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The relative suitability of the von Bertalanffy, Gompertz and inverse logistic models for describing growth in blacklip abalone populations (*Haliotis rubra*) in Tasmania, Australia

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ABSTRACT

Three candidate, non-nested, growth models (von Bertalanffy, Gompertz and inverse logistic) were fitted to multiple samples of tag-recapture data ($n = 27$ samples) to determine the best statistical model for blacklip abalone (*Haliotis rubra*) populations in Tasmania, Australia. Wild populations of blacklip abalone were sampled for growth data using tag-recapture methods. The best statistical model was identified for each sample using Akaike's Information Criteria and Akaike weights to measure the relative statistical fit. Using these criteria, the best fitting model was the inverse logistic for 21 of the 27 samples, both the von Bertalanffy and the Gompertz models were the best fitting model in three samples each. When the inverse logistic was the best fitting model it was the best unambiguously, as indicated by the high Akaike weight values (generally $w_i > 0.8$; 0.65–1.0). In contrast, when either the von Bertalanffy or the Gompertz growth models were statistically optimal, the highest Akaike weights ranged between 0.15 and 0.44 across both models. We conclude that the use of either the von Bertalanffy or Gompertz growth models in the assessment of Tasmanian blacklip abalone would be statistically sub-optimal and may mislead assessments of Tasmanian abalone stocks. The inverse logistic model can be considered as a good candidate growth model for other fished invertebrate stocks.

1. Introduction

Growth models are a key component of stock assessments used in the management of commercially important invertebrate marine species. This is especially the case for difficult to age species such as abalone, lobsters, and urchins, where size-based assessment models may be used to describe the population dynamics instead of age-based models. Despite their importance the growth models selected for abalone populations vary among studies resulting in different growth models being used for the same species in different regions (Troynikov et al., 1998; Worthington et al., 1995). In Australia, there has generally been little explicit consideration given to the selection of a length-based growth model from an array of candidate models used to fit tag-recapture data from blacklip abalone (*Haliotis rubra*) populations and the model selection methods adopted in earlier studies of abalone growth are not always clear. In a more recent study of *Haliotis rufescens* in northern California (Rogers-Bennett et al., 2007), the selection of a growth model was explicitly based on information criteria which is a widely accepted and standard method for model selection (Burnham and Anderson, 2002).

In a review of Australian abalone growth studies, Day and Fleming (1992) identified that model selection was usually limited to a choice of only two models: the von Bertalanffy and the Gompertz growth models. The von Bertalanffy growth model tends to be the default model in fisheries both currently and historically (Jákupsstovu and Haug, 1988; Katsanevakis and Maravelias, 2008). However, the systematic selection of an optimum growth model from a range of competing models does not appear to be common and the plausibility of the von Bertalanffy growth model has been questioned for blacklip abalone and other fish species (Day and Taylor, 1997; Katsanevakis and Maravelias, 2008). A characteristic of the von Bertalanffy is it predicts a linear decline in growth rate as small juveniles get bigger. Alternatively, the Gompertz predicts growth rates that initially increase for small juveniles and then decline (Fig. 1). However, neither of these characteristics have been observed in data from small juveniles. Instead the growth rate of small juveniles has been observed to remain constant rather than decline or increase (Day and Fleming, 1992; Prince et al., 1988). Both the von Bertalanffy and Gompertz growth curves may therefore

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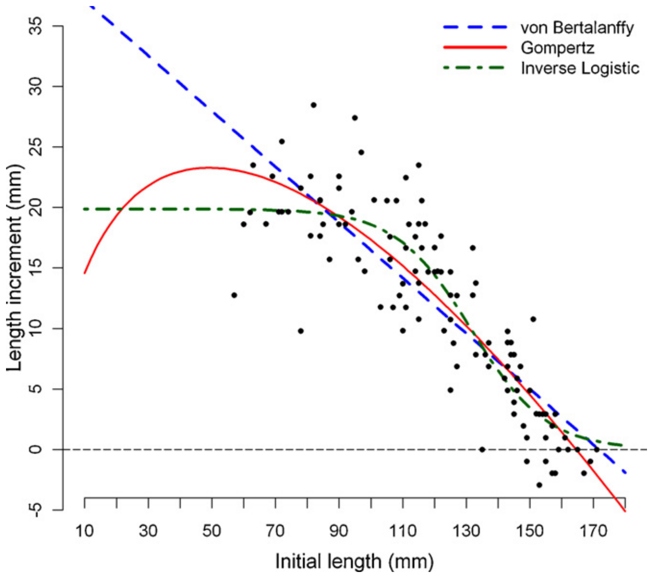

Fig. 1. The von Bertalanffy, Gompertz, and inverse logistic growth models fitted to a dataset that was the best example of tag recapture data in terms of sample size and initial size range. Presented are tag-recapture data from multiple years from site 458, Black Island 42.9687°S, 145.4924°E. Multiple years of tag-recapture data were pooled together.

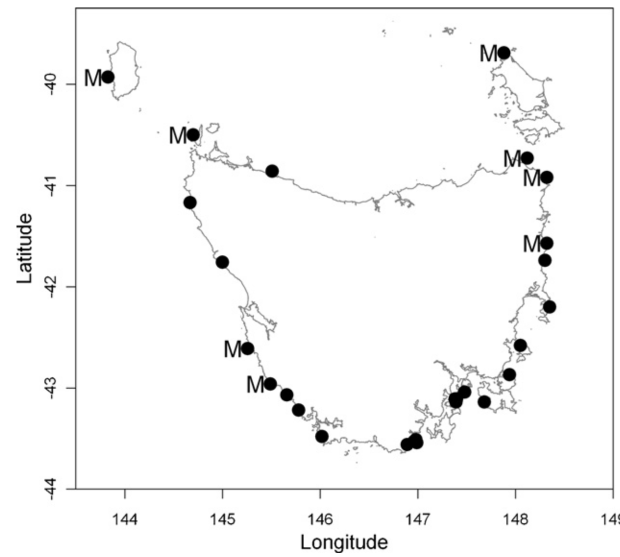

Fig. 2. Map of the distribution of the 27 samples of tagged blacklip abalone around Tasmania. The eight sites which had both growth and maturity data from the same site and year are indicated with an '*M*'.

be considered inappropriate for describing the growth of juvenile size classes. Even so, owing to its extensive use the von Bertalanffy model may be useful for making consistent comparisons between studies.

