2014

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

Amy Y. Then
Virginia Institute of Marine Science

John M. Hoenig
Virginia Institute of Marine Science

Recommended Citation
Then, A. Y., & Hoenig, J. M. (2014) Results of evaluating the performance of empirical estimators of natural mortality rate. Data report (Virginia Institute of Marine Science); no. 62. Virginia Institute of Marine Science, William & Mary. https://doi.org/10.21220/V5WW25

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

Amy Y. Then and John M. Hoenig

Department of Fisheries Science
Virginia Institute of Marine Science
The College of William and Mary

Data Report 62

July 2014

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.

References

Alverson, D. L., and Carney, M. J. 1975. A graphic review of the growth and decay of population cohorts. Journal du Conseil International pour l'Exploration de la Mer, 36: 133-143.

Beverton, R. J. H., and Holt, S. J. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *In* Ciba Foundation Symposium - The Lifespan of Animals (Colloquia on Ageing), Volume 5, pp. 142-180. Ed. by G. E. W. Wolstenholme and M. O'Conner. John Wiley & Sons, Ltd, Chichester, UK. 324 pp.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin, 82: 898-903.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour l'Exploration de la Mer, 39: 175.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Then, A. Y., Hoenig, J. M., Hall, N. G., Hewitt, D. 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.

List of Tables

List of Figures

Figure 7. Model residuals shown for the subset of literature M values < 0.5 (n = 132) for the updated weighted (composite) estimators of (t) $\text{Hoenig}_{\text{nls}}$ and $\text{Pauly}_{\text{nls}}$, (u) $\text{Hoenig}_{\text{nls}}$ and $\text{Pauly}_{\text{nls-T}}$, (v) one-parameter t_{max} and $\text{Pauly}_{\text{nls}}$, (w) one-parameter t_{max} and $\text{Pauly}_{\text{nls-T}}$, (x) one-parameter t_{max} and one-parameter K, and (y) $\text{Hoenig}_{\text{lm}}$ 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) $\text{Hoenig}_{\text{lm}}$ (c) $\text{Hoenig}_{\text{gm}}$ (d) $\text{Hoenig}_{\text{bc}}$ (e) $\text{Hoenig}_{\text{quad}}$ (f) $\text{Hoenig}_{\text{nls}}$ (g) $\text{Hoenig}_{\text{nls(weighted)}}$ (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) $\text{Pauly}_{\text{lm-T}}$, (p) $\text{Pauly}_{\text{nls}}$, (q) $\text{Pauly}_{\text{nls-T}}$, (r) $\text{Pauly}_{\text{nls}K}$, 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) $\text{Hoenig}_{\text{nls}}$ and $\text{Pauly}_{\text{nls}}$, (u) $\text{Hoenig}_{\text{nls}}$ and $\text{Pauly}_{\text{nls-T}}$, (v) one-parameter t_{max} and $\text{Pauly}_{\text{nls}}$, (w) one-parameter t_{max} and $\text{Pauly}_{\text{nls-T}}$, (x) one-parameter t_{max} and one-parameter K, and (y) $\text{Hoenig}_{\text{lm}}$ 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 $\text{Hoenig}_{\text{nls}}$. 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 $\text{Pauly}_{\text{nls-T}}$ 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).

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) $\text{Hoenig}_{\text{nls}}$, (c) $\text{Pauly}_{\text{nls-T}}$ 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) $Pauly_{nls\text{-}T}$ 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) $Pauly_{nls\text{-}T}$ 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) $Pauly_{nls\text{-}T}$ 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 $r^2 = 0.0028$.

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}	$M = a/\,\text{t}_{\text{max}}$	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}	$M = \exp(a + b\log(t_{max}) + \text{SE}^2/2)$	ls	this study
Hoenig_{quad}	$\log(M) = a + b\log(t_{max}) + c\log(t_{max}^{\,2})$	ls	this study
Hoenig_{nls}	$M = a t_{max}^{\,b}$	nls	this study
$\text{Hoenig}_{nls(weighted)}$	$M = a t_{max}^{\,b}$	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)
$\text{Pauly}_{lm\text{-}T}$	$\log(M) = a + b\log(K) + c\log(L_\infty)$	ls	this study
Pauly_{nls}	$M = aK^bL_\infty^{\,c}T^d$	nls	this study
$\text{Pauly}_{nls\text{-}T}$	$M = aK^bL_\infty^{\,c}$	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*	$M = \text{p}M_{\text{Estimator1}} + (1 - \text{p})\,M_{\text{Estimator2}}$	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
$\boldsymbol{t_{max}}$					
one-parameter t_{max}	$M = 4.934/\ t_{max}$	0.87	0.18	0.30	0.305
$\text{Hoenig}_{\text{lm}}$	$\log(M) = 1.717 - 1.01\log(t_{max})$	0.87	0.19	0.32	0.328
$\text{Hoenig}_{\text{gm}}$	$\log(M) = 1.966 - 1.1\log(t_{max})$	0.86	0.23	0.50	0.510
$\text{Hoenig}_{\text{bc}}$	$M = \exp(1.717 - 1.01\log(t_{max}) + 0.096)$	0.87	0.21	0.38	1.266
$\text{Hoenig}_{\text{quad}}$	$\log(M) = 1.46 - 0.789\log(t_{max}) - 0.042\log(t_{max})^2$	0.88	0.17	0.28	0.286
$\text{Hoenig}_{\text{nls}}$	$M = 4.504{t_{max}}^{-0.863}$	0.88	0.18	0.27	0.281
$\text{Hoenig}_{\text{nls(weighted)}}$	$M = 4.81{t_{max}}^{-0.908}$	0.88	0.18	0.28	0.285
$\text{Hoenig}_{\text{loess}}$	$M \sim t_{max}$	0.74	0.23	0.40	0.387
$\text{Hoenig}_{\text{loess(log)}}$	$\log(M) \sim \log(t_{max})$	0.88	0.17	0.27	0.284
$\boldsymbol{K}$					
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
$\boldsymbol{K, L_\infty, T}$					
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
$\text{Pauly}_{\text{lm-}T}$	$\log(M) = 1.091 + 0.545\log(K) - 0.361\log(L_\infty)$	0.50	0.35	0.60	0.610
$\text{Pauly}_{\text{nls}}$	$M = 2.338K^{0.619}{L_\infty}^{-0.435}T^{0.277}$	0.53	0.35	0.54	0.577
$\text{Pauly}_{\text{nls-}T}$	$M = 4.313K^{0.726}{L_\infty}^{-0.354}$	0.51	0.36	0.55	0.578
$\text{Pauly}_{\text{nlsK}}$	$M = 1.673K^{0.954}$	0.46	0.37	0.58	0.586
$\boldsymbol{K, t_{max}}$					
Alverson-Carney	$M = 3K/\ (e^{0.41Kt_{max}} - 1)$	0.81	0.26	0.40	0.414
Composites					
Weighted M	$M = 0.8M_{\text{Hoenignls}} + 0.2M_{\text{Paulynls}}$	0.86	0.19	0.29	0.302
	$M = 0.8M_{\text{Hoenignls}} + 0.2M_{\text{Paulynls-}T}$	0.87	0.19	0.29	0.301
	$M = 0.77M_{\text{one}tmax} + 0.23M_{\text{Paulynls}}$	0.86	0.19	0.30	0.307
	$M = 0.77M_{\text{one}tmax} + 0.23M_{\text{Paulynls-}T}$	0.86	0.19	0.30	0.303
	$M = 0.79M_{\text{one}tmax} + 0.21M_{\text{one}K}$	0.86	0.19	0.30	0.304
	$M = 0.77M_{\text{Hoeniglm}} + 0.23M_{\text{Paulylm}}$	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
$Hoenig_{nls}$	$M = 4.899t_{max}^{-0.916}$	0.89	0.19	0.30	226	0.323
$Hoenig_{nls(weighted)}$	$M = 4.992t_{max}^{-0.925}$	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
$Pauly_{lm-T}$	$\log(M) = 1.07 + 0.557\log(K) - 0.348\log(L_\infty)$	0.49	0.35	0.61	218	0.627
$Pauly_{nls}$	$M = 2.338K^{0.619}L_\infty^{-0.435}T^{0.277}$	0.53	0.35	0.54	215	0.577
$Pauly_{nls-T}$	$M = 4.118K^{0.73}L_\infty^{-0.333}$	0.50	0.36	0.56	218	0.597
$Pauly_{nlsK}$	$M = 1.683K^{0.946}$	0.46	0.37	0.58	218	0.597
K, t_{max}						
Alverson-Carney	$M = 3K/ (e^{0.41Kt_{max}} - 1)$	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$_{nls\text{-}T}$	$M = 4.118\, K^{0.73} L_{\infty}^{-0.33}$	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)

