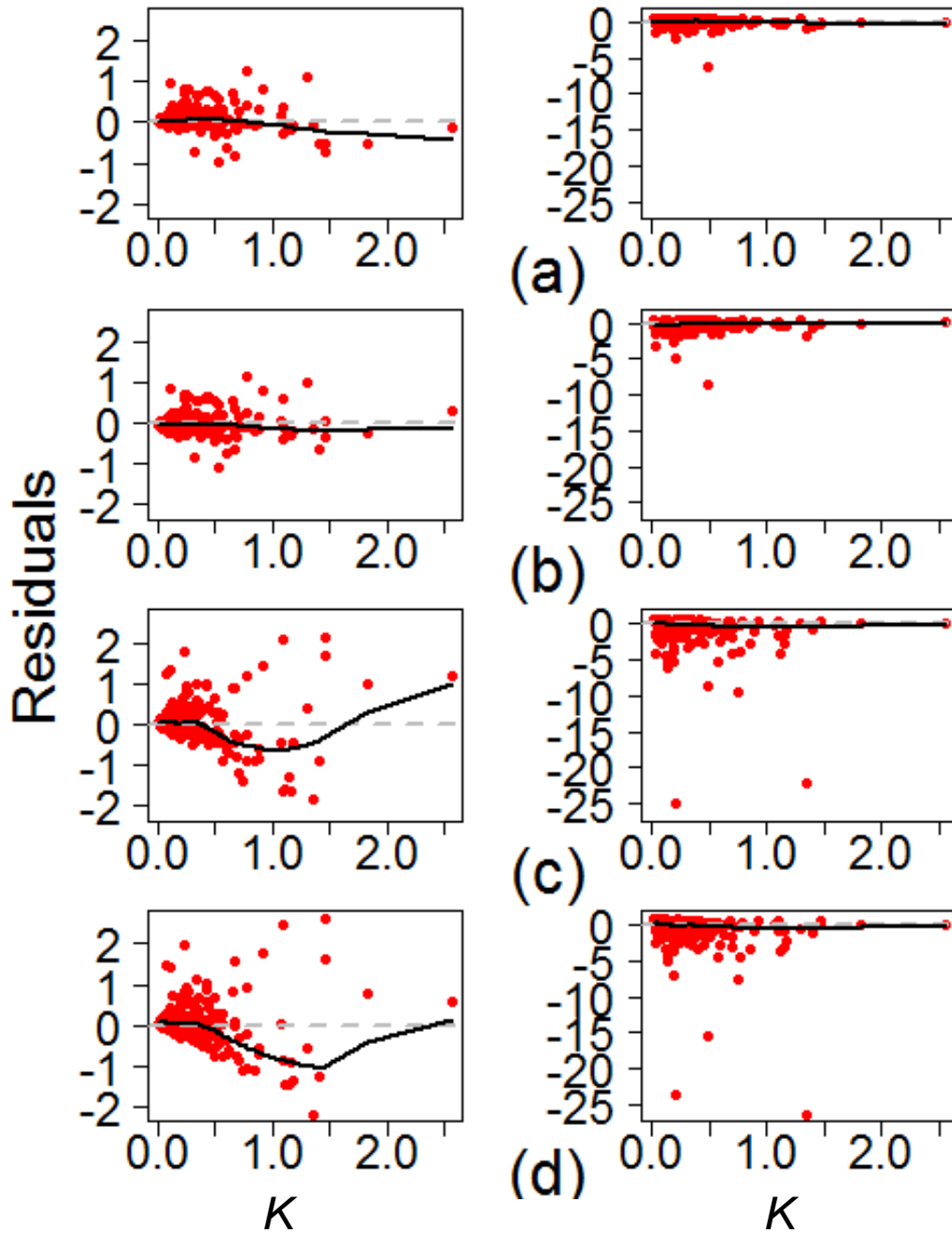
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Figure 13. (Left) Raw residuals and (right) residuals as fraction of the corresponding literature *M* estimates of updated empirical estimators as a function of maximum age (t_{max}). The estimators are (a) one-parameter t_{max}, (b) Hoenig$_{nls}$, (c) Pauly$_{nls-T}$ and (d) one-parameter *K*. Estimators were updated based on the common dataset (n = 215).

