

Abstract—Age estimates for striped trumpeter (*Latris lineata*) from Tasmanian waters were produced by counting annuli on the transverse section of sagittal otoliths and were validated by comparison of growth with known-age individuals and modal progression of a strong recruitment pulse. Estimated ages ranged from one to 43 years; fast growth rates were observed for the first five years. Minimal sexual dimorphism was shown to exist between length, weight, and growth characteristics of striped trumpeter. Seasonal growth variability was strong in individuals up to at least age four, and growth rates peaked approximately one month after the observed peak in sea surface temperature. A modified two-phase von Bertalanffy growth function was fitted to the length-at-age data, and the transition between growth phases was linked to apparent changes in physiological and life history traits, including offshore movement as fish approach maturity. The two-phase curve was found to represent the mean length at age in the data better than the standard von Bertalanffy growth function. Total mortality was estimated by using catch curve analysis based on the standard and two-phase von Bertalanffy growth functions, and estimates of natural mortality were calculated by using two empirical models, one based on longevity and the other based on the parameters L_{∞} and k from both growth functions. The interactions between an inshore gillnet fishery targeting predominately juveniles and an offshore hook fishery targeting predominately adults highlight the need to use a precautionary approach when developing harvest strategies.

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Age validation, growth modeling, and mortality estimates for striped trumpeter (*Latris lineata*) from southeastern Australia: making the most of patchy data

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Striped trumpeter (*Latris lineata*) are widely distributed around the temperate latitudes of southern Australia, New Zealand (Last et al., 1983), the Gough and Tristan Da Cunha Island groups in the southern Atlantic Ocean (Andrew et al., 1995), and the Amsterdam and St. Paul Island groups in the southern Indian Ocean (Duhamel, 1989). They are opportunistic carnivores associated with epibenthic communities over rocky reefs at moderate depths from 5 to 300 m along the continental shelf. The species can grow to a relatively large size, 1200 mm in total length and 25 kg in weight (Gomon et al., 1994). Spawning apparently occurs offshore, and females are highly fecund multiple-spawners (Furlani and Ruwald, 1999). Although there have been a number of ichthyoplankton surveys in Tasmanian waters, only a few striped trumpeter larvae have been collected, caught during the late austral winter through early spring months at near-shore (30–50 m) and shelf edge sites (~200 m) (Furlani and Ruwald, 1999). Larval rearing trials have shown that the presettlement phase is complex and extended; individuals can remain in this neritic-pelagic phase for up to 9 months after hatching before metamorphosis into the juvenile stage takes place (Morehead¹). As juveniles striped trumpeter settle on shallow rocky reefs.

In Tasmania striped trumpeter are taken commercially over inshore reefs (5 to 50 m), generally as a by-

catch of gillnetting, and are targeted with hook methods (handline, drop-line, longline, and trotline) on deeper reefs (80 to 300 m). Small, subadult individuals dominate inshore catches, whereas larger individuals are taken from offshore reefs. In recent years the combined annual commercial catch has been typically less than 100 metric tons (Lyle²). Striped trumpeter also attract significant interest from recreational fishermen, who use both hooks and gill nets. Furthermore, the aquaculture potential for this species is currently being assessed in Tasmania (Furlani and Ruwald, 1999; Cobcroft et al., 2001). Despite wide interest in this species, there is a general paucity of information on age, growth, and stock structure of wild populations.

Assessing the growth of a species is a fundamental part of fisheries population dynamics. Ever since Beverton and Holt (1957) introduced the von Bertalanffy growth model to fisheries research it has become ubiquitous in descriptions of the increase in size

¹ Morehead, D. 2003. Personal commun. Tasmanian Aquaculture and Fisheries Institute, Univ. Tasmania. GPO Private Bag 49, Hobart, Tasmania, Australia 7001.

² Lyle, J. M. 2003. Tasmanian scale-fish fishery—2002. Fishery assessment report of the Marine Research Laboratories, Tasmanian Aquaculture and Fisheries Institute, Tasmania. [Available from TAFI GPO Private Bag 49, Hobart, Tasmania, Australia 7001.]

of a species as a function of age. The parameters common to the von Bertalanffy growth function (VBGF) are used in stock assessment models such as empirical derivatives of natural mortality (Pauly, 1980) and assessments of yield per recruit and spawning stock biomass (Beverton and Holt, 1957). Despite the von Bertalanffy growth parameters being well established as cornerstones of many stock assessment models, several authors have highlighted limitations of the original derivation of the growth function to adequately represent growth of a population (Knight, 1968; Sainsbury, 1979; Roff, 1980; Schnute, 1981; Bayliff, et al, 1991; Hearn and Polacheck, 2003). This limitation becomes especially evident with limited or patchy data. The limitations of the von Bertalanffy growth function have created three scenarios: 1) use the VBGF and retain the use of the parameters to derive per-recruit estimates at the possible expense of physiological integrity; 2) derive or employ a model that is not based on the von Bertalanffy parameters (such as a linear or logistic model) or another polynomial function (for instance, the Gompertz equation [Schnute, 1981]) and in doing so the expediency of the von Bertalanffy parameters in stock assessments is compromised; 3), use or develop an extension of the von Bertalanffy equation with the caveat that, by introducing additional parameters, the problem of reduced parsimony by over parameterisation would need to be considered.

While investigating the life history characteristics of striped trumpeter, we became aware that the original description of the VBGF would not adequately represent growth of this species, in part because of the patchy data available for analysis.

This study aims to describe the age and growth of striped trumpeter from Tasmania. Seasonal growth oscillations are considered for the first four years by using actual length-at-age data from a strong cohort. We then employ and evaluate an extension of the VBGF that offers a better fit to the sample population of aged individuals and allows the flexibility of assigning representative growth and mortality parameters to different life phases of the population. Growth parameters derived from both the standard von Bertalanffy and extended von Bertalanffy models are used in our catch curve analyses, and the empirical models of Pauly (1980) and Hoenig (1983) are used to allow comparison of mortality estimates.

Materials and methods

Striped trumpeter were collected opportunistically from various sites off the east and southeast coasts of Tasmania from a variety of fisheries dependent and independent sources spanning the period 1990–2002 (Table 1). Inshore catches were predominately taken with gill nets ranging in mesh sizes from 64 to 150 mm. Offshore catches were taken by hook-and-line methods. Samples ranged from intact specimens, for which the full range of biological information was collected, to processed frames

Table 1

Composition of Tasmanian sampling data from 1990 through 2002 showing data from inshore gill net and offshore hook fisheries. Numbers in parentheses represent the number of individuals aged from each particular sampling regime.

Year	Gill net	Hook	Total
1990	—	45	45
1991	—	332	332
1992	—	126	126
1994	3	8	11
1995	228	12	240
1996	529	55	585
1997	193	2	195
1998	7	171	178
1999	205	902	1107
2000	—	91	91
2001	—	60	60
2002	—	97	99
Total	1165 (268)	1901 (508)	3069 (776)

from which length and, depending on condition of the body, sex and gonad weight were recorded. All specimens were measured for fork length (± 1 mm) and, where possible, total weight was recorded (± 1 gram). Otoliths were collected when possible. This *ad hoc* sampling approach created a temporally irregular data set.