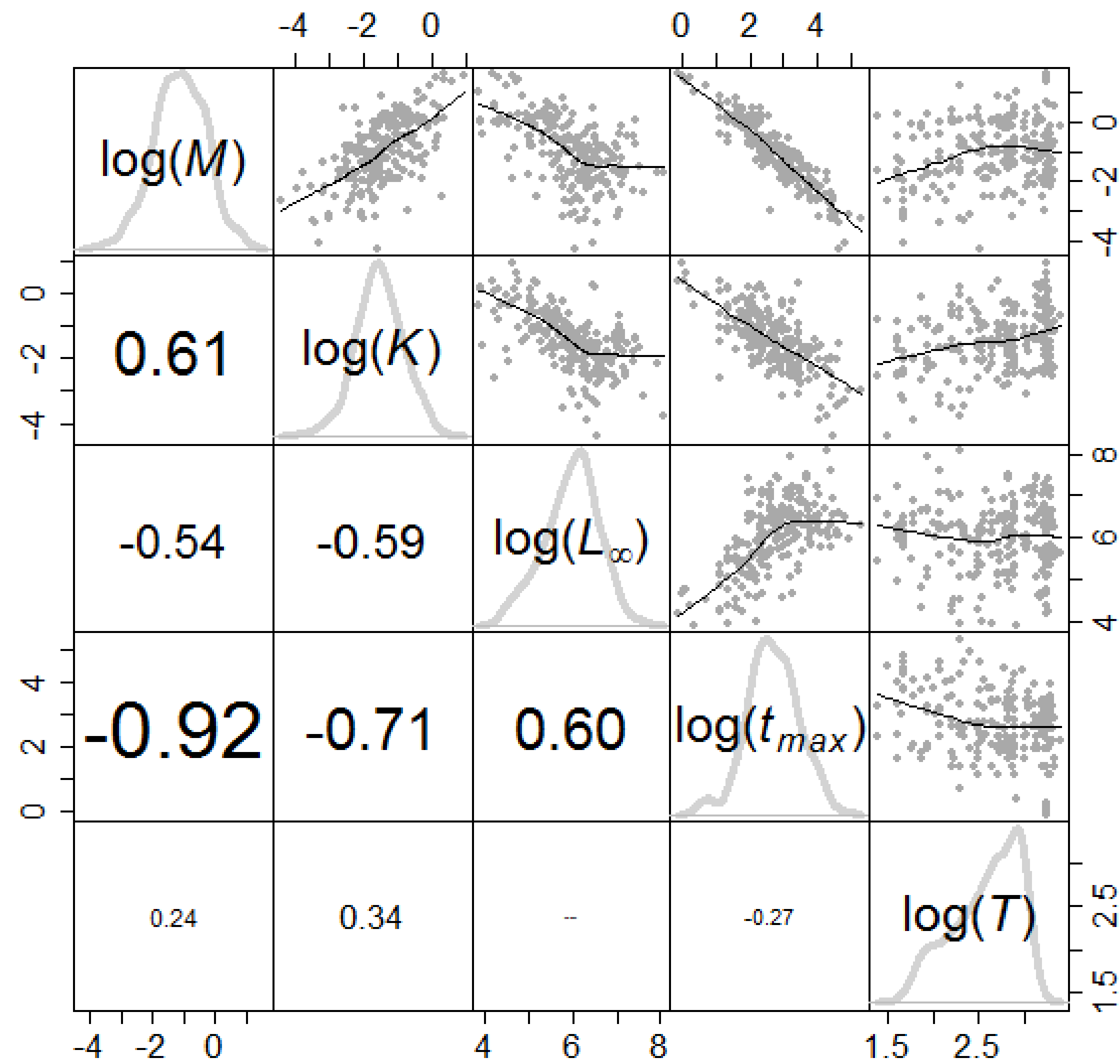

Figure 1. Scatterplot of pairs of log-transformed variables in the upper half of the panel, with locally weighted scatterplot smoothing (LOWESS) lines added (smoothing parameter f = 2/3). Variables: Natural mortality rate M, maximum age t_{max}, von Bertalanffy growth parameters K and L_∞, mean temperature 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.

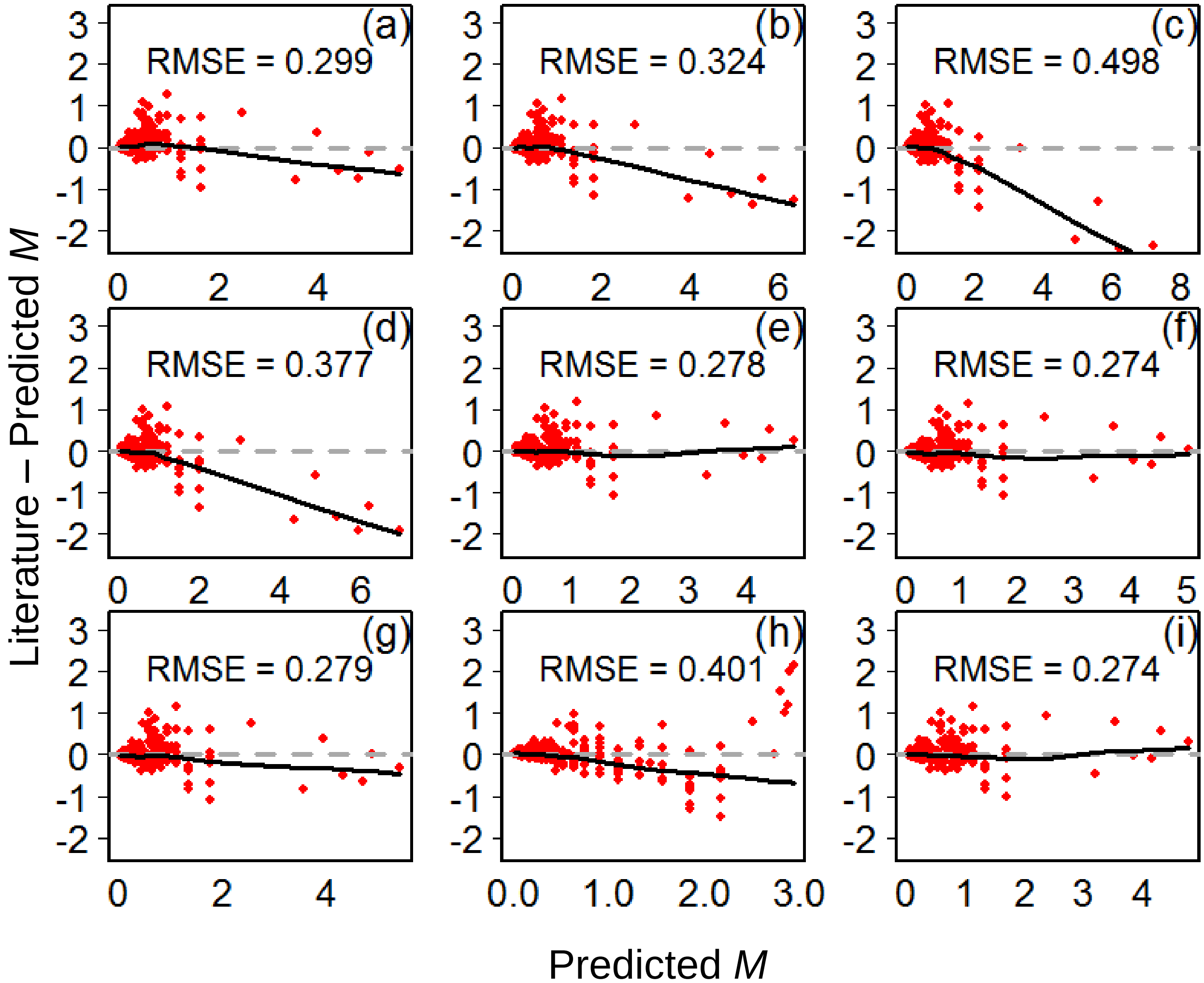

Figure 2. Model residuals for the updated t_{max}–based estimators of (a) one-parameter t_{max}, (b) $Hoenig_{lm}$, (c) $Hoenig_{gm}$, (d) $Hoenig_{bc}$, (e) $Hoenig_{quad}$, (f) $Hoenig_{nls}$, (g) $Hoenig_{nls(weighted)}$, (h) non-parametric regressions of M as a function of t_{max}, and (i) non-parametric 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.