Recently, the inverse logistic model was developed as a growth model for blacklip abalone populations in Tasmania and this model incorporates constant growth rates in the smaller juvenile size classes. The development of the inverse logistic model was influenced by a modal analysis of length frequencies that suggested constant growth rates for juvenile size classes (10–70 mm) (Haddon et al., 2008). Constant growth rates in small juveniles differs markedly from the predictions of the von Bertalanffy and Gompertz models and therefore the inverse logistic was proposed as being biologically more plausible.

In considering which models to include as a set of candidate growth models, it is important to assess the biological plausibility of the predicted growth trajectories in addition to statistical properties used in model selection (Burnham and Anderson, 2002). This consists of establishing a set of biologically plausible candidate models and selecting the best model according to statistical criteria, which measure the relative support for a model given the data (Sorensen and Gianola, 2002). With the exception of two studies (Haddon et al., 2008; Rogers-Bennett et al., 2007), multiple candidate growth models (i.e. greater than two models) have not been explicitly tested on abalone using formal model selection methods. However, both of these studies focused on only a single population in their comparisons and inter model comparisons were only a minor component in the study by Haddon et al. (2008). Where model selection is explicit, the minimum Akaike Information Criterion (AIC) is customarily used to identify the optimal model (Shono, 2000). Usually, the statistically best fitting candidate model is considered to be the optimal model, although biological factors are also important. For example, a candidate model with a growth trajectory similar to that of the inverse logistic, was the best fitting model to *H. rufescens* in northern California but the model was rejected because of the rapid decline in growth rate between the juvenile phase and adult phase (Rogers-Bennett et al., 2007). Under such circumstances the best fitting candidate growth model may be rejected following post hoc assessment of its biological validity.

In the present study, model selection is based on a combination of biological and statistical criteria. Three non-nested candidate growth models were fitted to tag-recapture data from 27 samples around Tasmania, Australia, to identify the optimal model in terms of statistical fit and parsimony guided by systematic model selection techniques. Each growth model was fitted to multiple populations of tag-recapture data from predominantly late-juvenile to adult-sized animals (80–210 mm shell length). The aims of this study were threefold; firstly to characterize typical variation in the parameters of three growth models for blacklip abalone populations around Tasmania, secondly to identify the best fitting growth model using goodness-of-fit tests and model selection techniques, and finally to examine whether the predicted growth trajectories could be given a biologically realistic interpretation.

2. Methods

2.1. Site selection

The sites sampled represent a range of currently fished abalone reefs in the Tasmanian fishery (Fig. 2). The sites selected were generally chosen on the advice of commercial divers who were actively fishing and familiar with the region.

2.2. Growth data

Length increment data were obtained from tag-recapture studies. Tag-recapture data used in the analyses were collected during multiple fishery independent surveys conducted by research divers. During the dives, the shell length of individual abalone were measured, allocated a numbered tag, and carefully returned to the same location, or at least proximal to where it was collected. Tagged abalone were then left at liberty for approximately one year before being removed and shell length measured. Growth increment data from different sites was accumulated in this way over a 15 year period, 1994–2008 by the Tasmanian Aquaculture and Fisheries Institute of the University of Tasmania (now part of the Institute for Marine and Antarctic Studies).

Data collected in different years from the same site were treated as separate samples for two reasons: (1) multi-year samples were not assumed to be identical and (2) growth parameters are assumed to be temperature variant; temperatures vary over time and temperatures may affect growth rate (Gilroy and Edwards, 1998). The possible effect of temperature was especially important as it is widely accepted that growth of poikilothermic species (e.g. abalone) may be affected by change in water temperatures. Therefore, it appears likely that mean somatic growth within a population may differ between years.

Four criteria had to be met for samples to be included in the analysis:

i. the sample must include juveniles to define the full growth curve, i.e. <100 mm shell length,
ii. large abalone with negligible or no growth increments had to be included in the sample so that the full range of growth was included,
iii. the time increment between mark and recapture was approximately one year (between 0.9 and 1.2 years),
iv. sample size was greater than 90 recaptures.

After applying the four data screening criteria, 27 samples were available for this study.

Negative increments were found to affect the parameters of the von Bertalanffy growth model (Sainsbury, 1980) so to minimize this effect, data with length increments greater than −3 mm were removed (−3 mm was selected to allow for some sampling error while only removing a minimum number of observations). Negative increments had negligible effects on model parameters fitted to the Gompertz and inverse logistic models (unpublished data). Because time increments are not explicit in the inverse logistic model, length increments were standardized for the time-at-liberty by dividing the observed length increment by the observed time-at-liberty (i.e. between 0.9 and 1.2 years) to normalize the length increments to one year exactly.

