

Abstract—Growth of a temperate reef-associated fish, the purple wrasse (*Notolabrus fucicola*), was examined from two sites on the east coast of Tasmania by using age- and length-based models. Models based on the von Bertalanffy growth function, in the standard and a reparameterized form, were constructed by using otolith-derived age estimates. Growth trajectories from tag-recaptures were used to construct length-based growth models derived from the GROTAG model, in turn a reparameterization of the Fabens model. Likelihood ratio tests (LRTs) determined the optimal parameterization of the GROTAG model, including estimators of individual growth variability, seasonal growth, measurement error, and outliers for each data set. Growth models and parameter estimates were compared by bootstrap confidence intervals, LRTs, and randomization tests and plots of bootstrap parameter estimates. The relative merit of these methods for comparing models and parameters was evaluated; LRTs combined with bootstrapping and randomization tests provided the most insight into the relationships between parameter estimates. Significant differences in growth of purple wrasse were found between sites in both length- and age-based models. A significant difference in the peak growth season was found between sites, and a large difference in growth rate between sexes was found at one site with the use of length-based models.

Estimates of growth and comparisons of growth rates determined from length- and age-based models for populations of purple wrasse (*Notolabrus fucicola*)

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Methods for estimating growth in wild fish stocks derive largely from two sources: 1) age-based models, such as the von Bertalanffy growth function (VBGF), from data for length-at-age, where fish ages are known or estimated from scales, otoliths, and other hard parts; and 2) length-based models, from recapture data from tagged fish to describe a growth trajectory over time at liberty (e.g., Fabens, 1965), or analysis of modal progressions in length-frequency data (e.g., MULTIFAN, Fournier, et al., 1990). Many of these models seek to characterize growth of the population in terms of the three standard von Bertalanffy parameters, *viz.* l_{∞} , the theoretical asymptotic mean length; k , the growth rate coefficient; and t_0 , the theoretical age at length zero.

Despite its wide use in descriptions of fish growth, the standard VBGF is often criticized because the function's parameters may represent unreasonable extrapolations beyond available data and hence lack biological relevance (e.g., Knight, 1968; Roff, 1980; Francis, 1988a; 1988b), estimates of l_{∞} produced by standard length- and age-based versions of the model lack mathematical equivalence (e.g., Francis, 1988b; 1992), the statistical properties of the parameters make comparisons between samples difficult (Ratkowsky, 1986; Cerrato, 1990; 1991), and individual variability introduces biases in parameter estimates (Wang, et al., 1995; Wang and Thomas, 1995; Wang, 1998; Wang and Ellis, 1998).

These criticisms have led to various reparameterizations of the VBGF (see Ratkowsky, 1986; Cerrato, 1991 for examples). Analyses of reparameterizations for age-based VBGFs indicate that the inclusion of parameters that are expected lengths-at-age, for age classes drawn from the data set, dramatically improve the statistical properties of the model (Cerrato, 1991) and also result in parameters that have direct biological interpretation. Reparameterizations that fit this criterion include the reparameterization of the Francis (1988b) model for length-at-age data, and GROTAG, a reparameterization of the Fabens model from tagging data with expected growth rates for length as parameters (Francis, 1988a). GROTAG in particular has the advantage of being readily parameterized to include seasonal growth terms, and, through the application of a likelihood function, can include estimators of measurement error, individual growth variability, and the proportion of outliers in a data set. It has been used to produce growth estimates for cartilaginous fishes (Francis and Francis, 1992; Francis, 1997; Francis and Mulligan, 1998; Sempendorfer, 2000; Sempendorfer, et al., 2000), bony fishes (Francis, 1988b; 1988c; Francis, et al., 1999), and bivalve mollusks (Cranfield, et al., 1996). Fitting of any growth model with maximum likelihood methods also permits straightforward application of LRTs in order to compare parameter estimates, and to deter-

Manuscript submitted 25 May 2004
to the Scientific Editor's Office.

Manuscript approved for publication
10 April 2005 by the Scientific Editor.
Fish. Bull. 103:697–711 (2005).

mine optimal parameterization of models (Kimura, 1980; Francis, 1988a). Computationally intensive methods such as bootstrapping and randomization tests provide a nonparametric method for approximating probability distributions of growth parameter estimates (Haddon, 2001), for generating confidence intervals to test for differences between parameter estimates, and for visualizing relationships between parameters (Mooij, et al., 1999). Drawing together these methods, it is possible to fit growth models, to produce parameter estimates that are biologically interpretable, and to use tests that are robust for comparing populations.

The purple wrasse (*Notolabrus fucicola*) is a gonochoristic, site-attached, reef-associated fish, common on moderate to fully exposed coasts in southeastern Australia and New Zealand (Russell, 1988; Edgar, 1997). Both *Notolabrus fucicola* and its Australian congener, the blue-throated wrasse (*N. tetricus*), are large benthic carnivores that play a significant role in the trophic dynamics of temperate reef systems (Denny and Schiel, 2001; Shepherd and Clarkson, 2001).

The development of a live fishery for *N. fucicola* and *N. tetricus* in southeastern Australia has made temperate wrasses increasingly important economically (Lyle¹; Smith, et al.²).

Most previous attempts to describe the growth of *N. fucicola* (Barrett, 1995a; 1999; Smith, et al.²) have been compromised by small sample sizes, lack of age validation, and the use of unsuitable statistical models to compare length-at-age between populations. Ewing et al. (2003) recently validated an aging method and developed growth models for *N. fucicola*, combining samples from many sites from eastern and southeastern Tasmania. Our study describes site- and sex-specific age- and length-based models for this species. We also compare methods for examining differences in growth model parameter estimates, such as confidence intervals and randomization tests based on bootstrap estimates, plots of bootstrap estimates, and LRTs where comprehensive coverage of age and length data is unavailable—a situation commonly faced in fisheries.

Materials and methods

Field methods

Notolabrus fucicola were trapped and tagged at two sites on the east coast of Tasmania. Trapping was conducted

at 1–2 month intervals, between July 1999 and April 2001 at Lord's Bluff (42.53°S, 147.98°E), and between July 2000 and March 2001 at Point Bailey (42.36°S, 148.02°E). Standard T-bar tags were inserted between the pterygiophores in the rear portion of the dorsal fin. Total length of each fish was recorded prior to release. Because *N. fucicola* display no external sexual characters, sex of fish could only be determined by the presence of extruded gametes if fish were running ripe when captured, or by dissection at the conclusion of the study.

At the conclusion of the tag-recapture study, each site was fished intensively. Recaptured tagged fish were euthanized by immersion in an ice-slurry. Fish captured at Lord's Bluff were measured immediately after sacrifice; gonads were dissected to determine sex, and sagittal otoliths were collected. Untagged fish were returned immediately; therefore otoliths that were analyzed came from tagged fish only. All fish captured at Point Bailey were processed in a similar fashion but were stored frozen prior to examination.

Otolith preparation and interpretation

Sagittal otoliths were mounted in a polyester resin block, and transverse sections (250–300 μm thick) were cut through the primordium with a lapidary saw. Sections were mounted on a slide and examined under a binocular microscope at $\times 25$ magnification. The primary author counted annuli and individuals were allocated to a year class, and fractional ages were assigned based on an arbitrary birthdate of 1 October, following the method of Ewing et al. (2003).

To determine if any significant differences existed within or between reader estimates, a random subsample of 55 otoliths, from both sites, was re-aged by the primary reader (DW) and another experienced otolith reader (GE). The frequency distribution of ages in each population was then compared with a Kolmogorov-Smirnov test. Consistency of age estimates was also compared by using age bias plots (Campana, et al., 1995) and the index of average percent error (IAPE *sensu* Beamish and Fournier, 1981).

