

Characterizing fish populations: effects of sample size and population structure on the precision of demographic parameter estimates

J.P. Kritzer, C.R. Davies, and B.D. Mapstone

Abstract: We examined precision of size, age, growth, and mortality parameters for four reef fishes at sample sizes ranging from 25 to 1000 using bootstrapped population samples. The results are illustrative rather than prescriptive in that we do not determine “optimum” sample sizes, but rather describe improvements in precision with increasing sample size. Furthermore, we do not address the related issue of accuracy. In general, a sample size needed to be tripled to halve precision at that sample size. Mean lengths and ages were most precise, reaching 10% by a sample size of 75 for all species. von Bertalanffy growth parameters were up to an order of magnitude more precise when constraints were placed upon the fitting process. Asymptotic lengths, L_{∞} , were up to eight times as precise as Brody growth coefficients, K . Catch curves were generally less precise than two other mortality estimators, but we cannot advocate any estimator until accuracy is addressed. We propose a general rule of collecting an average of 7–10 fish per age-class to estimate a variety of parameters. However, we more strongly suggest applying similar analyses for focal species and, where possible, with consideration of the application of parameters (e.g., sensitivity analyses).

Résumé : À l'aide d'échantillons de populations soumis au bootstrap, nous avons examiné la précision des paramètres de taille, d'âge, de croissance et de mortalité pour des échantillons de 25 à 1 000 individus chez quatre poissons de récifs. Nos résultats sont illustratifs plutôt que prescriptifs parce que nous n'avons pas déterminé la taille « optimale » des échantillons, mais plutôt décrit l'amélioration de la précision avec la taille croissante de l'échantillon. Nous n'avons pas non plus considéré le problème apparenté de l'exactitude. En général, il faut tripler la taille de l'échantillon pour réduire de moitié la précision à cette taille d'échantillon. Les longueurs moyennes et les âges sont les variables les plus précises, atteignant 10% pour une taille d'échantillon de 75 chez toutes les espèces. Les paramètres de croissance de von Bertalanffy sont plus précis par un facteur allant jusqu'à 10 lorsque des contraintes sont placées sur le processus d'ajustement. Les longueurs asymptotiques, L_{∞} , sont jusqu'à huit fois plus précises que les coefficients de croissance de Brody, K . Les courbes de capture sont généralement moins précises que deux autres estimateurs de la mortalité, mais nous ne pouvons en recommander aucun tant que la question de l'exactitude n'aura pas été étudiée. Nous proposons, comme règle générale, de récolter en moyenne sept à 10 poissons par classe d'âge pour l'estimation d'une variété de paramètres. Cependant, nous suggérons encore plus fortement de faire subir des analyses semblables aux espèces-cibles et, quand c'est possible, de tenir compte de l'application des paramètres (e.g., des analyses de sensibilité).

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Introduction

The precision and accuracy of a parameter estimate for a fish population will likely be a function of biological characteristics of the population, sampling gear used, sampling design, and number of samples obtained. While the effects of sampling biases on the accuracy of parameter estimates have received some attention (e.g., Goodyear 1995), precision is

less frequently considered. Methods exist for determining requisite precision and associated sample size for certain objectives, such as testing for specified differences between populations or treatments (Desu and Raghavarao 1990). However, the point at which differences are deemed “important” is effectively arbitrary and unlikely related to biological importance (Johnson 1999). Resource managers might need to determine precision required to detect specified “sig-

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nificant" differences to trigger management decisions, although the chosen significance level may be arbitrary. In contrast, researchers doing baseline fisheries biology or descriptive marine ecology should not aim for arbitrary precision levels, but rather should strive to attain the most precise yet cost-effective data possible to maximize the future utility of their results.

Features of tropical reefs pose practical difficulties for researchers. Reef fish assemblages are diverse (Thresher 1991) and coral reef fisheries are characterized by a multispecies catch (Russ 1991). Management requires assessment of multiple stocks, complicating selection of species-specific sample sizes. Additionally, spatially explicit data might be required because reef fishes have a complex spatial structure (e.g., Hart and Russ 1996). This will further restrict potential sample sizes. Finally, the high public profile afforded coral reefs generates social pressure to minimize sampling impacts. This is especially true for research in protected areas (ASTEC 1998), which can provide important insights into anthropogenic effects (e.g., Ferreira and Russ 1995).

Demographic traits of demersal tropical fishes, such as growth parameters, have been estimated with sample sizes ranging from less than 20 (e.g., Dee and Radtke 1989) to greater than 1000 (e.g., Manooch and Hassler 1978). Clearly, more attention to sample size effects on the precision of parameter estimates is needed. We apply a bootstrapping approach, akin to that proposed by Manly (1996), to assessment of precision of parameters of interest to marine ecologists and fisheries biologists (size, age, growth, and mortality parameters). Estimation of multiple parameters enables us to compare the relative precision of different parameters at common sample sizes. We apply the analysis to age-length data sets for four fish species caught in the Great Barrier Reef line fishery, which enables exploration of the effects of underlying population traits, such as longevity and growth trajectory, on precision.

Methods

Data sets analyzed

We used age-length data sets for four species of reef fishes commonly caught on the Great Barrier Reef: *Cephalopholis cyanostigma* (Serranidae), *Lethrinus miniatus* (Lethrinidae), *Lutjanus carponotatus* (Lutjanidae), and *Plectropomus leopardus* (Serranidae) (Fig. 1; Table 1). Real rather than simulated data were used to capture the inherent structure and variation of sampled populations. All data sets represent 1 or 2 years of data collected during fishery-independent sampling programs. The spatial scope of sampling ranges from a single reef (*P. leopardus*) to 24 reefs spanning 7° of latitude (*C. cyanostigma*). While spatial variation is an important focus of the three theses from which the *C. cyanostigma*, *Lethrinus miniatus*, and *Lutjanus carponotatus* data were obtained, our focus is not on the ecology of these species. However, inclusion of data from multiple locations increases the degree of variability in the data sets and makes our results more conservative.

Our data sets span not only four species but also two sampling gears: spear and hook and line. No species was sampled by both gears. Hence, species and gear are confounded and we cannot discern effects due to population biology from those due to gear selectivity. Furthermore, no data exist by which to assess whether the populations have been affected by fishing. Results are therefore interpreted in terms of differences between the *sampled* populations

and not those strictly due to real population structure, gear selectivity, and (or) history of exploitation.

The four data sets used in this analysis all contained at least 500 age-length data pairs and were considered by the authors to be large enough to encompass the range of natural variation in the population that could be observed for each species by a given sampling method. This largely subjective assessment, an alternative to which we advocate, was based in part on a cursory review of sample sizes reported in a range of publications on demersal tropical fish growth. A sample size of 500 falls above those used in many studies.

The four sampled populations exhibit diverse characteristics (Fig. 1; Table 1). The *P. leopardus* sample contains the largest fish and the greatest range of sizes but the shortest life span, while the *C. cyanostigma* data contain the smallest maximum size and the most restricted size range but the greatest longevity. The *Lethrinus miniatus*, *P. leopardus*, and *Lutjanus carponotatus* data show decreasing modal age-classes, respectively, and therefore increasing left-hand skew. Data for these species also show a regular decline in age frequencies beyond the modal age-class. In contrast, the *C. cyanostigma* data show no single pronounced mode and no trend of decreasing age frequencies until after age 25.