2.3. Growth models

The deterministic forms of the three candidate growth models include

(a) re-parameterized, size-based analogue of the von Bertalanffy model for tag-recapture data used for estimating length increments from time increments (Fabens, 1965) (Fig. 1):

$$\text{von Bertalanffy (VB)}: \quad \Delta\hat{L}_i = (L_\infty - L_i)(1 - e^{-K\,\Delta t}) + \varepsilon \tag{1}$$

(b) the re-parameterised Gompertz (Troynikov et al., 1998) for estimating length increments from time increments (Fig. 1):

$$\text{Gompertz (Gz)}: \quad \Delta\hat{L}_i = L_\infty \left(\frac{L_i}{L_\infty}\right)^{\exp(-g\,\Delta t)} - L_i + \varepsilon \tag{2}$$

(c) the inverse logistic model (Haddon et al., 2008), which assumes all size increments relate to the same time increment (Fig. 1):

$$\text{inverse logistic (IL)}: \quad \Delta\hat{L}_i = \frac{\text{Max}\,\Delta L}{1 + e^{\text{Ln}(19)((L_i - L_{50})/(L_{95} - L_{50}))}} + \varepsilon \tag{3}$$

where $\Delta\hat{L}_i$ is the expected length increment for individual i, L_∞ is the shell size where the mean length increment is zero (VB & Gz), L_i is the initial length for individual i when first tagged and released, K is the "destruction constant", (von Bertalanffy, 1938, p186) (VB), $g > 0$ (Gz), Δt is the time at liberty (as a fraction of a year; VB & Gz), Max ΔL is the maximum length increment, L_{50} is the initial length at 0.5 times Max ΔL, L_{95} is the initial length at 0.05 times Max ΔL.

The 19 in Ln(19) implies that the L_{95} parameter relates to the 95% point (Ln(15) would equate to the 75% point) (Haddon et al., 2008). The constant ε's are independent additive normal random error terms. Using an identical error structure for all three models simplifies their statistical comparison.

2.4. Model selection using statistical criteria

The optimal growth model was identified using three statistical criteria. The first criterion involved identifying the model with the minimum negative log-likelihood estimate (the best fitting model). In each case the minimum log-likelihood function based on length increments was,

$$-\text{LL} = -\sum_{i=1}^{n} \text{Ln}\left(\frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\left[\frac{(\Delta L_i - \Delta\hat{L}_i)^2}{2\sigma^2}\right]\right)\right) \tag{4}$$

where ΔL_i is the observed growth increment for each of the $i = 1$ to n observations at each site, $\Delta\hat{L}_i$ is the predicted growth increment for observation i from one of the three candidate growth models (Eqs. (1)–(3)), and σ is the standard deviation of the normal random errors. Rogers-Bennett et al. (2007) used least squared residuals when comparing six candidate models; in an equivalent manner we used normal random residuals errors. However, the use here of a maximum likelihood framework simplified the use of model selection methods and permitted the use of Akaike weights. The negative log-likelihood (−LL) was minimized in each case using the 'optim' function in R (R Development Core Team, 2008).

The growth models considered are simple low dimensional models described by only a few parameters. This makes it straightforward to locate the global minimum of the negative log-likelihood for each model (Sorensen and Gianola, 2002).

The second criterion was to identify the model with the smallest Akaike Information Criteria (AIC_{min}). The AIC balances the trade-off between the quality of fit and the number of parameters used (Burnham and Anderson, 2002) and is defined as $\text{AIC} = -2 \times \text{LL} + 2K$, where K is the total number of parameters (including σ^2) and $-2 \times \text{LL}$ is two times the negative log-likelihood at its optimum. The relative quality of fit of the three candidate growth models was determined for multiple sites in order to select the statistically optimum model for the majority of populations.

The third criterion was to determine the relative weight of evidence for each model (AIC_i, including the sub-optimum and optimum models) relative to the optimum model (AIC_{min}), using Akaike weights (w_i) (Buckland et al., 1997). These are defined by first calculating the relative AIC values, $\Delta_i = \text{AIC}_i - \text{AIC}_{\text{min}}$, where i indexes the three growth models, and substituting these into the expression

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{i=1}^{3} \exp(-0.5\Delta_i)} \tag{5}$$

2.5. Biological plausibility of growth model parameters

When examining the link between growth parameters and biology, two biological characteristics were used: median shell length of adults and size at maturity. For the median length, the percentage difference was calculated between estimates of the parameter values and the median length of catch; percent difference = 100 × $(P - M)/P$, where P is the estimated parameter and M is the median catch.

The L_∞ of the von Bertalanffy and Gompertz represents the initial shell length where the predicted mean increment is zero. The L_∞ of the von Bertalanffy and Gompertz models does not represent the asymptotic maximum shell length of the abalone population (Ratkowsky, 1986). Instead it represents the mean of the distribution of maximum lengths for the population as a whole (Sainsbury, 1980). The L_{95} of the inverse logistic is consistently close to the shell lengths where growth increments become small. Assuming

Table 1
Growth parameters for length increment data from 27 samples of blacklip abalone (*Haliotis rubra*); s.d. is the standard deviation. Three growth models, the von Bertalanffy, Gompertz and inverse logistic were fitted to 27 samples of tag-recapture data using maximum likelihood. Samples that differed in space and time were treated as separate samples.