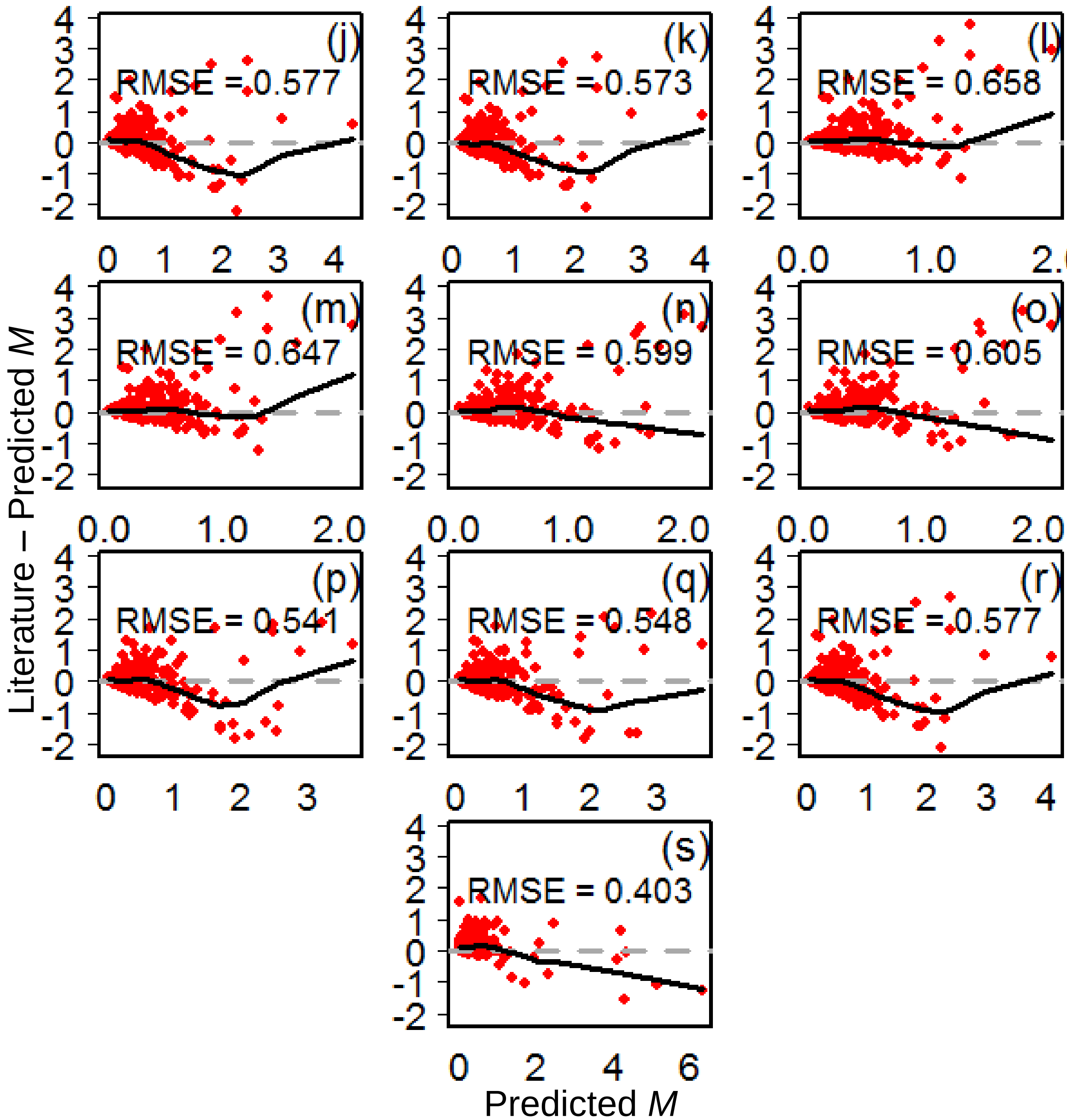

Figure 3. Model residuals for the updated growth-based and composite estimators of (j) one-parameter *K*, (k) two-parameter *K*, (l) log(one-parameter *K*), (m) log(two-parameter *K*), (n) $Pauly_{lm}$, (o) $Pauly_{lm\text{-}T}$, (p) $Pauly_{nls}$, (q) $Pauly_{nls\text{-}T}$, (r) $Pauly_{nlsK}$, and (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.

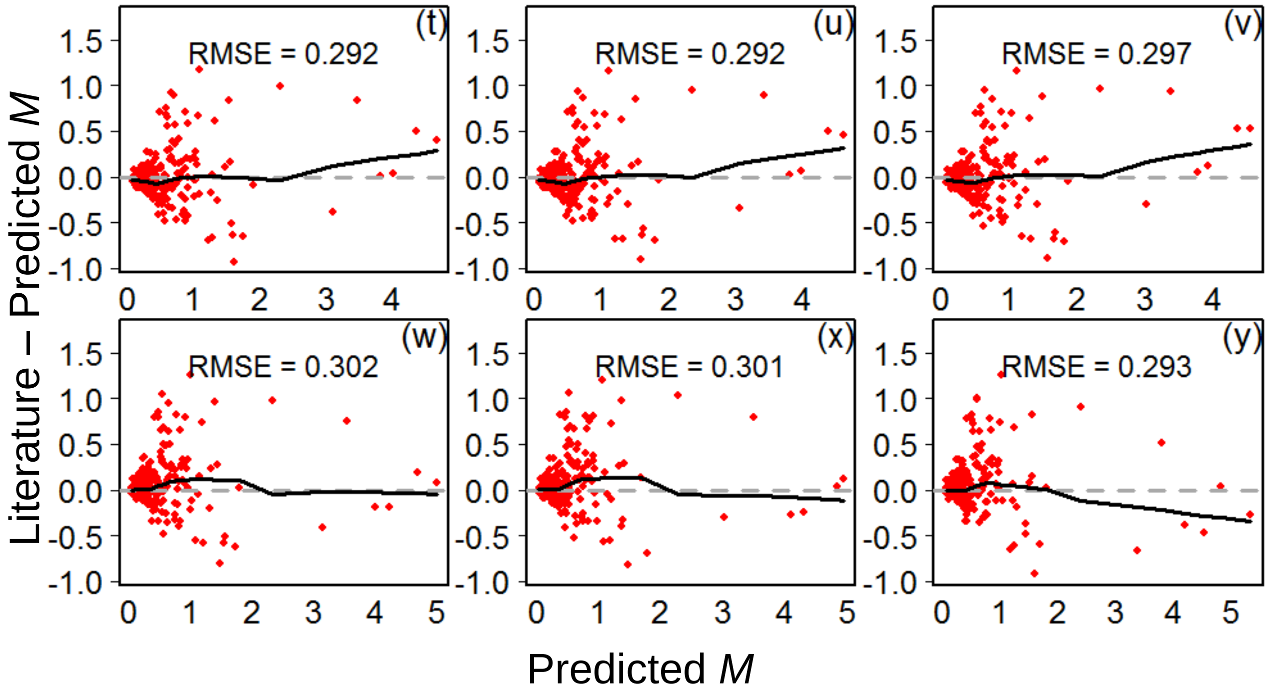

Figure 4. Model residuals for the updated weighted (composite) estimators of (t) $Hoenig_{nls}$ and $Pauly_{nls}$, (u) $Hoenig_{nls}$ and $Pauly_{nls\text{-}T}$, (v) one-parameter t_{max} and $Pauly_{nls}$, (w) one-parameter t_{max} and $Pauly_{nls\text{-}T}$, (x) one-parameter t_{max} and one-parameter 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.

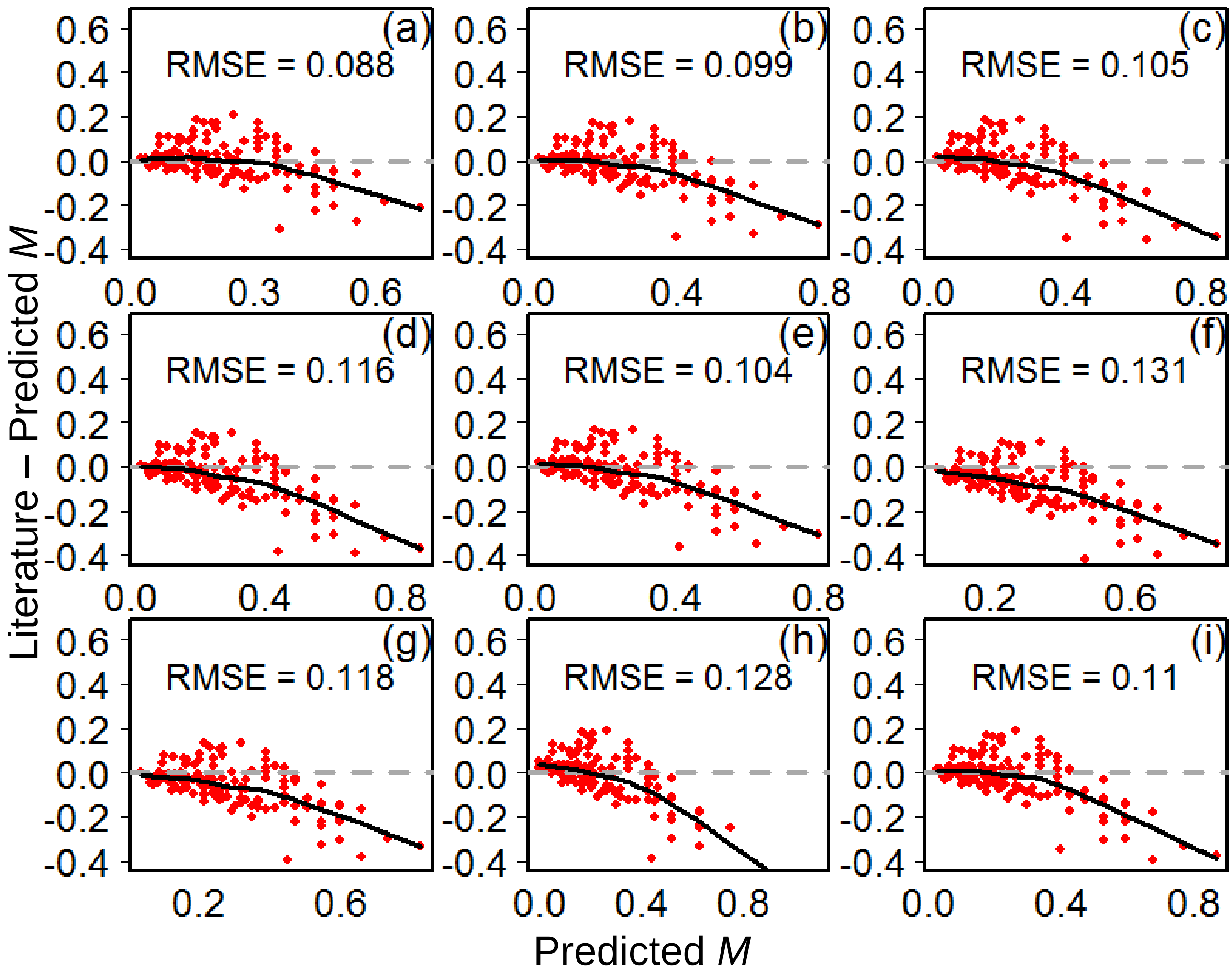

Figure 5. Model residuals shown for the subset of literature *M* values < 0.5 (n = 132) for the updated t_{max}–based estimators of (a) one-parameter t_{max}, (b) $\text{Hoenig}_{\text{lm}}$, (c) $\text{Hoenig}_{\text{gm}}$, (d) $\text{Hoenig}_{\text{bc}}$, (e) $\text{Hoenig}_{\text{quad}}$, (f) $\text{Hoenig}_{\text{nls}}$, (g) $\text{Hoenig}_{\text{nls(weighted)}}$, (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.

