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ARTICLE

Combining Samples from Multiple Gears Helps to Avoid Fishy Growth Curves

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Abstract

Size-at-age information is critical in estimating growth parameters (e.g., the von Bertalanffy growth function [VBGF]) that are used to assess fish populations. Due to gear selectivity, single sampling methods rarely sample all ages or all sizes equally well. Most growth estimates rely on samples from a single gear or a haphazard combination of gears, potentially leading to biased and imprecise growth parameter estimates. We evaluated the efficacy of combining samples from two gears with different size selectivity to estimate VBGF parameters; we then applied that approach to a case study on the Lochloosa Lake (Florida) population of Black Crappies *Pomoxis nigromaculatus*. Simulated age- and size-structured populations were randomly sampled with two gears characterized by different size-selectivity curves (one gear was selective for smaller fish; the other was selective for larger fish). Maximum likelihood VBGF estimates obtained for each gear separately were compared with estimates from a combined VBGF fitted to data from both gears. In every simulated scenario, a combined-gear approach reduced bias and increased precision for estimating the VBGF, but the gear-specific proportions that improved VBGF estimates depended on size selectivity. The VBGF estimates for the Black Crappie population showed that the combined-gear method yielded intermediate parameter values relative to single-gear approaches based on (1) trawl sampling (fishery-independent survey) and (2) angler harvest (as determined from carcass collections; fishery-dependent data). Furthermore, the combined-gear approach had greater precision in individual parameter estimates and much less variance than single-gear approaches when estimating the VBGF. Combining data from two gears can increase sample representativeness, leading to improvements in VBGF estimation. Such approaches can reduce uncertainty in VBGF estimation and can provide insight into key demographic processes occurring in fish populations for which ontogeny and gear selectivity lead to imperfect sampling.

An understanding of growth is fundamental in ecological studies and for managing exploited populations (Lorenzen and Enberg 2002; Paine et al. 2012). Changes in growth rates are one of the key compensatory responses to exploitation and

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influence sustainable harvest (Nicieza and Metcalfe 1997; Post et al. 1999; Lorenzen and Enberg 2002; Ali et al. 2003). Furthermore, growth parameter estimations are often very sensitive to variation in size at age, which is typically overlooked both in model fitting and in assessing growth trajectories (Sinclair et al. 2002). Estimated growth parameters are subsequently used to estimate natural mortality (e.g., Pauly 1980; Gislason et al. 2010), size-based survival (e.g., Lorenzen 2000), and expected abundances (e.g., Andersen and Beyer 2006). The development of size-based management regulations depends upon accurate growth estimates, which aid in establishing length limits, slot windows, and sustainable levels of harvest (Radomski et al. 2001; Walters and Martell 2004). Hence, accurate and precise estimates of growth are critical components for managing populations, as any sources of uncertainty or bias can scale disproportionately upward by affecting subsequent evaluations of survival, biomass, and optimal regulations (Walters and Martell 2004; Pardo et al. 2013).

Biologists sample composition information to obtain basic life history parameters, including growth parameters (Krebs 2001). Size-at-age samples that are used to estimate growth should be representative of the true extent of the age structure and the true variability in length at each age (Ricker 1975: 205; Walters and Martell 2004: 117). Unfortunately, the assumption of representativeness is often violated in fisheries assessments due to various forms of sampling selectivity (Myers and Hoenig 1997; Walters and Martell 2004) and problems with sampling designs (Peterman 1990; Legg and Nagy 2006), which can result in biased and incorrect statistical outcomes. Differential selectivity emerges for a number of reasons, including spatial variability in habitat selection; gear restrictions (Matthias et al. 2014); size selectivity (Myers and Hoenig 1997; Gwinn et al. 2010); and behavioral selectivity (Bryan and Larkin 1972; Nuhfer and Alexander 1994; Cooke et al. 2007; Philipp et al. 2009). Selectivity of the gear often causes small or large fish to be underrepresented in samples, thereby leading to bias in growth parameter estimation since only the fastest growing young individuals or the slowest growing old individuals will be sampled by a particular gear (Taylor et al. 2005). Growth parameters that are estimated from samples lacking representative observations of old or young fish will be biased (Gwinn et al. 2010).

Growth analysis should be made using data that cover as much of the age structure and size structure as possible (Lucena and O'Brien 2001). To circumvent the aforementioned problems, some fisheries assessments have combined size-at-age information from multiple gears that vary in selectivity (e.g., Murphy and Taylor 1994). This approach is based on the assumption that combining samples from multiple gears will improve model fit (Kritzer et al. 2001); however, the approach is not widely used and has been implemented haphazardly (Murphy and Taylor 1994; Begg and Sellin 1998; Potts et al. 1998), probably because formal guidance on when

and how to combine growth data from multiple gears is lacking. For example, Begg and Sellin (1998) pooled commercial and recreational catch data for Queensland Mackerel *Scomberomorus queenslandicus* and Australian Spotted Mackerel *S. munroi* to increase the overall sample size and the number of size-classes and age-classes used to model growth. However, Potts et al. (1998) combined samples of Vermilion Snapper *Rhomboplites aurorubens* captured in traps and trawls with samples from recreational and commercial hook-and-line fishing to compensate for the lack of individuals smaller than 250 mm TL in the hook-and-line catches, which was attributable to the minimum size limit of those fisheries. Given the increasing extent of combining fish samples from different gears, there is a need for rigorous guidance in evaluating which gears' selectivity to combine, how many samples are to be contributed by each gear, and the effects of combining gears on parameter estimation.