Preliminary inspection of the length data for thawed individuals from Point Bailey revealed many negative growth increments when compared to length data collected from recaptures prior to the conclusion of field sampling. Repeated measurements of *N. fucicola*, conducted independently of our study, have shown length changes in the order of 8–9% in frozen and thawed individuals compared to measurements from individuals alive or freshly euthanized (G. P. Ewing, unpubl. data³). Consequently, measurements taken from frozen fish were deemed to be incompatible with measurements taken from fresh fish and were removed from the tagging and otolith data sets. Where data from

¹ Lyle, J. M. 2003. Tasmanian scalefish fishery—2002. Fishery Assessment Report, 70 p. Tasmanian Aquaculture and Fisheries Institute, Marine Research Laboratories, Univ. Tasmania, Nubeena Crescent, Taroona, Tasmania 7053, Australia.

² Smith, D. C., I. Montgomery, K. P. Sivakumaran, K. Krusic-Golub, K. Smith, and R. Hodge. 2003. The fisheries biology of bluethroat wrasse (*Notolabrus tetricus*) in Victorian waters. Draft Final Report, Fisheries Research and Development Corporation No. 97/128, 88 p. Marine and Freshwater Resources Institute, 2a Bellarine Highway, Queenscliff, Victoria 3225, Australia.

³ Ewing, G. P. 2002. Unpubl. data. University of Tasmania, Tasmanian Aquaculture and Fisheries Institute, Marine Research Laboratories, Nubeena Crescent, Taroona, Tasmania 7053, Australia.

multiple recaptures allowed, the initial length and penultimate length measurement and their corresponding dates were used in length-based analyses at this site. Individual length-at-age estimates were also adjusted according to the date of any previous reliable length record.

Age-based growth modeling

Data consisted of ages estimated from otoliths (T) and lengths at final recapture (or last reliable length measurement at Point Bailey) (L). Kolmogorov-Smirnov tests were conducted between sites and between sexes within sites to determine if there were differences between the proportional frequency distributions of fish lengths in length-at-age data sets. Growth was modeled by using the standard von Bertalanffy growth function (VBGF):

$$L = l_{\infty}[1 - e^{-k(T-t_0)}]. \quad (1)$$

The VBGF for the two sites and sexes within sites were modeled separately (Table 1). Fish for which sex could not be determined were not included in the sex-specific models.

A reparameterized version of the VBGF was also estimated from Equation 4 in Francis (1988b):

$$L = l_{\tau} + \frac{[l_v - l_{\tau}][1 - r^{2(T-\tau)/v-\tau}]}{1 - r^2}, \quad (2)$$

where $r = \frac{l_v - l_{\omega}}{l_{\omega} - l_{\tau}}$ (3)

and where l_{τ} , l_v and l_{ω} , are the mean lengths at ages τ , v , and $\omega = (\tau + v)/2$ —ages chosen from within the observed range within the data set. The values chosen for all the otolith-based models were $\tau = 4$, $\omega = 7$ and $v = 10$ years, encompassing the range of ages represented in the data sets for both sites. Estimates of these parameters have a direct biological meaning and have more statistically favorable properties than the standard VBGF parameters l_{∞} , k , and t_0 (Francis, 1988b; Cerrato, 1991).

Models were fitted by minimizing a likelihood function and assuming normally distributed residuals (Eq. 4):

$$-\lambda = -\sum_i \ln \left(\frac{1}{\sqrt{2\pi}\sigma} \exp \left(-\frac{(L_i - \mu_i)^2}{2\sigma^2} \right) \right). \quad (4)$$

The measured length of the i^{th} fish, L_i , has its corresponding expected mean length at age μ_i , as determined from Equation 1 or 2 above, where μ_i is normally distributed and has a standard deviation σ . The quality of the fits was gauged visually in the first instance by the lack of trends in plots of residuals against length-at-age.

To further investigate each model, each data set was bootstrapped 5000 times. The bootstrapping procedure involved randomly resampling, with replacement, from the original data set, and then fitting the VBGF to this new data set, thereby generating new estimates of all model parameters (Haddon, 2001).

Based on the percentile distribution of bootstrap parameter estimates, 95% confidence intervals (CIs) around the original sample estimates were calculated for each VBGF parameter. To account for any skew in the distribution of bootstrap parameter estimates, a first-order correction for bias of CIs was performed, where bootstrap percentiles used to estimate the CIs were adjusted on the basis of the proportion of bootstrap estimates less than the original estimate (Haddon, 2001).

To determine whether growth showed any site or sex-within-site (referred to as “sex-“) differences, we compared the overlap of first-order corrected CIs and plots of bootstrap estimates. Simple comparison of CI overlap as a test for parameter difference has been shown to be overly conservative (Schenker and Gentleman, 2001). Hence the null hypothesis of no difference was accepted in the first instance only in cases where the amount of overlap was obviously large. In cases where the extent of overlap was small, and the chance of incorrectly accepting the null hypothesis existed, a randomization test was performed. This test involved constructing the distribution of the difference between the estimates of the parameter of interest. Parameter estimates were randomly selected with replacement from each set of bootstrap estimates for the two populations, and the differences were determined for these 5000 random pairs. Then a 95% first-order corrected CI was constructed as above, and the null hypothesis was rejected only if the CI did not include zero. Likelihood ratio tests were also conducted on the VBGFs and individual parameters (Kimura, 1980).

Length-based growth modeling

Growth trajectories consisted of the initial length (L_1), time at first capture (T_1), time at final recapture (or penultimate recapture at Point Bailey) (T_2), change in length from the first to the final recapture (ΔL), and duration in years between capture and last recapture (ΔT). T_1 and T_2 were measured in years from an arbitrarily chosen point, 1 January 1999—the first day in the earliest year in which tagging was conducted. For individuals recaptured more than once, only information relating to the initial and final captures was used in the analyses. This approach maximized the time between recaptures for any fish, increasing the chance of detecting growth, and gave equal weight to each fish sampled.

Because the two sites were sampled over different time periods, only samples from Lord’s Bluff that were taken at the same time as samples at Point Bailey were considered for the purposes of between-site growth comparisons (Table 1). The resulting data set, designated LB_{res} , reduced potentially confounding effects of longer sampling durations at Lord’s Bluff.

Table 1

Main model types (GROTAG and von Bertalanffy growth function [VBGF]), data sets, and sample sizes used to produce estimates of growth for *Notolabrus fucicola*. LB= Lord's Bluff, full data set; LB_{res} = Lord's Bluff, only fish captured over dates equivalent to the Point Bailey sample; PB=Point Bailey, full data set; ♂♂=males only; ♀♀=females only; *n*=sample size. The asterisk refers to one individual in this data set that was identified as an outlier during model parameterization and was excluded from bootstrapping.

Model type	Data set	Total <i>n</i>
GROTAG	LB _{res}	174
	PB	263
	LB♂♂	103
	LB♀♀	69*
	PB♂♂	96
	PB♀♀	89
VBGF	LB	101
	PB	178
	LB♂♂	47
	LB♀♀	54
	PB♂♂	68
	PB♀♀	104

A Kolmogorov-Smirnov test was conducted to determine whether differences existed in the proportional frequency distributions of lengths of fish at first capture (*L*₁) between sites and between sexes within sites.

Growth was modeled by using GROTAG (Eqs. 2 and 4 in Francis [1988a]), a reparameterization and extension of the Fabens growth model for tag-recapture data that incorporates seasonal growth:

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1 \right] \left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta} \right)^{\Delta T + (\phi_2 - \phi_1)} \right], \quad (5)$$

where $\phi_i = u \frac{\sin[2\pi(T_i - w)]}{2\pi}$ for $i = 1, 2$. (6)

The parameters g_α and g_β are the estimated mean annual growth (cm/yr) of fish of initial lengths α cm and β cm, respectively, where $\alpha < \beta$. The reference lengths α and β were chosen such that the majority of values of L_1 in each data set fell between them (Francis, 1988a). For site-specific estimates of growth, α and β were set at 20 and 30 cm, respectively, whereas β was set at 28 cm for sex-specific models. Seasonal growth is parameterized as w (the portion of the year in relation to 1 January when growth is at its maximum) and u ($u=0$ indicat-

Table 2

Parameters estimated in the five GROTAG models fitted to each tag-recapture data set to evaluate optimal model parameterization.