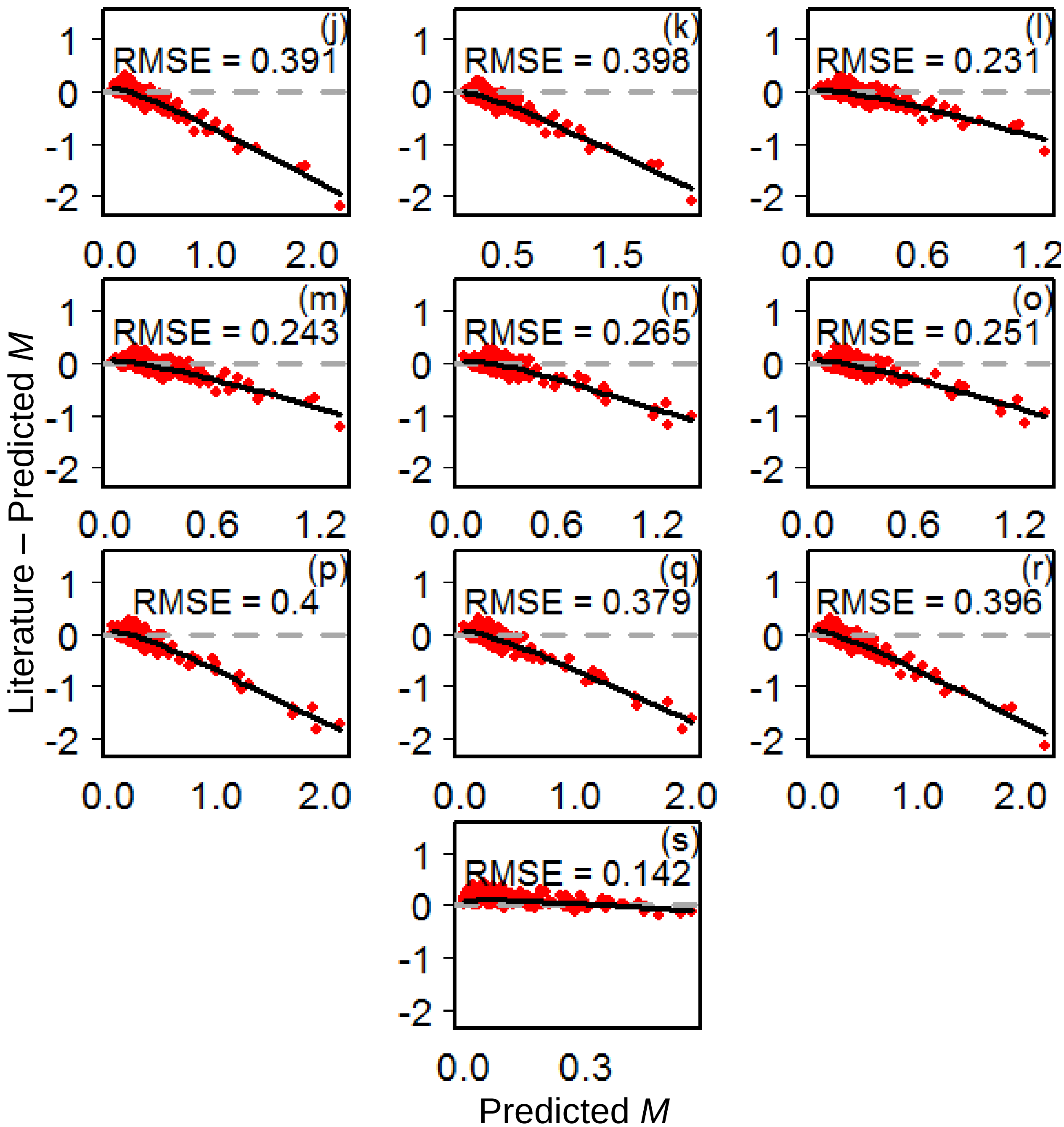

Figure 6. Model residuals shown for the subset of literature *M* values < 0.5 (n = 132) for the updated growth-based estimators of (j) one-parameter *K*, (k) two-parameter *K*, (l) log(one-parameter *K*), (m) log(two-parameter *K*), (n) Pauly_{lm}, (o) $\text{Pauly}_{\text{lm-T}}$, (p) $\text{Pauly}_{\text{nls}}$, (q) $\text{Pauly}_{\text{nls-T}}$, (r) $\text{Pauly}_{\text{nls}K}$, 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.

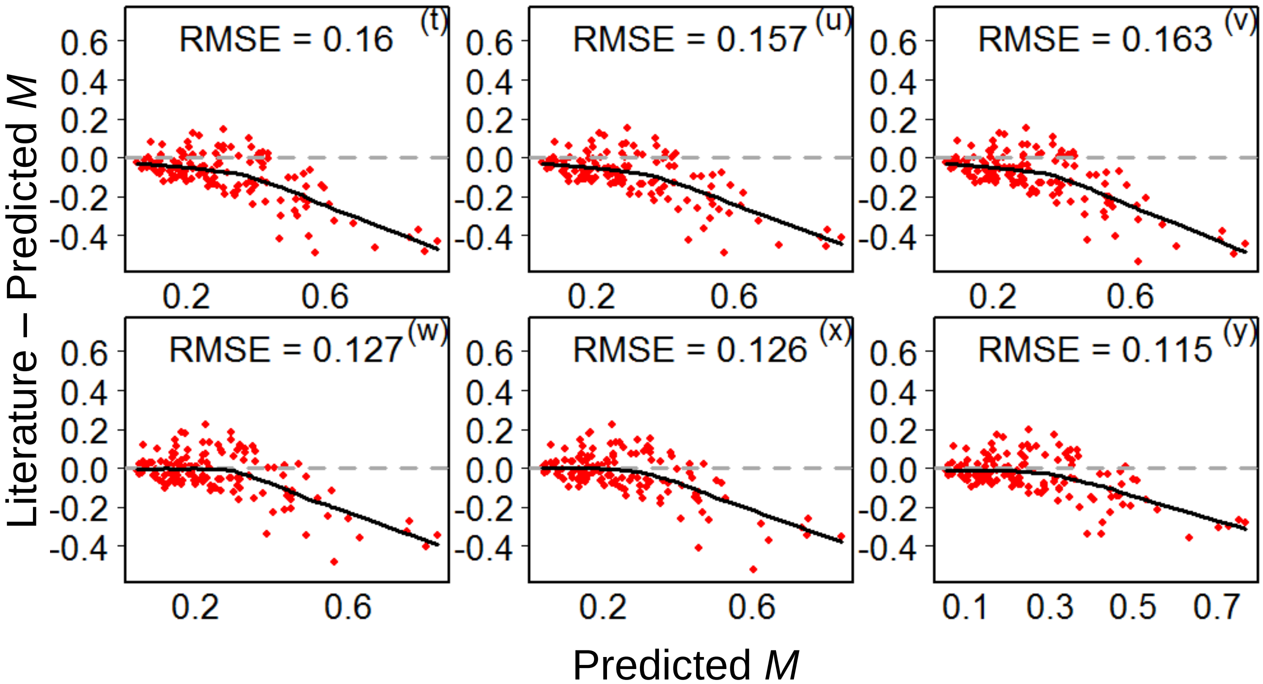

Figure 7. Model residuals shown for the subset of literature *M* values < 0.5 (n = 132) for the updated weighted (composite) estimators of (t) $Hoenig_{nls}$ and $Pauly_{nls}$, (u) $Hoenig_{nls}$ and $Pauly_{nls\text{-}T}$, (v) one-parameter t_{max} and $Pauly_{nls}$, (w) one-parameter t_{max} and $Pauly_{nls\text{-}T}$, (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.