Kolmogorov-Smirnov tests ($\alpha=0.05$) were used to determine whether significant differences existed between male and female length-frequency distributions or between length-frequency distributions by depth strata.

Analysis of residual sums of squares (Chen, 1992) was used to determine whether a significant difference existed between the sex-specific length-weight relationships that were fitted by minimizing the sum of square residuals and that are described by the power function

$$W = aL^b, \quad (1)$$

where W = whole weight (g);
 L = fork length (mm); and
 a and b = constants.

Sex ratios were compared for significant deviation from 1:1 by chi-square tests.

Aging technique

Sagittal otoliths were removed from 873 individuals and a subsample of 295 otoliths were individually weighed to the nearest milligram. One randomly selected otolith from each fish was embedded in clear polyester casting resin. A transverse section was taken through

the primordial region (width approximately 300 μm) and mounted on a microscope slide. A stereo dissecting microscope at 25 \times magnification was used to aid the interpretation of increments in the mounted sections. Increment measurements were made by using Leica IM[©] image digitization and analysis software (Leica Microsystems, Wetzlar, Germany). All counts and increment measurements were made without knowledge of fish size, sex, or date at capture to avoid reader bias.

Position of the first annual increment was determined by testing the close correspondence of otolith microstructure and body size between known-age individuals reared from eggs in aquaria and wild-caught specimens. To ensure that growth in cultured individuals also reflected growth in wild specimens, a hypothesis of comparable growth was tested by fitting traditional VBGFs to the length-at-age data of 288 cultured individuals (maximum known age: 4 years) and 268 wild specimens (maximum otolith-derived age: 4 years). A likelihood ratio test (Kimura, 1980) was then used to test for significance. The VBGF model was in the form

$$L_t = L_\infty(1 - e^{-(t - t_0)}) + \varepsilon, \quad (2)$$

where L_t = length at age t ;
 L_∞ = average asymptotic length;
 k = a constant describing how rapidly L_∞ is achieved;
 t_0 = the theoretical age where length equals zero; and
 ε = independent normally distributed (0, σ^2) error term.

Modal progression of length frequencies from a strong cohort of juvenile fish was sampled over a three-year period (1995–97). This cohort provided an opportunity to validate annual periodicity in increment deposition. By applying an aging protocol based on position of the first increment and assuming that each opaque+translucent zonal pair represented one year of growth, this recruitment pulse could be tracked over seven years in age-frequency progression.

A random subsample of 335 otoliths was read a second time by the primary reader, and a second subsample of 46 otoliths by a second reader, both experienced in otolith interpretation. Precision was assessed by determining percentage agreement between repeated readings, age bias plots (Campana et al., 1994), and calculating the average percent error (APE) (Beamish and Fournier, 1981).

Growth modeling

The length-frequency progression of a strong and discrete cohort of fish indicated that striped trumpeter may be subject to seasonal growth variability. This variability was described by integrating a sinusoidal function (Pitcher and MacDonald, 1973; Haddon, 2001) into a standard VBGF and by applying this function to the actual weekly length-at-age data of individuals

sampled from the strong 1993 cohort over the period 1995 through 1997, where the model was described as

$$L_t = L_\infty \left(1 - e^{-\left[C \sin\left(\frac{2\pi(t-S)}{52}\right) + k(t-t_0) \right]} \right) + \varepsilon, \quad (3)$$

where C = the magnitude of the oscillations above and below the nonseasonal growth curve of the sinusoidal cycle;

S = the starting point in weeks of the sinusoidal cycles; and

52 = the cycle period in weeks.

The timing of seasonal growth was compared with weekly average sea surface temperature (SST) on the southeast coast of Tasmania over the sampling period, calculated by using optimum interpolation (Reynolds et al., 2002) of raw remotely sensed data from the area (NOAA-CIRES³). A sine function was fitted to the weekly average SST by using least squares regression to compare the timing and phase of growth and temperature and test for a significant correlation.

All individuals aged were assigned a “decimal” age, where the decimal portion represented the proportion of the year between a nominal average date of spawning (1st October) and the date of capture. We assumed a nominal peak spawning date of 1 October based on an assessment of monthly averaged gonadosomatic index (Tracey, unpubl. data), which is consistent with that observed for wild-caught broodstock held under ambient conditions (Morehead¹).

Growth of the sampled population was initially described by using the standard von Bertalanffy growth function (Eq. 2). However, a preliminary visual assessment of the fit suggested it did not produce an adequate representation of the entire data set. In an attempt to find a model that better represented the data, the fit of the standard von Bertalanffy growth function (VBGF_s) was compared with an extension of the traditional von Bertalanffy growth model fitted by minimization of the sum of negative log-likelihood; normal distribution of the error term. The model chosen was similar to that used by Hearn and Polacheck (2003) and involved fitting a VBGF function either side of an age at transference, described as

$$L_t = \begin{cases} \left(L_{\infty 1} (1 - e^{-k_1(t-t_{01})}) \right) + \varepsilon & \text{for } t < t^\delta \\ \left(L^\delta + (L_{\infty 2} - L^\delta) (1 - e^{-k_2(t-t_{02})}) \right) + \varepsilon & \text{for } t \geq t^\delta \end{cases}, \quad (4)$$

³ Data sourced from the NOAA-CIRES Climate Diagnostics Center, Boulder, CO 80305. <http://www.cdc.noaa.gov/>. [Accessed 15 Sep. 2002]

where $L_{\infty 1}$, k_1 , t_{01} = VBGF parameters applied to the first growth phase;
 $L_{\infty 2}$, k_2 , t_{02} = VBGF parameters applied to the second growth phase;
 L^δ = length of transference from one growth phase to the next; and
 t^δ = age of transference from one growth phase to the next; calculated as,

$$t^\delta = t_{01} - \frac{1}{k_1} \ln \left(1 - \frac{L_t}{L_{\infty 1}} \right). \quad (5)$$

Having fitted Equation 4, we smoothed the discontinuity from the first growth stanza to the second, assuming normal distribution around the age at transference by integrating a normal probability cumulative distribution function (PDF) where the mean is equal to the age of transference (4.4 years) and where the standard deviation is arbitrarily set at 1.0. This model is referred to as the two-phase von Bertalanffy growth function (VBGF_{TP}) and is now represented as

$$L_t = \begin{cases} \left(1 - \int_{t=t_0}^{+t^\delta} \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(t-t_0)^2}{2\sigma^2}} \right) (L_{\infty 1}(1 - e^{-k_1(t-t_0)}) + \varepsilon) + \\ \left(\int_{t=t^\delta}^{+t_{\max}} \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(t-t^\delta)^2}{2\sigma^2}} \right) (L^\delta + (L_{\infty 2} - L^\delta)(1 - e^{-k_2(t-t^\delta)}) + \varepsilon) \end{cases}, \quad (6)$$

where t_{\max} = maximum age present in the sample;
 and
 σ^2 = standard deviation of cumulative density function with mean t^δ .

The model that best represented the data was judged on a combination of parsimony as determined by the Akaike information criterion (AIC) (Akaike, 1974), quality of fit by minimization of the negative log-likelihood value derived from each model, visual inspection of the residuals, and as an index of fit, the percent deviation of L_∞ for each model from the maximum observed length (L_{\max}).

