

# An assessment of sampling approaches for estimating growth from fishery-dependent biological samples

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Accuracy of fish growth estimates depends greatly on how samples are collected. A total of three common sampling strategies are random, fixed otolith sampling (FOS), and proportional otolith sampling (POS). Random sampling is inefficient and rarely random. While POS has been shown to produce more accurate estimates of growth compared to FOS under ideal conditions, it is unclear how variables such as sample size, fishery selectivity, and fishing mortality influence sampling bias. Simulated age-at-length observations from two tropical deepwater species were used to evaluate the accuracy of von Bertalanffy growth parameter estimates comparing FOS and POS for a fast-growing, short-lived fish (*Prisipomoides auricilla*) and a slow-growing, long-lived fish (*Etelis coruscans*). A total of 24 scenarios were tested to examine the influence of sample size, minimum size selected in the fishery, fishery exploitation rates, and supplemental sampling on growth parameter estimates. Furthermore, tests were applied to real fishery age-length observations for *P. auricilla*. POS consistently performed better than FOS, especially when the catch was representative of the population. However, FOS performed better when catch was not representative. This research demonstrates the importance of considering effects of fishery selectivity, fishing mortality, and sample size on sampling strategy and provides a tool to select an appropriate approach.

**Keywords:** age and growth, fisheries, fixed otolith sampling, independent-based model, population simulations, proportional otolith sampling, sampling bias.

## Introduction

Accurate estimates of population life history parameters such as somatic growth (length-at-age), longevity, age or length at sexual maturity, and population variance in length-at-age are requirements for reliable stock assessment and effective fisheries management (Aires-da-Silva *et al.*, 2015; Zhu *et al.*, 2016). Estimates of population life history parameters have associated error due to aging accuracy and sampling bias. Aging accuracy (the ability to accurately determine the age of individual fish by analyses of hard parts) has greatly improved in recent years due to method advancements (Campana, 2001; Newman *et al.*, 2015; Andrews *et al.*, 2016), but how specimens are selected (henceforth, sampling strategy) remains a persistent source of bias (Chih, 2009b; Gwinn *et al.*, 2010; Chang *et al.*, 2019; Goodyear, 2019). Specimens are often obtained from fishery-dependent sampling *via* commercial, recreational, or artisanal fishermen *via* fish markets, port sampling, fisheries observers, or contracted fishing trips. The crux of the problem for any fishery-dependent sampling design is that fisheries catch may not be representative of the population. Because fishermen rarely land fish randomly from the population, this can limit the range of fish sizes, ages, or individual growth characteristics available for sampling. The non-randomness of fishery catches is loosely termed fishery selectivity (or simply, selectivity) and can be driven by numerous mechanisms, such as: size selectivity of fishing gears (e.g. nets, which allow small fish to escape or hook-and-line configurations which allow large fish to break off); the tendency of spawning fish to aggregate; or fishermen modifying their behaviour to avoid species, ages, or sizes of fish for economic or regulatory reasons (Sampson, 2014). In addition to selecting for different sizes of fish, fisheries may select for characteristics of individual fish, for example,

the fastest-growing individuals of a given cohort, which can greatly bias growth parameter estimates (Lee, 1912; Sinclair *et al.*, 2002; Sampson, 2014). With these challenges in mind, there are three commonly implemented sampling strategies: (1) random otolith sampling, (2) fixed otolith sampling (FOS), and (3) proportional otolith sampling (POS; Goodyear, 2019). Each of these sampling strategies has different strengths and weaknesses and choosing which strategy to follow can be challenging.

Random sampling of fishery catch will yield statistically robust estimators of true population growth only if fishermen randomly catch fish from the population. More commonly however, fisheries are affected by issues such as size-based selectivity, something which often goes unaccounted for as the only real counter for this in a “randomly” sampled fishery is more samples, a solution that is neither cost nor time efficient. Additionally, further sampling in such cases can lead to over-sampling of the more common sizes (Brouwer and Griffiths, 2005; Chih, 2009b), which, again, can be inefficient and costly. To avoid this, researchers have several options. The von Bertalanffy theoretical time at length zero ( $t_0$ ) may be poorly defined. In these instances, researchers may simply constrain (fix)  $t_0$  to zero or another suitable value during parameter estimation. Alternatively, random sampling of fishery catch may be altered by supplementing the least abundant size classes with additional samples. However, this practice of targeted sampling of individuals within the tails of the distribution of available sizes may bias estimation of growth parameters. In particular, the targeting of large individuals (instead of older individuals) can lead to the overestimation of asymptotic length ( $L_\infty$ ; Chang *et al.*, 2019; Goodyear, 2019). Interestingly, the effects of disproportionate selection of samples from the lower size distri-

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bution on growth parameter estimation bias have not been investigated to our knowledge.

FOS sets a predetermined number of samples for each length bin (Chang *et al.*, 2019), a strategy which has been shown to lead to overestimates of mean length-at-age and  $L_{\infty}$  (Goodyear, 1995; Chih, 2009a; Coggins Jr *et al.*, 2013; Goodyear, 2019). Biased growth parameter estimates associated with FOS may be corrected by applying an age-length key (ALK; Lusk *et al.*, 2021; Goodyear, 2019). Problematically, ALKs require informed assumptions regarding the numbers at length in a fish population, which are likely lacking for data-poor fisheries in need of growth studies. In addition, the aged samples must accurately represent the true mean population length-at-age, which is especially challenging for older ages which may be rare in heavily fished populations (Kimura, 1977; Westrheim and Ricker, 1978; Goodyear, 2019). Finally, producing robust ALKs requires large sample sizes ranging from 500 to 1000 individuals, which may be impossible for small-scale fisheries or remote fish populations (Coggins Jr *et al.*, 2013).

POS entails allocating a previously determined total number of age samples across size bins based on abundance or catch at length within the overall population (hence, the population proportional length frequency (Chang *et al.*, 2019)). POS was identified as the preferred option over FOS based on population simulation studies (Chang *et al.*, 2019; Goodyear, 2019). Although POS performs well under simulated conditions where the population length frequency is known, researchers investigating growth of *in situ* marine fish populations often do not possess such detailed knowledge. It is unclear what would happen under POS if biological samples were fishery-dependent because the catch and the resulting biological samples may be a poor representation of the population.

Aside from sampling strategy, the total sample size can also influence growth parameter bias and uncertainty and must be carefully determined. Recommended total sample sizes for age and growth assessments range from 200 to 1000 for the sampling strategies discussed (Kritzer *et al.*, 2001; Brouwer and Griffiths, 2005; Coggins Jr *et al.*, 2013; Chang *et al.*, 2019). However, it can be difficult to obtain large sample numbers for less abundant species or when researchers are constrained by financial or other practical considerations. In such instances, quantifying the relationship between sample size and sampling strategy with bias and uncertainty of growth parameter estimates can inform study prioritization and design *a priori*. In cases where life history estimates based on small sample sizes are the best science available, *a posteriori* understanding of precision and bias would contribute to a more realistic representation of potential bias in assessment model outputs that could be integrated into risk analyses and management advice.

Tropical deepwater fisheries, composed mainly of snappers (Lutjanidae) and groupers (Epinephelinae), provide an example of the many challenges of life history sampling and parameter estimation. Much of the needed tropical deepwater fisheries biological information is lacking or shown to be spatially variable (Newman *et al.*, 2016; Williams *et al.*, 2017; O'Malley *et al.*, 2019). The small-scale and artisanal nature of many of these fisheries often makes it difficult to monitor catches and obtain biological samples. Many studies report small total sample sizes (Williams *et al.*, 2017; O'Malley *et al.*, 2019; Wakefield *et al.*, 2020), small individuals missing from

the catch (Trianni, 2011; Williams *et al.*, 2017; O'Malley *et al.*, 2019; Uehara *et al.*, 2020), or both (Williams *et al.*, 2017; O'Malley *et al.*, 2019). Additionally, many tropical deepwater species have long histories of exploitation and may be heavily fished (Newman and Dunk, 2003; Langseth *et al.*, 2019) meaning older individuals, which are necessary to inform estimates of maximum age and length as well as accurately estimate growth, may be rare or absent in the catch. Furthermore, fisheries can influence fish life history, such as selecting for faster growth and smaller size and age at maturity (reviewed in Kuparinen and Merilä 2007).

In this study, we examine the influences of these potential sources of bias by testing the effects of species life history, fishery exploitation, and length-based fishery selectivity on growth parameter estimation from fishery-dependent biological samples. We developed an individual-based model (IBM) to simulate ages at length of two tropical deepwater snapper species representing dissimilar life histories: a fast-growing, short-lived fish (yelloweye snapper, *Prisitipomoides auricilla*) and a slow-growing, longer-lived fish (longtail red snapper, *Etelis coruscans*). We evaluated a variety of sampling approaches including two widely used size-based sampling strategies (POS and FOS), constraining  $t_0 = 0$ , supplemental sampling (adding samples to lower and/or upper size classes), and total sample size during the estimation process. Random sampling was not investigated as it is not efficient and can lead to unintentional sample selection (i.e. is never truly random). Our objective was to determine the appropriate sampling approach to estimate fish growth parameters given sampled otoliths from fisheries catches with varying levels of representativeness to the true population. Finally, we applied the same sampling approaches to fishery-dependent length-at-age observations for yelloweye snapper from the hook-and-line fisheries around Guam and Saipan, Commonwealth of the Northern Marianas Islands to evaluate the consistency between the simulation results and a real-world case study. We highlight the importance of considering species life history and fishery characteristics when selecting biological samples and understanding potential biases in life history parameter estimates.

## Methods

### Growth models

We evaluated von Bertalanffy (von Bertalanffy, 1938), Gompertz (Gompertz, 1825), Schnute (Schnute, 1981), and Ricker (Ricker, 1975) growth models by parameterizing each one for a common set of fishery-dependent age-at-length observations for *P. auricilla*. Calculated Akaike Information Criteria for small sample sizes (AICc; Burnham and Anderson, 2002) suggested there was no difference ( $\Delta AICc < 4.0$ ) among compared models. We chose to use the von Bertalanffy growth function [VBGF; Table 1; Equation (1.1)] to simulate data in this study because it is widely used in life history studies of tropical deepwater fish (Mees, 1993; Newman and Dunk, 2003; Williams *et al.*, 2017; O'Malley *et al.*, 2019).

### Simulation modelling

We constructed an IBM incorporating individual variability in growth and a size-selective fishery operating at a range of fishery exploitation levels to simulate catches. The simulation model was built and run in R (R Development

**Table 1.** Summary of the individual-based fish population simulation model (IBM) equations used to generate age-at-length of the population and fishery catch.