GROTAG model	Parameters estimated
1	g_α, g_β, v, p
2	$g_\alpha, g_\beta, v, p, u, w$
3	$g_\alpha, g_\beta, v, p, s, m$
4	$g_\alpha, g_\beta, v, u, w, s, m$
5	$g_\alpha, g_\beta, v, p, u, w, s, m$

ing no seasonal growth through to $u=1$ indicating the maximum seasonal growth effect, i.e., where growth effectively ceases at some point each year).

The model was fitted by minimizing negative log-likelihood ($-\lambda$) function (Eq. 9 in Francis [1988a]). For each data set, made up of $i = 1$ to n growth increments:

$$\lambda = \sum_i \ln[(1-p)\lambda_i + p/R], \quad (7)$$

where $\lambda_i = \exp \frac{-\frac{1}{2}(\Delta L_i - \mu_i - m)^2 / (\sigma_i^2 + s^2)}{[2\pi(\sigma_i^2 + s^2)]^{\frac{1}{2}}}$. (8)

The measured growth increment of the i^{th} fish, ΔL_i , has its corresponding expected mean growth increment, μ_i , as determined from Equation 5 above, where μ_i is normally distributed with standard deviation σ_i . In this study, σ_i was assumed to be a function of the expected growth increment μ_i (Eq. 5, Francis, 1988a):

$$\sigma_i = v\mu_i. \quad (9)$$

where v is estimated as a scaling factor of individual growth variability, assuming a monotonic increase in variability around the mean growth increment as the size of the increment increases.

In its fully parameterized form, the likelihood function estimates the population measurement error in ΔL as being normally distributed, and having a mean of m and standard deviation of s . To estimate the proportion of outliers, Francis (1988a) also included p , the probability that the growth increment for any individual could exist erroneously in the data set as any value, within the observed range of growth increments R . This enables the proportion of outliers to be identified. Francis (1988a) suggested that an estimate of $p > 0.05$ indicates a high level of outliers and therefore some caution would be required in interpreting the overall model fit.

The optimal model parameterization was determined by fitting five different models, comprising different

combinations of parameters (Table 2), with unfitted parameters held at zero. A LRT was used to determine the improvement in model fit with the different parameterizations (Francis, 1988a). For models with an equal number of parameters, the model producing the lowest negative log likelihood ($-\lambda$) was considered the best fit.

As with the otolith models, LRTs were conducted on the GROTAG models to compare between sites and sexes, and models were also bootstrapped 5000 times. First-order corrected 95% CIs were calculated for parameter estimates (Haddon, 2001), and pairwise comparisons of growth parameters, by using CIs and randomization tests, as described above for otolith-based models.

Results

Otolith interpretation

Kolmogorov-Smirnov tests showed no significant difference in age-frequency distributions generated by repeat readings of 55 otoliths by the primary reader ($D_{0.05}=0.259$, $D_{\max}=0.072$, not significant) or between readers ($D_{0.05}=0.259$, $D_{\max}=0.109$, not significant). The IAPE score for all three readings was calculated as 6.9%, and no systematic under- or over-estimation of ages was apparent in age bias plots within or between readers. Therefore age estimates derived from the first readings by the primary author were used for modeling.

Age-based growth modeling

Site comparisons No significant differences in length frequencies were detected in a Kolmogorov-Smirnov test between sites ($D_{0.05}=0.169$, $D_{\max}=0.097$, not significant).

Length-at-age estimates showed high variability among individuals, as evidenced by the spread of data points around the fitted models (Fig. 1), and estimates of σ ranged from 1.16 to 2.17 cm across all models (Table 3). However, mean lengths-at-age were adequately described by the VBGf across the ages represented by the samples from the two sites. The plots of the site-specific VBGfs indicated that mean length-at-age at Lord's Bluff was higher than at Point Bailey.

Because of the absence of young (0+ and 1+) fish in the samples from both sites, and fish >14+ at Lord's Bluff, the standard VBGf parameters were difficult to interpret biologically. Confidence intervals for the three standard VBGf parameters largely overlapped in comparisons between sites (Table 3). Plots of the bootstrap parameter estimates showed strong nonlinear correlations, particularly between l_{∞} and k , revealing minimal overlap between sites, most easily visualized with logarithmic axes (Fig. 2A). Nonlinear correlation between parameter estimates and minimal overlap between sites were also true to a lesser extent in estimates of l_{∞} versus t_0 (Fig. 2B). LRTs showed that differences between sites were highly significant overall

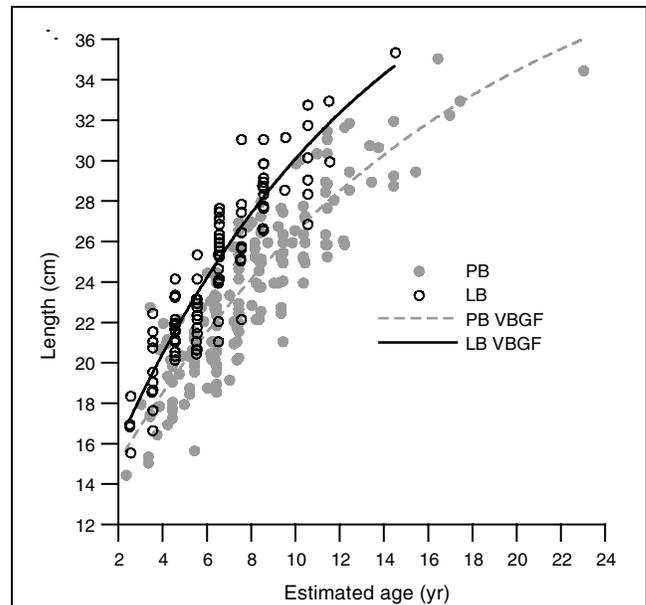


Figure 1

Length-at-age estimates for *Notolabrus fucicola*, derived from otoliths (symbols), and corresponding von Bertalanffy growth functions (VBGFs) fitted by least squares (lines). PB = Point Bailey, LB = Lord's Bluff.

but could not be attributed to significant differences in individual parameters (Table 4).

Confidence intervals for the Francis (1988b) reparameterized version of the VBGf clearly indicated significant differences in growth rates between sites in all three parameters, and no overlap between sites in the CIs of the estimates of mean length at 4, 7, or 10 years old (Table 3). These differences were also evident in plots of bootstrap parameter estimates, the two sites being clearly separated in the parameter space, and showed none of the high nonlinear correlations evident in the standard VBGf estimates (Fig. 3B). Randomization tests produced CIs of the difference between sites of 1.16–2.67, 2.48–3.50, and 2.82–4.44 cm for l_4 , l_7 , and l_{10} , respectively. Highly significant differences in all individual parameters growth parameters in the reparameterized model were also shown in LRTs between sites, but no significant difference in σ was detected (Table 4).

Sex comparisons Confidence intervals for the standard and reparameterized von Bertalanffy parameters significantly overlapped in all comparisons between sexes (Table 3). Likelihood ratio tests showed no significant differences between models of sexes within sites—a conclusion supported by considerable overlap in plots of bootstrap estimates (not shown).