We provide a general framework and statistical guidance for combining size-at-age samples from multiple gears to predict growth by using the von Bertalanffy growth function (VBGF). The VBGF is a flexible, nonlinear growth model that is fitted with size-at-age data and is commonly used to describe growth in fishes (Chen et al. 1992; Essington et al. 2001; Siegfried and Sansó 2006). Our objectives were to (1) use a mechanistic simulation model to assess the bias and precision of VBGF estimation based on both single-gear and combined-gear approaches for size-at-age samples; and (2) apply the single-gear and combined-gear approaches to a data set for Black Crappies *Pomoxis nigromaculatus* and evaluate the approaches' performance.

METHODS

Simulation model and population sampling.—A size- and age-structured population model was created in R software (version 3.1.3; R Development Core Team 2013) to simulate the sampling of a fish population for purposes of VBGF estimation (Table 1; see Supplementary Table S.1 [available in the online version of this article] for R code). The model allowed size to vary among ages, and the population was sampled with two gears to estimate the VBGF parameters. Model values for life history characteristics and sampling vulnerability were chosen to represent a fast-growing fish species, with application to fisheries.

The simulated population of 100,000 individuals with size and age information was sampled by two size-selective gears (one gear was selective for smaller, younger individuals; the other gear was selective for larger, older individuals) that had varying levels of overlap in size selectivity. The population was assumed to be at equilibrium and was not subject to harvest. Four vulnerability schedules were simulated to examine the influence of gear overlap on VBGF parameter estimation using combined gears: no overlap (scenario a); overlap occurring at ages 1 and 2 (scenario b); overlap at ages 2–4 (scenario c); and overlap at age 3 and older (scenario d; Table 2;

TABLE 1. Model characteristics, model structure, and parameter values used in the simulation to estimate the von Bertalanffy growth function by combining fish samples from multiple size-selective gears (κ = Brody growth coefficient; L_∞ = average asymptotic length; t_0 = theoretical age at a length of zero; M = natural mortality rate; a_{max} = maximum observed age; CV_{L_a} = coefficient of variation for length at age; cdf = normal cumulative density function; $MaxL_i$ = maximum capture length for gear i ; $MinL_i$ = minimum capture length for gear i).

Characteristic	Equation	Parameter
Length at age (L_a)	$L_a = L_\infty \{1 - e^{[-\kappa(\text{age}-t_0)]}\}$	$\kappa = 0.32$; $L_\infty = 800$ mm; $t_0 = -0.2$
Survival at age (S_a)	$S_a = \frac{1}{[1 + \frac{L_\infty}{L_a}(e^\kappa - 1)]^{-M/\kappa}}$	$M = 0.5$
Survivorship at age (l_a)	$l_a = l_{a-1} \cdot S_{a-1}$; $l_1 = 1$	
Proportion at age (P_a)	$P_a = \frac{l_a}{\sum_a^{a_{max}} l_a}$	$a_{max} = 10$ years
Vulnerability to capture (V_a) by gear i	$V_{a,i} = [\text{cdf}(\text{Max}L_i, L_a, L_a \cdot L_{cv}) - \text{cdf}(\text{Min}L_i, L_a, L_a \cdot L_{cv})]$	$CV_{L_a} = 0.15$
Capture probability (C_a) for gear i	$C_{a,i} = \frac{P_a V_{a,i}}{\sum_a^{a_{max}} (P_a V_{a,i})}$	

Figure 1). The four vulnerability schedules were further subdivided into scenarios in which the proportion of samples contributed by the large-size-selective gear varied from 0.00 to 1.00 in increments of 0.10. This allowed us to evaluate how the relative sample size for each gear influenced the parameter estimates.

Age-specific vectors for individual fish TL at age (L_a), survival at age (S_a), population proportion at age (P_a), and vulnerability at age (V_a) were created by using the equations presented in Table 1. Average L_a was simulated via the VBGF. We modeled S_a by using size-based survival from Lorenzen (2000). Values of P_a were calculated as survivorship at age (l_a) over the sum of survivorship-at-age vectors. Gear selectivity was calculated as the difference between two normal cumulative density functions incorporating the expected L_a , the growth variance, and the minimum and maximum capture sizes per gear type, showing that selectiveness was both age dependent and length dependent (see Table 1 for details and equations; see Table 2 and Figure 1 for selectivity curves).

A multinomial probability function was used to randomly generate the number sampled ($n_{a,i}$) in age-class a for gear i .

The probability of sampling a given age with a given gear was based on P_a and V_a (Table 1; Figure 1). Length-at-age samples were generated by randomly selecting $n_{a,i}$ individuals from the simulated population of 100,000 individuals that were vulnerable to capture. Variation in length across ages in the population was generated from a normal distribution with a mean of L_a and an SD equal to $L_a \times CV_{L_a}$ (where CV_{L_a} = coefficient of variation for L_a). In each scenario, 350 individuals were randomly sampled from the population of 100,000, but the proportion of samples contributed by each gear type varied. The total sample size of 350 was selected to be sufficient for VBGF estimation while maintaining the feasibility of capture and age estimation in terms of managers' time and budget.

