


Use and misuse of a common growth metric: guidance for appropriately calculating and reporting specific growth rate

Derek P. Crane¹ , Derek H. Ogle² and Daniel E. Shoup³

1 Department of Biology, Coastal Carolina University, Conway, SC, USA

2 Departments of Mathematical Sciences and Natural Resources, Northland College, Ashland, WI, USA

3 Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK, USA

Correspondence

Derek P. Crane, Department of Biology,
Coastal Carolina University, 107 Chanticleer
Drive East, Conway, SC 29526, USA.
Email: dcrane@coastal.edu

Received 21 June 2019; accepted 17 October
2019.

Abstract

Growth is an important metric in fisheries and aquaculture. Growth of small fish over relatively short periods of time is commonly modelled with an exponential function using instantaneous growth rate (g). Instantaneous growth rates are logarithmic and inherently difficult to interpret, but specific growth rates (SGR) express growth as the intuitively understandable per cent change in size per unit of time. A simple metric of SGR (G) is easily computed by exponentiating g , subtracting 1 and multiplying by 100. However, several prominent fisheries publications suggest that SGR should be calculated by simply multiplying g by 100 (we call this G^*). A search of the fisheries literature found that the number of papers that used SGR for fish increased significantly from 1830 papers in 2009 to 3170 papers in 2018. An extensive review of 300 papers from this search found that 92.6% were related to aquaculture and only 3.3% of all papers correctly used G to calculate SGR. We algebraically show that G^* is fundamentally different than G and cannot be interpreted as a per cent change in weight per unit of time. Furthermore we demonstrate, with three examples from the literature, that using G^* as if it were the same as G leads to biologically meaningful underestimates of true growth rates and estimated weights. Given these results and the simplicity with which G can be computed from g , we recommend that fisheries scientists abandon the pervasive practice of incorrectly measuring SGR as 100 times the instantaneous growth rate.

Key words: aquaculture, fisheries sciences, specific growth rate.

Introduction

Individual growth is one of the most commonly calculated vital rates in aquaculture and fisheries management (Quist & Isermann 2017) and is often related to the other vital rates, including survival (Post & Evans 1989; Olson 1996; Garvey *et al.* 1998) and fecundity (Danylchuk & Fox 1994; Michaletz 1998). Fish growth is of great interest for production aquaculture and commercial fisheries management because of its importance to yield (Ricker 1975) and to sport fish management because of its effect on population size structure. Growth is the net result of energy intake and expenditure and, as such, is usually influenced by environmental conditions such as prey availability (Hoxmeier *et al.* 2006; Michaletz 2014; Crane & Einhouse 2016), predation risk (Shoup *et al.* 2003; Westerberg *et al.* 2004), turbidity (Tomcko & Pierce 2001; Shoup & Lane 2015), temperature (Michaletz 2014; Weber *et al.* 2015) and water chemistry (Tomcko & Pierce

2001; Shoup *et al.* 2007). Growth can be expressed in many ways (e.g. relative growth, instantaneous growth, size-specific growth), but all growth metrics require knowledge of the size of fish at two or more points in time, either from direct or indirect measurements (Shoup & Michaletz 2017). The time interval between size measurements can range from days to decades depending on the species and question of interest.

It is often assumed that weight of fish, especially small fish, increases exponentially over short periods of time (e.g. hours, days, weeks or a few years). With this assumption, an exponential function can be used to model weight (w_2) at some future time (t_2) from weight (w_1) at time t_1 with:

$$w_2 = w_1 e^{g\Delta t}, \quad (1)$$

where g is the instantaneous growth rate and $\Delta t = t_2 - t_1$ is the elapsed time between t_1 and t_2 . Algebraic rearrangement of Equation 1 shows that g may be computed from:

$$g = \frac{\log_e(w_2) - \log_e(w_1)}{\Delta t}, \quad (2)$$

which is a well-known equation in the fisheries literature (Ricker 1975; Shoup & Michaletz 2017). Instantaneous growth rates are difficult to interpret because g represents the additive change in *log weight* per unit time (Elliott & Hurley 1995) and not a change in *weight* per unit time. A more interpretable metric of growth can be obtained by algebraically rearranging Equation 1 to:

$$\left(\frac{w_2}{w_1}\right)^{\frac{1}{\Delta t}} = e^g. \quad (3)$$

Thus, e^g is the multiplicative change in weight per unit time. Usually $w_2 > w_1$ such that $e^g > 1$ and $e^g - 1$ will give the proportional increase in weight per unit time. Multiplying this value by 100 gives:

$$G = 100(e^g - 1), \quad (4)$$

which is the per cent increase in weight per unit time, has units of per cent change (of weight) per unit time and has been called the specific growth rate (SGR; Houde & Schekter 1981). This concept of the SGR has become confused in the fisheries literature because several widely used publications (Busacker *et al.* 1990; Wootton 1990; Hopkins 1992; Cook *et al.* 2000; Westers 2001; Moyle & Cech 2004; Lugert *et al.* 2016; Shoup & Michaletz 2017) calculated SGR with:

$$G^* = 100g, \quad (5)$$

However, G^* does not have the same meaning as G . Multiplying g , an additive change in log weight, as noted above, by 100 does not make it a per cent change in weight. Furthermore, the equation for g (Eqn 2) can be algebraically rearranged to:

$$g = \frac{\log_e\left(\frac{w_2}{w_1}\right)}{\Delta t}, \quad (6)$$

which illustrates that multiplying by 100 does not coerce g into a per cent change in weight because g is on the log scale and the numerator in the log function is w_2 and not a change in weight (i.e. $w_2 - w_1$).

Most critiques of SGR have focused on whether the exponential model is appropriate to describe fish growth (Dumas *et al.* 2010; Lugert *et al.* 2016), which we do not address here. Our objectives here are to (i) demonstrate that G^* is commonly used and G is rarely used for estimating SGR in the fisheries literature and (ii) illustrate how using G^* instead of G can lead to errors in interpretation.

Literature review

Paper selection and data extraction

We reviewed the fisheries literature to determine the extent to which SGR is used, the rate at which G and G^* are used to calculate SGR, and other characteristics related to the use of SGR (described below). To estimate the overall use of SGR, we recorded the number of results returned by Google Scholar™ (hereafter, GS) using the search criteria ‘specific growth rate’ AND ‘fish’ for each year from 2009 through 2018. We then used PublishOrPerish™ (Harzing 2007) to efficiently obtain the specific citation information for a sample of about 1000 results each year from the GS search. To reduce possible ranking bias related to the GS search algorithm, we randomized the results from each year and then examined as many results as needed to obtain a sample of 30 results per year that met the following criteria: a result must be a journal article (i.e. a ‘paper’), be electronically accessible to us via the Internet or our library subscriptions, be written in English, be peer-reviewed, not be a synthetic review, specifically mention ‘specific growth rate’ or ‘SGR’ and have SGR be a substantive portion of the paper (i.e. SGR was calculated and reported as a result), be about fish (shellfish were excluded), provide the specific SGR equation and not use the mass-specific SGR (Ostrovsky 1995; Sigourney *et al.* 2008). We recorded the reasons why a paper was not included in our sample and the number of papers that we examined each year to reach 30 included papers. For papers included in our sample, we recorded whether G , G^* or some other equation was used to calculate SGR; the reference (if any) provided for the SGR equation; whether lengths or weights were used in the SGR equation; units reported for SGR; and whether SGR was used primarily in the context of an aquaculture or ecological study. For papers where either G or G^* was not used, we recorded whether it appeared that the authors attempted to use G^* but presented it with typographical errors (e.g. missing or mismatched parentheses), did not multiply by 100 (i.e. used g), did not use logarithms or used some other equation that was not at all similar to G^* .