Preliminary estimates of each species' mean asymptotic size were obtained by taking the average length of the 10 largest fish in each data set (Pauly 1984). We then calculated the percentage of each mean asymptotic size represented by the mean size at 25% of the maximum age. These percentages give an indication of the extent to which each species' growth trajectory reaches a plateau and suggest that *P. leopardus* has less asymptotic growth than the other species. *Cephalopholis cyanostigma*, *Lethrinus miniatus*, and *Lutjanus carponotatus*, on the other hand, all attain approximately three quarters of their mean asymptotic size by one quarter of their maximum age.

Bootstrapping procedure

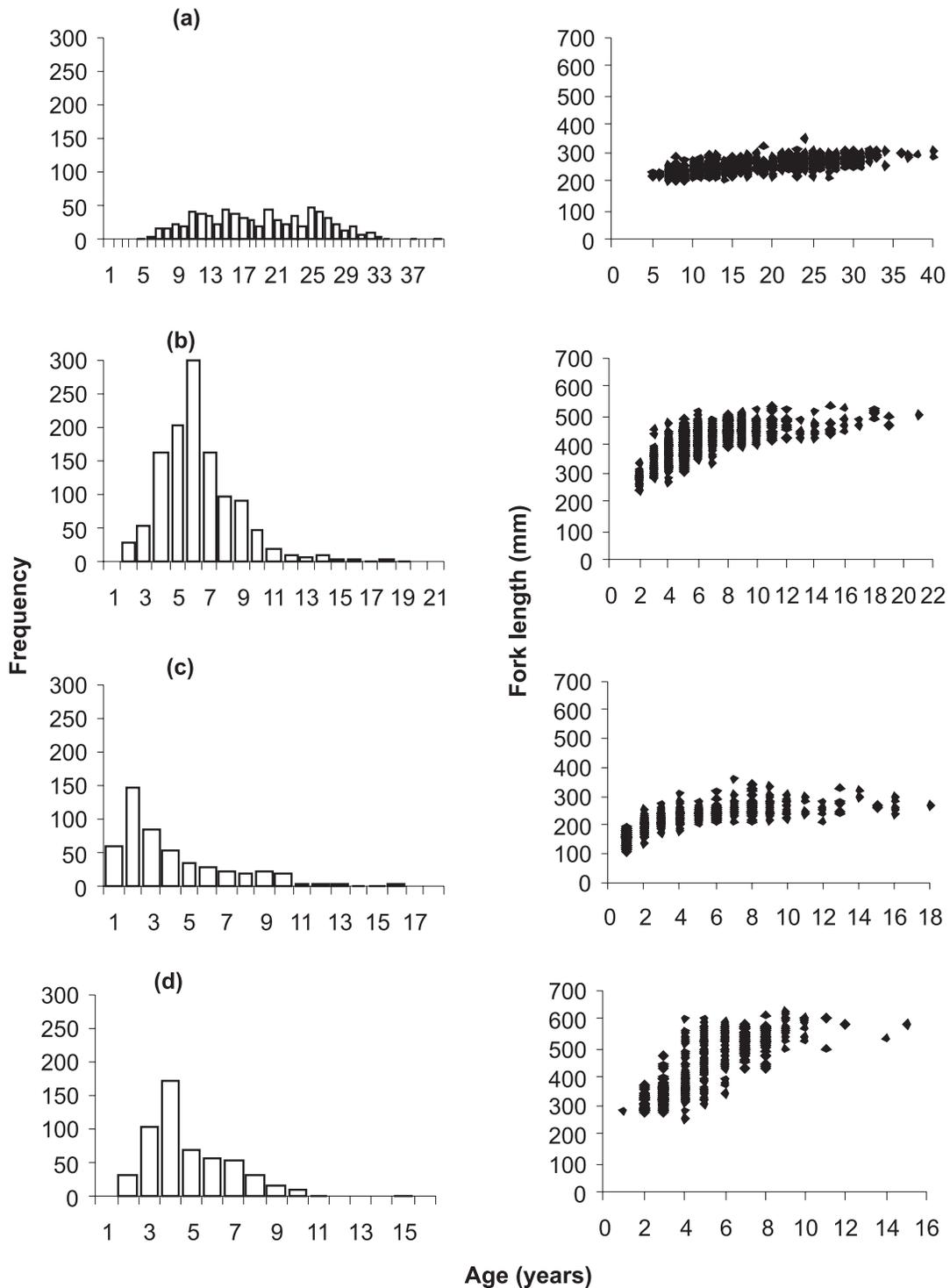
Random samples ranging in size from 25 to 1000 were drawn with replacement from a given age-length data set. Sampling with replacement implies an assumption that much of the range of variation in the vulnerable population has been captured in the available sample and any additional fish collected would fall within the bounds of our sample. For each sample size, 250 separate random samples were selected. Pilot simulations indicated that estimates of precision did not differ greatly between separate groups of 250 samples, nor did they differ between groups of 250 and 500 or 1000 samples.

Parameter estimation procedures

From each sample, a suite of population parameters was estimated and an age structure was constructed. Parameters included several measures of central tendency (mean length, \bar{L} ; mean age, \bar{t} ; modal age, t_{mode} ; median age, t_{med}), the estimation of which was straightforward. Due to the multimodal nature of its age structure, modal age was not estimated for *C. cyanostigma*. We also estimated longevity, t_{max} , as the oldest age-class in the sample.

Two von Bertalanffy growth functions (VBGFs) were fitted to each sample by least-squares nonlinear regression of length on age to estimate precision of the Brody growth coefficient, K , and the mean asymptotic length, L_{∞} . The first set of VBGF parameters, K_u and $L_{\infty,u}$, was estimated with the fitting procedure unconstrained (subscript "u"). However, estimation of VBGF parameters is sensitive to the distribution of sizes and ages in the sample (for an empirical example, see Ferreira and Russ 1994). Often, the youngest and smallest fish will be underrepresented due to sampling biases, irrespective of sample size. We addressed this sample size independent problem by estimating a second set of VBGF parameters from each sample, K_c and $L_{\infty,c}$, constraining (subscript "c") the y-intercept to a reasonable range of settlement sizes for reef fishes

Fig. 1. Age frequency and size at age data for the samples of (a) *C. cyanostigma*, (b) *Lethrinus miniatus*, (c) *Lutjanus carponotatus*, and (d) *P. leopardus*.



based on data reviewed by Victor (1991). The validity of these constraints is less important in the present study than the general comparison of constrained versus unconstrained fitting of VBGFs. (Note that the age at theoretical length 0, t_0 , is generally of little interest to biologists but does affect estimates of the other two parameters. We do not address the precision of t_0 herein but do indirectly address its influence by constraining the VBGF fits.)