The hypothesis of sexual dimorphism in growth was tested by using likelihood ratio tests (Kimura, 1980) for both the VBGF_S and VBGF_{TP} models fitted to the length-at-age data of all individuals whose sex had been determined.

Mortality estimation

Mortality estimates were calculated by using the parameters of both the VBGF_S and VBGF_{TP} functions. An estimate of instantaneous rate of total mortality (Z) for the offshore hook fishery was calculated for 1998 by applying a length converted catch curve analysis (LCCCA *sensu* Pauly, 1983) to the length-frequency data.

Estimates of instantaneous rate of natural mortality (M) were calculated by using two empirical equations. The first equation, derived by Pauly (1980), is described as

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_{\infty\gamma} + 0.6543 \log_{10} k_\gamma + 0.4634 \log_{10} T, \quad (7)$$

where $L_{\infty\gamma}$ and k_γ = parameters derived from the VBGF_S or from the second growth phase of the VBGF_{TP}; and
 T = average annual sea surface temperature (°C) at the area of capture.

The mean annual sea surface temperature on the east coast of Tasmania in 1998 was estimated as 14°C (NOAA-CIRES³). The second equation used was the regression equation of Hoenig (1983):

$$\ln Z = 1.46 - 1.01 \ln t_{\max}; \quad M \sim Z \text{ assuming } F \sim 0, \quad (8)$$

where t_{\max} = the maximum age for the species in years.

Estimates of fishing mortality (F) were calculated by subtracting natural mortality from total mortality.

Results

Males ranged in length from 203 mm to 815 mm ($n=504$) and females ranged from 269 mm to 950 mm ($n=565$). Length-frequency distributions did not differ significantly between sexes (Kolmogorov-Smirnov; $Z=0.91$ $P=0.38$).

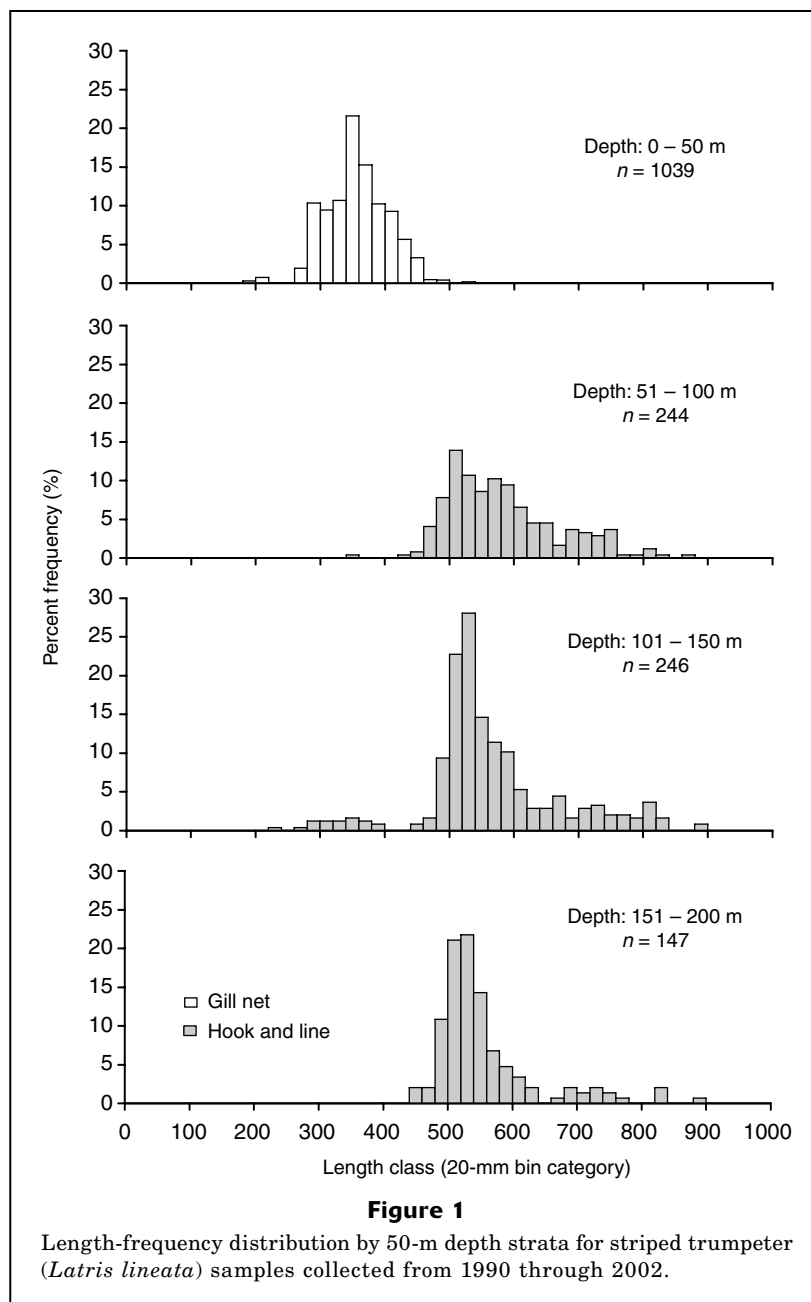
Pooling the length-frequency data of all individuals produced a bimodal frequency distribution. However, when grouped by depth (Fig. 1), the data revealed a significant depth-based stratification between the shallow (<50 m stratum) and the deeper strata (Kolmogorov-Smirnov; $Z=13.8$ $P<0.001$), occurring at around 450 mm in length.

Analysis of residual sums of squares indicated no significant difference between the sex-specific length-weight relationships ($F=0.02$ $df=2$ $P=0.10$); consequently a power regression was applied to the length-weight data of all individuals combined (Table 2).

The sex ratio of males to females (1.0:1.3) from the inshore net fishery showed a low level of significant difference from 1:1 ($\chi^2=3.88$ $P=0.049$ $n=232$), whereas, the ratio of males to females (1.0:1.1) caught from the offshore hook fishery did not show significant difference from 1:1 ($\chi^2=0.933$ $P=0.334$ $n=840$).