Number	Function	Description
1.1	$L_{a,i} = L_{\infty,i} (1 - e^{-K_i(a_i - a_{0,i})})$	von Bertalanffy Growth Function (VBGF) length of individual $i$ at age $a$ ( $L_{a,i}$ ). Asymptotic length for individual $i$ ( $L_{\infty,i}$ ) is drawn from a normal distribution with mean $\mu_{L_{\infty}}$ and standard deviation $\sigma_{L_{\infty}}$ . $\mu_{L_{\infty}} = 32.5$ cm ( <i>P. auricilla</i> ), 100 cm ( <i>E. coruscans</i> ) $\sigma_{L_{\infty}} = 2.5$ cm. Growth coefficient of individual $i$ ( $K_i$ ) is drawn from a normal distribution with mean $\mu_K$ and standard deviation $\sigma_K$ . $\mu_K = 0.60$ ( <i>P. auricilla</i> ), 0.14 ( <i>E. coruscans</i> ) $\sigma_K = 0$
1.2	$a_{0,i} = \frac{\ln(1 - L_{0,i}/L_{\infty,i})}{K_i}$	Theoretical age when individual $i$ has length = 0 ( $a_{0,i}$ ). Theoretical length at age 0 for individual $i$ ( $L_{0,i}$ ) is drawn from a normal distribution with mean $\mu_{L_0}$ and standard deviation $\sigma_{L_0}$ $\mu_{L_0} = 10$ cm, $\sigma_{L_0} = 2.5$ cm
1.3	$M_{constant} = 4.899A_{max}^{-0.916}$	Instantaneous natural mortality (year <sup>-1</sup> ) assumed constant over all ages ( $M_{constant}$ ). From the longevity ( $A_{max}$ ) based instantaneous natural mortality estimator of Then <i>et al.</i> (2015). $A_{max} = 55$ years ( <i>E. coruscans</i> ) $M_{constant} = 0.125$ year <sup>-1</sup> ( <i>E. coruscans</i> ) $M_{constant} = 0.18$ year <sup>-1</sup> ( <i>P. auricilla</i> , from O'Malley <i>et al.</i> , 2019)
1.4a	$L_a = L_{\infty} (1 - e^{-K(a - a_0)})$	Mean expected length at age $a$ ( $L_a$ ), calculated from the VBGF using mean values for $L_{\infty}$ , $K$ , and $L_0$ ( $\mu_{L_{\infty}}$ , $\mu_K$ , and $\mu_{L_0}$ , respectively). Mean theoretical age when length = 0 ( $a_0$ ) $a_0 = -0.61$ ( <i>P. auricilla</i> ), $-0.75$ ( <i>E. coruscans</i> ).
1.4b	$a_0 = \frac{\ln(1 - L_0/L_{\infty})}{K}$	
1.5	$t_0 = \frac{\ln(1 - L_0/L_{\infty})}{K} + 1$	Theoretical time at length = 0 ( $t_0$ ) calculated from the VBGF using mean values for $L_{\infty}$ , $K$ , and $L_0$ ( $\mu_{L_{\infty}}$ , $\mu_K$ , and $\mu_{L_0}$ , respectively). $t_0 = 0.39$ ( <i>P. auricilla</i> ), 0.25 ( <i>E. coruscans</i> )
1.6	$M_a = \frac{M1}{L_a}$	Mean expected instantaneous natural mortality at age $a$ ( $M_a$ , year <sup>-1</sup> ; Supplementary Figure S1). $M_a$ is assumed inversely proportional to $L_a$ , where $M1$ is the natural mortality rate at unit length (Lorenzen, 2005). $M1$ is estimated within the model by simultaneously solving Equations (1.5), (1.6), and (1.7). $M1 = 5.29$ ( <i>P. auricilla</i> ), 8.94 ( <i>E. coruscans</i> )
1.7	$\{ \text{Survivorship}_a = 1 \text{ for } a = 0 \}$	Survivorship to age $a$ ( $\text{Survivorship}_a$ )
1.8	$\{ \text{Survivorship}_a = \text{Survivorship}_{a-1} \times (e^{-M_a}) \text{ for } a = 1 \text{ to } A_{max} \}$	
1.9	$M_{a,i} = \frac{M1}{L_{a,i}}$	Instantaneous natural mortality (year <sup>-1</sup> ) of individual $i$ at age $a$ ( $M_{a,i}$ ). $M_{a,i}$ is assumed to be inversely proportional to $L_{a,i}$ where $M1$ is the natural mortality rate at unit length (Lorenzen 2005).
1.10	$p_{M_{a,i}} = \frac{M_{a,i}}{F_{a,i} + M_{a,i}} (1 - e^{-F_{a,i} - M_{a,i}})$	Probability of natural mortality of individual $i$ at age $a$ ( $p_{M_{a,i}}$ )
1.11	$Selex_{a,i} = \int_0^{L_{a,i}} \frac{1}{\text{mincatsd}\sqrt{2\pi}} e^{-0.5 \frac{(L_{a,i} - \text{mincat})^2}{2\text{mincatsd}^2}} dL_{a,i}$	Fishery selectivity of individual $i$ at age $a$ ( $Selex_{a,i}$ ) is the value of the normal cumulative probability density function at value $L_{a,i}$ with mean <i>mincat</i> and standard deviation <i>mincatsd</i> (Supplementary Figure S2) small individuals in catch: <i>mincat</i> = 10 cm small individuals absent from catch: <i>mincat</i> = 20 ( <i>P. auricilla</i> ), 30 ( <i>E. coruscans</i> ) <i>mincatsd</i> = 2.5 cm

Table 1. Continued

Number	Function	Description
1.12	$F_{a,i} = F' * Selex_{a,i}$	Instantaneous fishing mortality (year <sup>-1</sup> ) of individual $i$ at age $a$ ( $F_{a,i}$ ) is the product of $Selex_{a,i}$ and apical (fully selected) fishing mortality ( $F'$ ). A total of three different levels of fishery exploitation were simulated. low: $F' = 0.09$ ( <i>P. auricilla</i> ), 0.0625 ( <i>E. coruscans</i> ) medium: $F' = 0.18$ ( <i>P. auricilla</i> ), 0.125 ( <i>E. coruscans</i> ) high: $F' = 0.36$ ( <i>P. auricilla</i> ), 0.25 ( <i>E. coruscans</i> )
1.13	$p_{F_{a,i}} = \frac{F_{a,i}}{F_{a,i} + M_{a,i}} (1 - e^{-F_{a,i} - M_{a,i}})$	Probability of fishing mortality of individual $i$ at age $a$ ( $p_{F_{a,i}}$ )

Core Team, 2020) and it and the associated data are available for download from <https://github.com/evasschemmel-NOAA/LHsampling>.

Details of the simulation model are summarized in Equations (1.1)–(1.13) (Table 1). Within the IBM, a cohort of individuals was simulated over age and subjected to size-dependent natural and fishing mortality. Individual fish within the population were simulated in terms of integer age, not continuous time, because life history researchers examine sectioned otoliths and often assign only integer ages to long-lived fish species such as deepwater snappers. Hence, a fish having an otolith that lacks the first annular opaque zone would be assigned age = 0, but the true “age” of the individual since the moment of creation (time = 0) is essentially unknown. Each simulated cohort begins with  $N = 100\,000$  age 0 fish, which progress through ages 0 to  $A_{max}$  following the VBGF with individual-specific asymptotic length ( $L_{\infty,i}$ ) and length at assigned age 0 ( $L_{0,i}$ ) drawn from independent normal distributions with specified means ( $\mu_{L_{\infty}}$  and  $\mu_{L_0}$ ) and standard deviations [ $\sigma_{L_{\infty}}$  and  $\sigma_{L_0}$ ; Equations (1.1) and (1.2)].

For *P. auricilla*,  $\mu_{L_{\infty}} = 32.5$  cm,  $\sigma_{L_{\infty}} = 2.5$  cm,  $\mu_{L_0} = 10$  cm, and  $\sigma_{L_0} = 2.5$  cm based on published studies (O'Malley et al., 2019) or estimated from specimens collected from fishermen and research surveys in the western Pacific (Sundberg et al., 2015; O'Malley et al., 2019). For *E. coruscans*  $\mu_{L_{\infty}} = 100$  cm,  $\sigma_{L_{\infty}} = 2.5$  cm,  $\mu_{L_0} = 10$  cm, and  $\sigma_{L_0} = 2.5$  cm based on published studies (Williams et al., 2013). Our IBM also allows for individual variability in the von Bertalanffy growth coefficient ( $K_i$ ) by drawing individual values from normal distributions with mean  $\mu_K$  and standard deviation  $\sigma_K$ . However, for this investigation, we chose to incorporate variability in only  $L_{\infty,i}$  and  $L_{0,i}$ , while specifying  $K_i = \mu_K$  (i.e.  $\sigma_K = 0$ ) because adding variability to two highly correlated parameters  $L_{\infty}$  and  $K$  was redundant in order to simulate a population and catch of individuals with variable lengths at age. For *P. auricilla*,  $\mu_K = 0.60$  and for *E. coruscans*,  $\mu_K = 0.14$ . Maximum age ( $A_{max}$ ) was assumed equal to 32 years for *P. auricilla* (O'Malley et al., 2019) and 55 years for *E. coruscans* (Uehara et al., 2020).

At each 1-year interval within the simulation, individual fish may be removed from the population by natural mortality followed by harvest (fishing mortality) in a Bernoulli random process. Individuals removed by fishing mortality were set aside as harvested fish. Fish that survived both natural and fishing mortality remained in the population, underwent von Bertalanffy growth, and advanced to the next age. Within the IBM,  $A_{max} + 1$  cohorts (33 for *P. auricilla* and 56 for *E. corus-*

*cans*) were created and one age (from  $a = 0$  to  $A_{max}$ ) was taken from the harvest of each cohort to form the simulated catch from which individuals could be collected by each sampling approach (detailed in *Sampling Approaches*, below). The initial number of recruits, von Bertalanffy growth, and mortality at age were constant across cohorts in the simulated population and catch, which would be consistent with a steady-state population.

Individual natural mortality at age ( $M_{a,i}$ ) was assumed to be inversely proportional to length-at-age ( $L_{a,i}$ ) following Lorenzen (Lorenzen, 2000, 2005; Equations (1.3)–(1.9); Supplementary Figure S1). We estimated the natural mortality rate at unit length [ $M1$ ; Equation (1.8)] from the VBGF mean expected length-at-age ( $L_a$ ) assuming model-input natural mortality values were for a population where  $M_a$  was constant over all ages ( $M_{constant}$ ). We assumed  $M_{constant} = 0.18$  for *P. auricilla* based on published estimates (O'Malley et al., 2019) and  $M_{constant} = 0.125$  for *E. coruscans* based on the longevity-based estimator of (Then et al., 2015); for a maximum age of 55 years (Uehara et al., 2020).  $M1$  was scaled so that survivorship to  $A_{max}$  assuming length-based natural mortality was equal to  $A_{max}$  with  $M_a = M_{constant}$ . Fishing mortality at age was a function of apical (fully selected) fishing mortality ( $F'$ ) and length-dependent fishery selectivity modelled using a cumulative normal probability density of mean = *mincat* and standard deviation = *mincatsd* [Equations (1.10)–(1.12)].

### Fisheries scenarios

We simulated 12 fishery scenarios representing different life history, length-based selectivity, and level of fishery exploitation. Length-based selectivity was modelled at two levels: (1) small fish were vulnerable to the fishery and included in the catch (*mincat* = 10 cm); and (2) small fish were not available to the fishery (*mincat* = 20 cm for *P. auricilla* and *mincat* = 30 cm for *E. coruscans*; Supplementary Figure S2). Minimum size at fishery selectivity for both species reflected observations of the sizes of fish caught and retained in tropical deepwater fisheries of the western Pacific Ocean (Sundberg et al., 2015). We investigated three levels of exploitation for each species relative to  $M_{constant}$  in order to put results in context of life history strategies for each species. Apical fishing mortality was half of  $M_{constant}$  ( $F' = 0.5M_{constant}$ ) in the low exploitation scenarios, equal to  $M_{constant}$  ( $F' = M_{constant}$ ) in the moderate exploitation scenarios, and twice  $M_{constant}$  ( $F' = 2M_{constant}$ ) in the high exploitation scenarios. These mortality values are within



or near the common ranges for fisheries maximum sustainable yield (Deriso, 1982).