We estimated natural mortality using the method of Pauly (1980)

and total mortality using the methods of Ricker (1975) and Hoenig (1983). The regression method proposed by Pauly (1980), which predicts natural mortality from VBGF parameters and water temperature, was used to generate two estimates of the natural mortality rate: $M_{\text{Pauly,u}}$ using VBGF parameters estimated by the unconstrained fitting procedure and $M_{\text{Pauly,c}}$ using VBGF parameters estimated by the constrained fitting procedure. An estimate of the mean water temperature on the central Great Barrier Reef (26°C) (Lough 1994)

Table 1. Pertinent characteristics of fishery-independent data sets analyzed in this study.

Species	Sampling gear	Year(s)	Location(s)	n	t_c	t_r	t_{max}	Size range (mm fork length)	% L_{∞} at 25% t_{max}
<i>Cephalopholis cyanostigma</i>	Hook and line	1995–1996	24 reefs spanning 7° latitude, Great Barrier Reef	754	5	12	40	201–353	77
<i>Lethrinus miniatius</i>	Hook and line	1995	18 reefs spanning 3° latitude, Great Barrier Reef	1215	2	6	21	242–534	78
<i>Lutjanus carponotatus</i>	Spear	1997–1998	Palm Island group, central Great Barrier Reef	527	1	2	18	105–360	73
<i>Plectropomus leopardus</i>	Hook and line	1995	Bramble Reef, central Great Barrier Reef	556	1	4	15	257–625	62

Note: n , sample size of original data set; t_c , age at first capture; t_r , first mode in age structure, assumed age at full recruitment to the gear; t_{max} , oldest age-class in the sample; % L_{∞} , percentage of mean asymptotic size (L_{∞} estimated as the mean size of the 10 largest fish; Pauly 1984). Sources: *C. cyanostigma*: J.W. Mosse (James Cook University, Townsville, Queensland 4811, Australia, unpublished data); *Lethrinus miniatius*: Williams (1997); *Lutjanus carponotatus*: J.P. Kritzer (unpublished data); *P. leopardus*: Effects of Line Fishing Project, CRC Reef Research Centre, James Cook University (unpublished data).

was used in these calculations. The age-based catch curve of Ricker (1975) was used to estimate the total mortality rate, Z_{Ricker} . Catch curves were fitted from the first mode in the age structure of each random sample through to the last age-class before two consecutive frequencies of zero. Here, sample size refers to the number of fish in the sample and not the number of fish actually used in the final catch curve analysis given that fish that fell into age-classes before the first mode and beyond two consecutive zero frequencies were excluded from estimation of Z_{Ricker} . Because the age structure suggested excessive violations of the assumptions of constant recruitment and constant mortality, Z_{Ricker} was not estimated for *C. cyanostigma*. The longevity estimate, t_{max} , was used in Hoening's (1983) equation to generate a second estimate of total mortality rate, $Z_{Hoening}$.

Calculation of precision

Precision is typically defined as the ratio of the standard error of a parameter to the estimate of that parameter (Andrew and Mapstone 1987). However, the standard error is an estimate of the standard deviation of a hypothetical series of parameters estimated using repeated samples (Andrew and Mapstone 1987). Because our simulations produced an actual set of parameters estimated using repeated samples, we used the ratio of the standard deviation of the set of parameter estimates to the mean of those estimates as the estimate of precision. Specifically, we define the precision of parameter x at sample size n as

$$P_{x,n} = \frac{s_{x,n}}{\bar{x}_n}$$

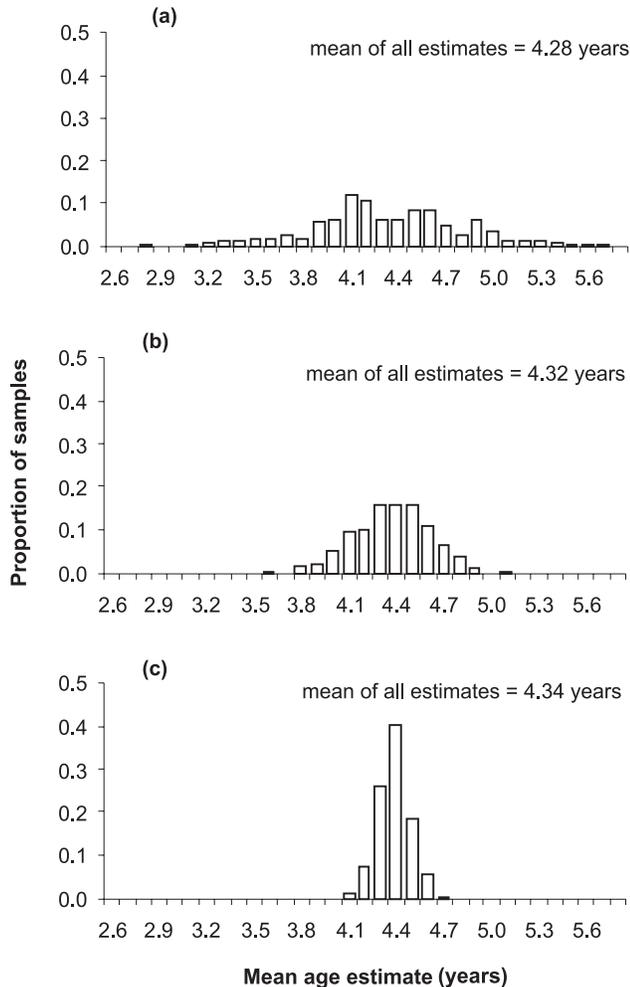
where $s_{x,n}$ is the standard deviation and \bar{x}_n is the mean of the 250 estimates of parameter x at sample size n . This provides a standardized, unitless index that can be compared between different parameters and populations (Andrew and Mapstone 1987).

Precision of predicted age structures was estimated by a modification of the Worthington et al. (1995) D index. Worthington et al. (1995) examined the effects of age determination and sampling errors on accuracy of estimated age structures by using the mean deviation of the proportion in each age-class in a predicted age structure from the proportion in each age-class in the true age structure. Because our focus is on precision rather than accuracy, we used an internal reference derived from the bootstrap data rather than an assumed true external reference. We calculated the deviation of the proportion in an age-class predicted by each random sample from the mean proportion in that age-class over 250 iterations at that sample size. The mean of these individual deviations over 250 iterations was then calculated for each age-class. Finally, precision was calculated as the sum of the mean deviations over all age-classes at that sample size. Specifically, the precision of an age structure estimated from 250 samples of size n is

$$D_n = \sqrt{\sum_{i=1}^{t_{max}} \left(\frac{\sum_{j=1}^{250} (\bar{p}_{i,n} - p_{i,j,n})^2}{250} \right)}$$

where t_{max} is the oldest age-class in the sample, $\bar{p}_{i,n}$ is the mean proportion in age-class i over all 250 samples of size n , and $p_{i,j,n}$ is the proportion of sample j in age-class i at sample size n . This index cannot be compared with precision estimates for other parameters. However, like the P index, it enables comparison of sample size effects on age structure estimation between different populations and can indicate where improvements from additional sampling are minimal.