Figure 14. (Left) Raw residuals and (right) residuals as fraction of the corresponding literature *M* estimates of updated empirical estimators as a function of the von Bertalanffy growth parameter *K*. The estimators are (a) one-parameter t_{max}, (b) Hoenig$_{nls}$, (c) Pauly$_{nls-T}$ and (d) one-parameter *K*. Estimators were updated based on the common dataset (n = 215).
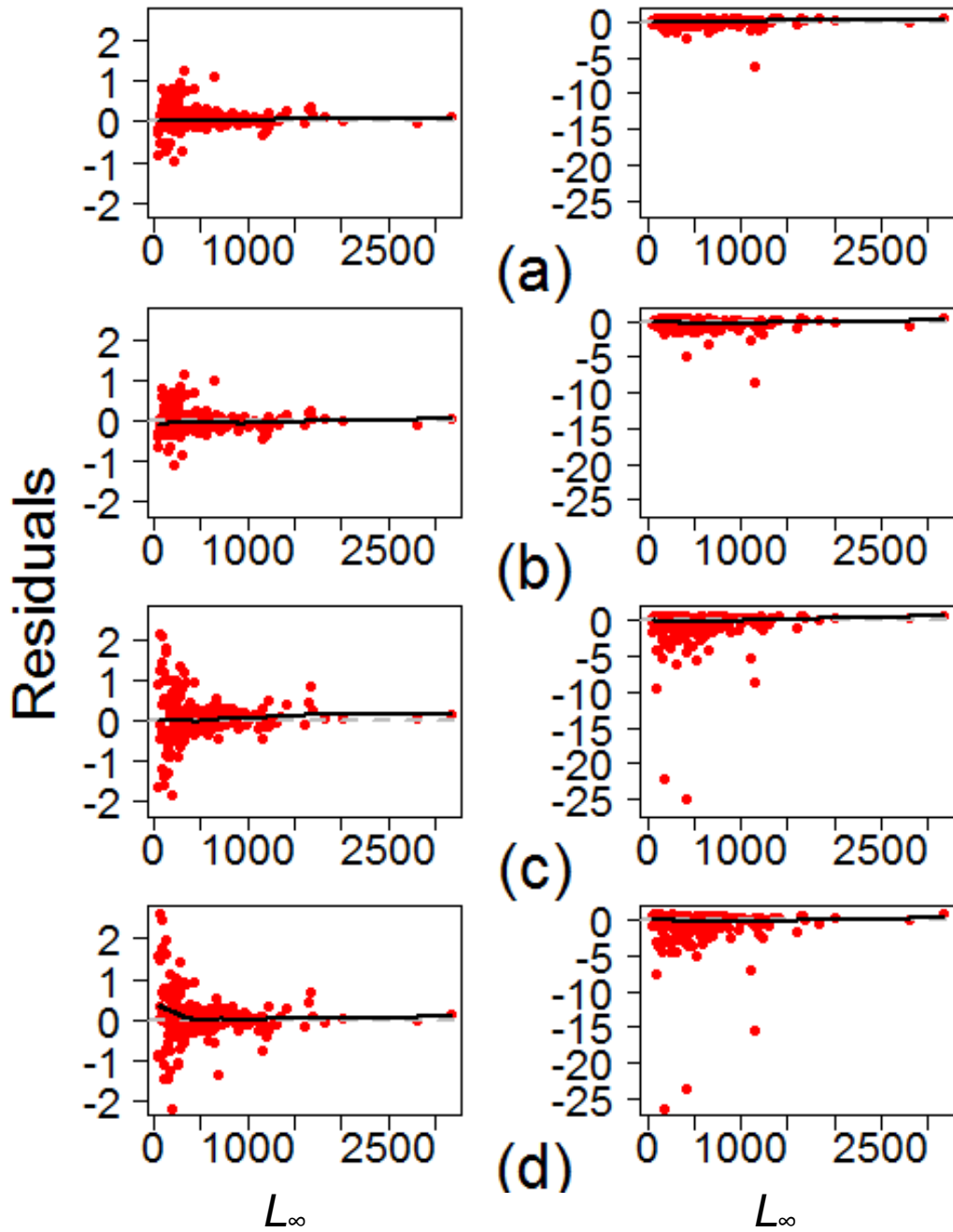
Figure 15. (Left) Raw residuals and (right) residuals as fraction of the corresponding literature M estimates of updated empirical estimators as a function of the von Bertalanffy asymptotic length parameter (L_∞). The estimators are (a) one-parameter t_{max}, (b) Hoenig$_{nls}$, (c) Pauly$_{nls-T}$ and (d) one-parameter K. Estimators were updated based on the common dataset (n = 215).