Statistical analyses

We estimated the proportion of papers per year that did not meet our inclusion criterion with $p_i = \frac{n_i - 30}{n_i}$, where n_i is the total number of papers we examined in year i . We then estimated the total number of papers returned by GS that would have met our inclusion criterion (if we would have completed a full census of papers returned by GS each year) with $N_i^* = N_i p_i$, where N_i is the total number of results returned by GS. We used simple linear regression to examine linear trends in N_i and N_i^* from 2009 through 2018.

Ninety-five per cent confidence intervals (CI) for percentages computed from binomial results (e.g. whether the paper had an aquaculture or ecological context) were computed with the method of Wilson (1927) as suggested by Agresti and Coull (1998), whereas those computed from multinomial results (e.g. type of equation used) used the method of May and Johnson (2000). All statistical analyses were conducted in the R environment (R Core Team, 2019) using `binom.wilson()` of the `epitools` package (Aragon 2017) and `multinomialCI()` from the `multinomialCI` package (Villacorta 2012). Results were deemed statistically significant when $P < 0.05$.

Rate of SGR usage in fisheries literature

The total number of articles returned by GS that met our search criteria increased significantly ($P = 0.0002$) from 1830 articles in 2009 to 3170 articles in 2018, an average increase of 142 (CI: 92–193) articles per year (Fig. 1). Between 38.8% (in 2016) and 68.1% (in 2009) of GS results per year did not meet our inclusion criterion. The primary reason for not being included was because the article was not about fish (54.8% of excluded articles) or not about SGR (8.8%). An additional 12.0% were excluded because the article did not present the SGR equation. The total number of articles that would have met our inclusion criteria increased significantly ($P = 0.0002$) from 584 in 2009 to 1865 in 2018, an average increase of 132 (CI: 84–181) articles per year (Fig. 1).

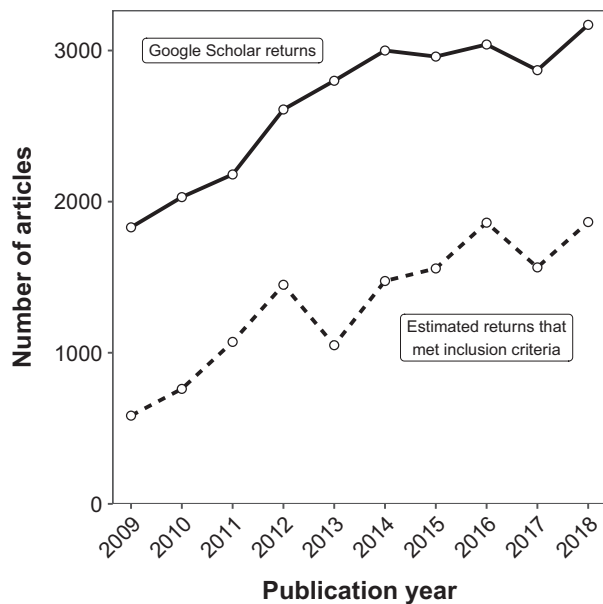


Figure 1 Number of articles returned from a Google Scholar search using 'specific growth rate' AND 'fish' and the estimated number of articles that met our inclusion criteria by year from 2009 to 2018.