### Representative index

We created a Representative Index (*RI*) to measure how well the lengths of individuals within the simulated fishery catches (hence available samples for life history studies) represented the lengths of individuals within the population, assuming no fishing had occurred (i.e. in the absence of fishing). The *RI* is a combined measure of the direct effects of size-based fishery selectivity on catches and indirect effects of length-truncation within a fish population due to fishery exploitation. The *RI* may be useful as an indicator of which sampling approaches are likely to minimize bias. The *RI* was calculated as the sum over all *Z* bins of the common area of the proportion of fish per length bin ( $prop_j$ ) between the simulated fishery catch ( $Catch_{prop_j}$ ) and the simulated population in the absence of fishing ( $Unfished_{prop_j}$ ):

$$prop_j = \frac{N_j}{\sum_{j=1}^Z N_j}$$

$$RI_j = \text{minimum}(Catch_{prop_j}, Unfished_{prop_j})$$

and

$$RI = \sum_{j=1}^Z RI_j,$$

where  $prop_j$  is the proportion of fish at length bin *j* and  $N_j$  is the number of fish at length bin *j*. We considered a *RI* < 0.5 as poor, 0.5–0.6 as moderate, > 0.6 as good.

### Preliminary analyses of total sample size and bin width

Choice of total sample size and bin width are central decisions when planning a sampling design (Kritzer *et al.*, 2001; Chih 2009b; Miranda and Colvin, 2017). Therefore, before running all combinations of fishing and sampling scenarios, preliminary screenings of total sample size and bin width were performed to understand how these sampling parameters could affect the accuracy and precision of estimated growth parameters. Our analysis included total sample sizes ( $N = 50, 75, 100, 150, 200, 250, 300, 400, 500, 750, \text{ and } 1000$ ) of each species for two levels of fishery exploitation (low:  $F' = 0.5M_{\text{constant}}$  and high: ( $F' = 2M_{\text{constant}}$ ) and high minimum size at selectivity ( $mincat = 20$  cm for *P. auricilla* and  $mincat = 30$  cm for *E. coruscans*). We also considered bin widths equal to 2, 4, 6, 8, and 10 cm for each species for low fishery exploitation and low minimum size at fishery selectivity ( $mincat = 10$ ).

Accuracy was measured as the % error:

$$\% \text{ error} = \frac{\bar{\tilde{x}}_{x,n,b} - \text{true}}{\text{true}} \times 100,$$

where  $\bar{\tilde{x}}_{x,n,b}$  is the mean of the bootstrapped sampling estimates ( $N = 1000$ ) of parameter *x* at sample size *n* and bin width *b*, and *true* is the true parameter value.

Precision across sample sizes was assessed following Kritzer *et al.* (2001):

$$P_{x,n,b} = \frac{s_{x,n,b}}{\bar{\tilde{x}}_{x,n,b}},$$

where  $s_{x,n,b}$  is the standard deviation and  $\bar{\tilde{x}}_{x,n,b}$  is the mean of the bootstrapped sampling estimates ( $N = 1000$ ) of parameter *x* at sample size *n* and bin width *b*.

### Sampling approaches

For each species and fishing intensity scenario, we investigated 24 sampling/fitting approaches, evaluating combinations of total sample size, sampling strategy (FOS vs. POS), supplemental sampling, and constraining  $t_0$  (Supplementary Table S1).

Based on preliminary analyses of total sample size, we chose  $N = 300$  as a large sample size because additional samples above  $N = 300$  resulted in diminished returns in precision for both species (see Results). We designated  $N = 75$  as the small total sample size in our analyses to reflect the lower end of sample sizes in published life history studies of deepwater snapper species (Fry *et al.*, 2006; Williams *et al.*, 2017).

Samples were taken from the simulated catch using either FOS or POS. For FOS, *n* individuals (calculated as total sample size, *N*, divided by the number of length bins) were assigned to each length bin. When less than *n* individuals were available in the catch of a length bin, additional samples were randomly drawn from the remaining length bins to ensure the total sample size (*N*) was consistent for all approaches. For POS, *N* total samples were divided among length bins in proportion to the total harvest. We used length bins equal to 2 cm for *P. auricilla* and 5 cm for *E. coruscans* based on preliminary analyses of length bin width and precision of life history parameter estimates (Supplementary Figure S6). We compared low ( $N = 75$ ) and high ( $N = 300$ ) total sample size for each sampling strategy, sampled without replacement to obtain 1000 replicates.

In addition to examining the relative performance of FOS, POS, and total sample size, we also investigated supplemental sampling, whereby researchers seek out specimens from the length bins that are absent or rare in fisheries catches. To simulate supplemental sampling, first a sample of *N* individuals was drawn from the fisheries catch following either the FOS or POS designs described above. Then, individuals were randomly eliminated from the more numerous length bins of the original FOS or POS sample. Additional samples were drawn from the population within the lower length bins, upper length bins, or both. Decreasing the number of samples per length bin in the most numerous length bins within the original FOS or POS sample allowed *N* to be held constant, avoiding the confounding effects of increased *N* that would otherwise occur with supplemental sampling. A total of three individuals were added to each supplemental sampling bin that previously contained less than three individuals.

### Model fitting constrained vs. unconstrained VBGF

We estimated VBGF model parameters from each fishery-dependent sample with nonlinear least squares regression assuming constant residual variance. The theoretical mean age when length equals zero ( $a_0$ ) can be derived from  $L_\infty$ ,  $K$ , and  $L_0$ , where  $L_\infty = \mu_{L_\infty}$ ,  $K = \mu_K$ , and  $L_0 = \mu_{L_0}$  [Equation (1.4b)]. For *P. auricilla*, true (simulated)  $a_0 = -0.61$ , and for *E. coruscans*, true  $a_0 = -0.75$ . In some life history studies, the length of an individual is assumed equal to zero at the time when growth commences (i.e. theoretical time at length zero,  $t_0 = 0$ ). The biological interpretation of  $t_0$  may be ambiguously defined by researchers as corresponding to various points in time, such as birth for viviparous fish (Von Bertalanffy, 1938), hatching from the egg, or settlement from the plankton to demersal habitat. The approach of fixing or “constraining”  $t_0 = 0$  is most often used when young fish are absent or underrepresented from samples of age-at-length (Berumen,

2005; O'Malley *et al.*, 2019). Within our population simulation model,  $t_0$  does not have a direct biological interpretation because fish were initiated at assigned age = 0 and then were subjected to natural and fishing mortality before advancing to the next age. We assumed the age-based index within our model lagged exactly 1 year behind an equivalent time-based index—fish were captured having existed for almost 1 year but assigned an age of 0—that would allow investigation of constraining  $t_0 = 0$ , i.e. we assumed at assigned age = 0, time = 1; therefore, theoretical  $t_0$  occurred exactly 1 year after theoretical  $a_0$  [ $t_0 = a_0 + 1$ ; Equation (1.5)]. For the simulated population in this study, *P. auricilla*  $t_0 = -0.61 + 1 = 0.39$ , and *E. coruscans*  $t_0 = -0.75 + 1 = 0.25$ . We investigated both the unconstrained model fitting approach (all VBGF parameters,  $L_\infty$ ,  $K$ , and  $L_0$ , were freely estimated) and the constrained model fitting approach where  $t_0$  was fixed = 0 and only  $L_\infty$  and  $K$  were estimated.

We report the relative % error (also referred to as bias) and mean and 95% CIs of the estimated VBGF parameters ( $L_0$ ,  $L_\infty$ , and  $K$ ). We also present an estimate of population variability (coefficient of variation, CV) in length at young and old ages ( $CV_{\text{young}}$  and  $CV_{\text{old}}$ ). We define young as age 0 for both species and old as age 15 and older for *P. auricilla* and age 20 and over for *E. coruscans*. If a sample did not contain any young or old individuals, then  $CV_{\text{young}}$  and  $CV_{\text{old}}$  were calculated by linear extrapolation from the available ages within the sample assuming a linear relationship between standard deviation of length-at-age and age.

### Application to *P. auricilla* samples collected from fisheries of the Mariana Islands

We used *P. auricilla* fishery-dependent data from Guam and Saipan as a case study to test sampling strategies for age and growth estimation. We used *P. auricilla* length data collected by the Guam and Saipan Biosampling Programs from 2010 to 2019 (Sundberg *et al.*, 2015). In total, 3623 fish were measured (fork length, cm) from the fisheries around Guam and Saipan (3144 Guam and 479 Saipan). Length-at-age estimates were obtained through thin section otolith processing and annual increment counts for *P. auricilla* using 135 aged samples collected from Guam ( $N = 89$ ) and the CNMI ( $N = 46$ ) during research cruises in the Mariana Archipelago in June and July 2014, and from the Guam Biosampling Program (O'Malley *et al.*, 2019).

We assigned ages to each of the 3623 fish with an ALK created following the methods of Kimura (1977). Aged samples were divided into 2-cm bins ranging from the minimum to the maximum length of the un-aged population and the probability of age given the length interval was estimated. The samples were then assigned an age based on the expected proportion of individuals in each age category. Analysis was done using the “alkIndivAge” function in the FSA R package (Ogle *et al.*, 2022). Decimal ages were rounded to integers. We then applied FOS and POS sampling strategies using a sample size of  $N = 300$  and compared estimates of VBGF parameters when  $t_0$  was constrained and unconstrained. Fishery-dependent observations were sampled 1000 times following each sampling strategy, and residual sum of squares tests were used to compare the growth curves for FOS and POS to the growth curve from the total fishery age-at-length observations. If differences were found, likelihood ratio tests were used to compare the %

of occurrence of different estimates from the different growth models.

## Results

### Simulated fish populations and catches

Older ( $> 15$  years) ages were well represented in IBM simulated catches of *P. auricilla* (5.1% of total catch by number) at low fishery exploitation, rare (2.0% of total catch by number) at medium exploitation, and virtually absent from the population ( $< 0.3\%$  by number) at high exploitation (Figure 1). For *E. coruscans*, the absence of older ( $> 20$  years) ages is apparent in the population under medium ( $< 2.8\%$  by number) and especially in the high exploitation scenario ( $< 0.4\%$  by number; Figure 1).

The length composition of simulated *P. auricilla* catches represented the available population length composition reasonably well ( $RI > 0.60$ ), even under high exploitation and large minimum size at fishery selectivity (Figure 2). Simulated *E. coruscans* catches ranged from providing a poor representation of the available population length composition under high exploitation and large minimum size at fishery selectivity ( $RI = 0.44$ ) to good representation of the length distribution of the unfished population under low exploitation and small minimum size at fishery selectivity ( $RI = 0.74$ ; Figure 2).