Fig. 2. Example of effects of sample size on the potential range of values that a parameter estimate is likely to take. Distribution of estimates of the mean age of *Lutjanus carponotatus* derived from 250 bootstrapped samples of size (a) 50, (b) 200, and (c) 1000.



Results

The complete set of precision estimates for each species – parameter – sample size combination is presented in the Appendix. Groups of informative results are plotted in Figs. 3–6.

The mean of the estimates of any given parameter was similar across sample sizes, but the variability about the mean of the estimates drastically decreased with increasing sample size (Fig. 2). The effect of this decreasing variability is that improvement in precision associated with increasing sample size for all species–parameter combinations follows a decreasing power function and illustrates the “law of diminishing returns” (Figs. 3–6). In general, to achieve a halving of the P value at a given sample size requires more than tripling that sample size. Despite this general pattern, both relative and absolute improvements in P for a common change in n varied between parameters and, to a lesser extent, species. For example, increasing the sample size from 50 to 100 *Lutjanus carponotatus* will improve the precision of K_u by

0.086, a change of 29% P at $n = 50$. However, the precision of $L_{\infty, u}$ will only improve by 0.033, a 49% change. Similarly, increasing n from 50 to 100 *P. leopardus* will improve the precision of t_{\max} by 0.029, a 14% change. An equivalent increase in the number of *C. cyanostigma* samples will only provide an improvement of 0.01, an 11% change.

For all species at all sample sizes, \bar{L} was the most precise parameter estimated. Differences in P values for this parameter at most sample sizes improved by roughly constant amounts from *P. leopardus* to *Lutjanus carponotatus* to *Lethrinus miniatus* to *C. cyanostigma*. Also consistently among the most precise parameters estimated was \bar{t} , although at many sample sizes, its precision was still an order of magnitude poorer than that of \bar{L} . *Cephalopholis cyanostigma* again exhibited the most precise estimates of this parameter, followed closely by *Lethrinus miniatus* and *P. leopardus* with similar precision levels (Figs. 3a, 3b, and 3d). In contrast, \bar{t} estimates for *Lutjanus carponotatus* across all sample sizes were typically up to twice as imprecise as those for the other species (Fig. 3c).

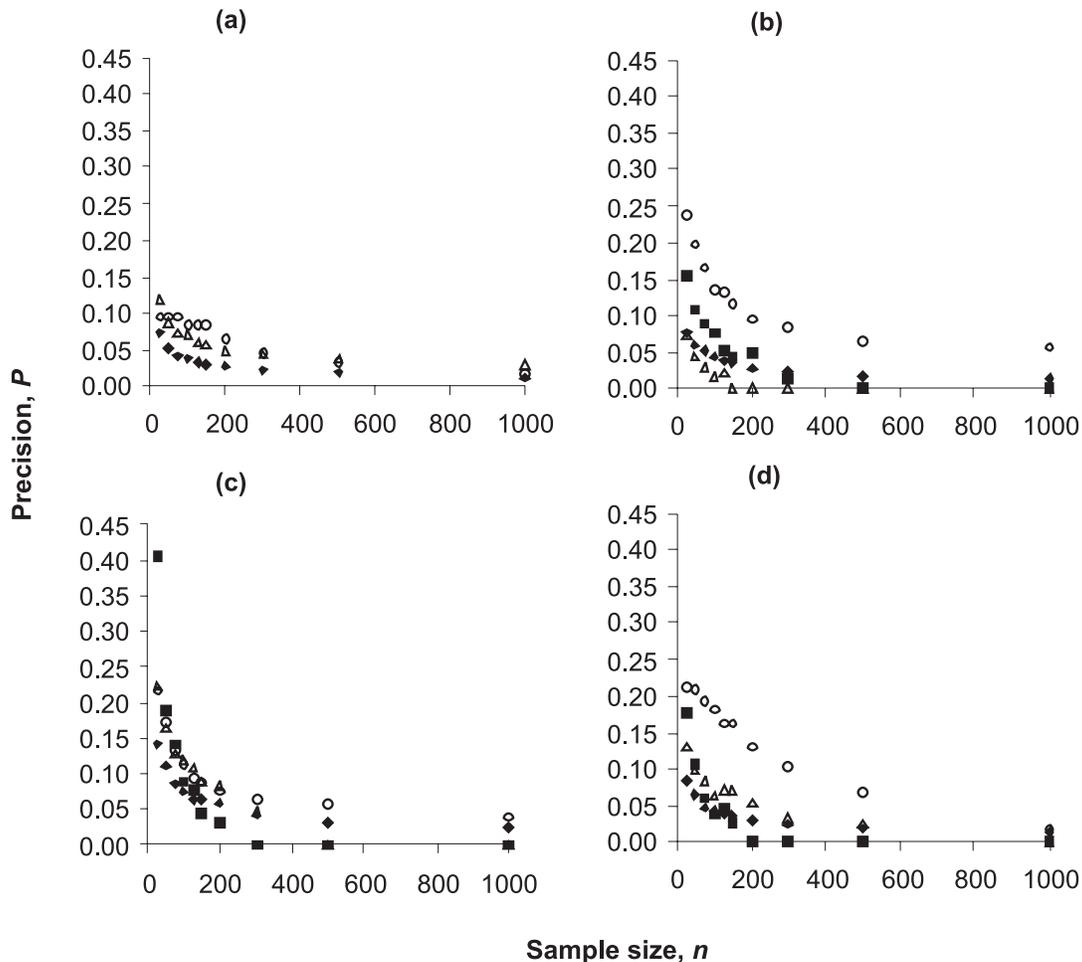
The precision of t_{\max} was generally the poorest of any age parameter (Figs. 3b–3d). The precision of t_{mode} was initially poorer than \bar{t} for all species (with the exception of *C. cyanostigma* for which t_{mode} was not estimated) but became slightly more precise at larger sample sizes and eventually showed no variation (Figs. 3b–3d). Estimates of t_{med} also showed high precision, reaching 0.01 or less at sample sizes less than 100 for all species (Figs. 3a, 3b, and 3d) except *Lutjanus carponotatus* (Fig. 3c).

Not surprisingly, placing constraints upon the fitting process led to more precise VBGF parameter estimates for all species. Parameters estimated by constrained fitting procedures were 2–10 times more precise than those estimated without constraints (Fig. 4). The magnitude of the difference between the two methods was always less for L_{∞} than for K (Fig. 4). The estimates of L_{∞} were 4–10 times more precise than those of K , with the greatest differences occurring when no constraints were placed upon the fitting process (Fig. 4). Estimates of L_{∞} for *P. leopardus* (Figs. 4b and 4d) and of K for *C. cyanostigma* (Figs. 4a and 4c) were always the least precise of all species, irrespective of estimation method.