Characteristics of SGR usage

The vast majority of papers that used SGR were related to aquaculture (92.6%; CI: 89.1–95.1%) and used weight (96.0%; CI: 93.1–97.7%) rather than length as the measure of size. Thirty-eight papers (12.7%; CI: 9.4–16.9%) provided a citation for use of SGR, with Ricker (1975; five citations), Houde and Schekter (1981; six citations) and Hopkins (1992; five citations) the most commonly cited sources. Interestingly, none of these cited papers suggested using G^* to calculate SGR; Ricker (1975) never mentions multiplying g (what he called G) by 100 and provides the equation $e^g - 1$ to describe proportional increases in weight, Houde and Schekter (1981) used G to calculate SGR, and although Hopkins (1992) provided the equation for G^* , he explicitly stated that it was incorrect and advised aquaculturists to report g (what he called G). Despite the most commonly cited sources for use of SGR either not providing the equation for G^* or advising against the use of G^* , only 10 of the 300 papers (3.3%; CI: 1.8–6.0%) we examined from 2009 to 2018 correctly used G to calculate SGR, all of which used the correct units of % per day. Six of the 10 papers that used G provided a reference for the equation, with five citing Houde and Schekter (1981) and one citing Ricker (1975). The SGR was incorrectly calculated using G^* in 85.7% (CI: 81.2–89.2%) of papers. Additional papers appeared to attempt to use G^* , but 4.7% (CI: 2.8–7.7%) presented the equation with a likely typographical error, 2.3% (CI: 1.1–4.7%) did not multiply by 100, and 1.7% (CI: 0.7–3.8%) did not use logarithms. Of the 290 papers that did not use G , 19.7% (CI: 15.5–24.6%) either did not present units for SGR or different units appeared throughout the paper. Of the 233 papers that did not use G and provided consistent units for SGR, 71.7% (CI: 65.6–77.1%) used % per day and 17.2% (CI: 12.9–22.5%) used %, with the remaining 11.2% (CI: 7.7–15.8%) using a variety of incorrect units.

G and G^* in practice

We examined the growth of fish from three published studies to provide a comparison of G and G^* in practice across a range of growth rates and times (Fig. 2). Bell *et al.* (2010) examined growth of Atlantic salmon (*Salmo salar*) intensively reared under a variety of diets for a 385 day trial. We used their results for the Caledonian strain of Atlantic salmon fed a fish oil diet as an example of a slow growth rate ($g \approx -0.01$); mean initial weight was 52.8 g, and mean final weight after 385 days was 2750 g (Fig. 2). Oliveira *et al.* (2012) investigated the effects of stocking density on growth of pirarucu (*Arapima gigas*). We used their results as an example of a moderate growth rate ($g \approx -0.02$); mean initial weight was 113.5 g, and mean final weight after 140 days was 2630 g (Fig. 2). Finally, Azaza *et al.* (2009)