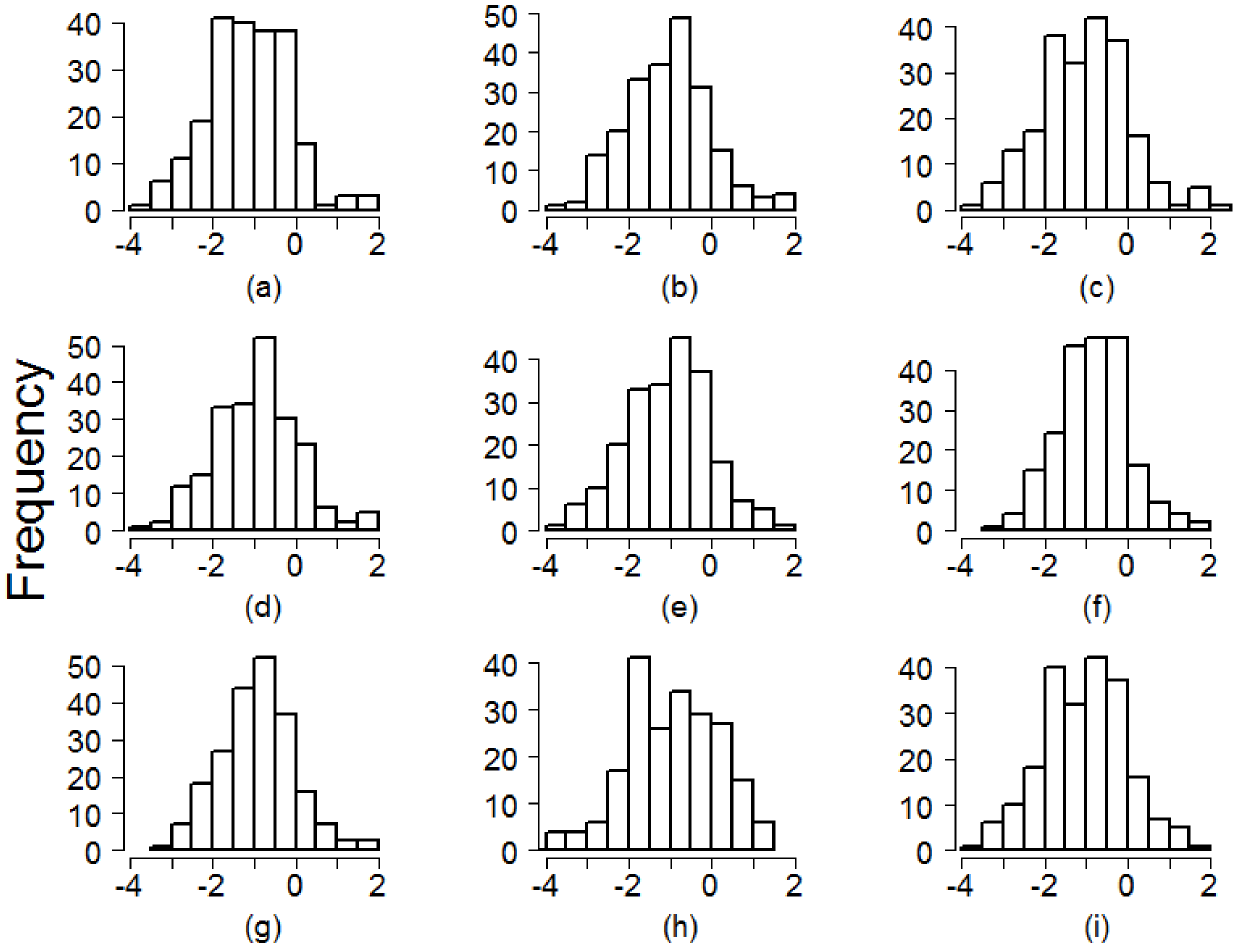

Figure 8. Histograms of model predicted M estimates (log-scale) for the updated t_{max}–based estimators of (a) one-parameter t_{max} (b) $Hoenig_{lm}$ (c) $Hoenig_{gm}$ (d) $Hoenig_{bc}$ (e) $Hoenig_{quad}$ (f) $Hoenig_{nls}$ (g) $Hoenig_{nls(weighted)}$ (h) non-parametric regressions of M as a function 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).

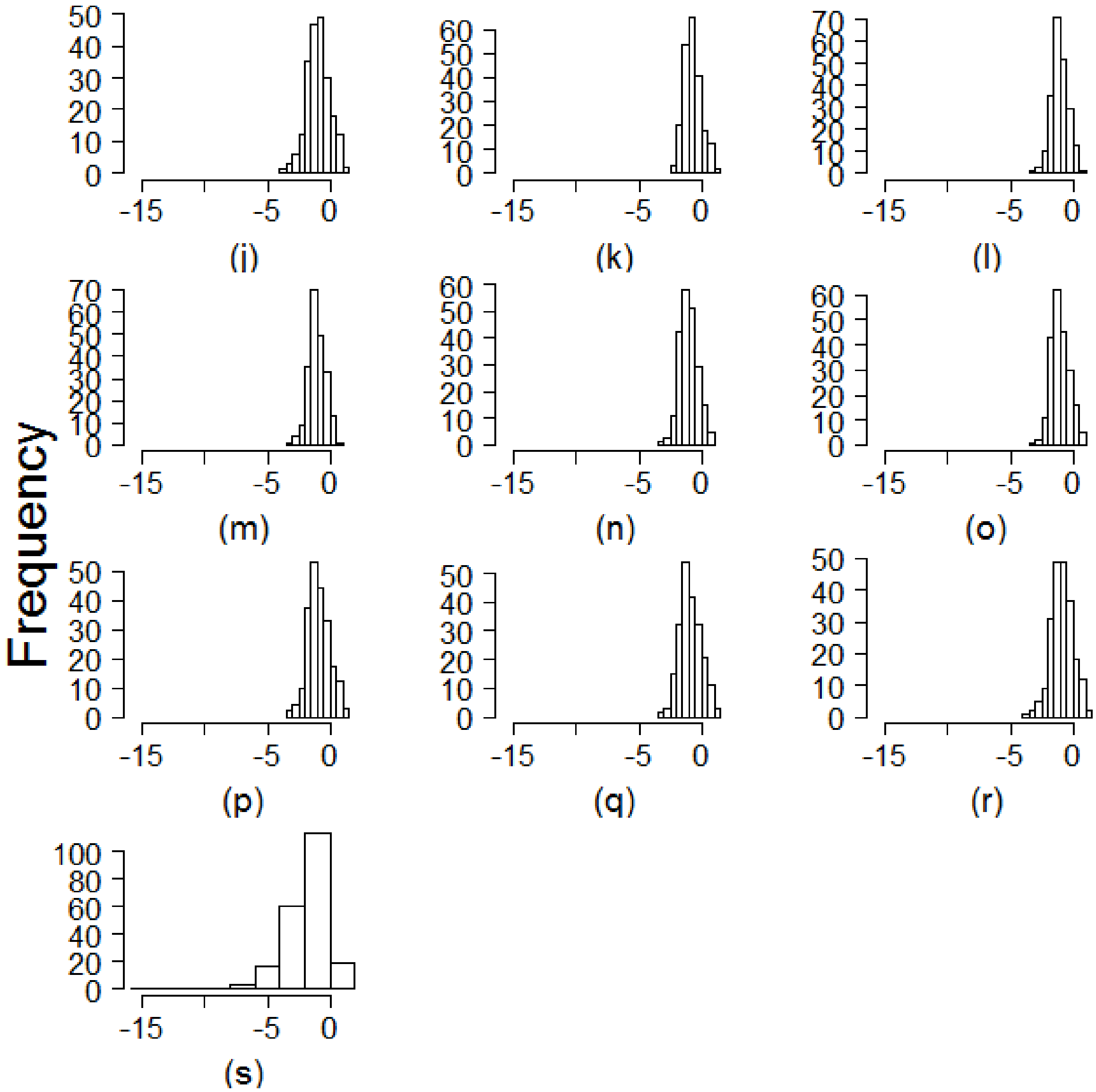

Figure 9. Histograms of model predicted *M* estimates (log-scale) for the updated t_{max}–based estimators of of (j) one-parameter *K*, (k) two-parameter *K*, (l) log(one-parameter *K*), (m) log(two-parameter *K*), (n) $Pauly_{lm}$, (o) $Pauly_{lm\text{-}T}$, (p) $Pauly_{nls}$, (q) $Pauly_{nls\text{-}T}$, (r) $Pauly_{nlsK}$, and (s) Alverson-Carney. Estimators were updated based on the common dataset (n = 215).

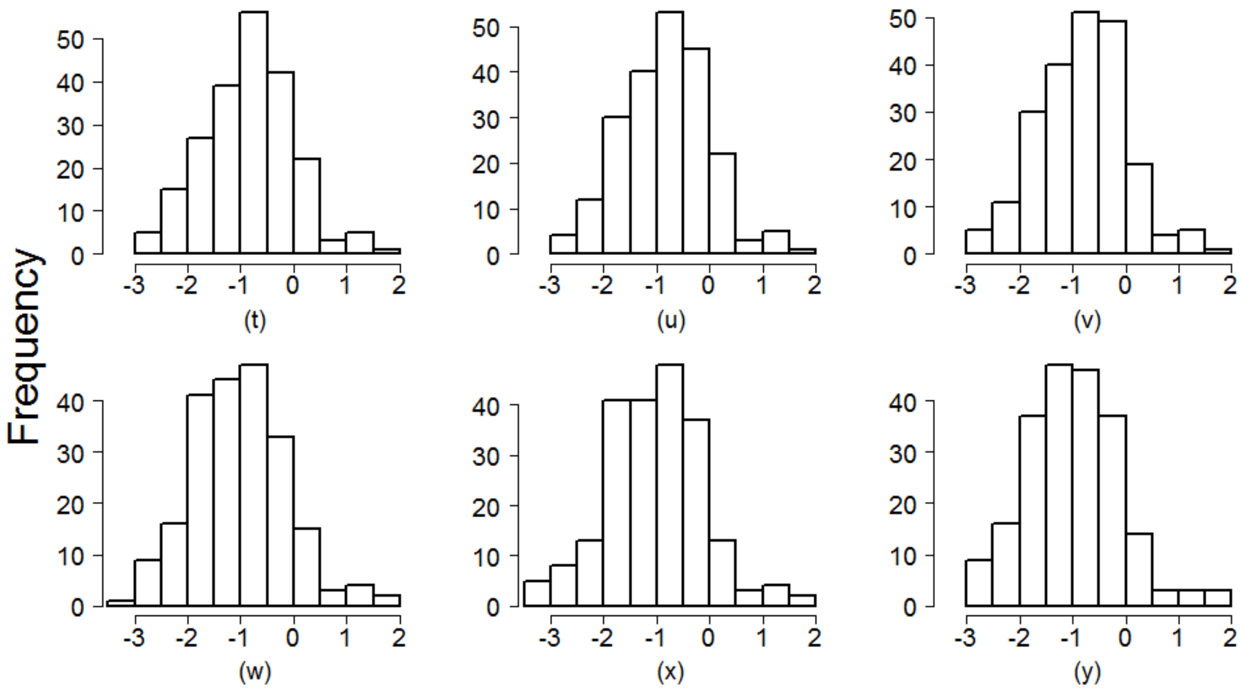

Figure 10. Histograms of model predicted *M* estimates (log-scale) for the updated weighted (composite) estimators of (t) $Hoenig_{nls}$ and $Pauly_{nls}$, (u) $Hoenig_{nls}$ and $Pauly_{nls-T}$, (v) one-parameter t_{max} and $Pauly_{nls}$, (w) one-parameter t_{max} and $Pauly_{nls-T}$, (x) one-parameter t_{max} and one-parameter *K*, and (y) $Hoenig_{lm}$ and $Pauly_{lm}$. Estimators were updated based on the common dataset (n = 215).