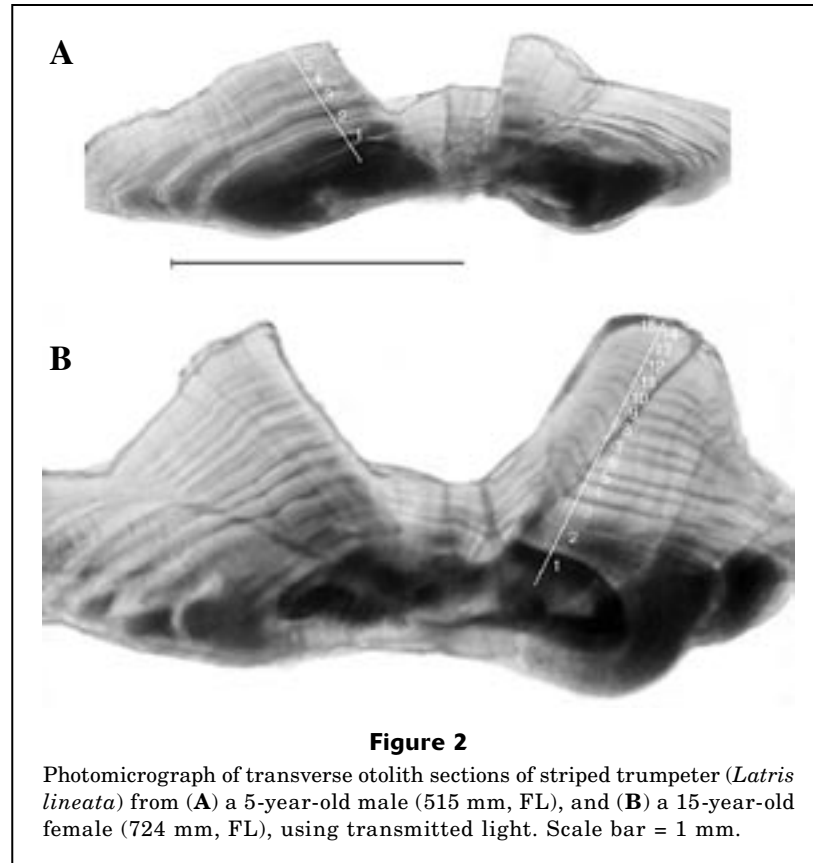
Age estimates

Age was successfully estimated for 776 (89%) individuals. Transverse otolith sections showed typical distinct alternate light and dark zone formations within the

**Table 2**

Predictive equations used to compare weight and length, otolith weight and age, and reader variability across age classes, for striped trumpeter (*Latris lineata*).

Dependent variable	Independent variable	<i>n</i>	Equation	<i>r</i> ²
Weight (<i>W</i>)	Fork length (<i>L</i>)	491	$W = 2 \times 10^{-5} \times L^{3.00}$	0.99
Otolith weight (<i>OW</i>)	Age (<i>t</i>)	295	$OW = 7.32 + (1.70 \times t)$	0.89
Primary reader, count 2 (<i>P</i> ₂)	Primary reader, count 1 (<i>P</i> ₁)	339	$P_2 = 0.05 + (0.99 \times P_1)$	0.99
Secondary reader, count 1 (<i>S</i> ₁)	Primary reader, count 1 (<i>P</i> ₁)	46	$S_1 = 0.27 + (0.97 \times P_1)$	0.97



otolith matrix. Viewed under transmitted light the zones showed as dark (opaque) and light (translucent) (Fig. 2). A robust linear relationship existed between otolith mass and individual age (Table 2).

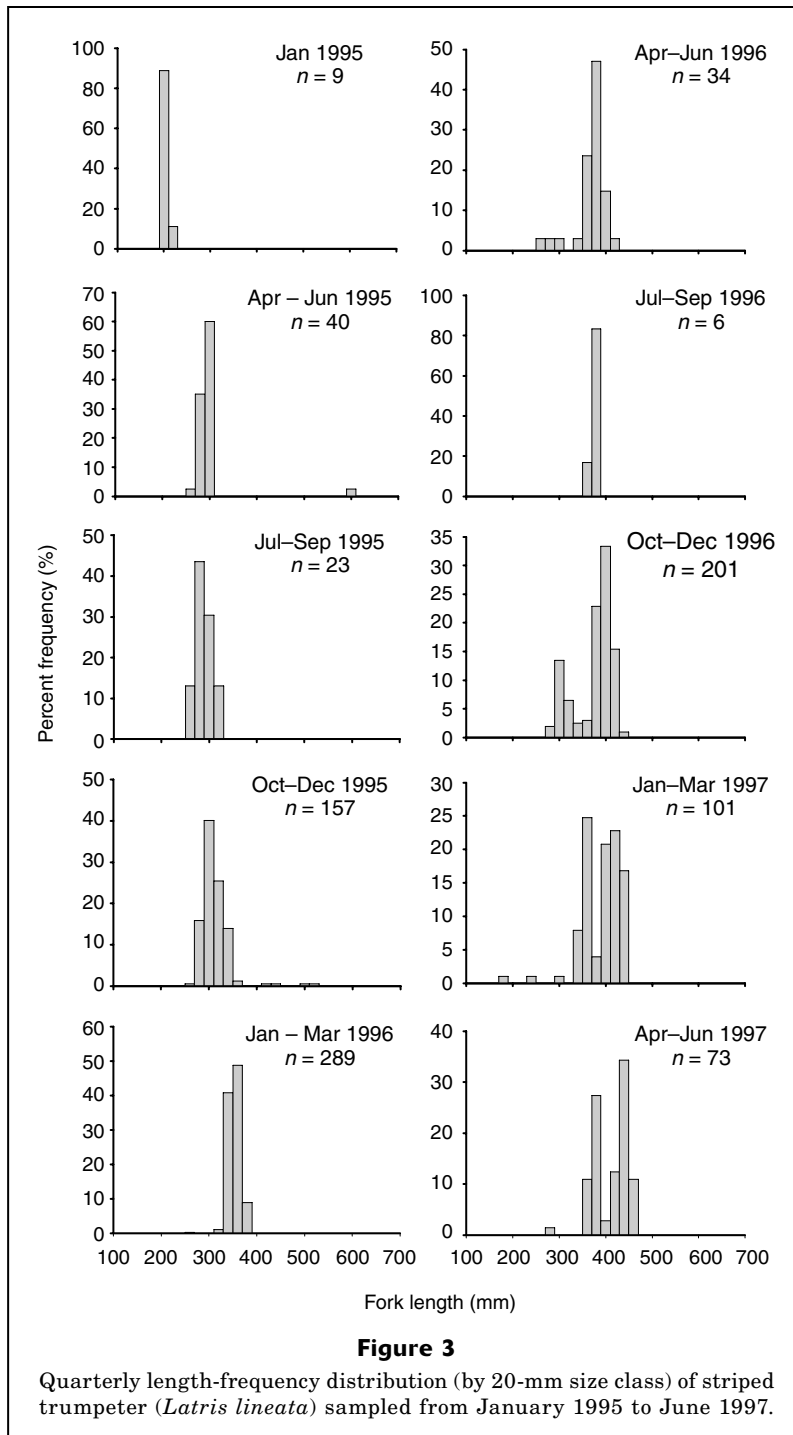
The core area of each section consisted of an opaque region. Immediately adjacent to this was a faint thin translucent zone followed by the first broad opaque annual increment. In some cases the transition from core to the first expected increment could not be discerned because of a continuation of the opaque region (the expected thin translucent zone was too faint to see). In such cases, increment measurements were required to ensure that the annulus was not overlooked. Mean increment radius (\pm SD) from the primordia to the first annulus was $491 \pm 63 \mu\text{m}$ ($n=122$); and the deposition of the second annulus occurred at a mean radius of $733 \pm 55 \mu\text{m}$ ($n=122$). The next four opaque and translucent zone pairs were relatively broad compared with subsequent zones that consistently narrowed as they approached the growing edge (Fig. 2).