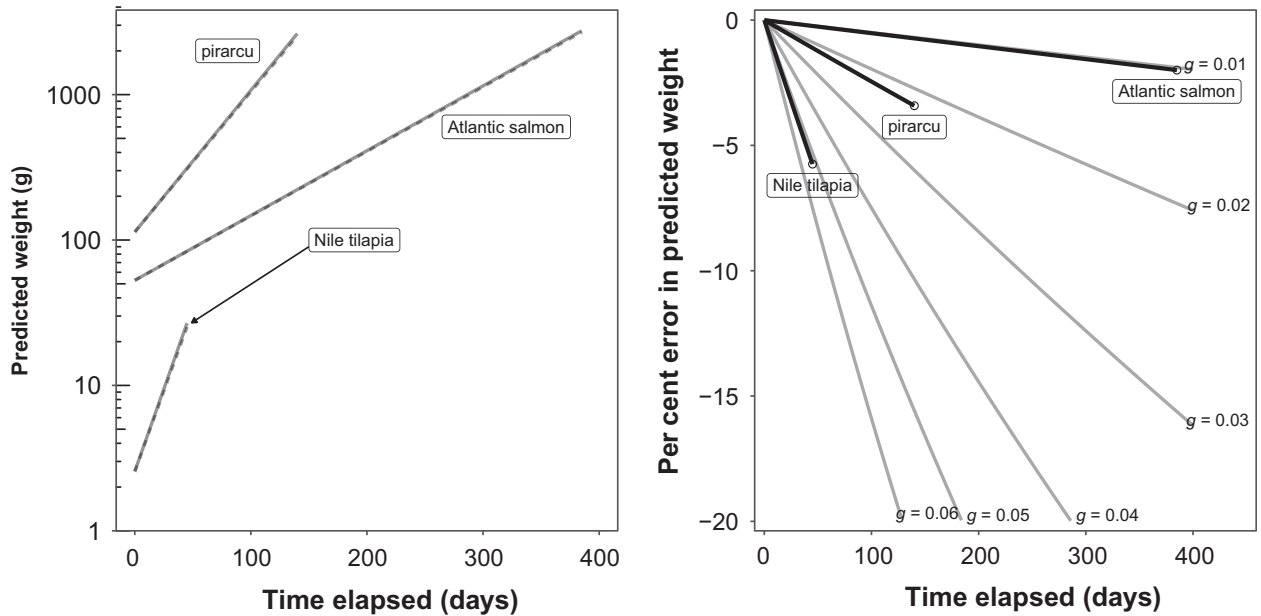


Figure 2 Predicted weight (Left) using G (solid line) and G^* (dashed line) and per cent error of calculated weight using G from calculated weight using G^* (Right) for the Atlantic salmon, pirarcu and Nile tilapia examples (black lines) and for six values of g for up to 400 days elapsed (grey lines). Note on the left plot that the y -axis is on a \log_{10} scale and that the solid and dashed lines are nearly coincident within species.

examined the effects of diet on growth of Nile tilapia (*Oreochromis niloticus*). We used their results for fish fed their control diet as an example of a fast growth rate ($g \sim 0.05$); mean initial weight was 2.56 g, and mean final weight after 45 days was 26.77 g.

The value of G^* will always be less than the value of G ; thus, the true growth rate (assuming exponential growth) will be underestimated when using G^* . If the unit of time used is small enough that only a small amount of growth occurs per unit time (i.e. G is near zero), then G^* will be only slightly less than G , for example $G = 1.032\%$ per day and $G^* = 1.027\%$ per day for the Atlantic salmon example, $G = 2.270\%$ per day and $G^* = 2.245\%$ per day for the pirarcu example and $G = 5.355\%$ per day and $G^* = 5.216\%$ per day for the Nile tilapia example. However, if the unit of time is such that more growth occurs during that time, then G^* will be substantially lower than G . For example, when SGR is computed per month (i.e. 30 days) instead of per day, then $G = 96.1\%$ per month and $G^* = 67.3\%$ per month for the pirarcu example. It is also evident from this example that the monthly G^* is simply 30 times the daily G^* , illustrating that daily growth did not compound over the entire month, as it should and as it does with G .

The discrepancies between G^* and G can be further illustrated by predicting final weights for the three examples

using G and G^* (but treated as a proportion rather than a percentage) in the familiar compound interest equation:

$$w_2 = w_1(1 + G[\text{or } G^*])^{\Delta t} \tag{7}$$

Predicted mean final weight was 2750 g using G but only 2695 g using G^* for Atlantic salmon after 385 days, was 2630 g using G and 2540 g using G^* for pirarcu after 140 days and was 26.77 g using G and 25.23 g using G^* for Nile tilapia after 45 days. These differences may not appear large and may not even be apparent when plotted (Fig. 2 Left). However, predicted weights using G matched the observed final mean weights, whereas using G^* resulted in predicted mean final weights that were 2.00% lower for Atlantic salmon, 3.42% lower for pirarcu and 5.75% lower for Nile Tilapia compared with measured weights at the end of their respective studies (Fig. 2 Right). The percentage error in predicted weights from using G^* rather than G is computed with

$$\left[\left(\frac{1+g}{e^g} \right)^{\Delta t} - 1 \right] \times 100. \tag{8}$$

which, along with the three examples (Fig. 2 Right), shows that the percentage error increases with g , Δt and the unit of time that per cent change in growth is measured over (e.g. % per day vs. % per month).