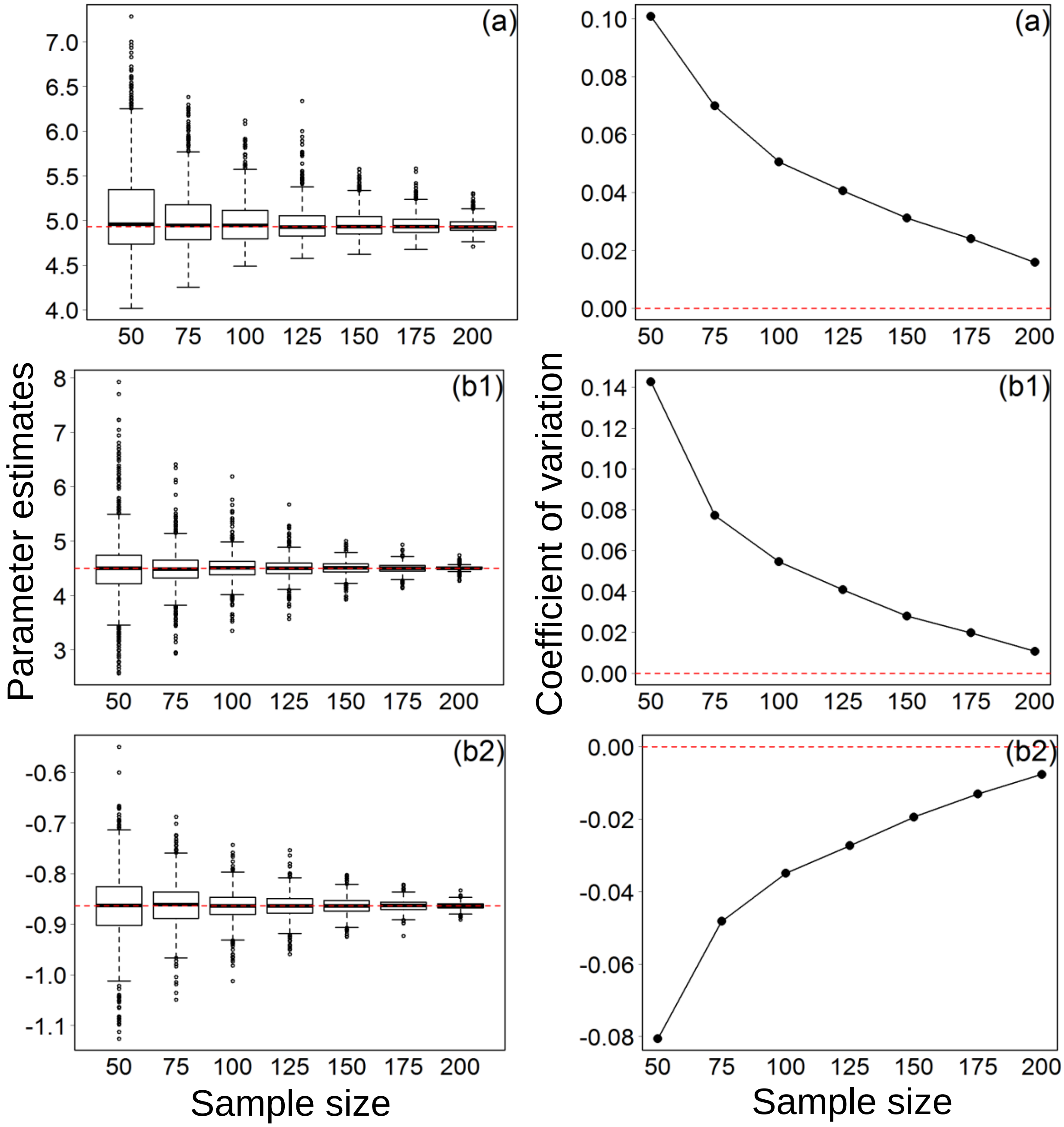

Figure 11. Effect of sample size on the accuracy and precision of the parameter estimates of select empirical estimators. Specifically, 1000 bootstrap samples were drawn with replacement from the complete dataset (n=215) with sample sizes of 50, 75, 100, 125, 150 and 200. The empirical models were fitted 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).

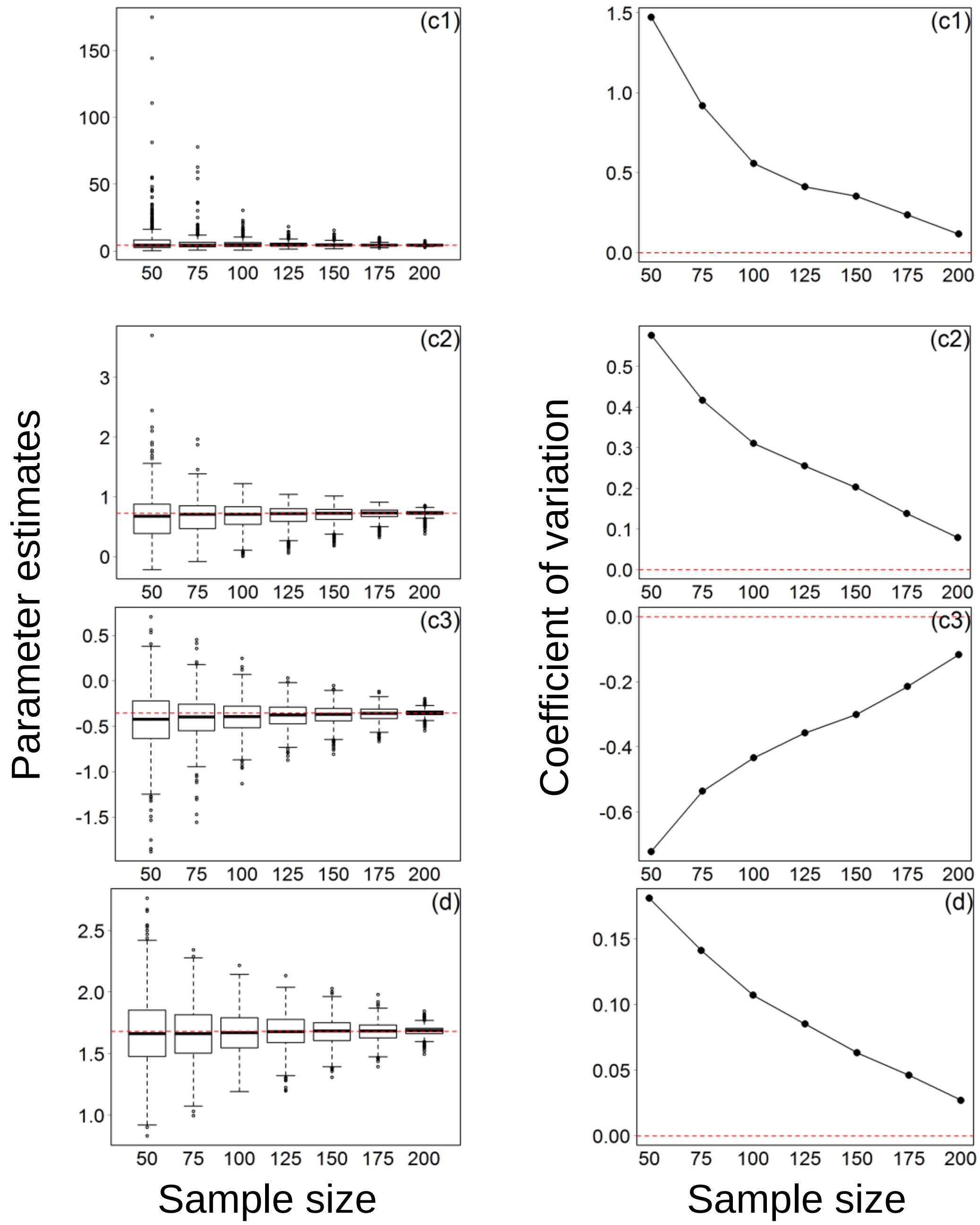

Figure 12. Effect of sample size on the accuracy and precision of the parameter estimates of select empirical estimators. Specifically, 1000 bootstrap samples were drawn with replacement from the complete dataset (n=215) with sample sizes of 50, 75, 100, 125, 150 and 200. The empirical models were fitted 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 $\text{Pauly}_{\text{nls-T}}$ 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).