Length-based growth modeling

Model parameterization Site-specific data sets were optimally parameterized under the most complex model,

Table 3

Von Bertalanffy growth function parameter estimates for *Notolabrus fucicola*. Numbers in bold text are parameter estimates from the original dataset. Numbers in parentheses are the proportion of parameter estimates from bootstrapped data sets that were less than the estimate from the original data set. Numbers in plain text are first-order corrected bootstrap 95% confidence intervals. LB = Lord's Bluff; PB = Point Bailey.

Dataset	Parameter estimate						
	l_{∞} (cm)	k (/yr)	t_0 (yr)	l_4 (cm)	l_7 (cm)	l_{10} (cm)	σ (cm)
LB	44.7 (0.48) 35.4 to 68.4	0.085 (0.51) 0.036 to 0.152	-3.23 (0.50) -5.82 to -1.59	20.4 (0.51) 20.0 to 20.9	25.9 (0.50) 25.4 to 26.3	30.1 (0.51) 29.4 to 30.8	1.61 (0.57) 1.39 to 1.87
PB	43.3 (0.66) 37.9 to 86.7	0.065 (0.51) 0.021 to 0.096	-4.65 (0.50) -8.71 to -2.83	18.5 (0.52) 17.9 to 19.2	22.9 (0.53) 22.6 to 23.2	26.5 (0.58) 26.1 to 26.9	1.79 (0.32) 1.57 to 1.92
LB♂♂	52.1 (0.51) 34.6 to 1210.1	0.059 (0.49) 0.001 to 0.157	-4.46 (0.48) -9.21 to -1.55	20.3 (0.51) 19.8 to 20.9	25.5 (0.48) 24.9 to 25.9	29.7 (0.50) 28.9 to 30.5	1.38 (0.64) 1.16 to 1.68
LB♀♀	43.2 (0.47) 33.1 to 187.8	0.095 (0.51) 0.007 to 0.192	-2.80 (0.48) -7.42 to -0.98	20.5 (0.51) 19.9 to 21.3	26.1 (0.48) 25.5 to 26.7	30.4 (0.49) 29.2 to 31.7	1.74 (0.62) 1.45 to 2.17
PB♂♂	43.3 (0.47) 33.3 to 163.3	0.060 (0.52) 0.007 to 0.138	-5.56 (0.51) -11.57 to -2.20	18.9 (0.54) 18.3 to 19.6	22.9 (0.53) 22.5 to 23.5	26.3 (0.55) 25.7 to 26.9	1.58 (0.60) 1.35 to 1.87
PB♀♀	43.2 (0.48) 37.0 to 199.4	0.065 (0.43) 0.002 to 0.093	-4.60 (0.53) -10.61 to -2.35	18.5 (0.45) 17.6 to 19.3	22.9 (0.47) 22.5 to 23.3	26.5 (0.45) 25.9 to 27.0	1.91 (0.62) 1.73 to 2.16

incorporating seasonal growth and measurement error estimates (Table 5). Estimates of proportion of outliers in the data set (p) greater than zero were due to lack of fit and dropped to zero in model 5. Preliminary bootstrap-

ping showed that fitting p regularly produced spurious model fits. Because the full data sets were estimated to have no outliers, it was considered reasonable to fit model 4 (equivalent to model 5, but with p held equal to zero) to all bootstrapped data sets for site-specific growth estimates and comparisons.

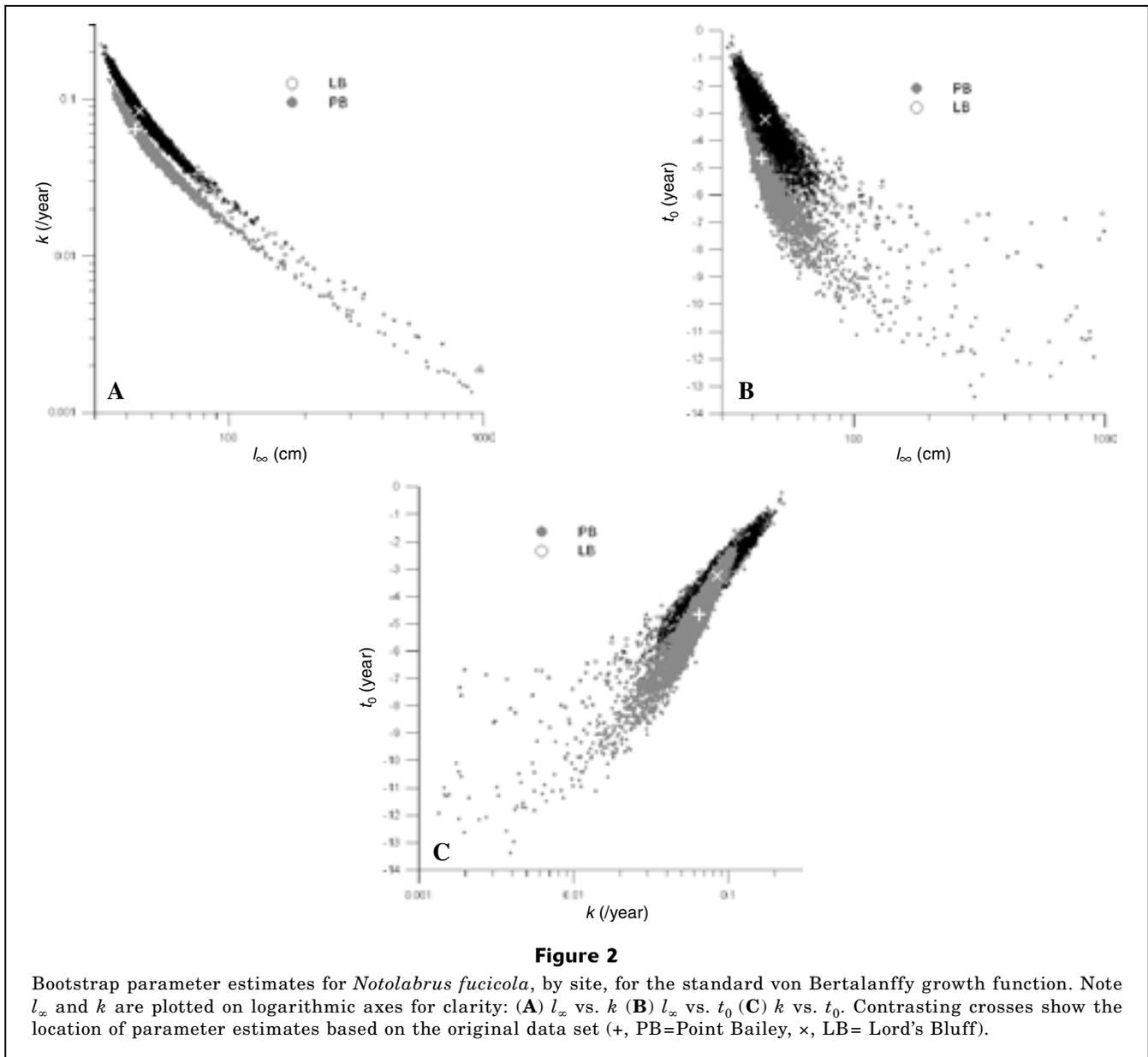
Estimates of p also dropped to zero in model 5 when this model was fitted to the sex-specific data sets, except for females at Lord's Bluff. Holding $p=0$ in model 4 for females at Lord's Bluff resulted in a less good fit compared to that of model 5 and also produced slightly different parameter estimates than those of model 5, namely increasing growth (g_{20} and g_{28}), growth variability (v), and measurement error (m) (Table 6). Visual inspection of residuals showed an obvious outlier in the data set. When this was removed and model 5 was refitted, p fell to zero and the other parameters estimates were very close to the values estimated from fitting model 5 to the original data set, and there was a large improvement in likelihood. Therefore the model for females at Lord's Bluff was based on the data set with the outlier excluded, and model 4 with p held at zero was fitted to all bootstrap data sets for sex-specific growth estimates and comparisons.