The magnitude of the differences in precision of M_{Pauly} utilizing the two sets of VBGF parameters mirrored the differences in precision between the two VBGF fitting methods, with the actual P values being approximately the average of the precision of the two parameters used in its estimation. Between-species differences likewise mirrored the differences in precision of the growth parameters, with more precise estimates of M_{Pauly} being produced for *Lutjanus carponotatus* and *Lethrinus miniatus*. Similarly, the precision of the Z_{Hoenig} estimator was nearly equivalent to the precision of t_{\max} . With few exceptions, these two mortality estimators based on the values of other parameters were generally as or more precise than Z_{Ricker} (Figs. 5b–5d). Estimates of Z_{Ricker} for *P. leopardus* and *Lutjanus carponotatus* were the most precise (Figs. 5b and 5d), followed by those for *Lethrinus miniatus* (Fig. 5c).

The precision indices for estimated age structures, D , were surprisingly similar among the four species at all sample sizes (Fig. 6). This was the case despite the pronounced difference between the overall character of the *C. cyanostigma*

Fig. 3. Precision, P , of estimates of the mean age, modal age, median age, and maximum age (i.e., longevity) of (a) *C. cyanostigma*, (b) *Lethrinus miniatus*, (c) *Lutjanus carponotatus*, and (d) *P. leopardus* across a range of sample sizes, n . The multimodal nature of the *C. cyanostigma* age frequency data meant that modal age estimation was not appropriate. \blacklozenge , mean age; \blacksquare , modal age; \triangle , median age; \circ , maximum age.



age structure and those for the other species and the differing modal and maximum ages between all species (Fig. 1). At small sample sizes, the precision of *C. cyanostigma* age structures was slightly poorer than for the other species, but by a sample size of 200, the four species' D values were nearly identical (Fig. 6). The pattern of flattening observed in the D versus n functions (Fig. 6) was similar to that observed in the various P versus n functions (Figs. 3–5). The precision of age structures showed steady improvement up to sample sizes of around 150–200 (Fig. 6). Thereafter, more than doubling the sample size from 200 to 500 improved precision by only approximately one third the D value at $n = 200$.

Discussion

Length and age parameters

Mean length, mean age, and modal age could consistently be estimated with high precision at small sample sizes relative to other parameters. This can prove useful when managing fisheries with a diverse multispecies catch. Changes in populations of less commercially important species can be

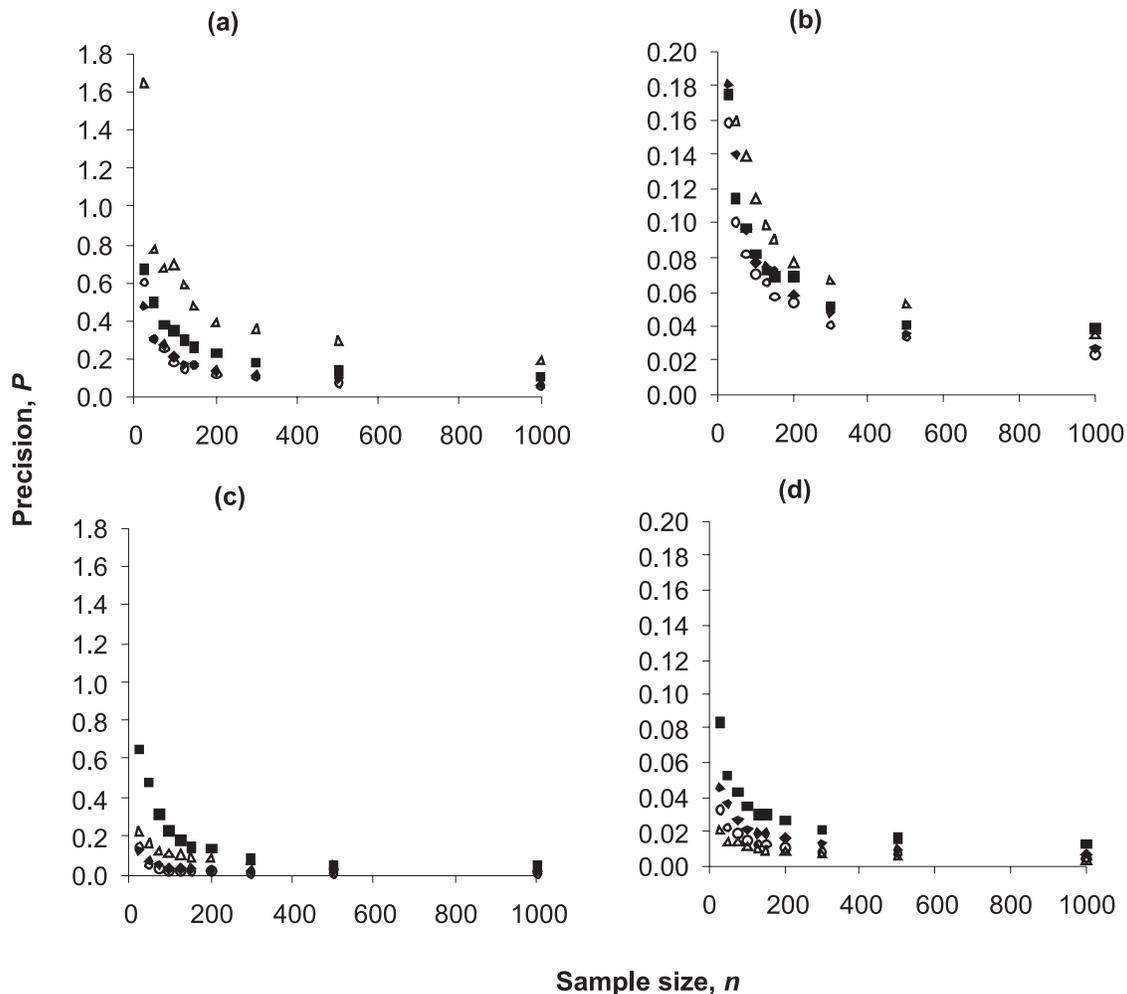
monitored by these simpler measures with low data requirements, while the bulk of resources is devoted to more sophisticated parameter estimation for primary target species. The high precision of mean lengths at small sample sizes (i.e., $P \ll 0.1$ at $n = 25$ for all species) is particularly relevant when data are collected dockside under time constraints amidst unloading of catch (see Gulland 1966).

Growth parameters

Constraining the VBGF fit might be regarded as artificially improving precision by restricting the potential range of values that each parameter can take. There is some truth to this assessment, but it misses the more important point that constraining the VBGF fit is essentially providing additional information not contained in the sample. If the VBGF is an appropriate model for the species in question, this will improve accuracy as well as precision by forcing the curve to better account for changes in size throughout life. Therefore, employing biologically meaningful constraints is likely to result in more accurate estimates and deliver equivalent precision using fewer samples.

The late age at first capture and little curvature in the

Fig. 4. Precision, P , of estimates of the von Bertalanffy growth parameters (a and b) K and (c and d) L_∞ for four species of coral reef fishes estimated with the y -intercept both unconstrained (Figs. 4a and 4c) and constrained (Figs. 4b and 4d) across a range of sample sizes, n . Precision differed by approximately an order of magnitude between constrained and unconstrained fits, so the left and right plots are presented with different y -axis scales. Δ , *C. cyanostigma*; \circ , *Lethrinus miniatus*; \blacklozenge , *Lutjanus carponotatus*; \blacksquare , *P. leopardus*.