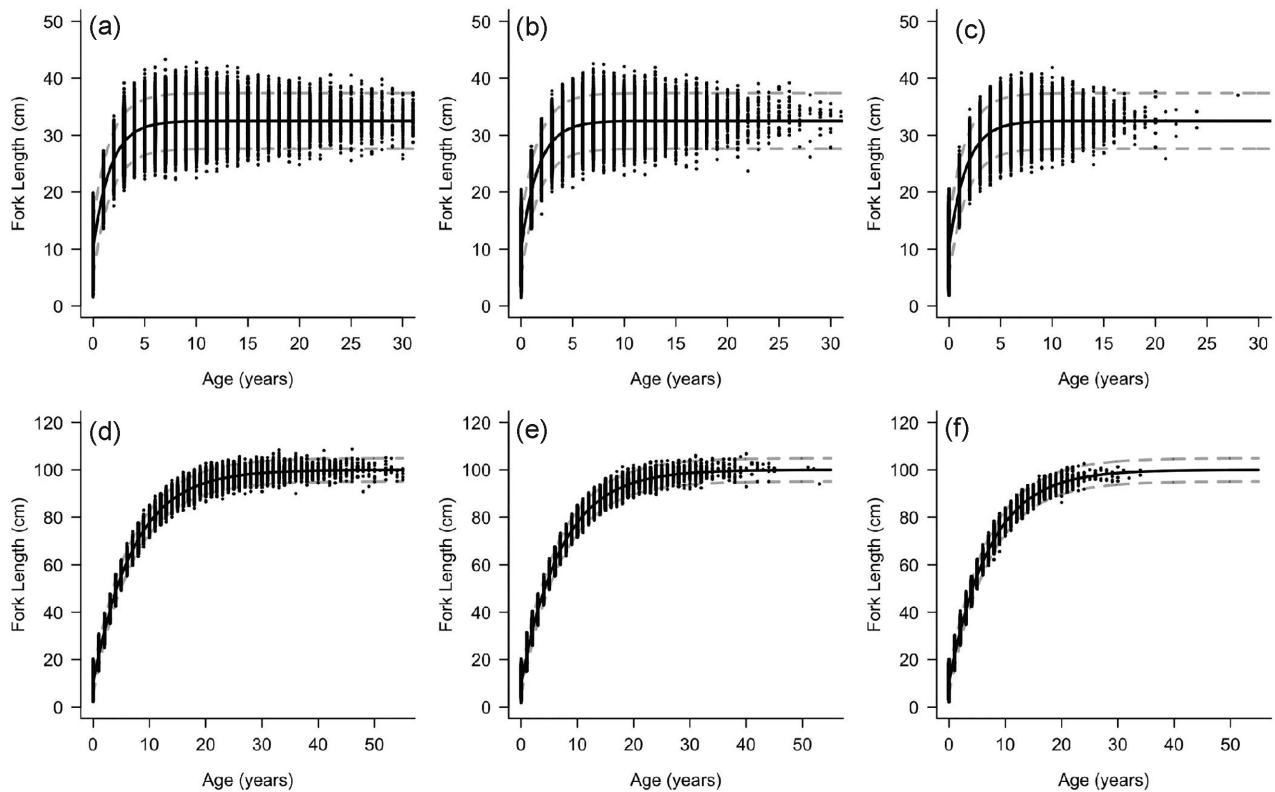
### Total sample size and bin width

There were improvements in accuracy and precision of growth parameter estimates with increasing sample size for both FOS and POS (Supplementary Figures S3 and S4). Precision of estimated  $L_\infty$  and  $K$  improved by up to 485% and 320%, respectively, when total sample size increased from 75 to 300. Accuracy of estimated  $L_\infty$  and  $K$  improved by up to 14% and 24%, respectively, when total sample size increased from 75 to 300; however, increases in accuracy were inconsistent. Total sample size of  $N = 300$  was the threshold beyond which additional samples resulted in very small improvements in precision of estimated  $L_\infty$  and  $K$  and accuracy stabilized. Additional samples beyond  $N = 300$  resulted in only marginal improvements in precision of  $L_\infty$  and  $K$ , averaging less than 28% change in precision per additional 100 samples. The low precision of small sample sizes was magnified at higher fishery exploitation. However, even at  $F' = 2M_{\text{constant}}$ , increasing sample size from  $N = 75$  to  $N = 300$  provided the largest improvements in precision of parameter estimates using FOS and POS for both species.

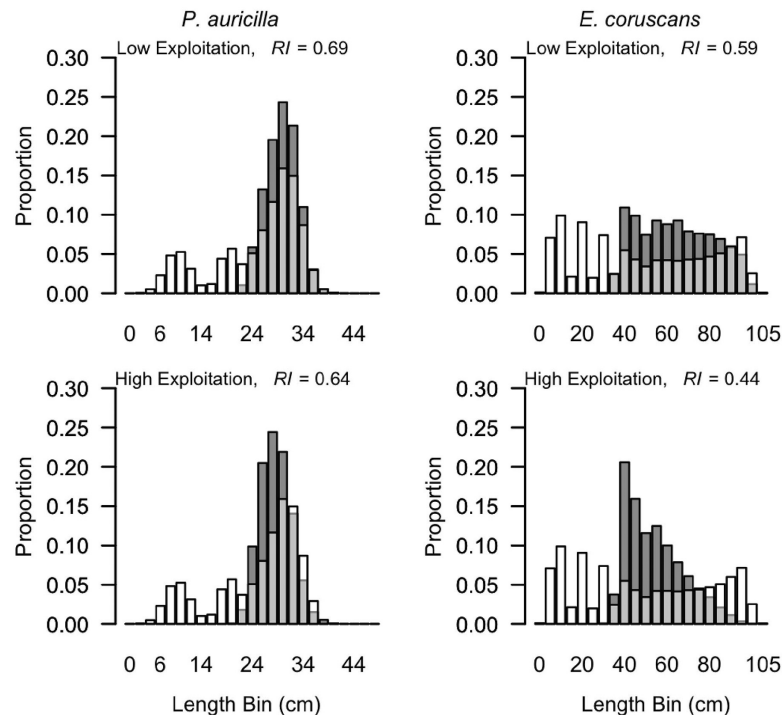
Ideal bin width for selecting samples will depend largely on the maximum length of the species. We found that a bin width of 2 cm and around 5 cm was ideal for *P. auricilla* and *E. coruscans*, respectively (Supplementary Figures S5 and S6). Accuracy of  $L_\infty$  and  $K$  under FOS improved with increased bin width, with FOS becoming more of a random sampling approach as bin width increases. POS accuracy remained stable for all growth parameters across all bin widths tested. For POS, precision around  $L_\infty$  and  $K$  diminished with increasing bin width; this was more pronounced in *P. auricilla*, the species with the shorter maximum length.

### Choosing a sampling approach

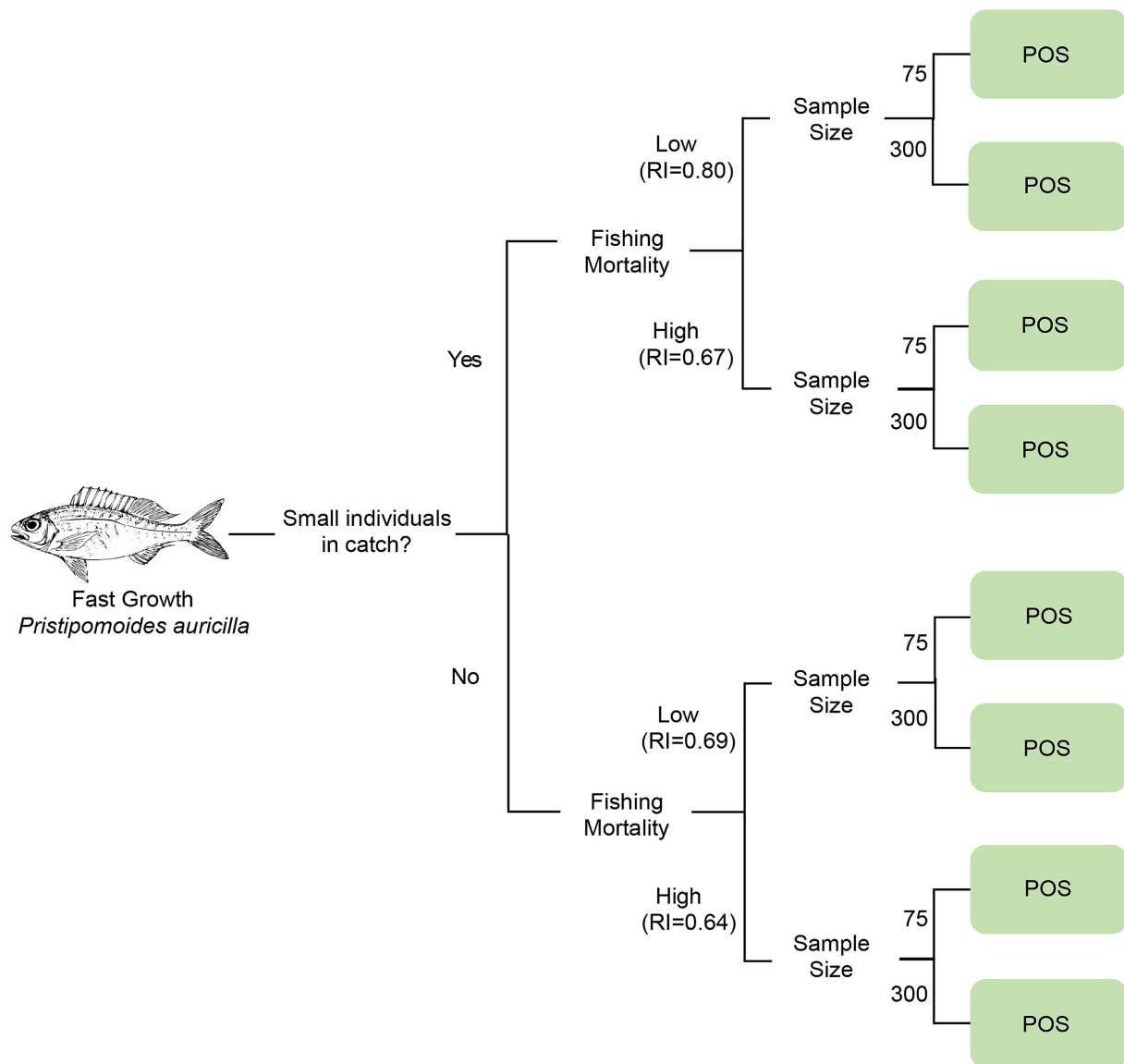
The interactive effects of life history and level of fishery exploitation affected the representativeness of fisheries catches



**Figure 1.** Population simulated length–age observations for *P. auricilla* (a)–(c) and *E. coruscans* (d)–(f) under three levels of fishery exploitation: low (a and d), medium (b and e), and high (c and f). Minimum size at fishery selectivity ( $mincat$ ) = 20.0 cm for *P. auricilla* and 30.0 cm *E. coruscans*. The points are individuals, solid black line is mean estimated length-at-age and the dashed lines are the center 95th percentile.



**Figure 2.** Proportion at length of fishery catches ( $Catch_{prop,i}$ ; dark grey bars), the unfished population ( $Unfished_{prop,i}$ ; white bars), and the  $RI$  ( $RI_i$ ; light grey bars) by length bin. Minimum size at fishery selectivity ( $mincat$ ) = 20 cm for *P. auricilla* and  $mincat$  = 30 cm for *E. coruscans*. For *P. auricilla*,  $RI$  = 0.69 and 0.64 under low and high fishery exploitation, respectively (left top, left bottom). For *E. coruscans*,  $RI$  = 0.59 and 0.44 under low and high fishery exploitation, respectively (right top, right bottom).