Parameter estimation.—The VBGF parameters (κ = Brody growth coefficient, a parameter with physiological interpretations; L_∞ = average asymptotic length; t_0 = theoretical age at a length of zero; and CV_{L_a}) were estimated by using age-length samples. For each scenario, parameters were estimated by minimizing the deviations of the collected age-length samples from the expected VBGF using the optim function in R software (R Development Core Team 2013).

TABLE 2. Scenarios simulated to combine fish samples from two different sampling gears with different capture probabilities and with varying contributions (0–100%) to the pooled sample ($n_{total} = 350$ fish).

Vulnerability scenario	Small-size-selective gear		Large-size-selective gear	
	Minimum TL (mm)	Maximum TL (mm)	Minimum TL (mm)	Maximum TL (mm)
a. No overlap occurs	40	225	400	1,200
b. Overlap occurs at ages 1–2	40	225	300	1,200
c. Overlap occurs at ages 2–4	40	575	475	1,200
d. Overlap occurs at age 3 and older	325	700	475	1,200

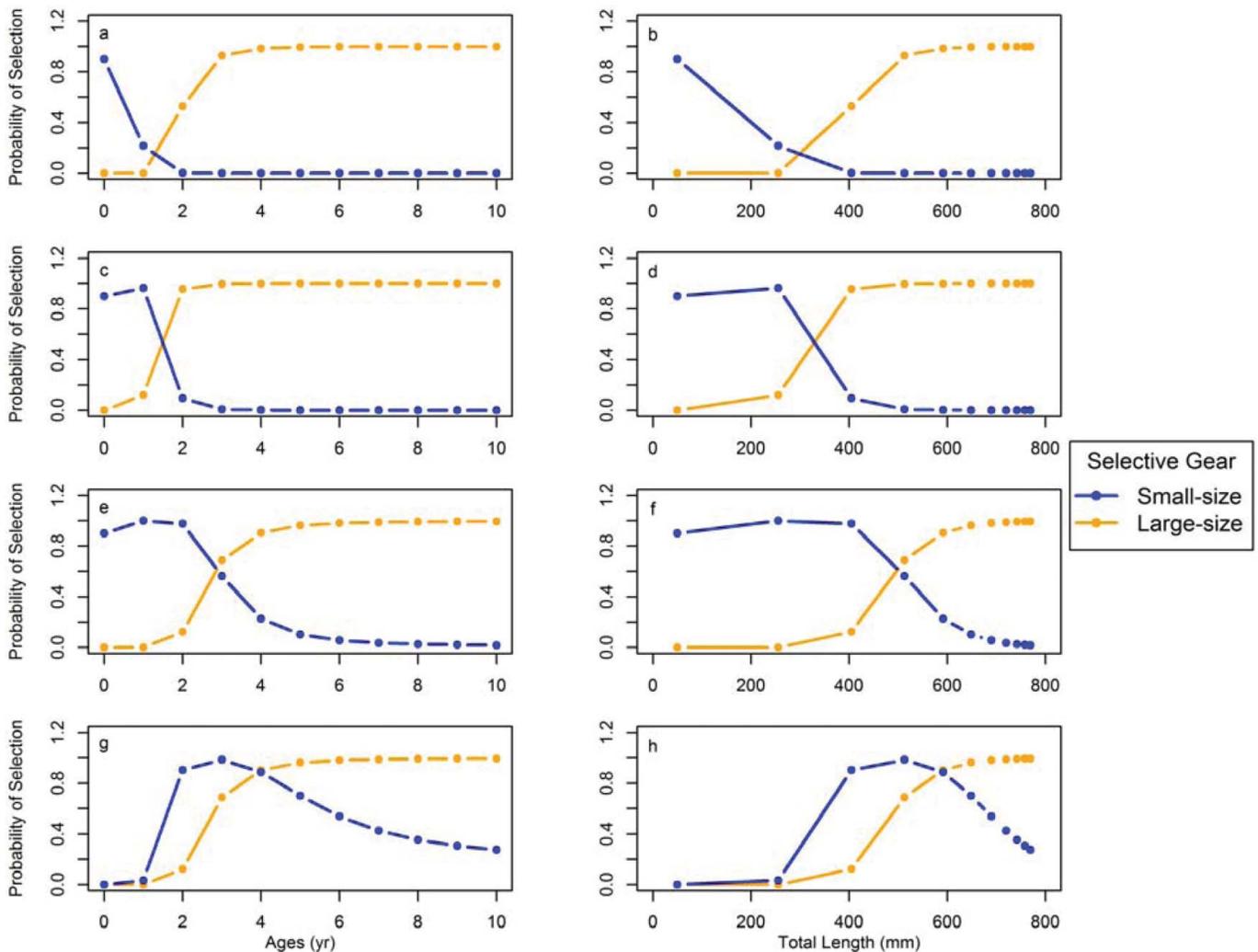


FIGURE 1. Vulnerability schedules used for simulations in which size-at-age samples from two gears (one gear was selective for smaller, younger fish; the other gear was selective for larger, older fish) were combined to estimate individual growth: (a), (b) age and size selectivity in the scenario of no overlap (see Table 2 for definitions of all scenarios); (c), (d) age and size selectivity in the scenario of overlap at ages 1–2; (e), (f) age and size selectivity in the scenario of overlap at ages 3–4; and (g), (h) age and size selectivity in the scenario of overlap at age 3 and older (i.e., smaller fish not sampled).