To validate the first increment we compared somatic and otolith growth of wild individuals with that of individuals cultured under ambient conditions. Larval-rearing trials of striped trumpeter juveniles have produced mean lengths of 190 mm at 14 months and 261 mm at 24 months. The smallest individuals recorded from the wild in our study were 190–220 mm and were captured in January 1995. From the rearing trials it seemed

reasonable to assume that the wild-caught individuals of this size were between 1 and 2 years of age. If a birth date of 1 October is assumed, these individuals would have been about 16 months old and therefore were spawned in 1993. Viewing the sectioned otoliths of these small wild-caught individuals revealed only one increment within the margin, analogous to the increment composition of cultured individuals at a similar length.

To test for comparable growth between wild and cultured individuals as a means to facilitate confident validation of the first increment deposition, von Bertalanffy growth curves were fitted to length-at-age data of both wild (based on otoliths) and cultured individuals (of known age) to age four. A likelihood ratio test indicated that wild-caught individuals increased in length slightly faster than those cultured to the same age ($\chi^2=5.3$ $df=6$ $P=0.51$); however, this trend was not significant ($F=4.4$ $df=23$ $P=0.04$).

Tracking length-frequency distributions (Fig. 3) from 1995 through 1997, from inshore gillnet samples, revealed progression of a strong cohort. Based on its size structure, the spawning year for this cohort was assumed to be 1993. A second cohort was evident in the last quarter of 1996, assumed to have been spawned in 1994. The progression of the cohort spawned in 1993 was clearly evident in the age structure of the samples over the period 1995–2001, proving useful in the valida-



tion of annual periodicity (Fig. 4). However, inferences about population age structure cannot be drawn from the age-frequency histograms because some sample sizes were low and there was discriminatory sampling (by gear type) over the period. For instance up to 1996–97 most of the aged samples were from inshore gillnet catches, whereas subsequent samples were derived primarily from hook catches.

Precision of repeated age estimation was high. Second readings by the primary reader were 79% in agreement with first readings, yielding an APE of 0.93%. Eighteen percent of second readings gave rise to a one-year difference and 3% of second readings differed by 2 years, and no significant tendency to overestimate or underestimate age was evident. An age bias plot did not differ significantly from 1:1 for the primary reader (Table 2).

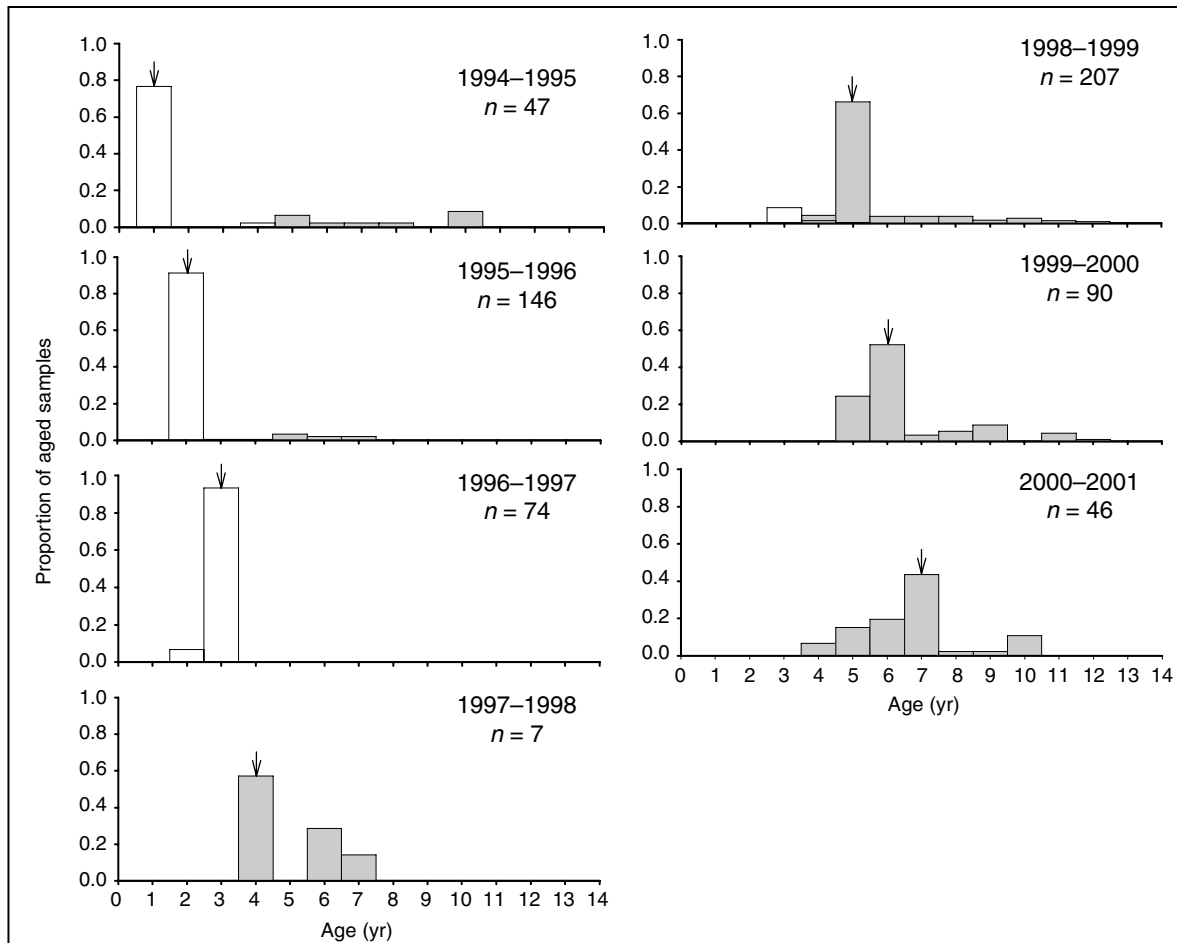


Figure 4

Age-frequency distribution (based on biological year, October–September) for striped trumpeter (*Latris lineata*) from 1994 through 2001. Gillnet-caught fish are represented by unshaded columns, hook-caught fish are represented by shaded columns. Arrows represent the progression of the cohort spawned in 1993.

Precision of the second reader's age estimates when compared with those of the primary reader were also satisfactory, yielding an APE of 1.59%, and no significant bias was revealed at any age class (Table 2).