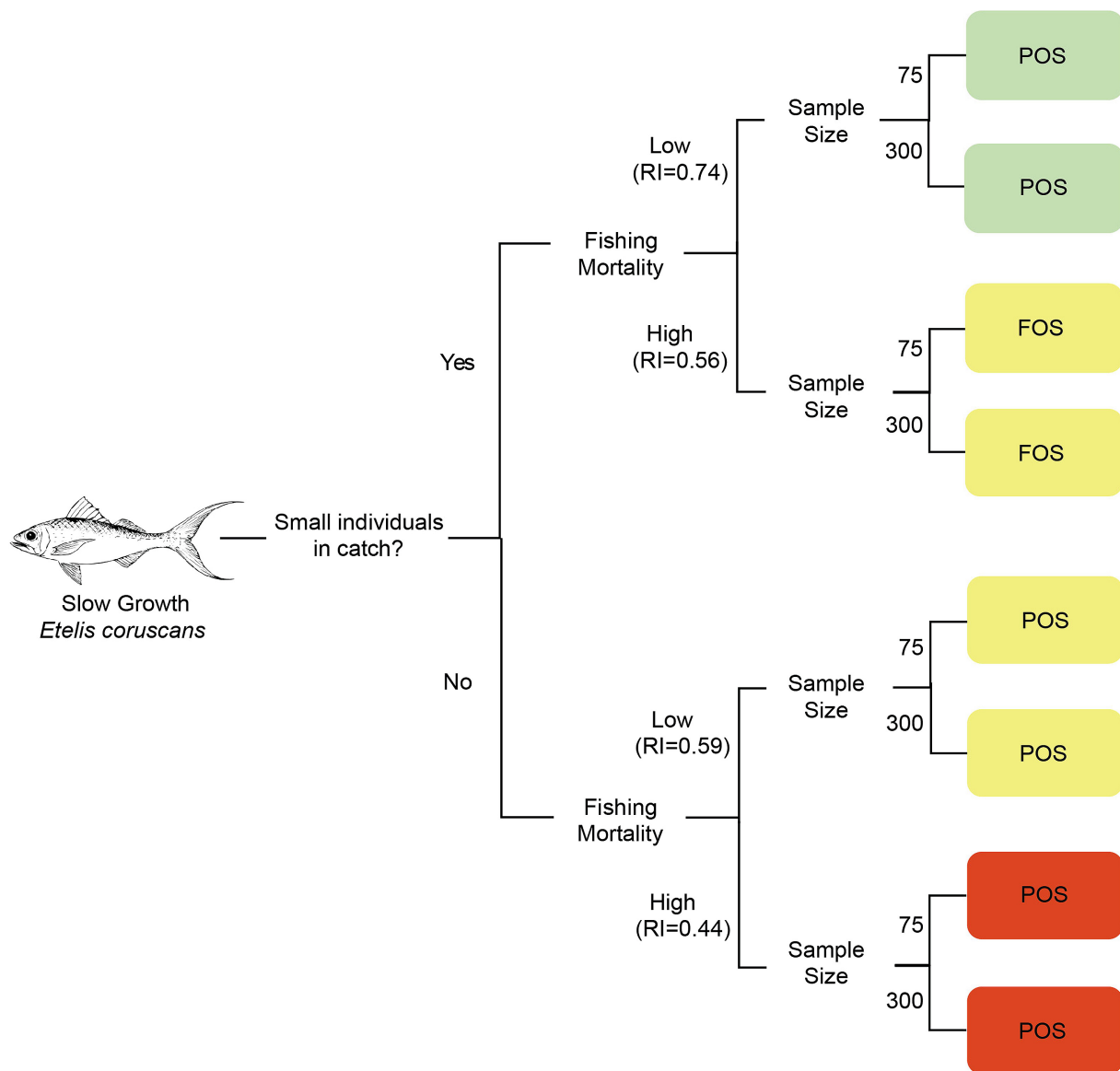
**Figure 3.** Decision tree showing optimal sampling strategy of fisheries catch for a *P. auricilla* type life history based on availability of small individuals in the catch (No: minimum size at fishery selectivity = 10 cm; Yes: minimum size at fishery selectivity = 20 cm minimum size limit), level of fishery exploitation (low,  $F' = 0.5M_{constant}$  and high,  $F' = 2M_{constant}$ ), and sample size. Sampling strategies are colour coded based on the *RI* (length-based representativeness of the catch to the unfished population) with green > 0.6, yellow 0.5–0.6, and red < 0.5.

relative to the available populations for the life histories of both tested species. These effects were further exacerbated when fishery selectivity limited the number of small fish in the catch. Ultimately, the representativeness of the catch determined which strategy produced the most accurate growth parameter estimates (Figures 3 and 4). Across all scenarios, FOS was more precise but consistently biased, overestimating  $L_{\infty}$  and underestimating  $K$  (Tables 2 and 3; Supplementary Tables S2 and S3; Supplementary Figures S7–S14). POS reduced bias in growth parameter estimates for the faster growing species, *P. auricilla*, regardless of the level of exploitation (Table 2; Figure 5). For *E. coruscans*, the best strategy (POS or FOS) depended on how well samples from the catch represented the population and if smaller sizes were selected. For *E. coruscans*, under high exploitation and with small individuals in the catch, POS produced highly variable parameter estimates because few to no samples were in the upper sizes to inform estimation of the asymptote of the VBGF curve ( $L_{\infty}$ ).

In these scenarios, FOS performed better because, by design, it ensured that large individuals were selected for in the upper size bins (Table 3; Figure 6).

We chose to rank sampling approaches assuming accuracy has a greater utility than precision. Although FOS resulted in more precise VBGF parameter estimates in many scenarios, the *CI*s did not encompass the true parameter value. In contrast, the high uncertainty of POS parameter estimates was preferred as long as the true parameter value fell somewhere within the 95% *CI*s, as this is likely a good indicator of the uncertainty in the true parameter values. For example, for *E. coruscans*, 95% *CI*s around POS estimated  $L_{\infty}$  was large but overlapped with the true value (estimated  $L_{\infty} = 101.3$  cm, *CI*: 95.9–108.5, true  $L_{\infty} = 100.0$  cm), while uncertainty of FOS estimated  $L_{\infty}$  was smaller but did not encompass the true value (FOS  $L_{\infty} = 103.0$  cm, *CI*: 101.5–104.9 cm, true  $L_{\infty} = 100.0$  cm). FOS did not produce *CI* for parameter estimates that encompassed the true value when exploitation was high,





**Figure 4.** Decision tree showing optimal sampling strategy of fisheries catch for an *E. coruscans* type of life history based on availability of small individuals in the catch (No: minimum size at fishery selectivity = 10 cm; Yes: minimum size at fishery selectivity = 30 cm minimum size limit), level of fishery exploitation (low,  $F' = 0.5M_{\text{constant}}$  and high,  $F' = 2M_{\text{constant}}$ ), and sample size. Sample strategies are colour coded based on the *RI* (length-based representativeness of the catch to the unfished population) with green > 0.6, yellow 0.5–0.6, and red < 0.5.

sample size was low ( $N = 75$ ), and small individuals were absent from the catch.

## FOS

Parameter estimates using FOS were consistently biased for both life histories, resulting in overestimated  $L_{\infty}$  and underestimated  $K$  (Tables 2 and 3; Figures 5 and 6). Bias in FOS VBGF parameter estimates was much greater for *P. auricilla* compared to *E. coruscans*. There was a maximum of +16.4% error in  $L_{\infty}$  and –42.8% error in  $K$  for *P. auricilla*, compared to a maximum of +2.7% error in  $L_{\infty}$  and –7.7% error in  $K$  for *E. coruscans* ( $N = 300$ ). For both life history types, the bias was greatest at high fishery exploitation.

The absence of small individuals from the catches resulting from larger minimum length at fishery selectivity had variable effects on the VBGF parameter estimates produced by FOS

(Tables 2 and 3). For *P. auricilla* at a low exploitation, the absence of small individuals in the catch had a minimal effect on bias in  $L_{\infty}$  estimates (0.4% at a high sample size and +0.6% at a low sample size) but was associated with reduced estimates of  $K$  (–5.6% at a high sample size and –12.7% at a low sample size). For *P. auricilla*, the absence of small individuals was more influential on the bias in estimates of  $L_{\infty}$  and  $K$  at high exploitation, increasing the bias in estimated  $L_{\infty}$  by +3.1% and +2.0%, and estimated  $K$  by –16.0% and –12.4% at a high and low sample size, respectively. For *E. coruscans*, selectivity had a minimal effect on estimated  $L_{\infty}$  and  $K$  at low exploitation, but bias increased at high exploitation. For example, at high exploitation, greater size at minimum selectivity increased bias in estimated  $L_{\infty}$  by +1.1% and  $K$  by –5.4%. Additionally, larger size at minimum selectivity greatly increased bias in  $L_0$  for both *P. auricilla* and *E. coruscans*.

**Table 2.** Relative % error of estimated  $L_{\infty}$ ,  $K$ , and  $t_0$  for *P. auricilla* under different levels of fishery exploitation (Table 1) and minimum size at fishery selectivity (*mincat* of 10 or 20 cm). Sampling strategies assessed were FOS and POS under low sample size ( $N = 75$ ), high sample size ( $N = 300$ ), and with no supplemental sampling (none), small individuals added (small), large individuals added (large), and both large and small individuals added (both).

Sampling strategy	N	Supplemental Sampling	Low F			High F			Low F			High F		
			<i>mincat</i> = 10 cm			<i>mincat</i> = 10 cm			<i>mincat</i> = 20 cm			<i>mincat</i> = 20 cm		
			$L_{\infty}$	K	$L_0$	$L_{\infty}$	K	$L_0$	$L_{\infty}$	K	$L_0$	$L_{\infty}$	K	$L_0$
FOS	300	None	12.3	-36.0	17.7	13.3	-26.8	-0.2	11.7	-41.6	32.7	16.4	-42.8	20.1
FOS	75	None	15.6	-39.8	11.7	16.2	-29.7	-7.2	16.3	-52.2	43.4	18.2	-42.1	12.5
FOS	300	Small	12.3	-36.2	18.1	13.8	-29.9	5.9	11.7	-40.6	27.8	16.9	-44.7	24.3
FOS	75	Small	16.0	-42.6	16.7	17.6	-36.1	4.9	15.8	-48.7	28.6	20.3	-48.0	25.0
POS	300	None	1.4	-10.9	26.0	1.2	-10.0	24.6	1.4	-17.3	57.8	1.4	-20.5	62.9
POS	75	None	1.0	-9.0	25.0	1.8	-12.7	28.1	0.9	-8.3	32.2	1.2	-13.8	45.9
POS	300	Large	3.7	-21.7	36.4	4.4	-21.9	33.5	3.3	-29.4	74.1	4.6	-36.0	79.9
POS	75	Large	11.1	-41.8	52.0	14.9	-42.8	45.4	11.1	-49.4	86.1	22.4	-57.4	87.6
POS	300	Small	1.3	-11.6	27.0	1.3	-11.5	26.8	1.0	-7.0	24.5	0.3	-4.4	25.4
POS	75	Small	2.0	-16.3	26.3	3.0	-17.6	27.7	2.0	-16.3	25.4	2.0	-14.9	25.6
POS	300	Both	3.6	19.6	30.1	4.3	-20.4	30.2	2.8	-14.0	26.5	2.6	-13.3	27.7
POS	75	Both	12.4	-38.5	29.7	14.5	-38.1	29.9	12.0	-38.4	28.5	15.5	-41.1	28.5

**Table 3.** Relative % error of estimated  $L_{\infty}$ ,  $K$ , and  $t_0$  for *E. coruscans* under different levels of fishery exploitation (Table 1) and minimum size at fishery selectivity (*mincat* of 10 cm or 30 cm). Sampling strategies assessed were FOS and POS under low sample size ( $N = 75$ ), high sample size ( $N = 300$ ), and with no supplemental sampling (none), small individuals added (small), large individuals added (large), and both large and small individuals added (both).