Site	Sample size	Latitude	Longitude	Year	von Bertalanffy			Gompertz			Inverse logistic			
					L_∞	K	s.d.	L_∞	g	s.d.	Max ΔL	L_{50}	L_{95}	s.d.
59	134	−41.57	148.32	1994	151	0.464	5.4	148	0.587	5.4	24.2	118	157	5.4
59	330	−41.57	148.32	1996	157	0.447	5.3	153	0.583	5.3	28.8	117	167	5.3
159	119	−42.58	148.05	1994	160	0.356	3.8	158	0.445	3.8	20.9	126	168	3.8
159	91	−42.58	148.05	1996	175	0.305	6.8	169	0.411	6.7	18.4	139	169	6.6
170	92	−41.17	144.67	1995	141	0.316	3.1	140	0.385	3.1	14.2	116	146	3.1
272	203	−42.61	145.26	2001	162	0.358	3.6	161	0.420	3.7	26.3	120	163	3.4
297	271	−42.2	148.35	2003	152	0.386	4.9	147	0.534	4.8	24.0	115	152	4.6
300	114	−41.74	148.3	2003	164	0.484	5.7	157	0.680	5.4	30.0	123	157	4.9
313	389	−40.5	144.7	2001	128	0.286	3.4	127	0.348	3.6	17.9	92	128	3.3
314	434	−39.93	143.83	2001	147	0.347	4.4	145	0.444	4.5	21.1	112	149	4.3
315	207	−39.69	147.88	2001	121	0.346	2.9	119	0.432	3.1	20.0	87	121	2.7
316	232	−40.73	148.12	2001	139	0.349	4.1	136	0.457	4.2	25.7	96	147	4.1
337	144	−42.87	147.94	2003	141	0.291	4.5	136	0.407	4.3	17.1	108	138	4.1
458	118	−42.96	145.49	2003	172	0.260	4.1	164	0.386	3.7	19.9	131	167	3.5
459	132	−43.48	146.02	2003	155	0.325	2.5	155	0.368	2.6	15.4	128	155	2.4
460	90	−43.07	145.66	2003	164	0.358	4.6	162	0.436	4.6	19.9	131	160	4.3
461	163	−43.11	147.38	2003	173	0.352	4.6	162	0.544	4.4	29.5	122	173	4.3
478	347	−43.54	146.99	2003	145	0.357	3.9	140	0.499	3.7	22.3	110	146	3.6
480	151	−43.56	146.89	2003	136	0.479	4.2	134	0.613	4.3	30.0	97	137	3.9
482	135	−43.11	147.397	2003	150	0.576	4.3	148	0.702	4.3	27.6	118	154	4.2
588	118	−40.92	148.32	2003	171	0.282	4.3	163	0.407	4.1	20.6	127	162	3.8
662	112	−40.86	145.51	2006	102	0.232	2.9	102	0.276	2.9	10.1	78	97	2.8
663	114	−43.04	147.48	2007	128	0.508	4.3	127	0.619	4.5	32.2	88	134	4.0
702	257	−43.14	147.39	2006	163	0.398	5.0	160	0.507	5.0	31.8	115	178	5.0
764	226	−43.14	147.68	2006	166	0.381	3.9	159	0.531	3.9	27.3	123	174	3.9
813	167	−43.51	146.98	2008	141	0.225	3.0	140	0.297	2.8	13.2	112	132	2.6
819	97	−41.76	145	2008	141	0.320	2.9	141	0.377	3.0	21.1	105	141	2.7

a normal distribution for the L_∞ and L_{95}, the most relevant biological estimate that could be compared to these parameters is the median length of catches. These are obtained annually from fishery-dependent commercial surveys and represent the median length of fished adult abalone from year to year. A range of median length estimates was accumulated over the years. In some years size selective fishing occurs where divers exclude very large abalone. This will affect year-to-year estimates of median length of catches causing a downward bias. To overcome this potential bias, only the maximum value within the range of median estimates was used for comparison with the L_∞ and L_{95} parameters. Fishing locations, for which median shell-length data were available, were matched as closely as possible to the locations of the tagging survey sites. The median shell length of catches was reported for 18 samples (Table 3). Parameter estimates of L_∞ (from the von Bertalanffy and Gompertz) and L_{95} (from the inverse logistic model) were compared with median shell length data using ANOVA.

The L_{50} parameter of the inverse logistic model is the initial shell-length at which the decline in growth rate is most rapid (Haddon et al., 2008). Declines in growth rate are associated with the onset of maturity as energy is transferred from somatic growth to reproductive investment and a reduction in shell growth rate is expected (Lester et al., 2004). This decline in growth rate was claimed to be biologically implausible in red abalone (*H. rufescens*) in northern California, as the decline in growth rate was considered to be too rapid (Rogers-Bennett et al., 2007). To explore if this rapid decline in growth rate is biologically valid in blacklip abalone, population estimates of size-at-maturity were compared with population estimates of the L_{50} parameter from the inverse logistic model (where L_{50} is the shell length where 50% of the population is mature). In total, eight sites (each representing a different population) were extracted from the database where each site had data for both growth and maturity taken at the same time (Fig. 2). The L_{50} parameter estimates were calculated for each site as well as the corresponding size-at-maturity (SM_{50}) and potential differences between these two variables were examined using a one-way ANOVA.

Finally, to demonstrate whether the selection of growth models has implications for the population dynamics, the age-at-maturity was calculated for the eight sites with size-at-maturity data using all three growth models. The earlier a species reaches maturity the shorter the expected generation time and hence the higher the expected productivity. These ages were determined as the time taken for 2 mm size animals to grow to the size-at-maturity.

3. Results

3.1. Statistical fit

The best fitting parameters of all three models exhibited wide variation around Tasmania (Table 1) and results clearly indicate that the inverse logistic is statistically optimal over a range of growth rates. The AIC values (Table 2) indicate that the inverse logistic model was statistically optimal in 21 samples out of the 27 samples of length-increment data considered. Both the von Bertalanffy and the Gompertz models were the best fitting models in only three samples each. In all cases, the ordering of the Akaike weights matched the minimum AIC, however, there were large differences in Akaike weights between the best inverse logistic model and best von Bertalanffy or Gompertz model (Table 2). The high Akaike weight values ($w_i > 0.8$) for the best inverse logistic model (e.g. sites 272–315; 337–663; 813 and 819, $n = 20$ sites with $w_i > 0.8$; Table 2) indicate that the best fitting inverse logistic models are generally more certain than the best fitting von Bertalanffy or Gompertz. The maximum Akaike weights ranged between 0.15 and 0.44 for the von Bertalanffy and Gompertz collectively, and indicate more uncertainty for the von Bertalanffy or Gompertz when either was the best fitting models in the presence of other candidate models.