C. cyanostigma data would appear to implicate sampling bias rather than biological traits in the relative imprecision of estimates of K . Further supporting this is the comparable precision seen in K for the other species, which all have some 1- and (or) 2-year olds represented, despite differing maximum sizes, size ranges, and growth trajectories. In contrast, the precision of L_∞ estimates appears heavily reliant upon underlying biology, as the poorest precision was associated with the least asymptotic growth trajectory (*P. leopardus*). However, sampling biases might also be important here if the selectivity function is domed rather than asymptotic, thereby undersampling larger and older individuals. Alternatively, the lower precision of L_∞ for *P. leopardus* might result because the von Bertalanffy function is not appropriate for the species, which might instead require a nonasymptotic model (Schnute 1981).

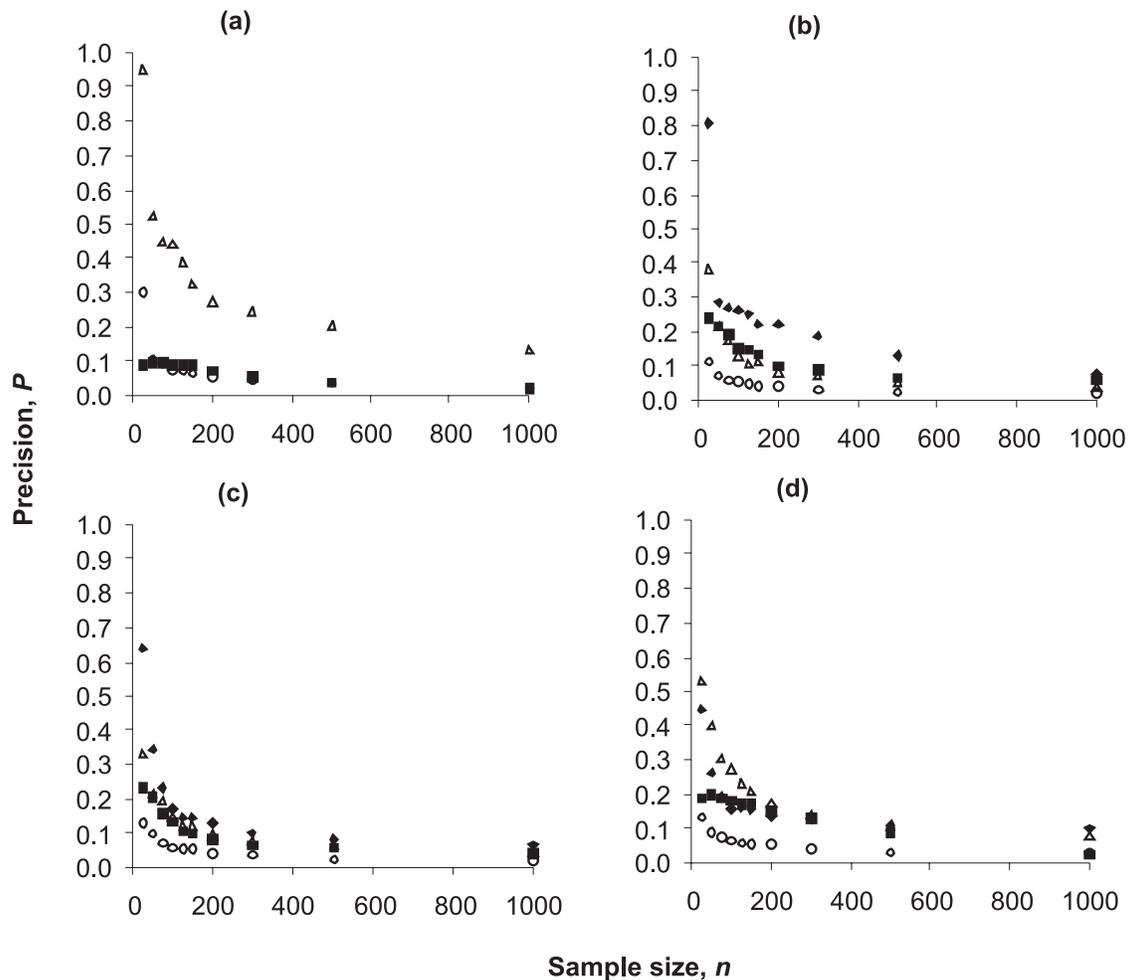
Longevity and mortality

Longevity does not appear to be important to its own estimation. Estimates of t_{\max} for the longest-lived species, *C. cyanostigma*, were most precise and estimates of t_{\max} for

the shortest-lived species, *P. leopardus*, were least precise. However, the distribution of fish among older age-classes seems to be important. The ranking of the species from highest to lowest percentage of fish in the last 20% of age-classes is the same as the ranking of t_{\max} estimates from most to least precise (i.e., *C. cyanostigma*, *Lutjanus carponotatus*, *Lethrinus miniatus*, *Plectropomus leopardus*). In other words, longevity estimates will be less precise for populations with a comparably thinner “tail” in their age distribution.

On the surface, the results suggest that the regressions of Hoenig (1983) and Pauly (1980) are less data-intensive mortality estimators than the age-based catch curve of Ricker (1975). However, we would be remiss not to briefly consider the question of accuracy before advocating use of any technique. We assumed that for all species, barring *C. cyanostigma*, the catch curve provides the most accurate, if not the most precise, mortality estimate given that it utilizes trends across a range of age-classes rather than one or a few potentially related parameters. We then compared the mean estimates (not presented) obtained by the methods across a range of sample sizes. For *Lutjanus carponotatus*, the Hoenig esti-

Fig. 5. Precision, P , of mortality estimators for (a) *C. cyanostigma*, (b) *Lethrinus miniatus*, (c) *Lutjanus carponotatus*, and (d) *P. leopardus* across a range of sample sizes, n . Two estimates of natural mortality were generated by Pauly's (1980) equation using von Bertalanffy growth parameters from unconstrained, $M_{\text{Pauly,u}}$, and constrained, $M_{\text{Pauly,c}}$, growth curve fits. Total mortality was estimated by the age-based catch curve of Ricker (1975), Z_{Ricker} , and by Hoenig's (1983) equation, Z_{Hoenig} . Estimation of Z_{Ricker} is not appropriate for *C. cyanostigma* due to excessive violations of the catch curve assumptions. Δ , $M_{\text{Pauly,u}}$; \circ , $M_{\text{Pauly,c}}$; \blacklozenge , Z_{Ricker} ; \blacksquare , Z_{Hoenig} .



mate was close to that generated by the catch curve. However, for *P. leopardus* and *Lethrinus miniatus*, the Hoenig estimate was 40% lower than the catch curve estimate. These two species are more heavily fished on the Great Barrier Reef than *Lutjanus carponotatus* (Mapstone et al. 1996). This supports Hoenig's observation that his estimator can underestimate Z if fishing changes the skew but not the extent of the age distribution (Hoenig 1983).