Sampling strategy	N	Supplemental sampling	Low F			High F			Low F			High F		
			<i>mincat</i> = 10 cm			<i>mincat</i> = 10 cm			<i>mincat</i> = 30 cm			<i>mincat</i> = 30 cm		
			$L_{\infty}$	K	$L_0$	$L_{\infty}$	K	$L_0$	$L_{\infty}$	K	$L_0$	$L_{\infty}$	K	$L_0$
FOS	300	None	1.7	-3.4	8.9	1.6	-2.3	5.7	2.3	-8.3	37.9	2.7	-7.7	32.5
FOS	75	None	2.8	-6.2	12.6	1.7	-1.9	2.2	3.0	-9.9	41.8	3.0	-8.4	33.3
FOS	300	Small	1.7	-3.7	9.9	1.7	-2.7	6.8	2.1	-6.3	25.3	2.5	-6.4	23.8
FOS	75	Small	2.9	-6.7	14.7	2.0	-3.2	6.4	2.7	-7.5	23.3	2.9	-7.3	22.2
POS	300	None	0.4	-1.6	14.1	2.1	-5.4	18.1	0.3	-1.1	13.7	1.3	-4.2	21.6
POS	75	None	0.7	-2.2	15.6	2.3	-5.7	19.0	0.3	-0.7	9.7	1.3	-3.4	19.1
POS	300	Large	0.4	-1.6	13.8	2.1	-5.4	18.1	3.4	-10.4	38.4	3.1	-8.3	29.1
POS	75	Large	0.7	-2.3	15.8	2.6	-6.1	19.2	0.6	-2.1	15.9	1.7	-4.7	22.4
POS	300	Small	0.5	-1.8	14.2	2.0	-5.2	17.9	0.7	-3.0	19.1	1.7	-5.2	22.0
POS	75	Small	0.9	-2.7	15.2	2.4	-5.8	17.7	1.0	-3.0	14.5	1.5	-3.7	15.5
POS	300	Both	1.5	-4.1	16.8	3.0	-7.1	19.0	3.4	-8.9	26.3	3.0	-7.5	23.6
POS	75	Both	3.5	-8.3	20.1	3.1	-7.0	17.8	3.6	-8.6	19.8	3.0	-6.5	16.6

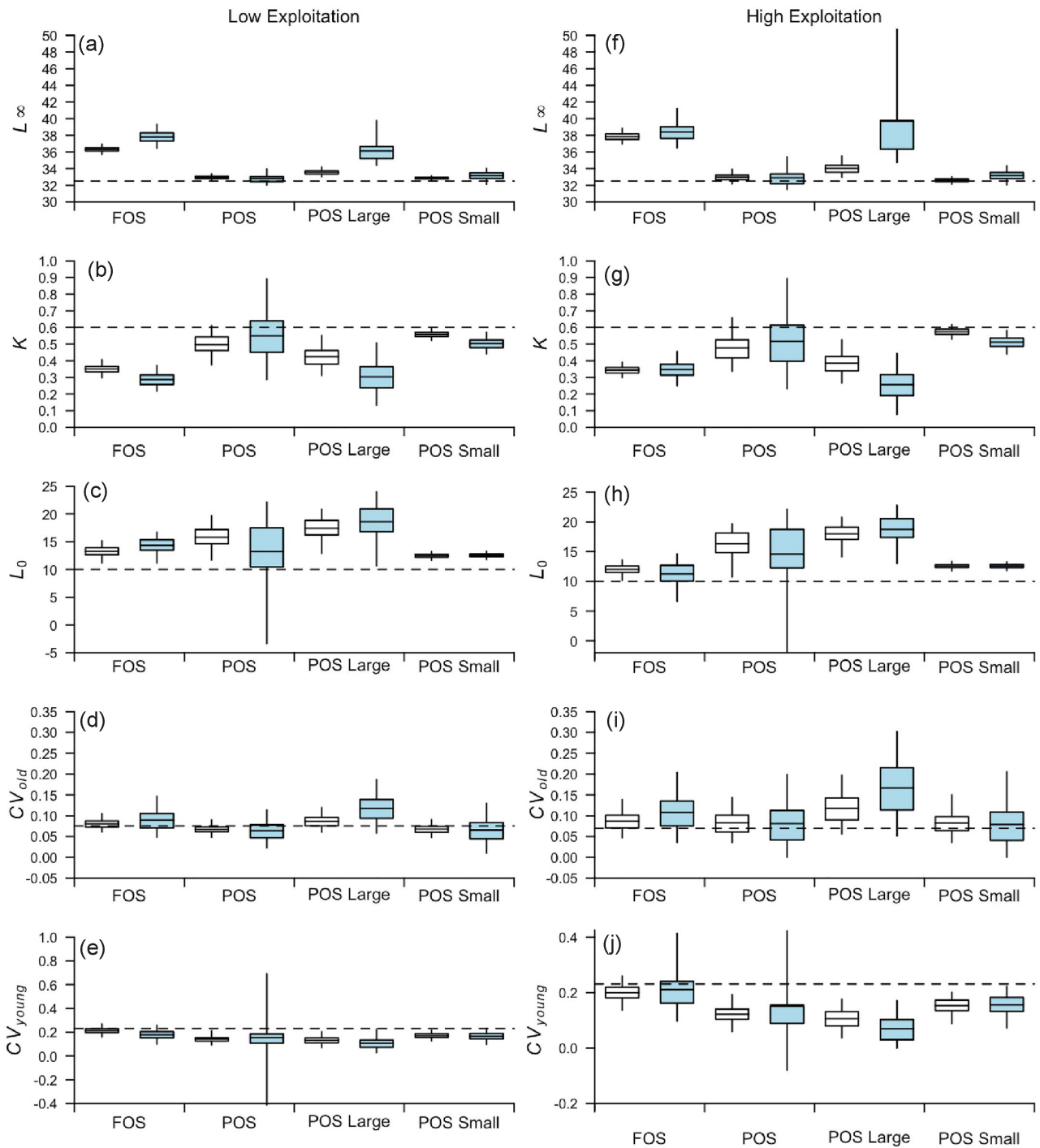
Low sample size increased bias and variability of  $L_{\infty}$  and  $K$  estimates with FOS for *P. auricilla* and *E. coruscans* (Tables 2 and 3; Figures 5 and 6). For example, reducing sample size from 300 to 75 increased the bias in estimated  $L_{\infty}$  by up to 4.6% and estimated  $K$  by up to 10.6% for *P. auricilla* and increased the bias in estimated  $L_{\infty}$  by up to 1.1% and estimated  $K$  by up to 2.8% for *E. coruscans*. Low sample sizes increased the variability of VBGF parameter estimates. For example, for both *P. auricilla* and *E. coruscans* under high exploitation, the standard deviation of estimated  $L_{\infty}$  was up to 2.3 times larger than the high sample size (Supplementary Tables S2 and S3). This increased variability with low sample size was observed around all VBGF parameter estimates.

## POS

POS resulted in VBGF parameter estimates that were closer to the true values compared to FOS in all but one scenario (Tables 2 and 3). In general, POS resulted in a slightly inflated  $L_{\infty}$  and underestimated  $K$  (Figures 5 and 6). At low fishing mortality, the bias in  $L_{\infty}$  was low ( $< 1.4\%$  for *P. auricilla* and  $< 0.7\%$  for *E. coruscans*) and the bias in  $K$  was high ( $> -17.3\%$  for *P. auricilla* and  $> -2.2\%$  for *E. coruscans*).

POS VBGF growth parameters deviated more from true values when the RI was reduced, which often occurred as fishing mortality increased. At high fishing mortality, there was a maximum of  $-1.8\%$  error in  $L_{\infty}$  and  $-20.5\%$  error in  $K$  for *P. auricilla* and a maximum of  $+2.3\%$  error in  $L_{\infty}$  and  $-5.7\%$  error in  $K$  for *E. coruscans*. For *E. coruscans*, there was also high variability (large 95% CI) around the POS VBGF parameter estimates at high fishing mortality. The one scenario that stood apart was for *E. coruscans* when small individuals were present and fishing mortality was high (Table 3; Supplementary Figure S12). In this scenario,  $L_{\infty}$  and  $K$  were slightly more biased under POS ( $L_{\infty} = 2.1\%$  and  $K = -5.4\%$ ) compared to FOS ( $L_{\infty} = 1.5\%$  and  $K = -2.3\%$ ), although neither method was able to replicate the true VBGF in this scenario.

Minimum length at selectivity had mixed effects on POS VBGF parameter estimates. The absence of small individuals did not have much of an influence on the accuracy of  $L_{\infty}$  for either *P. auricilla* or *E. coruscans* (Tables 2 and 3). However, larger size at minimum selectivity greatly increased the negative bias in  $K$  and the positive bias in  $L_0$  for *P. auricilla*. But for *E. coruscans*, greater size at minimum selectivity reduced the negative bias in  $K$  and had little to no effect on  $L_0$ .

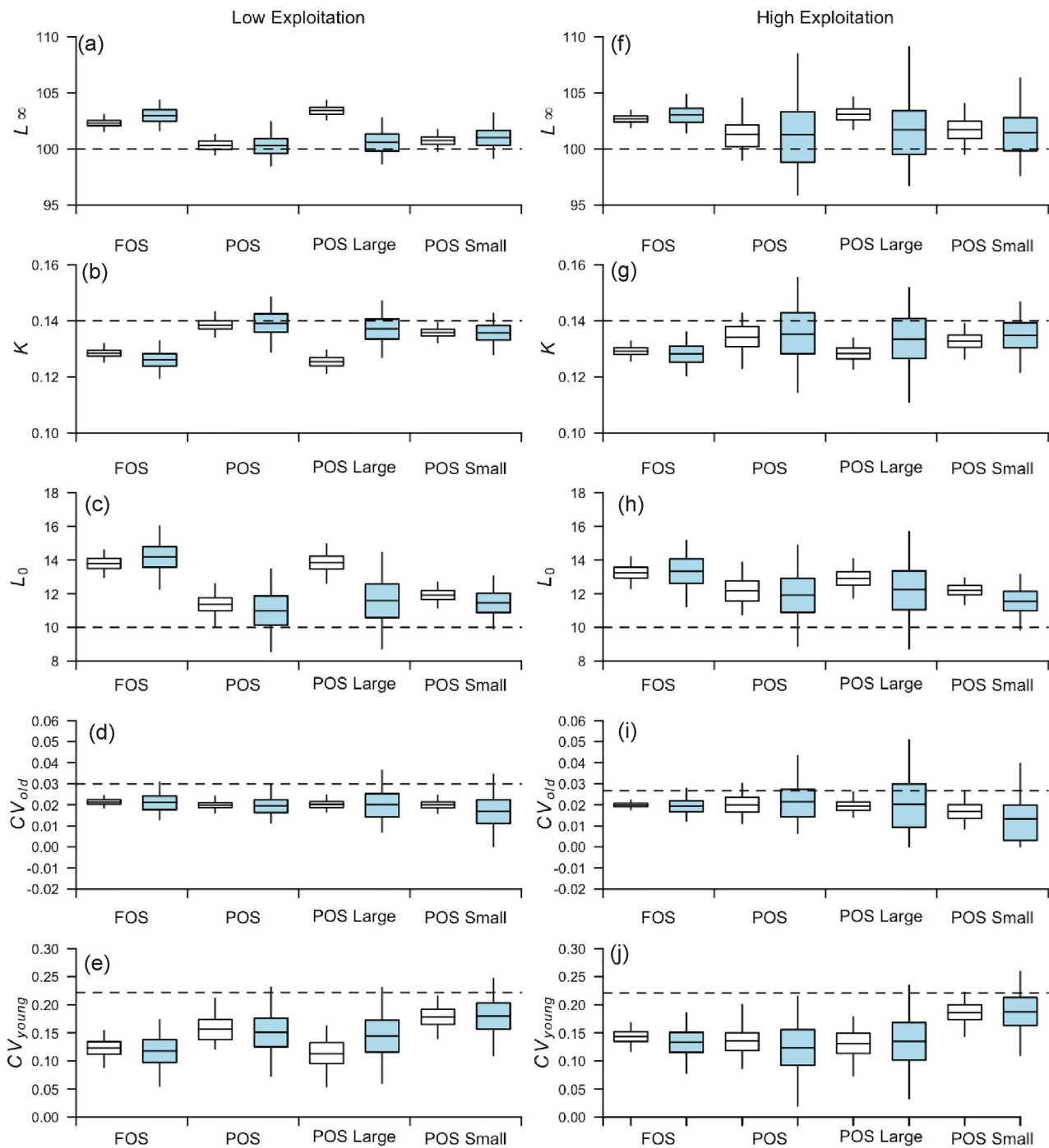


**Figure 5.** Estimated mean, interquartile, and 95% CIs of *P. auricilla* growth parameters for low (a)–(e) and high (f)–(j) fishery exploitation with minimum size at fishery selectivity = 20 cm. A total of four sampling approaches are shown: FOS, POS, POS Large (supplemental samples added to upper size bins), and POS Small (supplemental samples added to lower size bins) with two sample sizes ( $N = 300$ , white;  $N = 75$ , blue). Dashed lines are true parameter values.