As juveniles approach maturity energy is partitioned away from somatic growth toward reproductive development (Lester et al.,

Table 2
Information criteria associated with statistical model selection. Three growth models: von Bertalanffy (VB), Gompertz (Gz) and inverse logistic (IL), were fitted to 27 samples of tag-recapture data. Samples that differed in space and time were treated as separate samples.

Site	Year	Log likelihood			AIC			Minimum	Akaike weights		
		VB	Gz	IL	VB	Gz	IL	AIC	VB	Gz	IL
59	1994	416	416	415	838	838	839	Gz	0.31	0.46	0.23
59	1996	1020	1020	1019	2046	2046	2047	Gz	0.34	0.37	0.29
159	1994	329	329	329	664	664	666	VB	0.49	0.36	0.15
159	1996	304	303	301	614	612	610	IL	0.08	0.27	0.65
170	1995	235	235	234	476	476	477	VB	0.4	0.33	0.27
272	2001	547	555	539	1100	1117	1087	IL	0	0	1
297	2003	815	808	798	1636	1622	1604	IL	0	0	1
300	2003	359	353	344	724	713	696	IL	0	0	1
313	2001	1033	1046	1022	2072	2098	2051	IL	0	0	1
314	2001	1263	1265	1246	2532	2536	2499	IL	0	0	1
315	2001	516	526	502	1038	1059	1011	IL	0	0	1
316	2001	656	660	654	1317	1325	1316	IL	0.3	0.01	0.69
337	2003	421	414	408	847	833	823	IL	0	0.01	0.99
458	2003	333	321	315	673	648	638	IL	0	0.01	0.99
459	2003	309	311	302	625	628	612	IL	0	0	1
460	2003	264	266	259	534	538	527	IL	0.02	0	0.97
461	2003	479	472	469	963	950	946	IL	0	0.09	0.91
478	2003	962	947	936	1930	1900	1880	IL	0	0	1
480	2003	432	436	420	871	878	848	IL	0	0	1
482	2003	388	388	384	782	783	776	IL	0.04	0.03	0.93
588	2003	339	335	326	684	675	660	IL	0	0	1
662	2006	278	279	275	562	564	558	IL	0.09	0.04	0.88
663	2007	327	332	320	661	671	649	IL	0	0	1
702	2006	777	778	776	1559	1562	1560	VB	0.52	0.11	0.37
764	2006	631	629	628	1268	1263	1264	Gz	0.06	0.5	0.44
813	2008	419	412	395	844	829	797	IL	0	0	1
819	2008	240	245	235	485	496	477	IL	0.01	0	0.99

2004), resulting in an associated decline in somatic growth rates for larger size juveniles that appears to be non-linear (Fig. 3). Accordingly, the inverse logistic model is also able to capture the decline in growth rate for juveniles approaching maturity. The inverse logistic model is thus biologically consistent with the data insofar as it describes both constant and non-constant growth rates that may occur over the entire size range of the juvenile size classes. Note that within a given population, the size that constitutes small juveniles needs to be considered relative to the SM_{50} for that population, e.g. in Fig. 3, site 458, the growth of a 60 mm size abalone is predominantly somatic and is likely not confounded by reproductive development because it is far from the onset of maturity. By contrast, in site 315, a 60 mm abalone is likely approaching the onset of maturity and resources are thus divided between somatic and reproductive investment. It is expected that different samples will have different trajectories in the growth rate of abalone that are, for example, 60 mm in initial shell length, and this is a result of the size differential in the onset of maturity.

3.2. Biological plausibility

The estimated median shell lengths were proximal to the L_∞ parameters of the von Bertalanffy and Gompertz, and the L_{95} of the inverse logistic (Table 3). Overall, the maximum difference between the median shell length and the parameter value (as a percentage of the parameter value) was within 20% of the parameter value however the majority of samples were within 10% (15, 17 and 13 samples where within 10% for the von Bertalanffy, Gompertz and inverse logistic models respectively). For some sites there was strong agreement between the model parameters and the maximum length of catch (sites 170, 272, 460, and 482). For other sites (159, 337, 461, 480, 663 and 819) the percent difference ranged from −15.4% to 14.5% for von Bertalanffy, −17.2% to 10.7% for Gompertz, and −14.6% to 16.9% for the inverse logistic. Even so, there were no significant differences between the L_∞ and L_{95} parameters and the median shell length ($p > 0.05$).

There was no significant difference between the L_{50} parameter of the inverse logistic and the size-at-maturity (SM_{50}) ($p = 0.442$). Given only eight pairs of observations there was a strong correlation between the L_{50} of the inverse logistic model and the SM_{50} ($r = 0.891$, $p < 0.01$; Table 3, Figs. 3 and 4).

The von Bertalanffy model consistently resulted in the lowest estimates in age-at-maturity compared to the other growth models (Table 3). However, the trend in relative difference between sites was generally similar between growth models. The two most widely used growth models (i.e. the von Bertalanffy and Gompertz) produced the most disparate results differing by 2–3 years. The inverse logistic produced estimates that were consistently between the range of the von Bertalanffy and Gompertz.