Conclusions and recommendations

Specific growth rate is a widely used growth metric that has primarily been calculated in the aquaculture and fisheries literature by multiplying the instantaneous growth rate by 100 (i.e. using G^*). Although G^* may appear to be a close approximation of G in many cases, it leads to biologically meaningful differences in estimated weights. Thus, we urge commercial aquaculturists and scientists to use G instead of G^* when measuring SGR because (i) the calculation of G is technically sound and consistent with convention for other exponential equations used in fisheries science, ecology and economics; (ii) the calculation of G is simple and thus not necessary to approximate using G^* ; and (iii) the units of G are meaningful as an actual per cent change in weight. As a large body of literature using G^* already exists, authors of future works may also report g , but labelled as an instantaneous rather than specific growth rate and not multiplied by 100 to eliminate confusion. With this, comparisons between g and already published values of G^* divided by 100 can still be made.

Acknowledgements

We thank Prashant Sansgiry, John Hutchens and Andrew Jensen for meaningful discussions about the use of specific growth rate and its mathematical formulation.

References

- Agresti A, Coull BA (1998) Approximate is better than “exact” for interval estimation of binomial proportions. *The American Statistician* **52**: 119–126.
- Aragon TJ (2017) Epitools: Epidemiology tools. R package v0.5-10.
- Azaza MS, Kammoun W, Abdelmouleh A, Kraiem MM (2009) Growth performance, feed utilization, and body composition of Nile tilapia (*Oreochromis niloticus* L.) fed with differently heated soybean-meal-based diets. *Aquaculture International* **17**: 507–521.
- Bell JG, Pratoomyot J, Strachan F, Henderson RJ, Fontanillas R, Hebard A *et al.* (2010) Growth, flesh adiposity and fatty acid composition of Atlantic salmon (*Salmo salar*) families with contrasting flesh adiposity: effects of replacement of dietary fish oil with vegetable oils. *Aquaculture* **306**: 225–232.
- Busacker GP, Adelman IR, Goolish EM (1990) Growth. In: Schreck CB, Moyle PB (eds) *Methods for Fish Biology*, pp. 363–387. American Fisheries Society, Bethesda, MD.
- Cook JT, McNiven MA, Richardson GF, Sutterlin AM (2000) Growth rate, body composition and feed digestibility/conversion of growth-enhanced transgenic Atlantic salmon (*Salmo salar*). *Aquaculture* **188**: 15–32.
- Crane DP, Einhouse DW (2016) Changes in growth and diet of smallmouth bass following invasion of Lake Erie by the round goby. *Journal of Great Lakes Research* **42**: 405–412.
- Danylchuk AJ, Fox MG (1994) Age and size-dependent variation in the seasonal timing and probability of reproduction among mature female pumpkinseed, *Lepomis gibbosus*. *Environmental Biology of Fishes* **39**: 119–127.
- Dumas A, France J, Bureau D (2010) Modelling growth and body composition in fish nutrition: where have we been and where are we going? *Aquaculture Research* **41**: 161–181.
- Elliott JM, Hurley MA (1995) The functional relationship between body size and growth rate in fish. *Functional Ecology* **9**: 625–627.
- Garvey JE, Wright RA, Stein RA (1998) Overwinter growth and survival of age-0 largemouth bass (*Micropterus salmoides*): revisiting the role of body size. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 2414–2424.
- Harzing AW (2007) Publish or Perish. [Cited 1 May 2019.] Available from URL: <https://harzing.com/resources/publish-or-perish>.
- Hopkins KD (1992) Reporting fish growth, a review of the basics. *Journal of World Aquaculture Society* **23**: 173–179.
- Houde ED, Schekter RC (1981) Growth rate, rations and cohort consumption of marine fish larvae in relation to prey concentration. *Rapports et procès-verbaux des réunions/Conseil permanent international pour l'exploration de la mer* **178**: 441–453.
- Hoxmeier RJH, Wahl DH, Brooks RC, Heidinger RC (2006) Growth and survival of age-0 walleye (*Sander vitreus*): Interactions among walleye size, prey availability, predation, and abiotic factors. *Canadian Journal of Fisheries and Aquatic Sciences* **63**: 2173–2182.
- Lugert V, Thaller G, Tetens J, Schulz C, Krieter J (2016) A review on fish growth calculation: multiple functions in fish production and their specific application. *Reviews in Aquaculture* **8**: 30–42.
- May WL, Johnson WD (2000) Constructing two-sided simultaneous confidence intervals for multinomial proportions for small counts in a large number of cells. *Journal of Statistical Software* **5**: 1–24.
- Michaletz PH (1998) Effect of body size on fecundity, the gonadosomatic index, egg size, and timing of spawning of gizzard shad. *Journal of Freshwater Ecology* **13**: 307–315.
- Michaletz PH (2014) Temperature, plankton and conspecific density influence dynamics of age-0 gizzard shad: Implications for a gape-limited piscivore. *Ecology of Freshwater Fish* **23**: 322–335.
- Moyle PB, Cech JJ Jr (2004) *Fishes: An Introduction to Ichthyology*, 5th edn. Prentice Hall, Upper Saddle River, NJ.
- Oliveira EG, Pinheiro AB, Oliveira VQ, Silva ARM, Moraes MG, Rocha IRCB *et al.* (2012) Effects of stocking density on the performance of juvenile pirarucu (*Arapaima gigas*) in cages. *Aquaculture* **370**: 96–101.
- Olson MH (1996) Predator-prey interactions in size-structured fish communities: implications of prey growth. *Oecologia* **108**: 757–763.
- Ostrovsky I (1995) The parabolic pattern of animal growth: determination of equation parameters and their temperature dependencies. *Freshwater Biology* **33**: 357–371.