Pauly's estimator should produce M values that are at most equal and generally less than Z estimates. This only occurred for *P. leopardus*. As previously discussed, *P. leopardus* has a growth pattern qualitatively different from those of the other species, perhaps implicating the highly asymptotic nature of the other species' growth in the questionable values of M_{Pauly} . Consideration of L_{∞} alone does not account for the length of time spent at the asymptote, but Pauly's equation would estimate similar mortality rates for species with similar growth parameters but differing longevities. These hypotheses require more focused testing and we recommend careful consideration of the effects of population structure prior to use of any mortality estimator.

Age structures

Given that estimating age structures entails replicating entire distributions rather than generating single values, we expected that precision of age structures would improve with increasing sample size more slowly than most parameters. This did not prove to be the case. The explanation might be that the index D averages deviations across all age-classes. The effects of substantially overestimating or underestimating a few age frequencies using a given sample might therefore be negated. The remarkably similar D values derived at most sample sizes across species and the surprisingly rapid flattening of the D versus n curve perhaps suggest that an age distribution's general shape can be captured with relatively few samples.

While the basic shape of a distribution can be approximated with relatively few samples, it is important to clearly specify why an age structure is being generated. Approximating the shape of a distribution will not be adequate if the objective involves replicating a recruitment history, in which case, capturing peaks and troughs becomes critical and more samples might be needed (Worthington et al. 1995). On the

other hand, if the objective is to examine whether fishing has truncated the tail of the distribution (Hilborn and Walters 1992), approximating the general shape may suffice. In fact, objectives might often deal more with specific aspects of the distribution (e.g., modal age), and precision of those particular features should be considered.

Application of the analysis

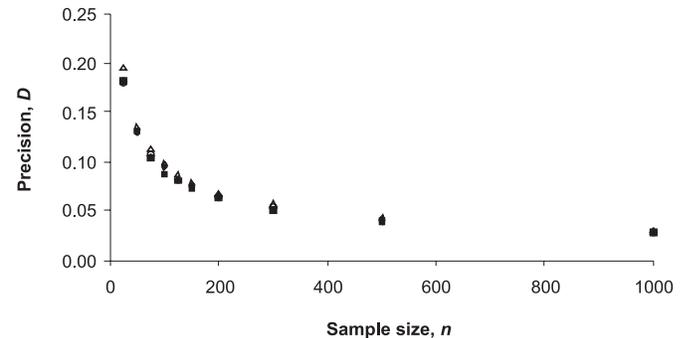
We did not aim to provide a prescriptive method for sample size determination. Rather, we have explored some factors affecting description of populations, including sample size but also underlying population structure and parameters being estimated. We strongly reiterate that an appropriate sample size can only be specified by consideration of resource expenditure per sample collected and (or) the degree of precision required to achieve specific objectives.

Still, some general comments on sample size requirements for baseline or descriptive studies can be made. As n increases and P decreases, one must sample more and more to gain less and less. For most parameters examined, relative improvements above sample sizes of around 300 were negligible unless the increase was on the order of several hundred. Absolute improvements were always minimal. Unfortunately, the question becomes more difficult at the lower end of the sample size spectrum where attention of researchers is more likely to be focused as they try to minimize costs. For most parameters, the P (or D) versus n function appeared very steep up to a sample size of at least 100 and began to appear quite flat by sample sizes of around 150–200. General rules for minimum sample sizes when statistically comparing frequency distributions range from an average of 5–10 observations per category (Sokal and Rohlf 1981). In light of our results, an average of 7–10 fish per age-class would be a useful although possibly overly conservative guideline for estimating age structures and a variety of parameters for all but those species living more than 25 or 30 years. Longer-lived species might require fewer samples per age-class. By our guideline, the target sample size for *C. cyanostigma* would be 400, which would not appreciably improve precision of most parameters from a sample half that size. Such exceptions highlight the limitations of general rules.

We used data sets in hand and retrospectively assessed different hypothetical samples. It might seem fruitless for other investigators to conduct similar analyses if samples need to have been collected first. However, one advantage of bootstrapping methods is their potential to build large numbers of hypothetical samples from relatively small amounts of data (Manly 1996). While extrapolating from small data sets is not without risk, our minimum sample size of 500 for the simulation data sets was excessively strict in light of our results. A modest pilot sample could roughly capture the population's characteristics and help determine the additional sampling required to attain more precise estimates.

Alternatively, extant data sets for species similar to focal species can also be used to approximate the population in question. For example, one species used herein, *Lutjanus carponotatus*, exhibits demographic traits similar to the congeneric *Lutjanus adetii* on the Great Barrier Reef (Newman et al. 1996). Data for this species could have been used as an initial approximation of a *Lutjanus carponotatus* population had data for *Lutjanus carponotatus* been unavailable. This

Fig. 6. Precision, D , of estimated age structures for four species of coral reef fishes across a range of sample sizes, n . Δ , *C. cyanostigma*; \circ , *Lethrinus miniatus*; \blacklozenge , *Lutjanus carponotatus*; \blacksquare , *P. leopardus*.



could lead to additional sampling if the newly researched population is revealed to be substantially different from the proxy population.

Sample size and (or) sampling method can be beyond the researcher's control, particularly when using fishery-dependent samples. In such cases, an analysis like ours can aid the researcher in assessing what parameters can be reliably estimated from a sample. For example, if a fisher provided a sample of 50 fish, mean age and length might be confidently estimated. Little faith would be placed in K estimates and corresponding M_{Pauly} estimates.

Future directions

The effects of sample size on the precision of descriptive parameters, such as density or mean size of organisms, have received previous attention (e.g., Andrew and Mapstone 1987; Downing 1989; Garner 1997). In contrast, precision of vital rate parameters, such as those related to growth and mortality, has largely been ignored (but see Jensen 1996). Given that such parameters are crucial to understanding the functioning and dynamics of ecological systems (Ebert 1999) and as such form central components of fisheries stock assessments (Hilborn and Walters 1992), our study can make an important contribution to both pure and applied marine ecology. A logical progression would be estimation of precision and associated sample sizes required to achieve objectives ranging from statistical comparisons of desired power to modeling with desired sensitivity. We stress that any selected target precision is essentially arbitrary unless project-specific objectives and real sampling costs (Downing 1989) are defined and related to precision. At the very least, consideration of these results or, better still, application of similar analyses to context-specific data should lead to more precise yet cost-effective parameter estimation with minimal impact on the population under study.

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Appendix

Table A1. Precision of population parameter estimates for four coral reef fish species across a range of sample sizes.