4. Discussion

For many fisheries, particularly fin-fish, the stock is considered to consist of one biologically homogenous population and the dynamic pool assumption applies (Pitcher and Hart, 1982). In contrast, the Tasmanian abalone fishery consists of hundreds of spatially explicit stocks which are ecologically dissimilar at fine spatial scales (tens or hundreds of metres) (Nash, 1992; Prince et al., 1987). It is therefore not feasible to impute growth parameters from one population onto another population.

The sites selected encompassed a diversity of geographic regions and resource states which is an important component of field sampling (Krebs, 1989). Two key factors that determine the diversity of resource states are food and habitat and both may influence the growth rate of blacklip abalone (Saunders and Mayfield, 2008). The geographical scale of the analyses presented in this study captures the naturally high levels of variation in growth in spatially discrete abalone populations, under widely varying environmental conditions. It is evident from the variability in growth parameters (Table 1) that the samples used in the analysis were representative of a wide diversity of resource states. Results demonstrate the inverse logistic is consistently selected as the optimal growth

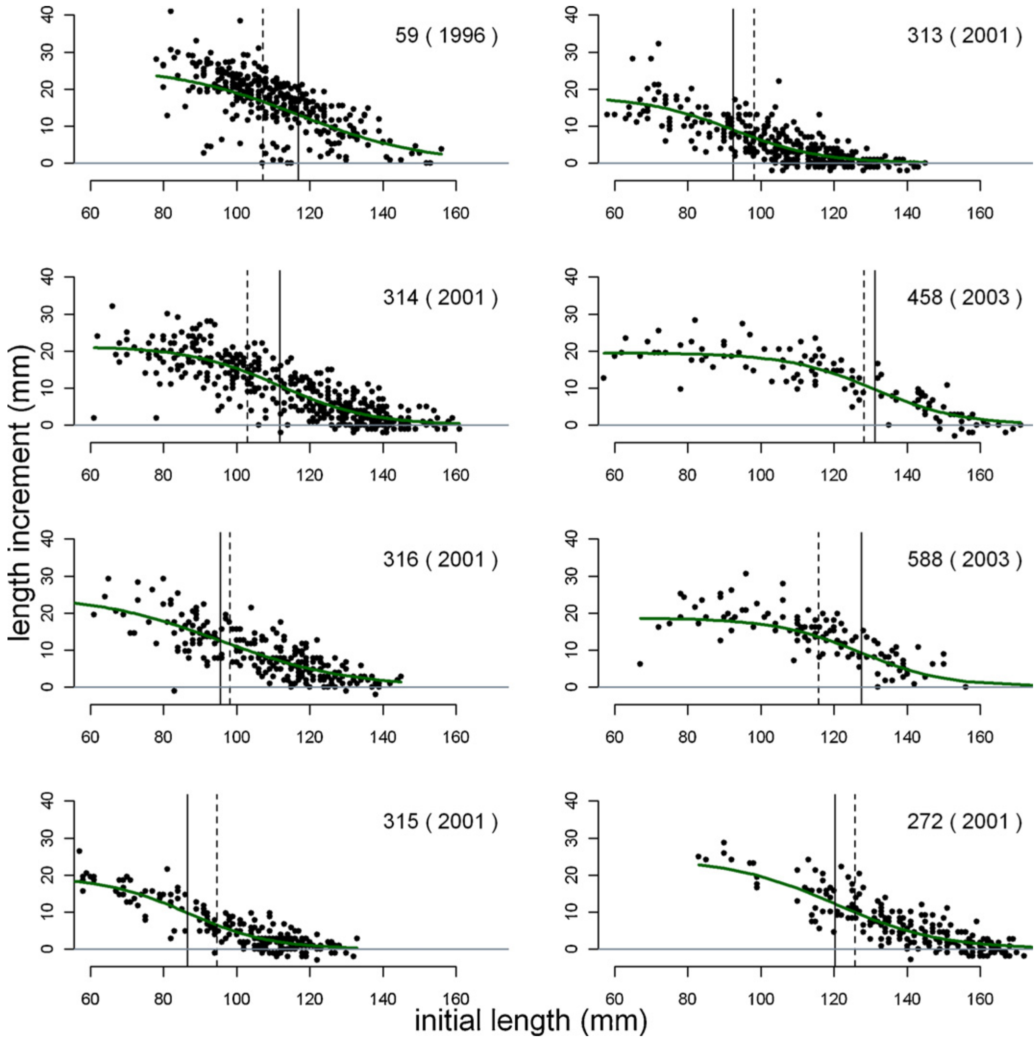

Fig. 3. Relationship between the estimates of size-at-maturity (SM_{50}, initial shell length at which 50% of the populations was mature) (dotted vertical line) and the L_{50} parameter of the inverse logistic model (solid vertical line) for eight sites. For each site growth and maturity data was collected in the same year. Site numbers are shown on each plot alongside the year (in brackets) the data were collected. The fitted growth curve in each case is the inverse logistic.

model in populations that occur across a range of environmental conditions. Although the sites sampled do not cover the entire geographic range of this species, the consistently favourable AIC, over the von Bertalanffy and Gompertz, clearly demonstrate the robustness of the inverse logistic to various resource states and can be potentially used for other regions. The inverse logistic may also be recommended for other species of abalone given that a growth model with a similar trajectory was also statistically optimal in a population of red abalone (*H. rufescens*) in California (Rogers-Bennett et al., 2007).