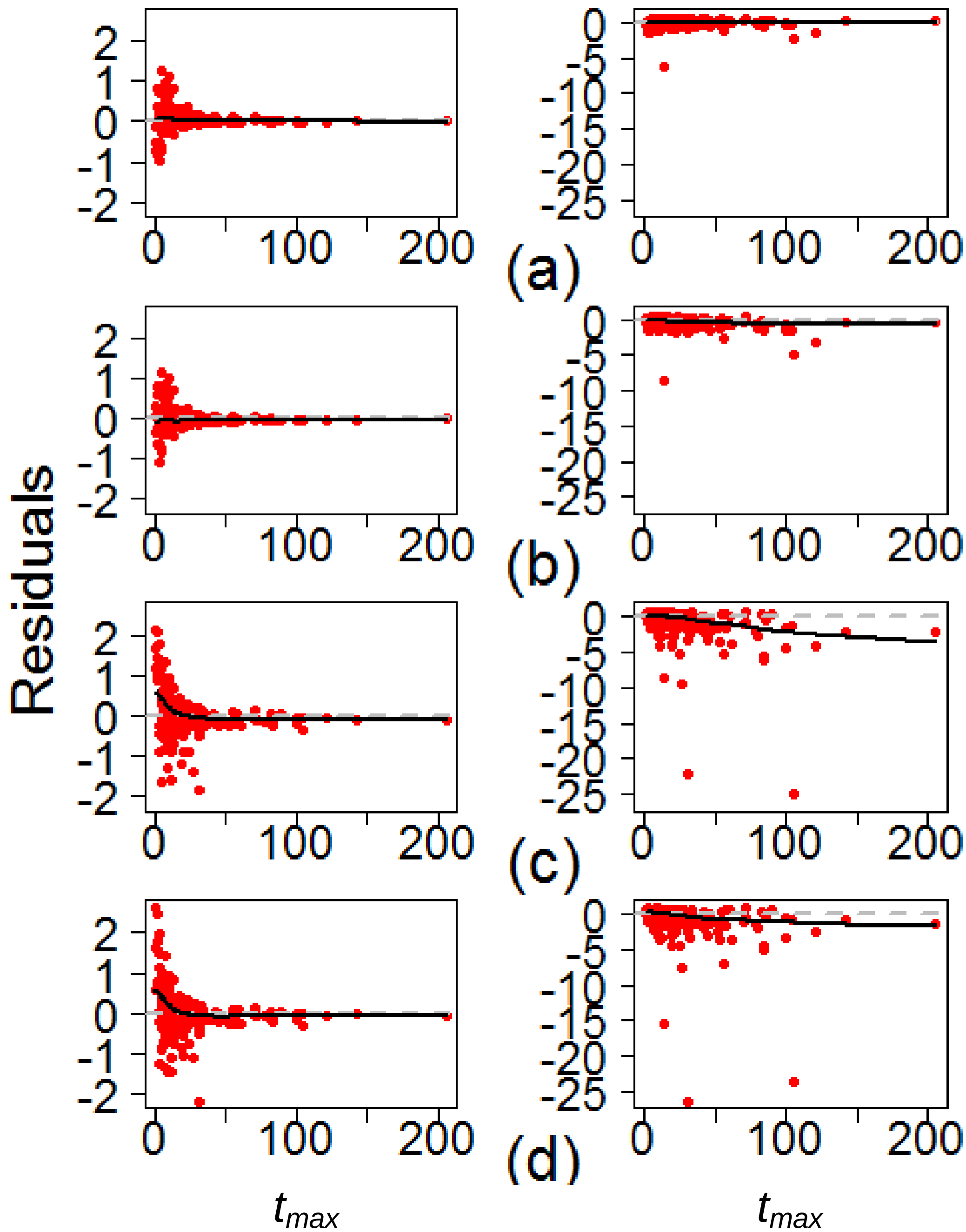

Figure 13. (Left) Raw residuals and (right) residuals as fraction of the corresponding literature *M* estimates of updated empirical estimators as a function of maximum age (t_{max}). The estimators are (a) one-parameter t_{max}, (b) $Hoenig_{nls}$, (c) $Pauly_{nls\text{-}T}$ and (d) one-parameter *K*. Estimators were updated based on the common dataset (n = 215).

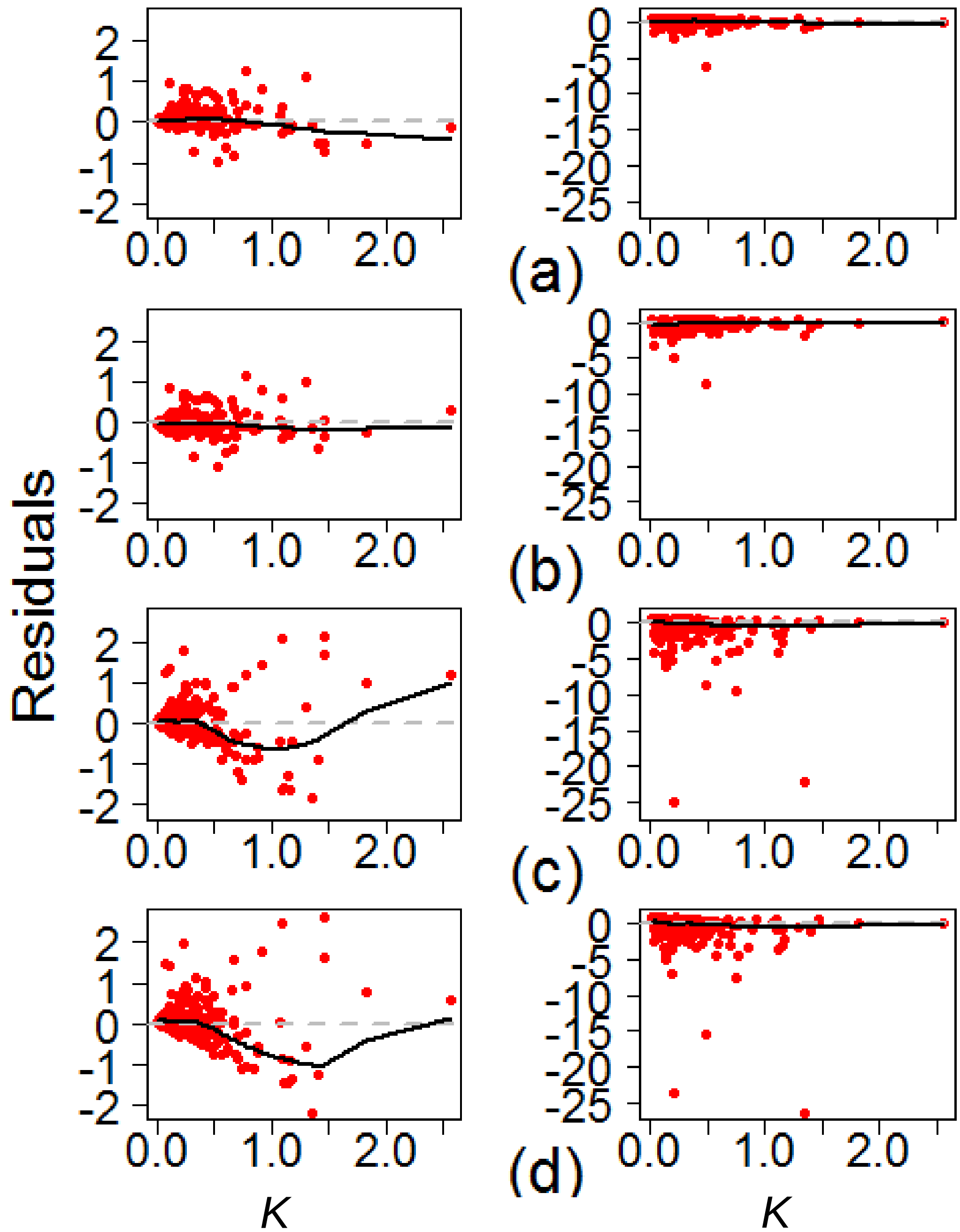

Figure 14. (Left) Raw residuals and (right) residuals as fraction of the corresponding literature *M* estimates of updated empirical estimators as a function of the von Bertalanffy growth parameter *K*. The estimators are (a) one-parameter t_{max}, (b) $Hoenig_{nls}$, (c) $Pauly_{nls\text{-}T}$ and (d) one-parameter *K*. Estimators were updated based on the common dataset (n = 215).