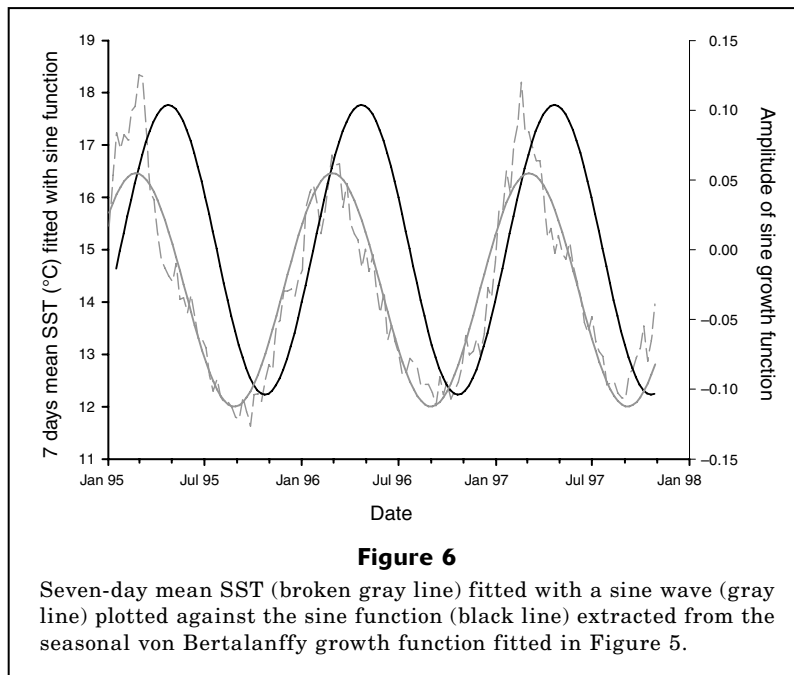
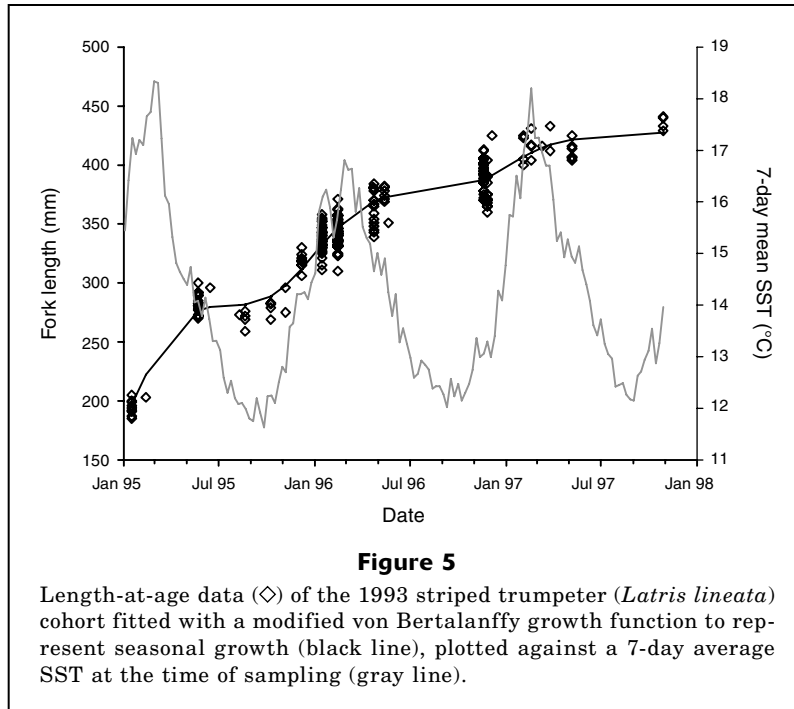
The maximum observed ages for males and females were 29 and 43 years, respectively. From the available data, it is unclear whether apparent differences in longevity between the sexes are representative because very few individuals over the age of 25 were sampled. However, there was no significant difference in the age-frequency composition of the pooled samples based on sex (Kolmogorov-Smirnov; $Z=1.05$ $P=0.22$).

Growth modeling

The strong 1993 cohort allowed us to closely monitor the actual length at age of striped trumpeter. Average size increased from 190 mm (1.3 years) in January 1995 to 300 mm (2.1 years) by November 1996 (Fig. 3) and 420 mm (4.0 years) by November 1997. The seasonal VBGF

model indicated that the majority of observed growth in this cohort occurred between January and May (late austral summer through autumn) and that there was little growth apparent between June and December (Fig. 5). The sine wave representing seasonal fluctuations indicated that the peak growth rate occurred in May. Comparing this sine function with that derived for SST (Fig. 6), we identified a first-order serial correlation—the strongest correlation identified when a 34-day lag period was incorporated in the growth phase.

The parameters of the $VBGF_S$ and $VBGF_{TP}$ fitted to the aged individuals are presented in Table 3. The $VBGF_{TP}$ gave the more parsimonious fit to the pooled length-at-age data according to the deterministic AIC value and underestimated L_∞ in relation to L_{max} to a lesser extent than the $VBGF_S$ (Table 3), reflecting a better fit to the data in the older age classes. In conjunction with a visual assessment of residuals, it was apparent that the $VBGF_S$ underestimated length at age above 20 years (Fig. 7). The better fit by the $VBGF_{TP}$



supports the hypothesis that a more complex growth model was required for striped trumpeter.

The $VBGF_{TP}$ was sensitive to the value *age at transference*. A profile of negative log likelihood for a range of age-at-transference values (Fig. 8) assisted in determining the correct absolute minima. The negative log-likelihood profile revealed a low minima range across age at transference from 3.5 to 4.6 years, which, however,

converged to a lowest value at age 4.4 years. Fitting the PDF to the growth curve substantially smoothed the point of transition, producing a curve that represented the data well. Setting an arbitrary standard deviation of 1.0 around the age at transference provided a normally distributed two-tailed range at transference (90 percent confidence adjusted for bias) from 1.3 to 7.8 years.

A likelihood ratio test (LRT) identified a slight significant difference between male and female VBGF_S growth curves ($\chi^2=13.20$ $df=3$ $P=0.04$), but there was no significant difference when the VBGF_{TP} was tested ($\chi^2=10.83$ $df=6$ $P=0.09$).

Mortality estimation

Ages 9–23 and 7–25 were included in the LCCCA regressions of the VBGF_S and the VBGF_{TP}, respectively, to

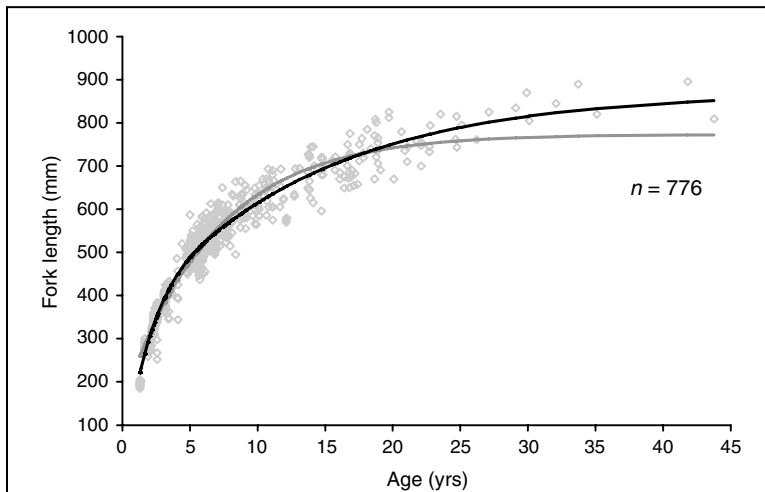


Figure 7

Pooled length-at-age data for striped trumpeter (*Latris lineata*). The black line represents the optimal two-phase von Bertalanffy growth function (VBGF_{TP}), with a mean age at transference of 4.4 years and a standard deviation equal to 1; the gray line represents the optimal standard von Bertalanffy growth function (VBGF_S).