A strength of this study is that numerous populations were considered relative to other studies on wild abalone growth. The only other study of comparable scale was conducted in New Zealand, where 30 sites were also examined for growth (Naylor et al., 2006). Other similar Australian studies consist of fewer sites, e.g. 16 sites in South Australia (Saunders and Mayfield, 2008) and seven sites in NSW (Worthington et al., 1995). Overseas studies have far fewer populations owing to a relatively small geographical extent of these fisheries, e.g. six sites in a study of *Haliotis midae* in South Africa (Tarr, 1995) and only one population in a growth study from California USA (Rogers-Bennett et al., 2007). With fewer sites there is a greater potential for sampling more adequately, however if unchecked there is also the possibility that biological conclusions may be biased by data that misrepresent the biology through sampling error due to low size range or low sample size.

Biological validity is important in model selection because if the candidate set of models is biologically arbitrary (for example a polynomial could be used to describe mean growth increments) it is still possible to obtain a statistically optimum model based on AIC estimates. The AIC estimates only evaluate the relative statistical fit of the candidate models presented (relative to each other). The best-fitting statistical model, identified as the one with lowest relative AIC value, may still be biologically implausible if it lacks realism. Every effort should therefore be made to gain relevant biological knowledge of the models relative to the species in question before establishing an *a priori* set of candidate models (Burnham and Anderson, 2002).

Recently the inverse logistic growth has been proposed as a candidate growth model for abalone populations (Haddon et al., 2008). In a study of *H. rufescens* in northern California the dose–response model (a growth model visually similar to the inverse logistic model) was statistically the best fitting model, based on AIC results (Rogers-Bennett et al., 2007). However the dose–response model was rejected on the basis that the sharp transition in growth rate from constant growth in juveniles to slow growth in adults was not considered biologically plausible. The inverse logistic has a similar rapid transition and this transition appears to represent

Table 3
Biological plausibility of model parameters for three growth models (von Bertalanffy (VB), Gompertz (Gz) and inverse logistic (IL)). Estimated values between median lengths of catches correspond to the parameters of three growth models that describe maximum shell length (L_∞ for both the von Bertalanffy and Gompertz and L_{95} for the inverse logistic). Estimated values of size at maturity (SM_{50}) correspond to the parameter of the inverse logistic model where the growth rate declines most rapidly (L_{50}). Each of the three growth models were fitted to tag-recapture data for 27 populations. The median length of catches represents the median length of adults in the population collected over a six year period between 2004 and 2009. Only the maximum values of the range collected over the six year period are presented. The age at maturity (AM_{50}) is presented only for samples that had growth and maturity data collected from the same point in time and space.

Site	VB	Gz	IL	Median length catch (mm)	IL	Size at maturity	Age at maturity		
	L_∞ (mm)	L_∞ (mm)	L_{95} (mm)		L_{50} (mm)	SM_{50} (mm)	VB	Gz	IL
59	151	148	157	–	118				
59	157	153	167	–	117	107	2.9	4.8	4.3
159	160	158	168	150	126				
159	175	169	169	151	139				
170	141	140	146	145	116				
272	162	161	163	162	120	126	4.5	7.4	5.6
297	152	147	152	149	115				
300	164	157	157	–	123				
313	128	127	128	–	92	98	5.0	7.9	6.3
314	147	145	149	–	112	103	3.4	5.6	5.0
315	121	119	121	–	87	95	4.5	6.8	5.6
316	139	136	147	–	96	98	3.6	5.7	4.4
337	141	136	138	154	108				
458	172	164	167	162	131	128	5.4	7.6	6.7
459	155	155	155	163	128				
460	164	162	160	159	131				
461	173	162	173	148	122				
478	145	140	146	157	110				
480	136	134	137	157	97				
482	150	148	154	148	118				
588	171	163	162	–	127	116	4.4	7.0	6.3
662	102	102	97	–	78				
663	128	127	134	146	88				
702	163	160	178	148	115				
764	166	159	174	147	123				
813	141	140	132	150	112				
819	141	141	141	157	105				

the size where growth increments are decreasing due to resources being allocated away from somatic growth and toward reproductive development (Fig. 3). It is possible that the onset of maturity may result in a rapid decrease in somatic growth rate (Lester et al., 2004) and this is clearly demonstrated here (Fig. 3). Furthermore the strong correlation between the L_{50} parameter of the inverse logistic model and the SM_{50} in the present study (Fig. 4) supports the biological validity of the inverse logistic model for blacklip abalone in Tasmania.

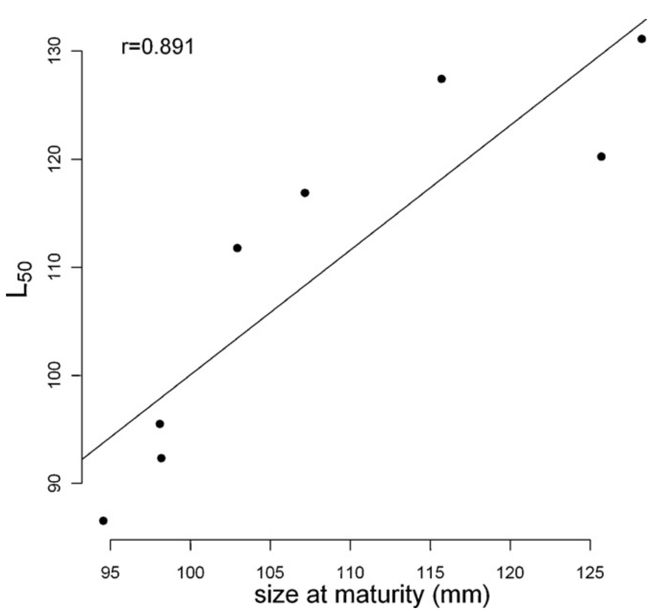

Fig. 4. Correlation between size at maturity (SM_{50}) and the L_{50} of the inverse logistic fitted to tag-recapture data for eight populations where growth and maturity data were collected in the same site and year. The correlation coefficient of $r = 0.890$ is significant at $p < 0.01$ ($n = 8$).