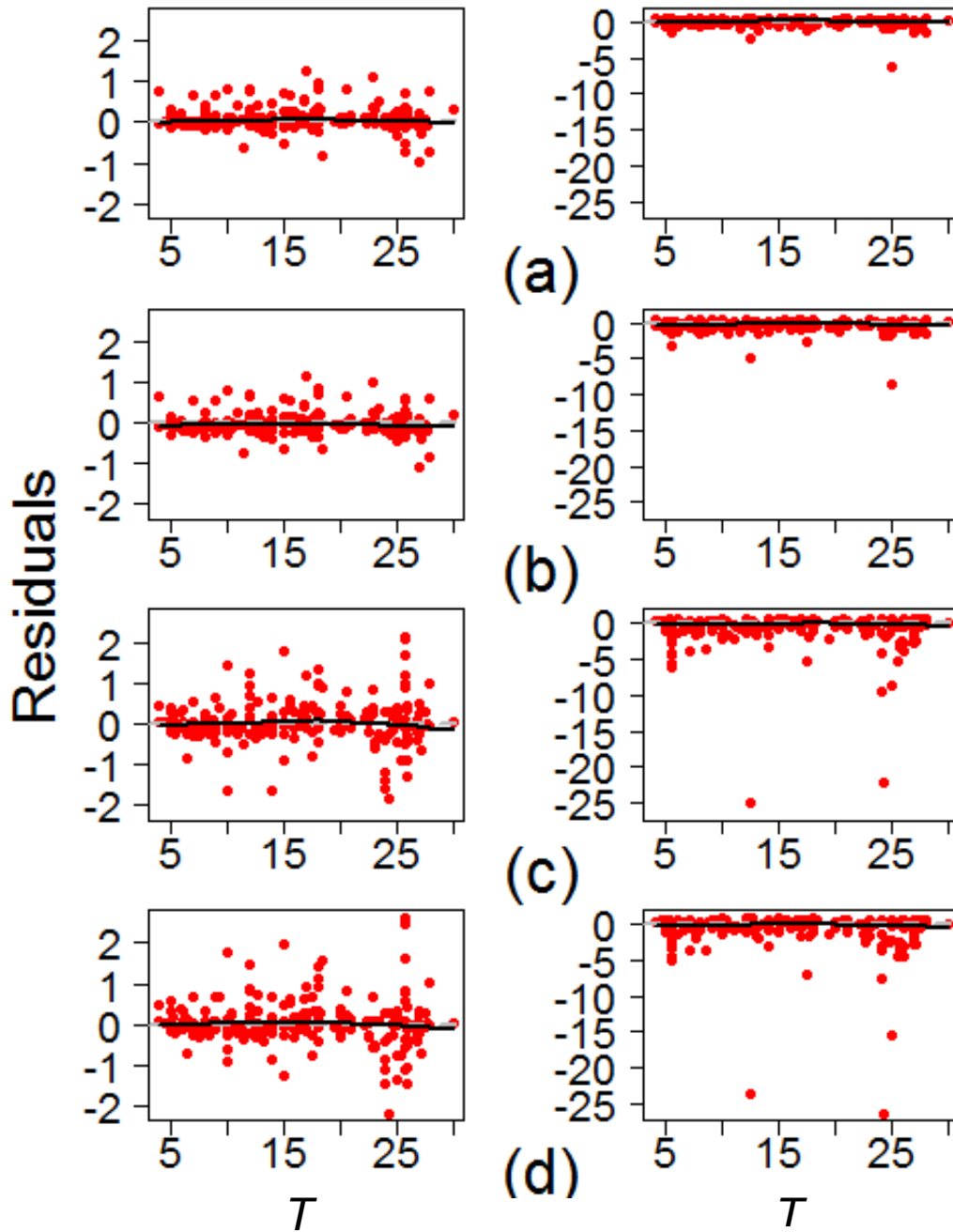
Figure 16. Residuals (left column) and residuals as fraction of the corresponding literature M estimates (right column) of updated empirical estimators as a function of mean water temperature (T). The estimators are (a) one-parameter t_{max}, (b) Hoenig$_{nls}$, (c) Pauly$_{nls-T}$ and (d) one-parameter K. Estimators were updated based on the common dataset (n = 215).
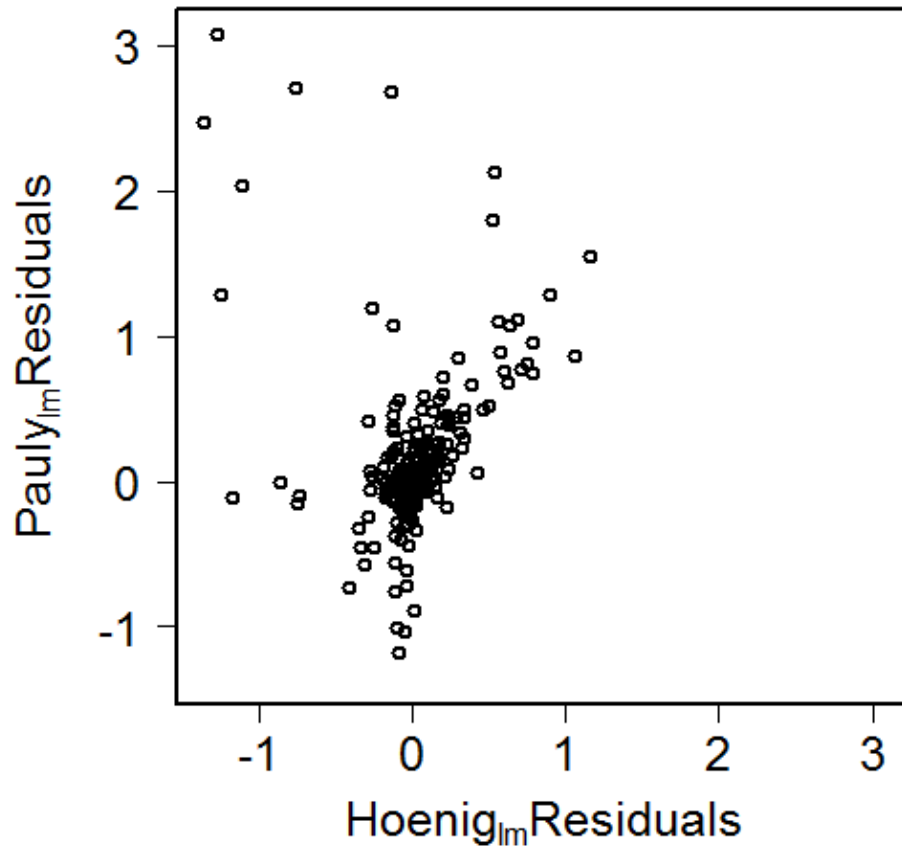
Figure 17. Biplot of the residuals of the updated Hoenig$_{lm}$ and Pauly$_{lm}$ models (n = 215). The coefficient of determination between both model residuals is r^2 = 0.0028.