Site comparisons With the exception of s at Lord's Bluff, the proportion of bootstrap parameter estimates

Table 4

Likelihood ratio tests of site differences in the von Bertalanffy growth functions fitted to *Notolabrus fucicola* length-at-age data and individual VBGF parameters, both standard and reparameterized. $-\lambda$ = negative log-likelihood. The base case represents the summed likelihood for both curves fitted separately.

Hypothesis	$-\lambda$	χ^2	df	P
Base case	553.0	—	—	—
Coincident curves	617.8	129.75	3	<0.001
= l_{∞}	553.0	0.03	1	0.870
= k	553.2	0.36	1	0.548
= t_0	553.4	0.78	1	0.376
= l_4	565.7	25.47	1	<0.001
= l_7	602.9	99.78	1	<0.001
= l_{10}	589.2	72.53	1	<0.001
= σ	554.2	2.49	1	0.114



were more or less evenly distributed around the original parameter estimates, resulting in approximately symmetrical first-order corrected 95% CIs (Table 7). Based on the lack of overlap of CIs, only g_{20} differed significantly between sites. A randomization test of the difference in g_{20} produced CIs of 0.75–2.85 cm/yr faster growth at Lord's Bluff.

Plots of bootstrap parameter estimates clearly indicate differences in growth rates between sites, and little overlap in the parameter clouds along the g_{20} axis when g_{20} is plotted against g_{30} (Fig. 4A). Plots of bootstrapped estimates of the seasonal growth parameters u and w showed a high level of nonlinear correlation. A region of overlap between site estimates along the w axis is evident in Fig. 4B. However, the randomization test for

this parameter produced a CI of the difference between the two sites of 0.02–0.33 yr, corresponding to significantly different maximum in seasonal growth occurring at Lord's Bluff 8–120 days after Point Bailey. Estimates of w at Point Bailey ranged from –0.14 to 0.05 years in relation to 1 January (Table 7), corresponding to peak growth between austral mid-spring and mid-summer (early November through mid-January), contrasting with the Lord's Bluff estimate of –0.08 to 0.20 years and indicating peak growth from austral late spring to early autumn (mid-December through mid-March).

Site differences in growth were also indicated in the results of LRTs. The overall models were significantly different; the growth parameter g_{20} and the timing of maximum seasonal growth were significantly different

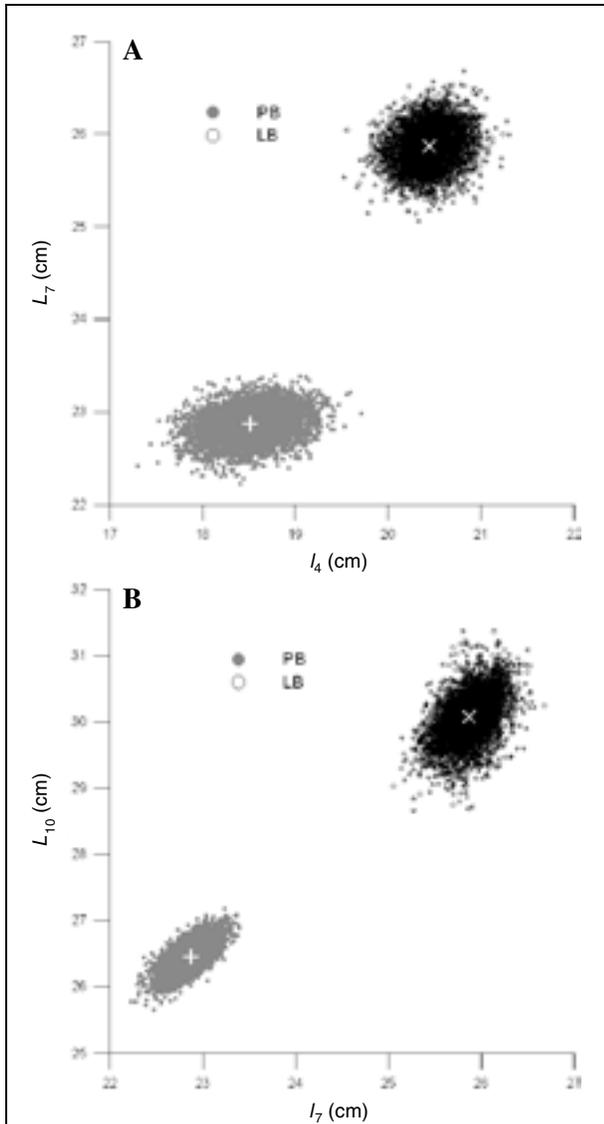


Figure 3

Bootstrap estimates of reparameterized von Bertalanffy growth function mean lengths at age for *Notolabrus fucicola*, by site. (A) l_4 versus l_7 , (B) l_7 versus l_{10} mean length-at-ages at 7 and 10 years. Contrasting crosses show the location of parameter estimates based on the original data set (+, PB=Point Bailey, x, LB=Lord's Bluff).

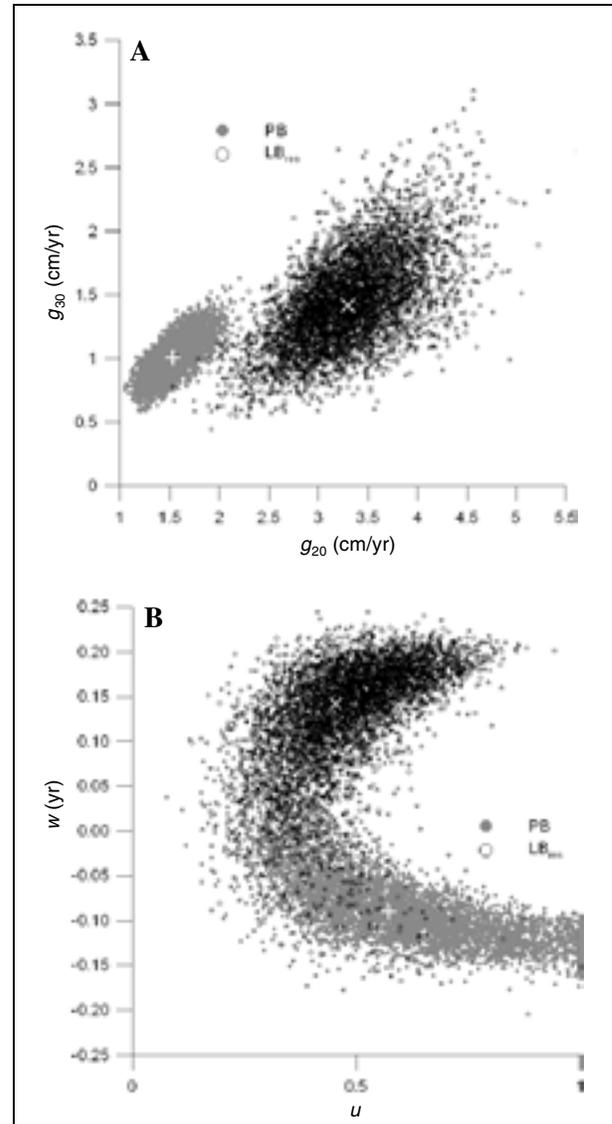


Figure 4

Bootstrap estimates of GROTAG parameters for *Notolabrus fucicola*, by site: (A) g_{20} versus g_{30} , mean annual growth at initial length 20 and 30 cm and (B) u versus w , magnitude and timing of seasonal growth. Contrasting crosses show the location of parameter estimates based on the original data set (+, PB = Point Bailey, x, LB_{res}=Lord's Bluff).

at $\alpha=0.05$ when tested individually (Table 8A), in agreement with the results of the randomization tests.