The inverse logistic model is able to describe both constant initial growth increments as well as a non-linear decline in growth rates of larger juveniles as they approach maturity. The inverse logistic is thus biologically plausible for the entire juvenile size range as well as being statistically optimal. The von Bertalanffy and Gompertz are also consistent with the non-constant decline in growth rates of larger juveniles but were not statistically optimal (Table 2). This does not eliminate the von Bertalanffy and Gompertz as suitable growth models, although it does demonstrate that the inverse logistic, being only recently implemented and previously untested, is biologically and statistically a sound candidate growth model; this has not previously been demonstrated for growth trajectories that incorporate constant growth rates in small juvenile size classes.

This study therefore partly overcomes one problem of model uncertainty – the thin choice in model selection (Katsanevakis and Maravelias, 2008). This may lead to "retrospective regret" in model selection because a larger range of plausible models was not considered (Hamilton et al., 2007; Katsanevakis and Maravelias, 2008). Historically, there has been strong reliance on the von Bertalanffy model to characterize growth and if the von Bertalanffy was not the best fitting model, then typically the Gompertz was selected, effectively by default. This study provides clear evidence that the inverse logistic model can be a plausible growth model thereby improving the degrees of freedom in the choice of candidate models.

A well known disadvantage of the deterministic Faben's version of the von Bertalanffy is that parameter estimates are biased if the growth variation of individuals is ignored (Eveson et al., 2007; Sainsbury, 1980; Wang and Thomas, 1995). The issue of the biases has been researched extensively for over 30 years (Sainsbury, 1980). A solution is to use probability density functions (pdfs) around the k and L_∞ parameters (Eveson et al., 2007; Troynikov, 1998). However, this solution leads to the practical disadvantage concerning the difficulty in incorporating probabilistic growth models into stock assessments. This means that the inherently biased von Bertalanffy continues to be used because of its relative simplicity. The deterministic Gompertz model may be used to overcome this bias and also other model options are readily available that could be considered and tested (Rogers-Bennett et al., 2007).

Although the Gompertz may be an alternative to the biased von Bertalanffy another well known disadvantage to both deterministic models is that they predict negative growth increments (Sainsbury, 1980; Troynikov, 1998). For many species negative growth is biologically implausible, and fitting these models to data that includes negative increments may skew parameter estimates. The deterministic von Bertalanffy and Gompertz models require pdfs around the L_∞ in order to avoid predicting negative increment for larger size classes. The inverse logistic model achieves this without requiring a pdf around its parameters.

A disadvantage of the inverse logistic is that it requires data from small juvenile size classes to define the Max ΔL parameter. The deterministic von Bertalanffy and Gompertz models have the advantage of being simpler to use than the inverse logistic and are less demanding in their data requirements. However, this needs to be evaluated against the disadvantage of parameter biases and/or predictions of negative growth. The inverse logistic may be equally appealing insofar that it does not predict negative growth increments and is therefore easier to implement than the probabilistic von Bertalanffy or Gompertz thereby offering the same advantage as these probabilistic models without the complications.

The main advantage of the inverse logistic is that it is consistent with the description of growth from observed data for juvenile size classes of abalone. This model has also been used to describe the growth increments of echinoderms in Australia (Ling et al., 2009) and rock lobsters in New Zealand (Starr et al., 2009).

In summary, the problem of bias and or negative growth increments is an issue for tag-recapture data of any species. Overall, the advantages of the inverse logistic outweigh the disadvantages when evaluated against the biases of the von Bertalanffy and the negative growth predictions of the both the von Bertalanffy and Gompertz.

The selection of a growth curve has implications for stock productivity and may influence many aspects of the population dynamics of a species. For example, the Gompertz model consistently estimates relatively older age-at-maturity, which would imply lower productivity than predicted by the von Bertalanffy, which consistently predicted younger age-at-maturity. The productivity of the stock implied by the inverse logistic model, as indicated by the age-at-maturity, would be intermediate between the Gompertz and the von Bertalanffy models. Estimates of age-at-maturity are used in age based stock assessment model for calculating spawning biomass. While age-at-maturity is only one of many potential implications of growth model selection on the population dynamics of the species concerned, the large differences in relative productivity predicted by different growth models clearly demonstrate the importance of defensible model selection techniques.

This paper resolved the problem of selecting a growth model among the main candidate models across many population samples. Previously the majority of studies of growth in abalone have indiscriminately used the Gompertz, the von Bertalanffy or variants of them (probability distribution on some of the parameters) or the Schnute growth model (which usually defaulted to the von Bertalanffy or Gompertz equivalents). To further characterize variation, and potentially include samples that were excluded by the data screening criteria, it may now be useful to use a Bayesian analysis of a hierarchy of inverse logistic models. Such a Bayesian approach may be applied now that an optimum model structure has been identified.

5. Conclusion

The inverse logistic model adequately describes the growth of blacklip abalone populations over the geographic range of the species in Tasmania. The inverse logistic model was selected as the best statistically fitting model for many more sites and outperformed the von Bertalanffy or Gompertz. Akaike weights for when the inverse logistic was the best fitting model were also high leading to more confidence in the selection of this growth model. This finding is limited to models fitted to data with normal random errors. Nevertheless, not only did the inverse logistic fit the data well but the model parameters were biologically plausible. It is recommended that the inverse logistic be used in stock assessment modelling where a description of growth is included, because the von Bertalanffy or Gompertz growth models may introduce biases. The inverse logistic model is suitable for all abalone species including *H. rufescens* in the USA. The inverse logistic may also be suitable for any species that are difficult to age including rock lobster (Starr et al., 2009) and sea urchins (Ling et al., 2009).

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