The bias in POS  $L_0$  was as much as +62.9% for *P. auricilla* and +21.6% for *E. coruscans* at high fishing mortality when small individuals were absent, compared to +28.1% for *P. auricilla* and +19.0 for *E. coruscans* at high fishing mortality when small individuals were present. However, without small individuals, the VBGF has no observations at its base to help establish the origin of the growth curve; therefore, under cer-

tain scenarios,  $L_0$  becomes more variable (Supplementary Tables S2 and S3; Supplementary Figures S7–S14).

Low sample size greatly increased the probability of inaccurate VBGF parameters under POS. While low sample size did not have much of an effect on the mean POS VBGF parameters from the 1000 bootstraps (Tables 2 and 3), it greatly increased the variability in the POS VBGF param-



**Figure 6.** Estimated mean, interquartile, and 95% CIs of *E. coruscans* growth parameters for low (a)–(e) and high (f)–(j) fishery exploitation with minimum size at fishery selectivity = 30. A total of four sampling approaches are shown: FOS, POS, POS Large (supplemental samples added to upper size bins), and POS Small (supplemental samples added to lower size bins) with two sample sizes ( $N = 300$ , white;  $N = 75$ , blue). Dashed lines are true parameter values.

ters (Figures 5 and 6; Supplementary Figures S7–S14). For example, under high fishing mortality,  $L_{\infty}$  standard deviation was up to 2.2 times larger than the high sample size for *P. auricilla* and up to 2.5 times larger than the high sample size for *E. coruscans* (Supplementary Tables S1 and S2). Regardless of sampling approach, low sample size was associated with increased variability in estimates of all VBGF parameters.

#### Model fitting constrained vs. unconstrained VBGF

Constraining  $L_0$  (or  $t_0$ ) is often done to constrain the growth curve to a reasonable value when small individuals are not in the catch. Because the true value of  $L_0$  in real world situations is often unknown, we employed the commonly used  $t_0 = 0$  ( $a_0 = -1$ ) instead of the population simulations actual estimated  $t_0$ . Constraining the VBGF tended to slightly increase bias in estimates of  $L_{\infty}$ ,  $K$ , and  $L_0$  (Supplementary Figures S7–S14).



The exception was for *P. auricilla* under FOS when small individuals were absent and *E. coruscans* when small individuals were absent and fishing mortality was high, with constraining slightly improving  $L_{\infty}$ ,  $K$ , and  $L_0$ . Additionally, constraining slightly improved VBGF parameters under POS for *P. auricilla* but not *E. coruscans* when small individuals were absent and for *P. auricilla* when small individuals were present and fishing mortality was low.

### Supplemental sampling

Supplemental sampling of small individuals was tested for FOS because additional sampling of small individuals is commonly seen as advantageous for this method. However, we found a minimal influence on estimates of  $L_{\infty}$  and  $K$ , and only a slight improvement in the accuracy of estimates of  $L_0$  with the addition of more small individuals (Tables 2 and 3). Inversely, POS with supplemental sampling can produce highly variable growth curves that are dependent on the type of supplemental sampling done (adding small individuals, adding large individuals, or adding both small and large individuals), the species life history, and the level of fishing mortality.

POS with supplemental sampling of large individuals increased bias in VBGF parameters for both life history types and most scenarios. The bias introduced by supplemental sampling was highest when small individuals were not in the catch and under high fishing mortality (Tables 2 and 3; Figures 6 and 7). For *P. auricilla*, supplemental sampling of large individuals resulted in up to a 21.2% increase in bias for  $L_{\infty}$  and a 43.6% increase in bias for  $K$  at low sample sizes and a 3.2% increase in bias for  $L_{\infty}$  and a 15.5% increase in bias for  $K$  at high sample sizes. For *E. coruscans*, supplemental sampling of large individuals resulted in up to a 0.4% increase in bias for  $L_{\infty}$  and a 1.4% increase in bias for  $K$  at low sample sizes and a 1.8% increase in bias for  $L_{\infty}$  and a 9.3% increase in bias for  $K$  at high sample sizes. Supplemental sampling of large individuals did not have much effect on *E. coruscans* when small individuals were present, with < 0.3% change in  $L_{\infty}$  and < 0.4% change in  $K$  compared to POS without supplemental sampling.

POS with supplemental sampling of small individuals had opposite effects for *P. auricilla* and *E. coruscans* (Tables 2 and 3; Figures 5 and 6). For *P. auricilla* in the absence of small individuals, supplemental sampling of small individuals greatly improved the accuracy of growth parameters, especially  $K$  and  $L_0$ . For example, using a POS sampling strategy combined with supplemental sampling of small individuals improved accuracy for  $L_0$  by 1.1%,  $K$  by 16.1%, and  $L_{\infty}$  by 37.5% compared to POS without supplemental sampling under high fishing mortality ( $N = 300$ ;  $\text{mincat} = 20$  cm). However, for *E. coruscans* in the absence of small individuals, supplemental sampling of small individuals increased the bias of VBGF parameters. For example, POS with supplemental sampling of small individuals reduced the accuracy for  $L_0$  by 0.4%,  $K$  by 3.0%, and  $L_{\infty}$  by 0.3% compared to POS without supplemental sampling under high fishing mortality ( $N = 300$ ;  $\text{mincat} = 30$  cm). Supplemental sampling had no effect or slightly increased bias in VBGF parameters for both *P. auricilla* and *E. coruscans* when small individuals were already present ( $\text{mincat} = 10$  cm).

Supplemental sampling of both small and large individuals resulted in biased VBGF parameters as seen for *P. auricilla* and

*E. coruscans* under all scenarios tested (Tables 2 and 3). Bias in VBGF parameters was highest with small sample sizes.

### Application to *P. auricilla* samples collected from the fisheries of the Mariana Islands

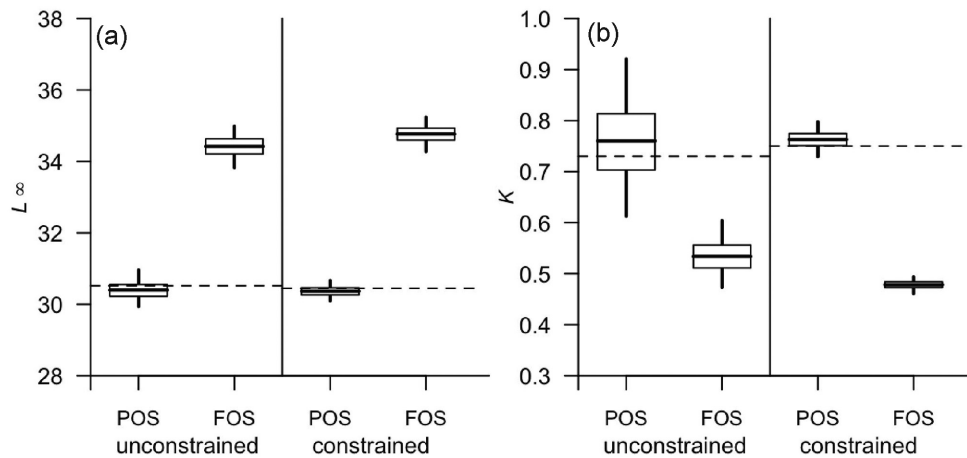
We compared POS and FOS growth parameter estimates from fishery-dependent age-length observations to determine if the best sampling approaches based on the simulation results were consistent with real fishery observations. Known lengths along with ages derived from sectioned otoliths ( $N = 135$ ) used to create the ALK had a higher mean length (+1.1 cm) compared to the distribution observed in fishery catch at length in Guam and Saipan ( $t = 3.40$ ,  $df = 140.72$ ,  $p\text{-value} < 0.01$ ). However, the distributions were considered adequate, with the upper distribution of otolith-aged fish mirroring the fishery catch distribution (Supplementary Figure S15).

The optimum sampling strategy from the simulation results and the fishery-dependent age-at-length observations for a fast-growing fish such as *P. auricilla* was POS. Proportional and FOS growth parameters followed similar patterns to what we observed from simulated *P. auricilla* length-age observations. As would be expected, POS performed better than FOS in providing VBGF parameter estimates close to estimates based on all fishery length-age observations (Table 4, Figure 7). For both POS and FOS, constraining the VBGF (fixing  $t_0 = 0$ ) did not notably affect estimates of  $L_{\infty}$ . However, constraining the VBGF considerably reduced the variability in  $K$  estimated with POS and further underestimated  $K$  under FOS (Table 4, Figure 7).

### Discussion

Our findings support those of previous studies that POS is generally advisable for fast-growing fish species such as *P. auricilla*, Pacific Bluefin Tuna (*Thunnus orientalis*; Chang *et al.*, 2019), Striped Marlin (*Kajikia audax*; Goodyear, 2019), and Vermilion Snapper (*Rhomboplites aurorubens*; Goodyear, 2019). However, the choice of sampling approach for slow-growing, long-lived species, which support many valuable fisheries (e.g. some species of snappers and groupers (Chan and Sadovy, 2002; Newman *et al.*, 2016), Sablefish (*Anoplopoma fimbria*; King and McFarlane, 2003), rockfish (*Sebastes spp.*), and flatfish (i.e. *Hippoglossus stenolepis*; King and McFarlane, 2003)), is often not as straightforward. The impacts of fishery exploitation on population size structure occur much faster, and at lower levels of fishing mortality, for slow-growing, long-lived species compared to fast-growing, shorter-lived species. Therefore, for slow-growing, long-lived species, the best sampling approach will be much more sensitive to factors such as the selectivity of the fishery and level of exploitation, in comparison to faster growing longer lived species. In these cases, the *RI* will help to discern if the catch is representative of the population and if additional sampling considerations (increasing sample size, supplemental sampling, or constraining the growth model) may need to be applied to minimize bias in growth parameter estimation.

Sample size must be considered when choosing a sampling approach. There is a much greater loss in precision with POS at low sample sizes compared to FOS; however, FOS produces less accurate growth parameter estimates than POS (this study) or random otolith sampling (Chih, 2009a; Goodyear, 2019). The precision in growth parameters was found to have



**Figure 7.** Estimated  $L_{\infty}$  (a) and  $K$  (b) for *P. auricilla* from 1000 iterations of sampling for proportional otolith sample (POS) and 1000 iterations of sampling for the fixed otolith sample (FOS) and the resulting  $t_0$  estimated and  $t_0$  fixed ( $t_0 = 0$ ) growth parameter means, interquartile, and 95% CIs from the fishery-dependent length-age observations. The estimated growth parameters from all of the fishery-dependent observations are represented by the dashed line.

**Table 4.** Estimated VBGF parameters (mean and 95% CI, based on 1000 bootstraps) for *P. auricilla* from fishery-dependent POS ( $N = 300$ ) and FOS ( $N = 300$ ). Parameter estimates based on all available age-length specimens (All,  $N = 3623$ ) are included for comparison.