Sex comparisons Bootstrapped parameter estimates from sex-specific data sets were approximately symmetrical about the original estimates (Table 7). The largest divergence from 0.5 was evident in estimates of s for females at Lord's Bluff and males at Point Bailey. Bootstrap estimates of u for Lord's Bluff males occasionally extended into spurious negative values, lowering

confidence estimates of the extent of seasonal growth in this data set (Table 7).

Based on simple overlap of CIs, no single parameter differed significantly between sexes at either site (Table 7). Plots of the bootstrap estimates of the growth parameters g_{20} and g_{28} showed minimal overlap between males and females, and separation was most evident along the g_{20} axis (Fig. 5A). Plots of bootstrapped estimates of the seasonal growth parameters u and w (Fig. 5B), and the measurement error parameters m and s

Table 5

Parameter estimates and negative log-likelihoods ($-\lambda$) of models used in likelihood ratio tests to determine the optimal parameterization of GROTAG models for *Notolabrus fucicola* tagging data, by site. Bold text in $-\lambda$ column indicates the optimally parameterized model for each data set. Model 4 is equivalent to model 5 with $p = 0$ in these instances. LB_{res} = residents of Lord's Bluff; PB = Point Bailey.

Data set	Model	Parameter estimate								$-\lambda$
		g_{20} (cm/yr)	g_{30} (cm/yr)	v	u	w (yr)	s (cm)	m (cm)	p	
LB _{res}	1	1.84	1.07	0.88	—	—	—	—	0.07	57.06
	2	3.00	1.67	0.88	0.59	0.22	—	—	0.07	50.46
	3	2.60	1.12	0.29	—	—	0.22	-0.12	0.00	20.59
	4 and 5	3.30	1.42	0.26	0.45	0.14	0.22	-0.10	0.00	12.97
PB	1	1.50	1.01	0.73	—	—	—	—	0.16	87.82
	2	1.55	1.15	0.82	0.31	0.13	—	—	0.07	79.02
	3	1.87	1.18	0.36	—	—	0.19	-0.08	0.00	36.16
	4 and 5	1.53	1.01	0.35	0.57	0.91	0.18	-0.07	0.00	23.52

Table 6

Parameter estimates and negative log-likelihoods ($-\lambda$) of models used in likelihood ratio tests to determine the optimal parameterization of GROTAG models for *Notolabrus fucicola* tagging data, by sex within site. Bold text in $-\lambda$ column indicates the optimally parameterized model for each data set. * indicates the parameter estimates and likelihoods when GROTAG is fitted to the Lord's Bluff (LB) ♀♀ data set with a single outlier removed. Model 4 is equivalent to model 5 with $p = 0$ in all other instances. PB = Point Bailey.

Data set	Model	Parameter estimate								$-\lambda$
		g_{20} (cm/yr)	g_{30} (cm/yr)	v	u	w (yr)	s (cm)	m (cm)	p	
LB♂♂	1	1.98	1.49	0.52	—	—	—	—	0.00	43.07
	2	1.88	1.54	0.50	0.23	0.04	—	—	0.00	39.24
	3	2.09	1.62	0.27	—	—	0.21	-0.05	0.00	32.21
	4 and 5	2.04	1.67	0.27	0.23	0.19	0.20	-0.04	0.00	29.44
LB♀♀	1	2.05	1.40	0.52	—	—	—	—	0.16	60.58
	2	1.99	1.20	0.48	0.41	0.98	—	—	0.15	58.19
	3	2.88	1.87	0.26	—	—	0.25	-0.29	0.00	41.15
	4	2.75	1.75	0.25	0.32	0.96	0.24	-0.31	—	38.40
	5	2.66	1.48	0.22	0.47	0.94	0.22	-0.26	0.03	36.23
4 and 5*	2.66	1.48	0.22	0.48	0.94	0.23	-0.26	0.00	30.36	
PB♂♂	1	1.31	1.02	0.60	—	—	—	—	0.24	21.31
	2	1.15	0.96	0.61	0.41	0.90	—	—	0.19	19.93
	3	1.54	1.21	0.33	—	—	0.19	-0.03	0.00	6.43
	4 and 5	1.15	0.93	0.32	0.81	0.88	0.18	-0.04	0.00	2.49
PB♀♀	1	1.49	1.15	0.68	—	—	—	—	0.16	30.55
	2	1.43	1.16	0.90	0.33	0.12	—	—	0.00	28.85
	3	1.96	1.32	0.38	—	—	0.20	-0.11	0.00	19.06
	4 and 5	1.46	1.01	0.39	0.77	0.87	0.18	-0.12	0.00	15.78

(Fig. 5C) showed distinct relationships within the two sexes. Randomization tests confirmed significant differences in g_{20} , m , and w . The CIs of these differences were estimated to be 0.2–1.09 cm/yr faster for females

with an initial size of 20 cm, with an annual peak in female growth 3–152 days earlier than males, and with a measurement error that overestimated female length by 2–40 mm more than the measurement error for males.

Table 7

GROTAG parameter estimates derived from *Notolabrus fucicola* tag-recapture data. For all data sets, g_{α} is the mean annual growth of individuals with an initial length of 20 cm. g_{β} represents the estimated mean annual growth of individuals with an initial length of 30 cm for Lord's Bluff (LB_{res}) and Point Bailey (PB), or the estimate for 28-cm individuals for all other data sets. Numbers in bold text are the parameter estimates from the original data sets. Numbers in parentheses are the proportion of parameter estimates from bootstrap data sets less than the original estimate. Numbers in plain text are first-order corrected bootstrap 95% confidence intervals.

Data set	Parameters estimate						
	g_{α} (cm/yr)	g_{β} (cm/yr)	v	u	w (yr)	s (cm)	m (cm)
LB _{res}	3.30 (0.50) 2.32 to 4.34	1.42 (0.48) 0.80 to 2.19	0.26 (0.54) 0.14 to 0.40	0.45 (0.43) 0.23 to 0.68	0.14 (0.47) -0.08 to 0.20	0.22 (0.60) 0.18 to 0.26	-0.10 (0.48) -0.18 to -0.03
PB	1.53 (0.51) 1.21 to 1.94	1.01 (0.51) 0.76 to 1.31	0.35 (0.50) 0.27 to 0.44	0.57 (0.46) 0.25 to 1.00	-0.09 (0.54) -0.14 to 0.05	0.18 (0.55) 0.15 to 0.22	-0.07 (0.56) -0.12 to -0.01
LB♂♂	2.04 (0.48) 1.77 to 2.31	1.68 (0.51) 1.32 to 2.01	0.27 (0.58) 0.20 to 0.40	0.23 (0.45) -0.06 to 0.43	0.19 (0.48) -0.02 to 0.29	0.20 (0.57) 0.12 to 0.28	-0.04 (0.49) -0.14 to 0.06
LB♀♀	2.66 (0.49) 2.27 to 2.98	1.48 (0.50) 1.18 to 1.83	0.22 (0.50) 0.13 to 0.30	0.48 (0.39) 0.16 to 0.69	-0.06 (0.52) -0.16 to 0.12	0.23 (0.62) 0.14 to 0.34	-0.26 (0.49) -0.41 to -0.10
PB♂♂	1.15 (0.41) 0.83 to 1.69	0.93 (0.43) 0.61 to 1.41	0.32 (0.57) 0.17 to 0.47	0.81 (0.51) 0.18 to 1.00	-0.12 (0.43) -0.20 to 0.10	0.18 (0.62) 0.14 to 0.24	-0.04 (0.53) -0.14 to 0.06
PB♀♀	1.46 (0.50) 1.08 to 2.33	1.01 (0.47) 0.70 to 1.01	0.39 (0.56) 0.23 to 0.74	0.77 (0.46) 0.14 to 1.00	-0.13 (0.47) -0.20 to 0.14	0.18 (0.56) 0.09 to 0.27	-0.12 (0.51) -0.22 to 0.00