The percent relative bias (deviation of the estimated parameter value from the true value) was calculated as

$$\text{Relative bias} = 100 \times [(\hat{x}_i - x_i)x_i^{-1}], \quad (1)$$

where x_i is the true parameter for gear i ; and \hat{x}_i is the estimated parameter for gear i . Each simulation scenario was repeated 1,000 times to compare precision and bias from each gear.

Lochloosa Lake Black Crappie population.—The combined-gear approach from the simulation was applied to estimate the VBGF for the Black Crappie population in Lochloosa Lake, Florida. We included Black Crappie data that were collected during 2006–2012 via two sampling methods:

(1) trawling (selective for smaller sizes); and (2) angler harvest (selective for larger sizes) as indicated by carcass collections. Fishery-independent sampling of the Black Crappie population was conducted via annual trawling by the Florida Fish and Wildlife Conservation Commission; this method captured the majority of available sizes but primarily selected for young fish (Bonvechio et al. 2008; Binion et al. 2009). Fishery-dependent catch data were obtained by asking anglers to place the carcasses of filleted Black Crappies into collection bins, which were positioned at fish camps and boat launches around the lake. Carcasses were collected from the bins several times per week from January to March; the carcasses were measured for TL, and sagittal otoliths were removed for age estimation (Campana 2001). The Black Crappie fishery on Lochloosa

Lake does not have a minimum length limit, and anglers are free to harvest individuals of any size (up to 25 individuals·angler⁻¹·d⁻¹). However, anglers typically keep adult Black Crappies larger than 200 mm TL. Although Miranda and Door (2000) found that anglers expressed intermediate size selectivity among all harvested Black Crappies, the majority of harvested Black Crappies were greater than 270 mm TL for a species that commonly has an asymptotic size of 280–350 mm (Jackson and Hurley 2005). As such, angler harvest can be considered selective for larger fish relative to the overall size structure, as evident for Lochloosa Lake Black Crappies. For this study, the trawl represented a small-size-selective gear from fishery-independent surveying, and angler harvest (as indicated by carcass collections) was a large-size-selective gear from fishery-dependent surveying. Therefore, the Black Crappie population in Lochloosa Lake served as an ideal case study for combining samples from multiple gears to estimate the VBGF.

Black Crappie size-at-age data were used to estimate κ , L_∞ , t_0 , and CV_{La} from the 2006–2012 data set by using (1) trawl samples only, (2) angler harvest (carcass samples) only, and (3) the combination of both gear types based on simulation results (see R code in Table S.2). To avoid subjectively following one of the four simulation scenarios, we compared VBGF parameter estimates from the trawl-only approach, the angler harvest-only approach, and the combined-gear approach by using 1,000 random samples for each single-gear approach and 500 samples/gear for the combined-gear approach. The use of equal sample sizes when comparing the single-gear approaches to the combined-gear approach allowed us to (1) directly test how combining samples from the two gears influences sample representativeness in growth estimation and (2) analyze this influence independently from the potential effect of different gear-specific sample sizes on the accuracy and precision of parameter estimates. Using maximum likelihood estimation, the VBGF parameters were fitted to size-at-age samples from all seven sampling years, and 95% confidence intervals were generated by bootstrapping the size-at-age samples and VBGF estimates from each approach 10,000 times (Table S.2).

RESULTS

Simulation Model

Compared with most single-gear approaches, combining samples from two gears improved VBGF parameter estimation for the simulated age- and size-structured populations. When the two gears had little to no overlap and when one gear sampled smaller individuals particularly well in vulnerability scenarios a–c, estimating the VBGF via the combined-gear approach increased precision and reduced relative bias in comparison with estimates from the single-gear approaches (Figure 2). Use of only samples from the large-size-selective gear

tended to result in overestimation of L_∞ and underestimation of κ , t_0 , and CV_{La} (Figure 2). Estimation of the VBGF by using only the small-size-selective gear led to highly biased and imprecise estimates of L_∞ and κ (Figure 2). The CV_{La} parameter was generally not estimated without bias, but this is expected when using a maximum likelihood approach. Any gear combination in which the large-size-selective gear contributed 0.10 to 0.90 of the samples tended to improve VBGF parameter estimation. Specifically, the combination in which sample proportions were 0.90 for the small-size-selective gear and 0.10 for the large-size-selective gear consistently performed the best in reducing bias and improving precision of the VBGF parameters, except for CV_{La} in scenarios a–c (Figure 2). This result suggests that when information on small individuals is available, the proportion of older, larger fish that must be sampled to achieve an accurate growth curve is relatively small.

When neither gear sampled smaller, younger individuals (e.g., scenario d), growth estimation was marginally improved by combining samples (Figure 2d). For example, any proportional combination of the two gears led to reduced bias in estimates of L_∞ . The parameter κ was estimated equally well by (1) the single-gear approach using the small-size-selective gear and (2) the combined approach with proportions of 0.60–0.80 for the large-size-selective gear. Severe negative bias (ranging from –1,400% to –320%) in t_0 estimates was observed for all approaches, but the use of combined gears produced the lowest amount of bias. Compared with single-gear approaches, estimates of CV_{La} (i.e., growth variation) were improved by the combined approach in which the sample proportion from the small-size-selective gear was 0.10–0.70. Unlike scenarios a–c, for which a combined approach with sample proportions of 0.90 (small-size-selective gear) and 0.10 (large-size-selective gear) was generally the best for VBGF estimation, no single combination of proportions generally worked best to reduce bias and improve precision under scenario d (Figure 2). However, the combined-gear approach with any combination of proportions was the least biased overall.