	<i>n</i>									
	25	50	75	100	125	150	200	300	500	1000
<i>Cephalopholis cyanostigma</i>										
\bar{L}	0.014	0.012	0.010	0.008	0.007	0.006	0.006	0.005	0.004	0.003
\bar{i}	0.074	0.052	0.042	0.038	0.032	0.029	0.026	0.021	0.018	0.011
t_{mode}	na	na	na	na	na	na	na	na	na	na
t_{med}	0.119	0.088	0.074	0.070	0.061	0.056	0.050	0.043	0.038	0.030
t_{max}	0.095	0.095	0.095	0.085	0.084	0.083	0.066	0.046	0.033	0.017
K_u	1.651	0.774	0.679	0.693	0.588	0.478	0.391	0.357	0.294	0.191
$L_{\infty,u}$	0.226	0.163	0.122	0.109	0.102	0.089	0.080	0.071	0.054	0.039
K_c	0.632	0.160	0.139	0.115	0.100	0.092	0.078	0.067	0.053	0.035
$L_{\infty,c}$	0.021	0.014	0.014	0.011	0.010	0.010	0.008	0.007	0.005	0.004
$M_{Pauly,u}$	0.951	0.523	0.449	0.444	0.392	0.325	0.274	0.245	0.204	0.135
$M_{Pauly,c}$	0.301	0.106	0.093	0.077	0.067	0.062	0.053	0.045	0.036	0.024
Z_{Ricker}	na	na	na	na	na	na	na	na	na	na
Z_{Hoenig}	0.090	0.091	0.095	0.086	0.086	0.087	0.071	0.051	0.036	0.018
<i>Lethrinus miniatus</i>										
\bar{L}	0.022	0.017	0.015	0.012	0.010	0.010	0.009	0.007	0.005	0.004
\bar{i}	0.075	0.060	0.051	0.043	0.038	0.035	0.028	0.024	0.017	0.013
t_{mode}	0.153	0.110	0.089	0.077	0.051	0.044	0.048	0.015	0	0
t_{med}	0.074	0.045	0.030	0.017	0.021	0	0	0	0	0
t_{max}	0.238	0.197	0.164	0.135	0.133	0.118	0.095	0.083	0.065	0.057
K_u	0.604	0.309	0.256	0.183	0.152	0.165	0.119	0.102	0.073	0.053
$L_{\infty,u}$	0.147	0.047	0.035	0.024	0.020	0.021	0.016	0.013	0.010	0.007
K_c	0.159	0.101	0.082	0.070	0.065	0.058	0.054	0.041	0.034	0.024
$L_{\infty,c}$	0.032	0.022	0.018	0.015	0.013	0.013	0.011	0.009	0.007	0.005
$M_{Pauly,u}$	0.386	0.215	0.175	0.125	0.105	0.113	0.082	0.070	0.050	0.037
$M_{Pauly,c}$	0.111	0.071	0.058	0.050	0.046	0.041	0.038	0.029	0.024	0.017
Z_{Ricker}	0.809	0.286	0.266	0.263	0.249	0.224	0.222	0.187	0.126	0.075
Z_{Hoenig}	0.240	0.212	0.194	0.149	0.148	0.134	0.101	0.087	0.066	0.059
<i>Lutjanus carponotatus</i>										
\bar{L}	0.036	0.027	0.022	0.018	0.015	0.015	0.015	0.011	0.008	0.006
\bar{i}	0.143	0.112	0.086	0.075	0.063	0.065	0.057	0.042	0.031	0.024
t_{mode}	0.405	0.189	0.141	0.088	0.077	0.045	0.032	0	0	0
t_{med}	0.222	0.163	0.129	0.119	0.108	0.089	0.083	0.049	0	0
t_{max}	0.216	0.172	0.134	0.115	0.093	0.088	0.076	0.064	0.058	0.038
K_u	0.469	0.300	0.274	0.214	0.173	0.172	0.136	0.113	0.094	0.064
$L_{\infty,u}$	0.127	0.068	0.052	0.035	0.030	0.031	0.024	0.019	0.016	0.011
K_c	0.181	0.141	0.096	0.078	0.075	0.073	0.058	0.048	0.035	0.026
$L_{\infty,c}$	0.045	0.036	0.027	0.021	0.019	0.019	0.016	0.013	0.009	0.007
$M_{Pauly,u}$	0.330	0.214	0.192	0.148	0.121	0.120	0.094	0.078	0.066	0.044
$M_{Pauly,c}$	0.129	0.100	0.070	0.056	0.053	0.052	0.042	0.035	0.025	0.019
Z_{Ricker}	0.638	0.342	0.231	0.171	0.147	0.144	0.128	0.100	0.079	0.065
Z_{Hoenig}	0.235	0.201	0.171	0.131	0.102	0.098	0.081	0.065	0.059	0.042
<i>Plectropomus leopardus</i>										
\bar{L}	0.044	0.032	0.025	0.023	0.019	0.018	0.016	0.013	0.010	0.007
\bar{i}	0.083	0.064	0.047	0.042	0.039	0.035	0.029	0.025	0.019	0.014
t_{mode}	0.176	0.106	0.059	0.039	0.047	0.027	0	0	0	0
t_{med}	0.129	0.097	0.085	0.063	0.071	0.070	0.054	0.033	0.024	0
t_{max}	0.210	0.209	0.193	0.180	0.161	0.163	0.131	0.104	0.067	0.019
K_u	0.669	0.494	0.380	0.345	0.293	0.266	0.229	0.180	0.136	0.102
$L_{\infty,u}$	0.656	0.482	0.313	0.228	0.174	0.146	0.135	0.084	0.052	0.038

Table A1 (concluded).

	<i>n</i>									
	25	50	75	100	125	150	200	300	500	1000
K_c	0.175	0.115	0.097	0.819	0.073	0.069	0.069	0.052	0.041	0.038
$L_{\infty,c}$	0.084	0.052	0.043	0.035	0.031	0.030	0.027	0.021	0.016	0.013
$M_{\text{Pauly},u}$	0.531	0.399	0.302	0.271	0.231	0.208	0.177	0.139	0.103	0.077
$M_{\text{Pauly},c}$	0.136	0.089	0.074	0.063	0.056	0.053	0.052	0.039	0.031	0.029
Z_{Ricker}	0.448	0.262	0.193	0.159	0.165	0.157	0.133	0.127	0.112	0.099
Z_{Hoenig}	0.189	0.197	0.186	0.183	0.167	0.174	0.151	0.127	0.086	0.024

Note: Precision is defined as the ratio of the standard deviation of 250 distinct parameter estimates to the mean of those same estimates. *n*, sample size; \bar{L} , mean fork length; \bar{i} mean age; t_{mode} , modal age-class; t_{med} , median age-class; t_{max} , maximum age-class; K_u , von Bertalanffy growth coefficient, estimated with *y*-intercept unconstrained; $L_{\infty,u}$, von Bertalanffy mean asymptotic size, estimated with *y*-intercept unconstrained; K_c , von Bertalanffy growth coefficient, estimated with *y*-intercept constrained; $L_{\infty,c}$, von Bertalanffy mean asymptotic size, estimated with *y*-intercept constrained; $M_{\text{Pauly},u}$, natural mortality rate estimated by Pauly's (1980) regression using von Bertalanffy parameters from unconstrained fit; $M_{\text{Pauly},c}$, natural mortality rate estimated by Pauly's (1980) regression using von Bertalanffy parameters from constrained fit; Z_{Ricker} , total mortality rate estimated by Ricker's (1975) catch curve; Z_{Hoenig} , total mortality rate estimated by Hoenig's (1983) regression; na, features of the age structure meant that estimation of these parameters was not appropriate.

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