Table 8

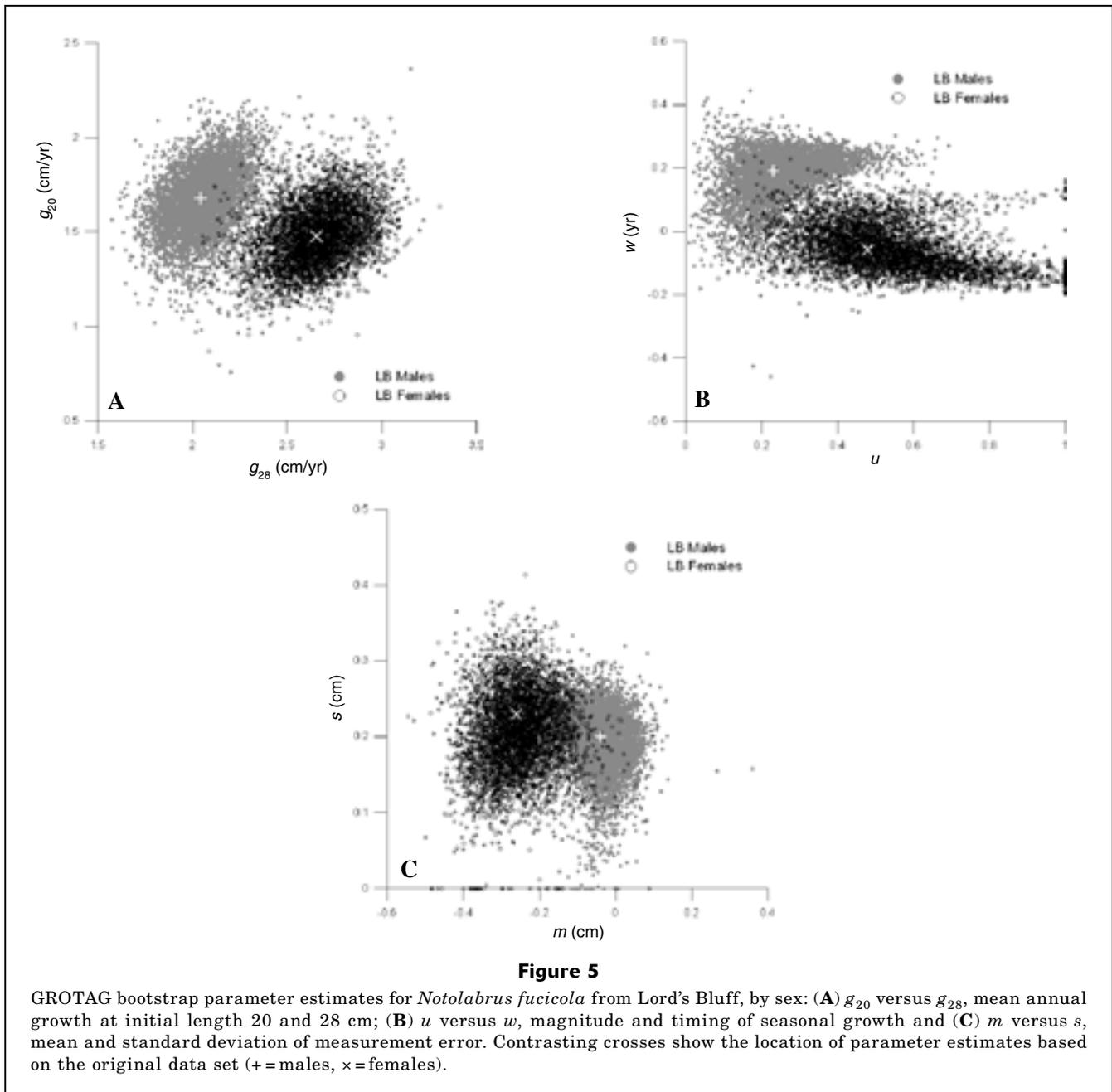
Likelihood ratio tests of the GROTAG models for which bootstrap parameter estimates were generated (Tables 5 and 6): (A) Point Bailey (PB) against Lord's Bluff (LB_{res}) (B) LB♀♀ against LB♂♂. $-\lambda$ = negative log-likelihoods. The base case is the negative log-likelihood of the data sets fitted with two wholly separate models. * = significant at $\alpha=0.05$.

A Hypothesis	$-\lambda$	χ^2	df	P	B Hypothesis	$-\lambda$	χ^2	df	P
Base case	36.49	—	—	—	Base case	59.80	—	—	—
Coincident curves	51.98	30.98	7	<0.001*	Coincident curves	72.17	24.75	7	<0.001*
= g_{20}	42.19	11.38	1	<0.001*	= g_{20}	63.43	7.27	1	0.007*
= g_{30}	37.36	1.72	1	0.189	= g_{28}	60.21	0.83	1	0.362
= v	37.35	1.72	1	0.190	= v	60.11	0.62	1	0.431
= u	36.62	0.12	1	0.623	= u	60.64	1.69	1	0.194
= w	38.91	4.84	1	0.028*	= w	62.05	4.50	1	0.034
= s	37.64	2.28	1	0.130	= s	59.94	0.30	1	0.583
= m	36.66	0.33	1	0.565	= m	62.51	5.43	1	0.020*

These conclusions agreed with the LRTs, which indicated highly significant differences between g_{20} between sexes at Lord's Bluff, and significant differences between m and w at $\alpha=0.05$ when tested individually (Table 8B). This contrasts with the results of age-based

modelling of sex-specific growth at Lord's Bluff, where no difference between the sexes was detected in any test.

Sex comparisons at Point Bailey revealed no sex-specific growth differences, and neither CIs (Table 7)



nor LRTs indicated significant difference in any of the model parameters, and bootstrap plots showed large regions of overlap (not shown).

Discussion

Comparisons of models

In this study, two methods, based on mathematically different concepts, produced similar conclusions, namely that growth in *N. fucicola* was faster at Lord's Bluff than

at Point Bailey. The results of length-based and age-based models also produced similar conclusions regarding the methods most suitable for robust comparisons of models and parameter estimates for different groups of fish. Confidence intervals were only reliable indicators of difference in cases where parameters showed low levels of correlation between estimates and where highly significant differences existed, such as in site comparisons of the reparameterized VBGF parameters, and hence were of limited utility.

Likelihood ratio tests provided a robust method of testing differences between models. However, we believe

that evidence from more than one source is required before conclusions can be drawn about differences between models designed to describe nonlinear processes such as growth. In the present study, bootstrapping techniques proved to be informative as a way of visualizing the behavior of the models used, and the distributions and correlations of parameter estimates that could not be determined readily from model likelihoods alone. They also provided a basis for estimating nonparametrically with randomization tests the differences, and CIs, of growth estimators between populations. Hence we recommend bootstrapping, plots of parameter estimates, and randomization tests to complement the “traditional” statistical tests such as the LRTs.

The standard VBGF has been criticized for the difficulty it causes in extracting biological meaning from parameters (Knight, 1968; Roff, 1980; Francis, 1988b; 1992). The problem is particularly acute where only a part of the size or age range (or both ranges) of animals is available—a situation regularly faced in analyses of fisheries data (Haddon, 2001). Data sets in our study were limited, particularly by the lack of fish in the lower age classes (*cf.* Ewing et al., 2003). Hence, any attempt to interpret or compare l_{∞} or t_0 as descriptors of the growth of *N. fucicola* would be spurious. Furthermore, because k and l_{∞} are highly correlated, comparisons of k cannot be independent of the effects of size or age selectivity on a data set. Because of the limitations of such parameters, and as l_{∞} and k are often inputs into population dynamics models and empirical models estimating parameters such as natural mortality (e.g., Pauly, 1979), extreme caution should be exercised when extrapolating these values from limited data. However, this instance exemplifies the utility of the reparameterization, because even with limited data, the useful parameters of mean lengths at age can be estimated and compared.