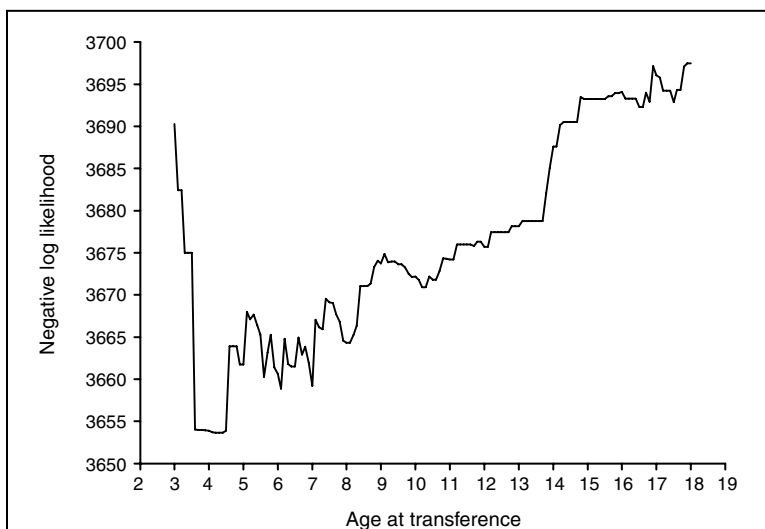


Figure 8

Negative log-likelihood profile plot of increasing age-at-transference values for striped trumpeter (*Latris lineata*).

estimate Z (Fig. 9). Individuals below these ranges were assumed, by their respective model, not to have fully recruited to the offshore fishery, and individuals over the age of 25 were excluded due to poor sample size. These age ranges effectively excluded the strong 1993 recruitment pulse from the regression, thereby avoiding the complication of including a known strong year class in the analysis.

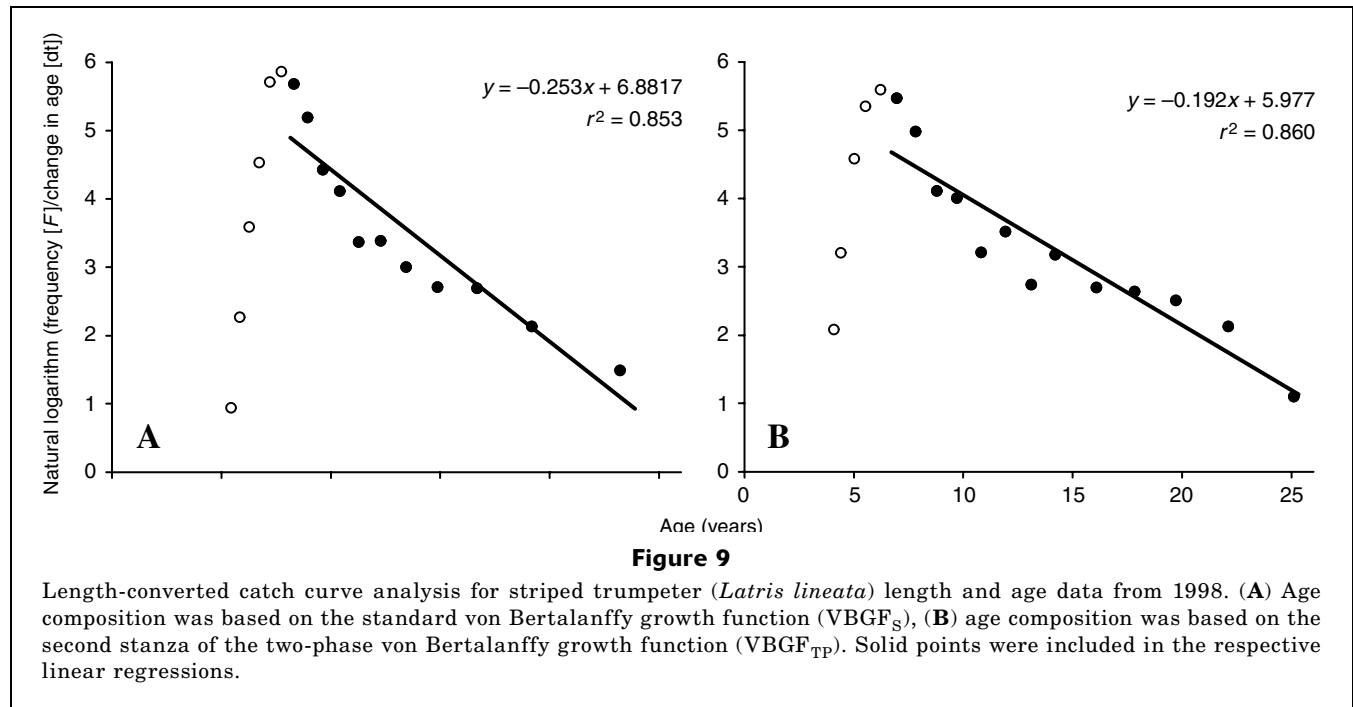
Application of the VBGF_{TP} model resulted in lower estimates of Z and M (based on the Pauly equation), compared with those calculated by using the VBGF_S parameters (Table 4). The estimate of Z based on the Hoenig (1983) equation was assumed to be close to M because F is low for this species. The Hoenig M was very similar to the Pauly estimate when VBGF_{TP} parameters were used. In this case M was just below 0.1, indicating an annual natural mortality rate of about 9%. The VBGF_{TP} estimates indicate that F was slightly higher than M in the offshore fishery. By contrast, the standard VBGF_S parameters produced a substantially higher estimate of M (0.15) based on the Pauly equation than predicted by the Hoenig approximation, indicating an annual natural mortality rate of about 14%. Derived estimates of F with the VBGF_{TP} were slightly higher than M , whereas F in relation to M was variable for the VBGF_S, depending on the equation used to derive M .

Discussion

The present study represents the first report of age and growth of striped trumpeter. Despite having available a patchy data set, we were able to validate age and overcome the limitations of the von Bertalanffy equation to represent these data by the use of a robust growth model. Striped trumpeter are long lived, have a maximum age in excess of 40 years, and growth is particularly rapid up to age five, after which it slows dramatically.

The species has a complex early life history involving a long planktonic larval phase of around nine months (Morehead¹), an in-shore juvenile phase, and then movement offshore into deepwater.

Gear selectivity (gill nets in the shallow and hook catches in the deeper waters) may have influenced the fish-size structure of our samples, especially when grouped by depth, although it is highly unlikely that the size differences could be completely attributed to gear type alone. For instance, small individuals (<400 mm) were occasionally taken by hooks in the deeper strata and individuals over 500 mm were taken by gill nets in less than 50 m. The commercial hook fishery



for striped trumpeter is largely restricted to depths of greater than 50 m, and despite considerable hook-fishing effort at shallower depths targeting other demersal reef species, notably the wrasses *Notolabrus fucicola* and *N. tetricus*, minimal catches of striped trumpeter are taken and those that are caught tend to be small in size (Lyle²). Rather, size structuring by depth is believed to reflect the movement of striped trumpeter offshore into deeper water as they grow and mature.

Seasonal growth was dramatic in young striped trumpeter (Fig. 5). This phenomenon is common in temperate species (Haddon, 2001; Jordan, 2001; McGarvey and Fowler, 2002), and has been linked to fluctuations in environmental factors, such as water temperature and oceanographic conditions, as well as biotic factors, such as seasonality in primary productivity (Harris et al., 1991; Jordan, 2001). Our study supports a correlation between water temperature and seasonal growth (Fig. 6); maximum growth was observed to take place consistently over a three-year period, approximately one month after the peak sea-surface temperatures.