Black Crappie Case Study

Gear selectiveness was evident for the Black Crappie population in Lochloosa Lake from 2006 to 2012. Trawling sampled a high proportion of small, young fish; 83% of the 2,348 individuals sampled were less than 200 mm TL, with ages ranging from 0 to 3 years (Figure 3a, c). Conversely, anglers mainly harvested larger, older fish; 96% of the 2,039 individuals sampled were greater than 200 mm TL, with ages ranging from 2 to 6 years (Figure 3a, c). The overlap in size-at-age samples from trawling and angler harvest was similar to simulation scenarios c and d and therefore seemed to support proportions of 0.50/0.50 for a

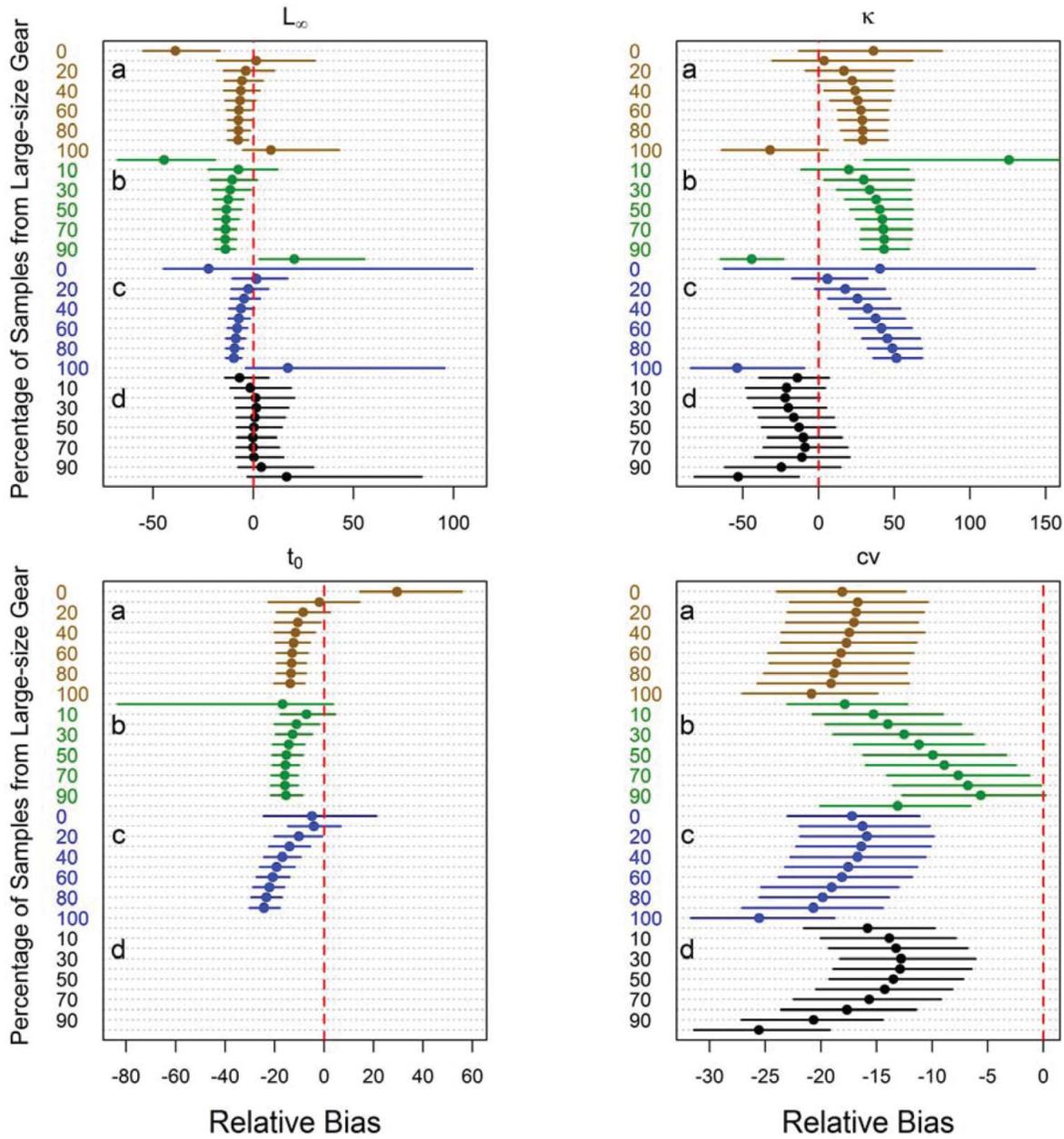


FIGURE 2. Percent relative bias (red dashed line = zero bias) and 95% confidence intervals for the estimated von Bertalanffy growth function (VBGF) compared with the true VBGF (L_{∞} = average asymptotic length; κ = Brody growth coefficient; t_0 = theoretical age at a length of zero; M = natural mortality rate; cv = coefficient of variation for length at age). Individuals were sampled under varying scenarios of single-gear and combined-gear approaches from a simulated age-structured model. Scenarios involved varying the percentage (0–100%) of samples that were contributed by a large-size-selective sampling gear under differing vulnerability scenarios (as summarized in Table 2), including (a) no overlap between samples from the two gears (brown); (b) overlap at ages 1–2 (green); (c) overlap at ages 2–4 (blue); and (d) overlap at age 3 and older (black; scenario letters correspond to the letters on each panel). Note that the upper confidence interval for estimates of κ under scenario b with 0% contribution from the large-size-selective gear fell outside the plot range; all t_0 estimates for scenarios a–c under a 100% contribution from the large-size-selective gear were below the plot range; and all t_0 estimates under scenario d were below the plot range.