Variability in growth

Models of growth can be used to estimate length-dependent processes in fish populations, such as reproductive output, increases in biomass due to individual growth, selectivity of fishing gear, and the impact and appropriateness of size limits as management tools. The results of the present study demonstrate that growth varies significantly across individuals, seasons, sexes, and sites in *N. fucicola*.

Although the significance of estimating the variability in growth around the population mean (v) was not explicitly tested during model parameterization, values of v around 0.2 to 0.7 were estimated for all data sets modeled. Values in this range have been estimated with GROTAG from other species of bony fishes (Francis, 1988a; b; 1988c; 1992; Francis, et al., 1999) and cartilaginous fishes (Francis and Francis, 1992; Francis, 1997; Francis and Mulligan, 1998; Simpendorfer, 2000; Simpendorfer, et al., 2000), indicating that considerable individual variability in annual growth of size classes is common. The extent of variability in individual growth

is an important factor when quantifying growth because it may obscure other sources of growth variation, particularly in situations where data are limited. This effect may partially explain why age-based models failed to detect any significant effect of sex on growth rates in our study, whereas length-based modeling indicated that among smaller size classes, females grew faster than males at Lord’s Bluff. On the basis of a large data set (>1000 individuals), Ewing et al. (2003) demonstrated that average length-at-age was significantly higher for females than males in *N. fucicola* although the magnitude of this difference was small. No growth differences between the sexes were evident at Point Bailey but given slower growth rates, the absolute magnitude of any expected growth differences related to sex would be relatively small and difficult to detect statistically.

Our study is the first to show that growth rates of *N. fucicola* vary significantly across small spatial scales; the two sites in our study were separated by less than 25 km. At Point Bailey, few individuals reach the minimum legal size limit of 30 cm until 10 years of age, whereas at Lord’s Bluff they do so at least two years earlier (Fig. 1). An equivalent conclusion is evident from the GROTAG estimates, indicating that a 28-cm fish at Point Bailey will take nearly 2 years on average to exceed 30 cm, whereas fish of the same size are likely to reach legal size in just over a year at Lord’s Bluff. Hence relative yields and rates of replacement of recruited size and age classes are likely to be lower at Point Bailey than at Lord’s Bluff. However, because *N. fucicola* can be sexually mature at lengths of 12 cm (Patterson, 2000), some individuals are likely to have spawned for 6–8 years before recruitment to the fishery at Lord’s Bluff (Fig. 1). This size at maturity suggests that the minimum legal size limit provides effective protection of the reproductive output of the prerecruit population of *N. fucicola* at both sites.

Using length-at-age estimated from whole otoliths, Barrett (1999) found no growth differences between several populations of *N. fucicola* in southeastern Tasmania and used these findings to support the hypothesis that populations are not resource limited. Our study did not specifically address any hypothesis about resource limitation but has clearly demonstrated that growth rates can vary between populations at the scale of individual reefs. *Notolabrus fucicola* are site-attached once they settle out of the plankton, rarely having an ambit of more than 500 m on contiguous reef, and rarely crossing soft bottom habitat if they are resident on smaller patch reef habitat (Barrett, 1995b). Intuitively, it follows that if productivity varies between reefs, then the potential for growth of individual site-attached reef fish may be limited. A variety of factors have been cited in other temperate reef species where spatial variability in length-at-age is evident, such as habitat type (Gillanders, 1997; Barrett, 1999), conspecific competition and variation in juvenile recruitment (Jones, 1980, 1984), and impacts of exploitation (Buxton, 1993). Further study is advocated to determine the factors that influence *N. fucicola* growth at this scale.

Parameterization of seasonal growth significantly improved the fit of the GROTAG models, indicating that seasonal variability in growth is significant for *N. fucicola*. The estimates of seasonal growth from our study constitute the first for this species. The LRTs indicated significant differences in the timing of maximum growth (w) between sites and between sexes at Lord's Bluff. This result was repeated in the randomization tests based on the outputs of bootstrapping. Peak growth in *N. fucicola* at both sites is estimated to occur over the austral spring–summer, during maximum water temperatures and increased productivity off the coast of Tasmania (e.g., Halpern, et al.⁴), and peak growth occurs significantly later in the season at Lord's Bluff than at Point Bailey. The mechanism affecting the timing of seasonal growth at this reef-by-reef scale is worthy of further investigation but is likely to include variability in seasonal cycles of oceanography, in availability of food (Denny and Schiel, 2001; Shepherd and Clarkson, 2001) and in temperature effects on metabolism, controlling the amount and timing of resources for allocation to growth throughout the year.

The estimate of the size of the difference in w between the sexes at Lord's Bluff had very broad CIs, and it is difficult to propose a hypothesis that could result in seasonal growth varying between the sexes by as much as five months, although resource allocation for reproduction could be involved. It may be that the particularly small size of the female data set at this site limited our ability to estimate seasonal growth accurately with GROTAG, and further study is required to more precisely determine how important seasonal growth differences between the sexes are in temperate reef fishes such as *N. fucicola*.

Sex-specific GROTAG analyses indicated a significant difference in measurement errors; females were under measured by a mean of 3 mm, compared to less than 1 mm for males at Lord's Bluff. Greater measurement errors for females have been detected in other studies with GROTAG (e.g., Sempendorfer, 2000), but a reason for greater difficulty in measuring females is difficult to determine. A possible explanation from our study is the high individual growth variability and small sample sizes. Both of these factors have been shown to affect accurate estimation of measurement error in GROTAG (Francis and Mulligan, 1998), and therefore the high estimate of m in our study may be an artifact of the data set.

⁴ Halpern, D., V. Zlotnicki, P. M. Woicheshyn, O. B. Brown, G. C. Feldman, M. H. Freilich, F. J. Wentz, and C. Gentemann. 2000. An atlas of monthly mean distributions of SSM/I surface wind speed, AVHRR sea surface temperature, TMI sea surface temperature, AMI surface wind velocity, SeaWiFS chlorophyll-*a*, and TOPEX/POSEIDON sea surface topography during 1998. Jet Propulsion Laboratory Publication 00-08, 102 p. National Aeronautics and Space Administration, Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Drive, Pasadena, CA 91109.

A significant difference in growth between the sexes at Lord's Bluff indicates that under conditions of rapid growth, females may grow significantly faster than males. As discussed above, the current minimum legal size limit is effectively protecting the reproductive output of the prerecruit population of *N. fucicola*. However, any significant lowering of the legal minimum size is contraindicated where, in prerecruitment size classes, females grow more rapidly than males, because lowering the legal size may result in differences in sex-specific fishing mortality.

As demonstrated in the present study, the choice of growth model and the methods used to compare parameter estimates are critical to ensuring that growth is adequately described, differences in growth are detected, and if detected, are interpretable. In combination, the tests we employed are shown to be generally robust, even in situations where data sets are limited in sample size or by coverage across the full range of age and length classes. We recommend the use of a combination of approaches, including growth models with biologically interpretable parameters, statistical tests such as LRTs, plots of bootstrap parameters, and nonparametric randomization tests, to provide insight into the growth dynamics of fish species.

Acknowledgments

We wish to thank Malcolm Haddon, John Hoenig, Craig Johnson, Paul Burch, and Philippe Ziegler for their constructive suggestions for the manuscript. Alan Jordan and Graeme Ewing made invaluable contributions to the field and laboratory analyses. This study was conducted as a part of a Ph.D. program by the primary author, through the Faculty of Science and Engineering at the University of Tasmania.

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