Samples	$L_{\infty}$	$L_{\infty}$ CI		$K$	$K$ CI		$t_0$	$t_0$ CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Unconstrained									
All	30.5	30.3	30.7	0.73	0.55	1.04	-0.1	-0.2	0.1
POS	30.4	29.9	31.0	0.75	0.70	0.93	-0.2	-0.5	0.3
FOS	34.4	33.9	35.0	0.53	0.48	0.60	0.2	0.0	0.4
Constrained									
All	30.5	30.3	30.6	0.75	0.74	0.77			
POS	30.3	30.8	30.7	0.75	0.73	0.80			
FOS	34.6	34.3	35.3	0.47	0.46	0.49			

diminishing returns around a total sample size of 300, which is within the recommended range from previous studies (Kritzer *et al.*, 2001; Brouwer and Griffiths, 2005; Chang *et al.*, 2019). For tropical deepwater fish, if expected sample sizes are at or above 300, sample size is unlikely to be a factor in deciding which approach to apply. Optimum sample size will depend on the variability in age-length observations and maximum size of the fish (Kritzer *et al.*, 2001). For this reason, we recommend evaluating the optimal sampling size for each study species when possible.

While there are many benefits of POS, such as reduced sampling effort compared to FOS and random sampling (Goodyear, 2019), it is seldom used as a sampling strategy. This may be due to the added logistical complexity of setting up and operating such a sampling approach or the need to understand population-level length composition in order to inform a POS sampling approach. Such length composition data are also needed to apply a weighted ALK which may correct for bias from FOS (Kimura, 1977; Goodyear, 2019; Lusk *et al.*, 2021). Our models assumed that samples were available for the upper and lower size bins for FOS, but in reality, the largest and smallest individuals are not regularly encountered in many fisheries, and significant sampling effort would need to be allotted to obtain them. POS may also rarely be used because fishery researchers target individuals from the tails of the size distribution to provide information on longevity, age, and

size at maturity, juvenile growth rates, and validation of ageing criteria (Campana, 2001; Newman *et al.*, 2015; O'Malley *et al.*, 2016). However, it is fairly easy to account for this by sampling additional individuals from the tails of the distribution for other purposes but excluding them from the growth assessment.

While it may be tempting to add additional samples to the tails of size distributions to increase precision in growth parameter estimates or simply because including the smallest and largest fish “feels” reasonable, doing so can result in large increases in growth parameter bias (Coggins Jr *et al.*, 2013; Goodyear, 2019). Our findings are in agreement with prior research that indicated supplemental sampling of large fish can increase bias in growth parameters when applied to POS, with bias upwards of 18% (this study), 100% in  $L_{\infty}$  (Goodyear, 2019), and 50% in  $K$  (Goodyear, 2019). This was especially true for fast-growing fish and was further intensified at low sample sizes (*P. auricilla*: > 18% error in  $L_{\infty}$ , > 57% error in  $K$ ). The primary mechanism to explain this is, fish that grow faster (e.g. in our analysis have higher  $L_{\infty}$ ) reach a large size at a younger age and will have experienced fewer annual opportunities for mortality than a slower-growing (and hence older) fish of equal length. As a result, for a given large size, the fastest growing individuals will be most numerous and will have the highest probabilities of being sampled, whereas the slowest growing individuals will have comparatively lower

probabilities of being sampled and may even be absent. In POS with supplemental sampling, these few large, fast-growing individuals have a disproportionate influence on the linear regression of the growth curve and anchor estimated  $L_\infty$  at a biased value, while concurrently underestimating  $CV_{old}$ . The magnitude of the bias in estimation of  $L_\infty$  depends on how heavily skewed larger sizes are to the fastest growing individuals, which was greatest for the *P. auricilla* because that species approaches  $L_\infty$  in fewer years than *E. coruscans*. In our analysis,  $K$  was underestimated with supplemental large sampling due to the strong negative correlation between  $K$  and  $L_\infty$  rather than direct variability in individual  $K$  because all simulated individuals had identical  $K$  (i.e.  $\sigma_K = 0$ ).

The effect of supplementing small individuals on VBGF parameters was hard to predict and depended on sample size, sampling strategy, fishing mortality, and life history. In general, supplemental sampling of small individuals increased bias in growth by reducing the flexibility of the growth curve near maximum length. Even when small individuals were absent, supplemental sampling of small individuals did not have the expected benefit of increased accuracy in growth parameters for both life history types examined. The effect of supplemental sampling of small individuals was inconsistent between life history types, with improvements in accuracy of VBGF parameters for *P. auricilla* but not *E. coruscans* with the exception of small sample sizes. This is the first study to evaluate sample selection that favours small fish and demonstrates that selecting for small fish is typically not worth the effort and can increase bias in growth parameters. Ultimately, this study and prior research show that if samples are representative of the population, supplemental sampling introduces bias.

Another common correction applied when juveniles are missing from sampling is to constrain the growth model (Kritzer *et al.*, 2001; Williams *et al.*, 2017; O'Malley *et al.*, 2019), such as fixing  $t_0 = 0$  in the VBGF. Our research is in agreement with Kritzer *et al.* (2001) who showed that when small individuals are absent, constraining the VBGF can provide additional information not contained in the sample, improving accuracy and precision of growth parameters. For example, when small individuals are absent and unconstrained models are used, estimates of  $t_0$  may be illogical, with some studies reporting  $t_0 < -8$  years (Craig, 2007). For tropical deepwater fish, it is not uncommon to see estimates of  $t_0 < -3$  years (Uehara *et al.*, 2020). The problem is not the very low estimates of  $t_0$  but rather the reduction in  $K$  (and the increase in  $L_\infty$ ) that corresponds to the model fit; constraining  $t_0$  can improve  $K$  estimates under these conditions which can ultimately effect estimates of natural mortality depending on the method used. Under certain conditions, constrained VBGF can also produce biased estimates of growth. Pardo *et al.* (2013) found no benefit to constrained VBGF over unconstrained models and found that slight deviations in  $L_0$  and the resulting  $t_0$  can cause large increases in bias of VBGF parameters. This makes estimating  $L_0$  and constraining the VBGF inherently risky. Constraining the VBGF should be avoided when small individuals are already present, as we found increased bias or no benefit to constrained models under these conditions. Additionally, in situations where large individuals were missing from the sample, anchoring the lower limit of the VBGF by constraining  $t_0$  reduced the influence of sample length-at-age observations in informing the parameterized VBGF, hence increasing the probability of bias in  $L_\infty$  and  $K$  estimates. Constraining the VBGF should be done with caution

and only under circumstances such as when small individuals are missing from the sample but large individuals are present, a clear asymptote in length-at-age is reached, and/or the unconstrained VBGF is producing illogical estimates of  $K$  and  $t_0$ . Otherwise, our research shows constraining the VBGF will increase bias in growth parameter estimates.

Our IBM combines variability in individual growth and size-selective fisheries to demonstrate the challenges of estimating growth parameters from sampling fishery-dependent catches which were first recognized by fisheries scientist and statistician Rosa Mabel Lee in 1912. Lee noted the average length of fish at the age of harvest was greater than the length-at-age predicted from examining the distances between scale annuli over the lifetimes of fish harvested at older ages (Lee, 1912). She suggested faster-growing individuals were caught at younger ages, whereas slower-growing fish were more likely to survive to be harvested at older ages because fishing gears select fish based on length. This “phenomenon of apparent change in growth rate” is commonly referred to as the Rosa Lee Phenomenon. In our simulated size-selective fisheries, the fastest-growing individuals are over-represented in the catch, and we have shown a strong tendency to overestimate  $L_0$  and  $L_\infty$ . Concurrently, slower-growing individuals and their contribution to the variability of length-at-age are under observed such that  $CV_{young}$  and  $CV_{old}$  are consistently underestimated. This phenomenon is driven by length-selective fisheries, so any of the fishery-dependent sampling approaches we investigated in our study failed to account for its effects. Instead, the prudent researcher may select the best sampling strategy based on our findings but should also report details of the sampling design and estimates of parameter uncertainty and possible bias that can be integrated into stock assessment and in turn inform fisheries management.

The implications of relying on biased estimates of fish growth and population variance in length-at-age are becoming more relevant with increasing reliance on statistical age-structured population models for stock assessment (Lynch *et al.*, 2018; Punt *et al.*, 2020). Time series observations of catch at age are highly informative in age-structured assessment models (Maunder and Piner, 2017), but require collection and analyses of a great number of otoliths or hard parts over many years. Such resource-intensive historic data collection programs are absent from much of the world's smaller fisheries in developing nations, which are often the fish stocks most in need of life history studies and stock assessments (Amorim *et al.*, 2019; Hilborn *et al.*, 2020). Instead, age-structured stock assessments are more likely to use weight or length composition data as model inputs, relying on growth parameters to generate the expected age composition within the assessment model. Inflated length-at-age within the assessment model, especially for older fish, will cause overestimation of fishing mortality and depressed spawning stock biomass, as fish must be removed from the population at a higher rate to account for the observed rarity of large individuals in the catch (Maunder and Piner, 2017; Minte-Vera *et al.*, 2017). Overestimating fishing mortality would in turn lead to management recommendations to reduce catches in an attempt to stop the perceived overfishing and unnecessarily burden fishing communities because of lost yield. Estimates of population variance of length-at-age are of equal importance to estimates of length-at-age themselves in integrated stock assessments, but are rarely included in published age-growth studies (Maunder and Piner, 2017). If variance of length-at-age is low or under-



estimated as is predicted by our results, length–composition data will gain an over-inflated importance within the assessment model (i.e. contributes to the heavy weighting of composition data and the false confidence in their informativeness; Ono *et al.*, 2015). The relationship between assessment advice and misspecifying variance of length-at-age is less clear than for growth parameters such as  $L_{\infty}$ , but several studies suggest underestimating population variance in length-at-age would lead to underestimates of  $F$  resulting in overly risky harvest advice (Zhu *et al.*, 2016). Hence, even when relying on our recommendation of using POS for species which exhibit fast growth, it is likely that population variance in length-at-age will be underestimated. Researchers may wish to weigh length composition data within the assessment model appropriately (Francis, 2017) or include sensitivity analyses of higher population variance in length-at-age estimates in order to generate more risk-adverse harvest recommendations.

We have demonstrated fishery dynamics and life history are important when selecting a sampling approach. Additionally, we have provided a tool to simulate length-selective fisheries catches and investigate how sampling approaches can influence bias and uncertainty in life history parameter estimation. The tool is flexible to account for a range of life histories and realistic fishery dynamics, while including common sample design options. Although we focused on von Bertalanffy growth for our analysis of sampling approaches for deepwater snappers, the IBM also includes the option to model linear-von Bertalanffy multi-stanza growth, which may be more realistic for some fish species (Quince *et al.*, 2008; Zhu *et al.*, 2016). We suggest future research focus first on additional aspects of individual and fishery-level processes, including multi-stanza growth, variability in  $K$ , covariance among growth parameters, more diverse fish life history strategies (including a finer time step to more accurately represent fast-growing species), and dome-shaped fishery selectivity (e.g. large fish are not vulnerable to capture by fishermen). Furthermore, an inherent assumption in our simulation model is that all cohorts comprising the population experienced identical conditions and had underlying individual growth parameters selected from a common distribution, hence the system was assumed to be in a steady state. Future extensions of our IBM may include additional dynamics such as time-varying growth, recruitment, and exploitation.

## Supplementary material

**Supplementary material** is available at the ICES/JMS online version of the manuscript. Supplementary material includes tables of growth parameters for all scenarios, additional information on model mortality and selectivity, precision of growth parameters under varying bin and sample sizes, and additional graphical representations of tested scenarios on growth parameters.

## Conflicts of interest

The authors declare that there are no conflicts of interest.

## Authors' contributions

ES and EB had equal contribution in the analysis and writing of the manuscript. JO generated the research idea and supported the development and review of the manuscript.

MK supported the development, analysis, and review of the manuscript.

## Data availability

The majority of the data underlying this article comes from simulated populations and the code to generate the data is available at <https://github.com/evasschemmel-NOAA/LHsampling>. Fishery dependent observation data are available at Pacific Islands Fisheries Science Center. 2021. *Life History Program Life History Estimates*, <https://inport.nmfs.noaa.gov/inport/item/59002>.

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