combined approach. The VBGF approach that relied solely upon angler harvest data (i.e., large-size-selective gear) yielded a higher L_{∞} and lower κ , t_0 , and CV_{La} values than the trawl-only and combined-gear approaches (Table 3; Figure 3). Furthermore, the angler harvest-only approach

resulted in the least precise parameter estimates (Table 3; Figure 3). Estimation of the VBGF based on only the trawl samples produced the lowest L_{∞} , the highest t_0 and CV_{La} , and an intermediate value of κ (Table 3; Figure 3). When the combined-gear approach was used to fit the VBGF,

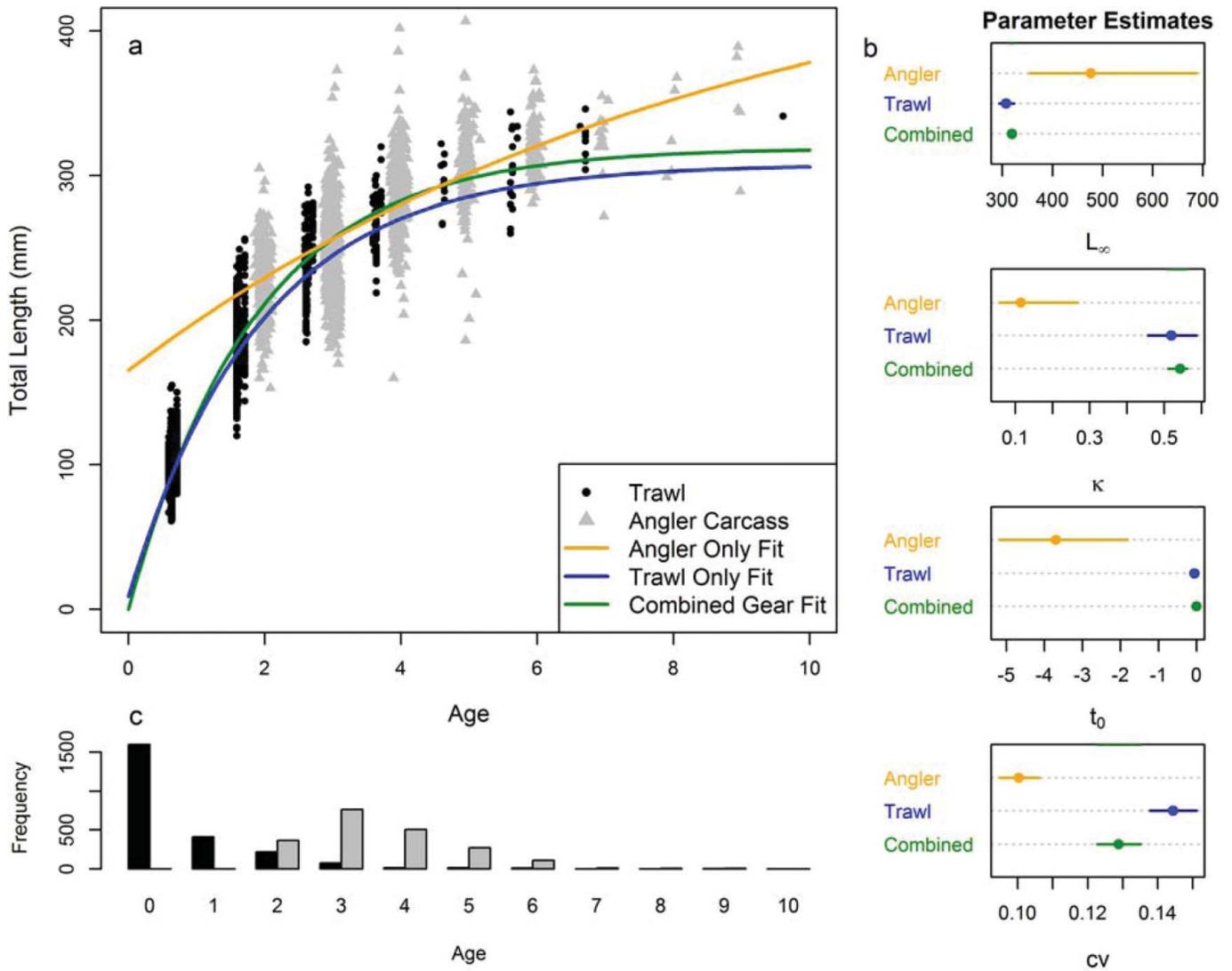


FIGURE 3. (a) Three approaches for estimating the von Bertalanffy growth function (VBGF) for Black Crappies in the Lochloosa Lake fishery based on samples collected via trawling (black circles) and angler harvest (carcass collections; gray triangles) from 2006 to 2012. Growth functions were fitted using a total of 1,000 fish for each approach and were bootstrapped 10,000 times; the combined-gear approach used 500 fish/gear. (b) Median and 95% confidence intervals for the VBGF parameters (L_{∞} = average asymptotic length; κ = Brody growth coefficient; t_0 = theoretical age at a length of zero; cv = coefficient of variation for length at age) show relative uncertainty among the three approaches. (c) The frequency of observed ages in Black Crappie samples from trawling (black bars) and angler harvest (gray bars) depicts the gear selectivity across ages.

estimates were intermediate to those obtained from either gear individually but appeared to be closest to the trawl-only estimates (Table 3; Figure 3). Precision was higher for the trawl-only and combined-gear approaches than for the angler harvest-only approach; however, the combined-gear approach typically generated the most precise parameter estimates. All of the case study results were consistent with the simulation results and appeared to support the initial findings that combining samples from two gears generally led to improvements in VBGF estimation by improving sample representativeness.