Knowledge of growth and growth variability is essential to the understanding of a stock's population dynamics. To achieve an accurate assessment of these characteristics, several issues need to be addressed. Foremost, is a rigorous approach to the validation and precision testing of age estimates (Campana, 2001). In this study, a combination of age validation protocols outlined by Fowler and Doherty (1992) and Campana (2001) were subscribed to: 1) otoliths must display an internal structure of increments, (Fig. 3); 2) otoliths must grow throughout the lives of fish at a perceptible rate, which was confirmed by the otolith weight-at-age

Table 3

Parameter estimates derived from the two growth functions (standard von Bertalanffy growth function, [VBGF_S] and the two-phase von Bertalanffy growth function [VBGF_{TP}]) applied to the length-at-age data of striped trumpeter (*Latris lineata*) in Tasmania. Growth parameters are defined in the text, NOP = number of parameters in the model, AIC = Akaike information criterion, and L_{max} = the maximum length of all individuals included in the growth models.

		VBGF _S	VBGF _{TP}
Growth parameters	$L_{\infty 1}$	773.27	532.77
	k_1	0.15	0.43
	t_{01}	-1.46	0.03
	L^δ	—	450.11
	$L_{\infty 2}$	—	871.59
	k_2	—	0.08
	t_{02}	—	3.49
	t^δ	—	4.4
	σ^2 of t^δ	—	1.0
	Diagnostics	NOP	3.0
-log likelihood		3759.98	3700.13
AIC		5335.12	5211.30
% deviation of $L_{\infty 2}$ from L_{max}		-13.7	-2.7

regression (Table 2); 3) the age of first increment formation must be determined; and 4) increment periodicity across the entire age range of interest must be veri-

Table 4

Estimates of instantaneous rates of total (Z), natural (M), and fishing (F) mortality for striped trumpeter (*Latris lineata*) determined with age-based catch curve analysis and the empirical equations of Hoenig (1983) and Pauly (1980). $VBGF_{TP}$ = estimates derived from the parameters of the two-phase von Bertalanffy growth function, $VBGF_S$ = estimates derived from the parameters of the standard von Bertalanffy growth function and LCCCA = length converted catch curve analysis.

Method	Z		M		F	
	$VBGF_S$	$VBGF_{TP}$	$VBGF_S$	$VBGF_{TP}$	$VBGF_S$	$VBGF_{TP}$
LCCCA	0.253	0.192	—	—	—	—
Hoenig	—	—	0.096	0.096	0.157	0.096
Pauly	—	—	0.151	0.092	0.102	0.100

fied. We used cultured individuals to determine which opaque or translucent zone represented the first growth increment, although the accuracy of age validation with cultured individuals has been questioned by Campana (2001). In our study, the close correspondence between the growth of cultured and wild fish over a period of several years gives us confidence in using this approach to validate first increment position. The slightly slower growth rate observed in cultured striped trumpeter can be attributed to jaw malformation—a phenomenon that has been shown to affect feeding ability (Cobcroft et al., 2001).

Modal progression of the 1993 cohort through time provided indirect validation for annual periodicity in increment formation up until age seven. Validation across all age classes was not possible in our study, although validation after the age of five years was significant. That is, validation was achieved past the average age at which fish moved offshore into deeper water, and past the age at which there was a significant reduction in growth rate.

The second consideration to address when studying animal growth is model selection. Akaike's information criterion is a standard method for model selection that provides an implementation of Occam's razor, in which parsimony or simplicity is balanced against goodness-of-fit (Forster, 2000). However, model selection should not rely on statistical fit alone; it should also provide a biologically sensible interpretation across the entire range of ages in the sampled population (Haddon, 2001). In the case of striped trumpeter, the standard von Bertalanffy function provided a poor representation of growth in older individuals, resulting in an unrealistically low L_{∞} . This problem was largely overcome by the application of a two-phase growth function. Similar to that used on large pelagics, such as *Thunnus maccoyii* (Bayliff et al., 1991; Hearn and Polacheck, 2003). In their application of the model, Hearn and Polacheck (2003) considered biological traits when discussing the justification for age at transference, namely the reduction in growth rate, and inshore to offshore migration. In the present study we have considered analogous traits to seed the age of transference for striped trumpeter.

In this species there is a marked transition in size structure between shallow and deeper reefs that occurs at around 450 mm or between 4 and 5 years (Fig. 8). In addition, a visual assessment of the length-at-age data highlighted a marked decrease in growth rate at a similar age.

Solving for the age at transference produced a point estimate that results in a sharp discontinuity in the growth curve; an observation that Hearn and Polacheck (2003) highlighted as biologically unrealistic. The range of low negative log likelihood values described by the age at transference profile is due to the patchiness of data around these ages, creating uncertainty in the model. We have assumed in this case that the converged value of 4.4 years is accurate and that the variability around this point is normally distributed with a standard deviation equal to one. By including the normal probability distribution function we have effectively created a smooth transition between growth phases. This function implies that age at transference has some level of inherent variability, which is likely to be more biologically plausible than knife-edge transition.

A further extension of the two-phase model was tested by applying the seasonal growth version of the VBGF (described in Eq. 3) to the first phase and a standard VBGF to the second phase, but was disregarded because of the effect of over parameterization on parsimony. However, this approach did highlight the flexibility of the two-phase model to allow for a more dynamic representation of population growth characteristics.

This study supports the assertion by Hearn and Polacheck (2003) that discontinuity in growth rate may be a more common phenomenon in fish than implied by growth models reported in the literature. Such a two-phase growth model, where age at transference coincides with the transition phase from one fishery to another, has proven useful. It allows separate growth parameters to be tracked to each fishery, and as such, provides a precursor to developing a more biologically robust production model with dynamic parameters at age and for fishing method.

The predictive regression developed by Pauly (1980) that estimates natural mortality is based on the direct

relationship between longevity (t_{max}) and the magnitude of the physiological growth parameters k and L_{∞} . As such, it would be reasonable to assume that if a good fit exists between length at age that the growth parameters, when employed in such an empirical model, would yield a natural mortality estimate approximately equal to that determined by a regression model that is based on t_{max} (Hoenig, 1983). The two-phase growth function also provided a more conservative estimate of M than the standard von Bertalanffy model. Overestimates of M can lead to unrealistically high estimates of productivity and a potential yield that may in turn lead to overexploitation of a stock.

Protracted longevity, slow growth in later life, large body size, recruitment variability, and relatively low natural mortality once individuals reach adulthood are all characteristics typical of a K-selected species (where equilibrium is the biological strategy). Such species are often regarded as being susceptible to growth over-fishing and stock depletion (Booth and Buxton, 1997). For instance, increased fishing effort on the inshore fishery, as has been observed with the recruitment of strong cohorts, will affect subsequent recruitment to the off-shore fishery and spawning stock. The current analysis indicates that fishing mortality is slightly higher than natural mortality and, in the absence of further strong recruitment, a decline in the stock size is likely if fishing pressure is not reduced.

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