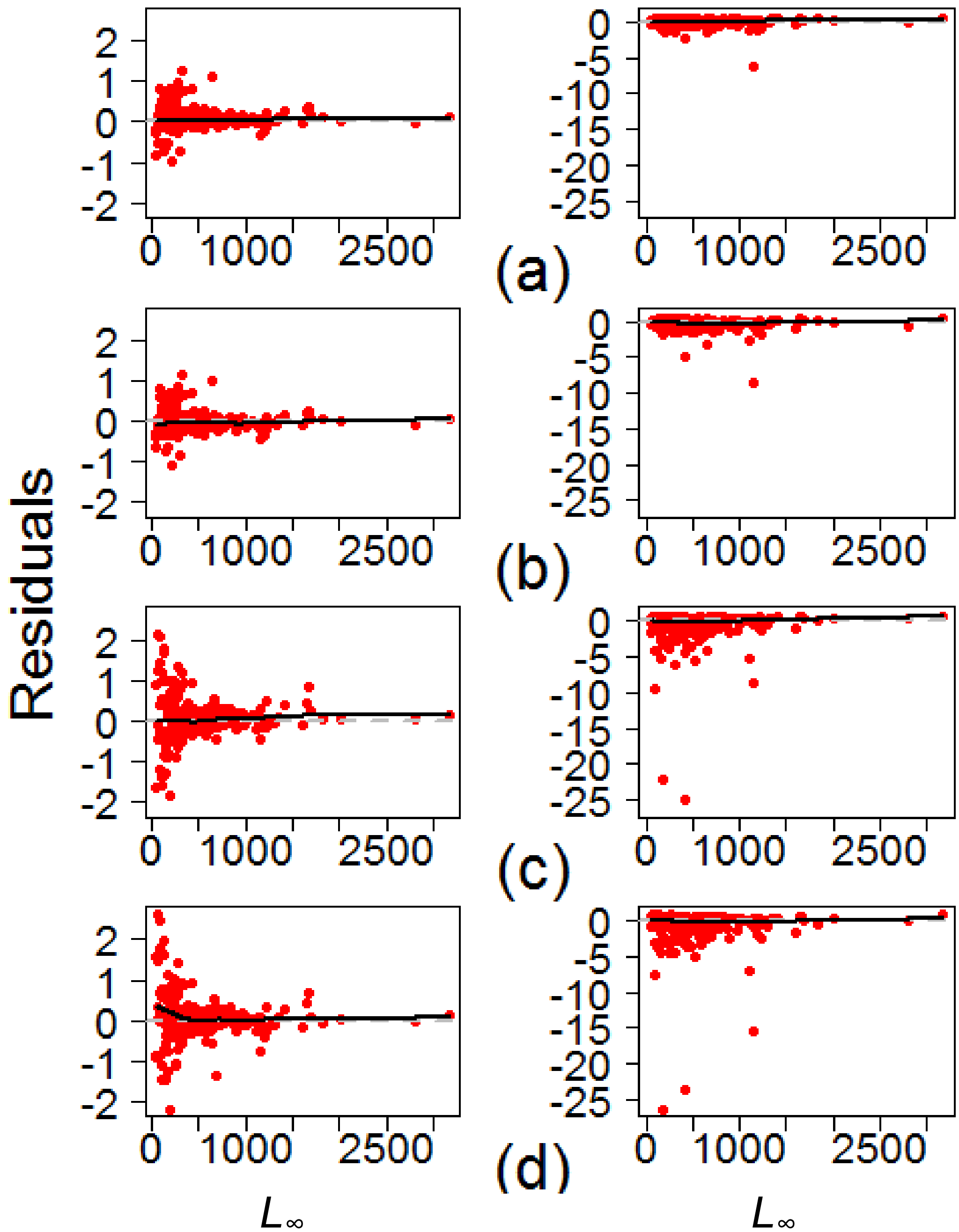

Figure 15. (Left) Raw residuals and (right) residuals as fraction of the corresponding literature *M* estimates of updated empirical estimators as a function of the von Bertalanffy asymptotic length parameter (L_∞). The estimators are (a) one-parameter t_{max}, (b) $\text{Hoenig}_{\text{nls}}$, (c) $\text{Pauly}_{\text{nls-T}}$ and (d) one-parameter *K*. Estimators were updated based on the common dataset (n = 215).

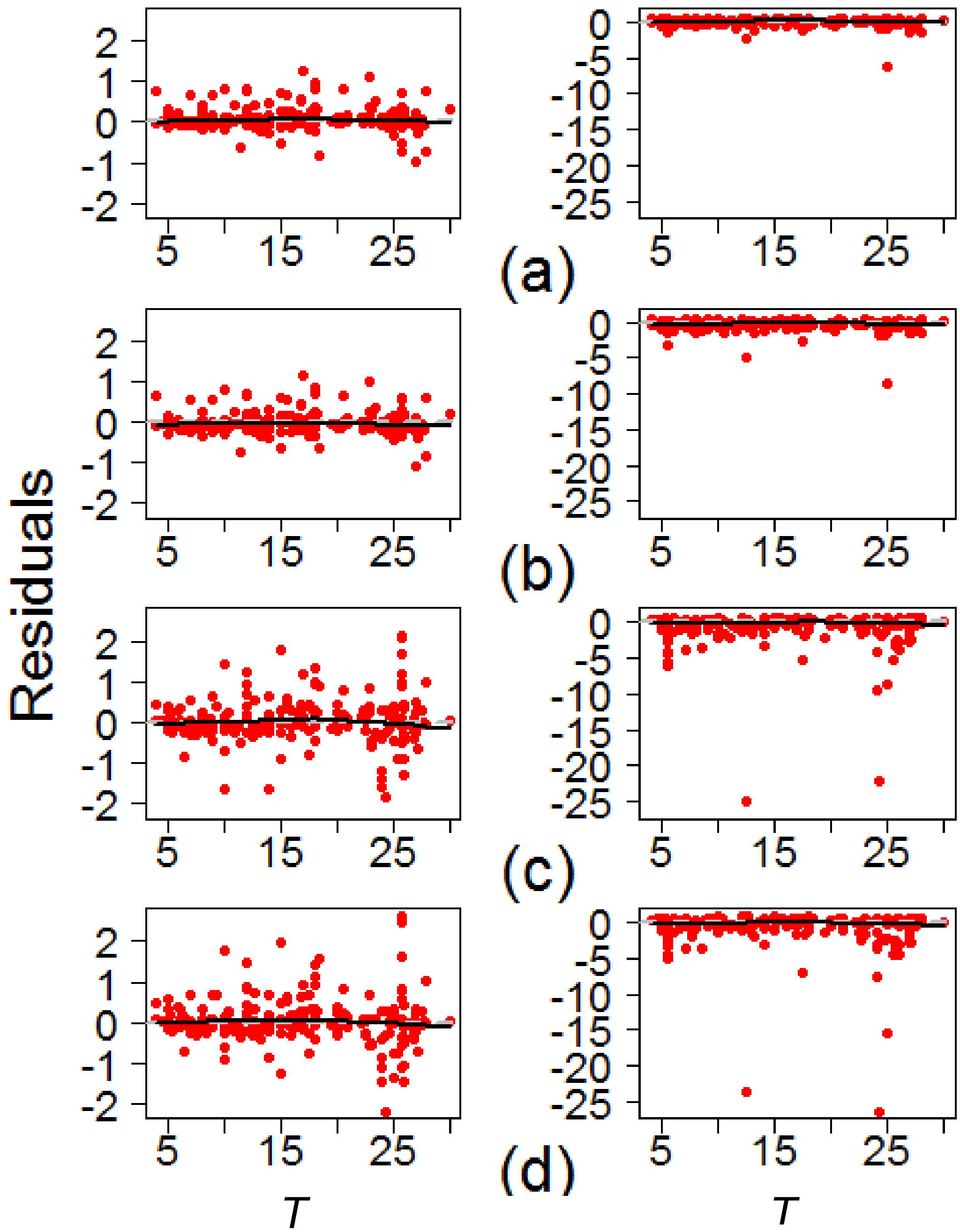

Figure 16. Residuals (left column) and residuals as fraction of the corresponding literature *M* estimates (right column) of updated empirical estimators as a function of mean water temperature (*T*). The estimators are (a) one-parameter t_{max}, (b) Hoenig$_{nls}$, (c) Pauly$_{nls\text{-}T}$ and (d) one-parameter *K*. Estimators were updated based on the common dataset (n = 215).

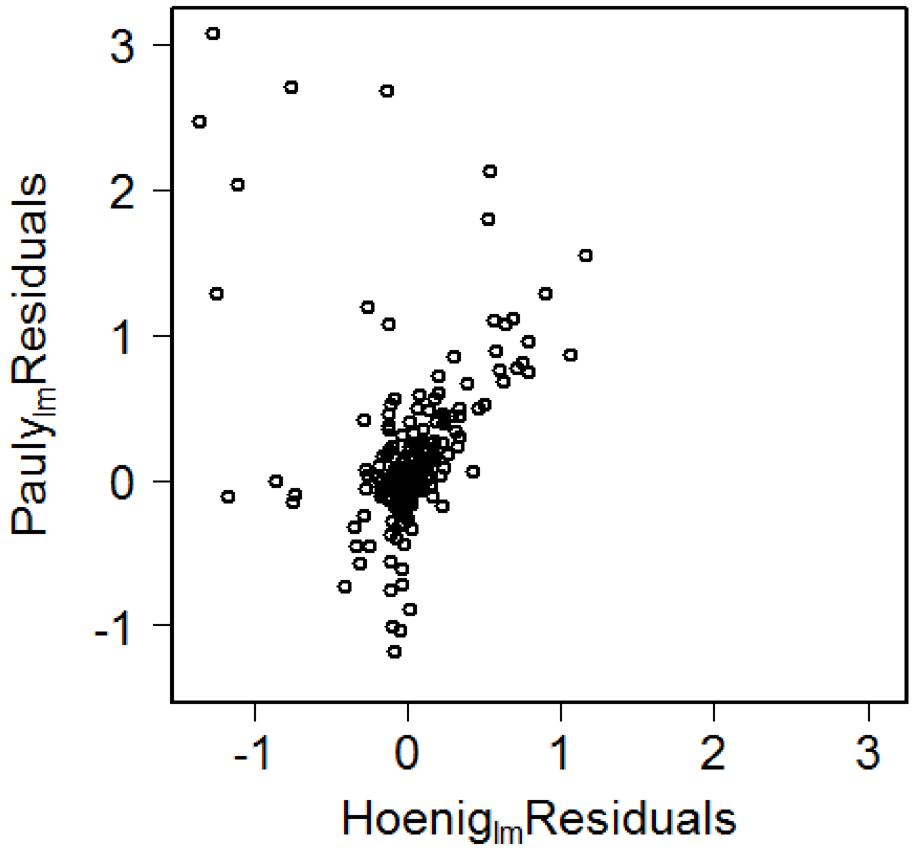

Figure 17. Biplot of the residuals of the updated $Hoenig_{lm}$ and $Pauly_{lm}$ models (n = 215). The coefficient of determination between both model residuals is $r^2 = 0.0028$.