DISCUSSION

Overall, combining samples from multiple gears had two important benefits for improving growth estimates: reduced bias and increased precision. At first glance, these benefits might appear statistically intuitive. However, we highlight that many fisheries managers are currently unsure of how to handle data from multiple gears, whether they should consider sampling with more gear types, and how much benefit is gained by changing gears or implementing additional sampling trips. Current practitioners either have been haphazardly combining samples from multiple gears (Murphy and Taylor 1994; Zhao

TABLE 3. Median values (with 95% confidence intervals; from 10,000 bootstrap iterations) of estimated von Bertalanffy growth function (VBGF) parameters (L_∞ , κ , t_0 , and CV_{La} ; defined in Table 1) for the Lochloosa Lake population of Black Crappies. The fish were sampled with two size-selective gears from 2006 to 2012: (1) trawling (fishery-independent survey), which was selective for smaller fish; and (2) angler harvest (fishery-dependent data), which was selective for larger fish (harvest was estimated from carcass collections). Estimated VBGF parameters were fitted to random size-at-age samples across all years by using three approaches: trawl-only samples (1,000 samples), angler harvest-only samples (1,000 samples), and combined-gear samples (500 samples/gear).

Parameter	Approach	Median (for all years)
L_∞ (mm)	Trawl only	308 (294–323)
	Angler harvest only	475 (356–683)
	Combined gears	319 (314–325)
κ	Trawl only	0.519 (0.458–0.588)
	Angler harvest only	0.116 (5.73×10^{-2} to 0.270)
	Combined gears	0.543 (0.511–0.563)
t_0	Trawl only	-0.0567 (-0.110 to -7.56×10^{-3})
	Angler harvest only	-3.69 (-5.168 to -1.803)
	Combined gears	-1.70×10^{-4} (-3.46×10^{-2} to -3.26×10^{-7})
CV_{La}	Trawl only	0.144 (0.138–0.151)
	Angler harvest only	0.100 (9.50×10^{-2} to 0.106)
	Combined gears	0.129 (0.123–0.135)

et al. 1997; Potts et al. 1998) or have not combined the samples at all. Hence, the problem has been longstanding, but rigorous advice and solutions have not been available. The general design of our simulation scenarios, the Black Crappie case study, and the age- and size-structured model code provide such clarity.

In our simulations, we showed that combining samples from different size-selective gears improved sample representativeness and generally led to reduced bias and increased precision in growth parameter estimation. Improvements in sample representativeness and increases in sample size are direct consequences of combining samples, but our simulation and case study results documented the benefits of combining gears independently from the effect of increased sample size. Combining two gears generally decreased bias even when both gears selected for larger fish—which is often the case with many sampling techniques—but the inclusion of smaller individuals in the assessment produced a much greater decrease in bias. The results suggest that adding any amount of data from smaller individuals may reduce the bias in VBGF parameter estimates. For example, in the Black Crappie case study, sample sizes were constant, and combining trawl and angler harvest data increased the precision in parameter estimates to a greater extent than the use of either gear alone. The two gears' selectivity overlapped substantially at 150 to 300 mm TL, but very little overlap occurred outside of this range. This overlap likely yielded the greater similarity in parameter estimates between the trawl-only and combined-gear approaches compared with the data for angler harvest only, which missed small fish.

Managers' decisions about how or whether gears should be combined must be made carefully. Similar to Kritzer et al. (2001) and Gwinn et al. (2010), we cannot prescribe one rule that applies across species and selectivity scenarios and that will always lead to improved parameter estimates. The results from this study and other studies have shown how using data from different gears can influence growth parameters (Zhao et al. 1997; Potts et al. 1998; Lucena and O'Brien 2001). The specific proportions that should be used in combining samples from multiple gears remain for managers to decide and will be rather case specific depending upon the apparent overlap in size selectivity for the gears being considered. Because we found that combining gears sometimes increased bias in the VBGF parameters (i.e., when both gears missed smaller individuals: Figure 2, scenario d), combining samples from two or more gears may not always be preferable to single-gear approaches. Our recommendation is for managers to (1) create rules that can be consistently followed and (2) avoid ad hoc rules for excluding catch-at-age data that appear to not conform to an assumed size-selective curve. Ad hoc rules are often followed in fisheries, such as when selecting the minimum ages to include in mortality estimation via catch curves (Kritzer et al. 2001; Lester et al. 2014), fixing L_∞ at the maximum lengths sampled (Sammons and Maceina 2009), fixing the x -intercept of the VBGF (i.e., t_0) at zero (Gwinn et al. 2010), or alternatively by fixing the y -intercept (L_0 ; length at an age of zero) at some observed value (Pardo et al. 2013). We cannot dispute the efficacy of creating or following such rules when specific to each fishery, but the tradeoffs behind such decisions should be critically examined in each case. For example, Table S.1 provides a model that could be adapted

relatively easily by fisheries managers to decide their own best approaches specific to their gears' selectivity. The leading parameters for the code (i.e., growth, maximum age, and capture sizes) can be based on minimum and maximum capture sizes from recent catches and on previous growth studies of the species. Such an approach can expose gaps in monitoring programs and can help to allocate limited sampling effort toward underrepresented ages or sizes.