- Post JR, Evans DO (1989) Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 1958–1968.
- Quist MC, Isermann DA (2017) *Age and Growth of Fishes: Principles and Techniques*. American Fisheries Society, Bethesda, MD.
- R Core Team (2019) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**: 1–382.
- Shoup DE, Lane WD (2015) Effects of turbidity on prey selection and foraging return of adult largemouth bass in reservoirs. *North American Journal of Fisheries Management* **35**: 913–924.
- Shoup DE, Michaletz PH (2017) Growth estimation: summarization. In: Quist MC, Isermann DA (eds) *Age and Growth of Fishes: Principles and Techniques*, pp. 233–264. American Fisheries Society, Bethesda, MD.
- Shoup DE, Carlson RE, Heath RT (2003) Effects of predation risk and foraging return on the diel use of vegetated habitat by two size-classes of bluegills. *Transactions of the American Fisheries Society* **132**: 590–597.
- Shoup DE, Callahan SP, Wahl DH, Pierce CL (2007) Size-specific growth of bluegill, largemouth bass and channel catfish in relation to prey availability and limnological variables. *Journal of Fish Biology* **70**: 21–34.
- Sigourney DB, Letcher BH, Obedzinski M, Cunjak RA (2008) Size-independent growth in fishes: patterns, models and metrics. *Journal of Fish Biology* **72**: 2435–2455.
- Tomcko CM, Pierce RB (2001) The relationship of bluegill growth, lake morphometry, and water quality in Minnesota. *Transactions of the American Fisheries Society* **130**: 317–321.
- Villacorta PJ (2012) MultinomialCI: Simultaneous confidence intervals for multinomial proportions according to the method by Sison and Glaz. R package v1.0.
- Weber MJ, Brown ML, Wahl DH, Shoup DE (2015) Metabolic theory explains latitudinal variation in common carp populations and predicts responses to climate change. *Ecosphere* **6**: 1–16.
- Westerberg M, Staffan F, Magnhagen C (2004) Influence of predation risk on individual competitive ability and growth in Eurasian perch, *Perca fluviatilis*. *Animal Behaviour* **67**: 273–279.
- Westers H (2001) Production. In: Wedemeyer GA (ed) *Fish Hatchery Management*, 2nd edn, pp. 31–90. American Fisheries Society, Bethesda, MD.
- Wilson EB (1927) Probable inference, the law of succession, and statistical inference. *Journal of the American Statistical Association* **22**: 209–212.
- Wootton RJ (1990) *Ecology of Teleost Fishes, Fish and Fisheries Series 1*. Chapman & Hall, London.