Combining gears can allow both fishery-dependent and fishery-independent data to be directly used in growth estimates. Application of this approach has primarily been limited to some data-rich marine stock assessments conducted by fisheries management councils, such as Southeast Data, Assessment, and Review (SEDAR; e.g., Murphy and Taylor 1994; Zhao et al. 1997; Potts et al. 1998). For example, Lombardi-Carlson (2006a, 2006b) combined all available length-at-age data from commercial, recreational, and scientific samples to express growth of various serranid species (sea basses) for SEDAR reports. However, we have found no literature to suggest that managers of inland fisheries (where managers also conduct the stock assessments) have similarly adopted this approach or that the combined approach has been widely adopted across stock assessment personnel. Current approaches appear haphazardly implemented, with most published records indicating that all available data were combined or that combining samples was not decided upon. To our knowledge, no previous studies have provided guidance on specific tradeoffs in combining samples from gears that vary in their relative number of samples and that vary in size selectivity. Catch-at-age data are often sampled with independent scientific surveys to avoid the biases that are common in fishery-dependent data (Hilborn and Walters 1992; Chen et al. 2003). Typically, these two sources of data are indirectly combined by (1) assuming that fishery-independent data indicate the true ecological pattern and then (2) using the fishery-independent data to calibrate stock assessment models or to inform Bayesian priors for the fishery-dependent data (Latour et al. 2003; Walters and Martell 2004). However, both fishery-dependent and fishery-independent surveys can selectively sample a fishery. Combining samples into a single population may increase the number of age-classes and size-classes such that they match the number of classes available in the stock and more accurately approximate growth trajectories and population structure. For example, the Black Crappies sampled from angler harvest included the largest, oldest individuals, which trawl surveys tended to avoid; likewise, the trawl samples included younger, smaller individuals, which were not harvested by anglers. Combining catch-at-age samples seems an intuitive response to the selective and imperfect sampling of fish populations.

Our case history example used data from Black Crappies that were sampled with two gears (trawling and angling), but the results in combination with our simulation model are generalizable to a wide range of fish populations. For example,

many monitoring programs include gears that sample both young fish and adults and therefore vary substantially in size selectivity. Bryan and Scarnecchia (1992) used a variety of gears to monitor the abundances of juvenile Yellow Perch *Perca flavescens*, Bluegills *Lepomis macrochirus*, and Smallmouth Bass *Micropterus dolomieu* in an Iowa lake, and the adults of these same species are typically monitored with creel surveys and electrofishing (e.g., Bonar et al. 2009). Beach seines have been used extensively to quantify the growth and mortality of juvenile and age-1 estuarine predators, such as Striped Bass *Morone saxatilis* and Bluefish *Pomatomus saltatrix* (Hurst and Conover 1998; Richards and Rago 1999; Buckel and McKown 2002); the age structure of these species is also monitored in the adult phase by using fishery-dependent and fishery-independent data (e.g., Richards and Rago 1999; Robillard et al. 2009). Our results indicate that combining gears for growth curve estimation would generally improve parameter estimates relative to the use of a single gear that samples only large fish or only small fish. Thus, our results should be applicable to a wide range of fish sampling applications.

Gear selectivity can confound an accurate understanding of key processes affecting population dynamics. Combining samples from multiple gears appeared to alleviate some of the problems caused by selectivity, and this approach improved sample representativeness in nearly all cases. For example, the slope of the VBGF (i.e., κ) varied between approaches; the κ estimated with combined gears ranged from 0.51 to 0.56 and was more precise than single-gear estimates. This range is higher than the average κ (0.44) that was estimated based on 81 Black Crappie populations (Jackson and Hurley 2005). Lochloosa Lake is a eutrophic, subtropical lake, and we would expect κ to be higher than the North American average because Black Crappies grow fastest under productive, eutrophic conditions (Maceina et al. 1996). Combining gears helped to surmount sampling bias caused by selectivity, thus allowing reasonable VBGF estimates to be generated for Black Crappies in Lochloosa Lake.

Future research could include a focus on assessing the tradeoffs associated with combining samples from multiple gears to estimate fish abundance and survival (e.g., using catch curves to estimate total annual mortality; Chapman and Robson 1960; Lester et al. 2014) or alternative growth models (e.g., biphasic growth; Lester et al. 2004). Estimating year- or site-specific growth parameters is an increasingly common recommendation (e.g., Booth 2000), but a greater number of samples and sufficient representativeness are required at such resolution. Combining samples from multiple gears allows for a finer spatiotemporal resolution of growth parameter estimates by improving the range of ages that are collected from different size-selective gears and by increasing the number of samples that are available for model fitting (Kritzer et al. 2001). Managers of size- and age-structured populations should begin evaluating whether and how to combine

information from multiple sampling gears that are subject to selective biases, as this approach can lead to drastically improved estimates of the critical processes regulating population dynamics. Such improvements will avoid “fishy growth curves” and will facilitate management decisions and regulation changes that are more informed and appropriate for their respective populations (Pardo et al. 2013).

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