

# Life-history characteristics of coral reef gobies.

## I. Growth and life-span

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**ABSTRACT:** Life-history theory predicts that small species will exhibit short life-spans and fast growth rates; however, previous studies indicate that a positive relationship between size and maximum age may not be universally applicable to coral reef fishes. Here, we investigate the growth and life-span of 5 small species of coral reef goby (family Gobiidae): *Istigobius goldmanni*, *Asterropteryx semipunctatus*, *Amblygobius bynoensis*, *Amblygobius phalaena* and *Valenciennea muralis*. All 5 species were relatively short-lived, with the oldest individual sampled ranging from 11 to 16 mo depending on species and sex. Rapid growth occurred over much of the size range of all 5 species and, in contrast to most reef fishes, relatively little or no time was spent at an asymptotic size. Patterns of growth were best described by a Broken Stick model for *I. goldmanni*, and by either a Broken Stick model or the von Bertalanffy growth function for the other 4 species. Summer-growing individuals had higher growth rates than winter-growing individuals, but this did not affect the overall patterns of growth. Sex-specific differences in growth were evident for *I. goldmanni* and *A. semipunctatus*, with males growing faster and attaining a larger maximum size than females. In contrast, there was no significant difference in growth between male and female *A. bynoensis*, *A. phalaena* and *V. muralis*. This pattern may be related to interspecific differences in intensity of sexual selection, mating system, and reproductive behaviour. Overall, the patterns of growth and life-span of these 5 small species conformed to traditional concepts of life-history theory.

**KEY WORDS:** Longevity · Growth · Body size · Life history · Gobiidae · Otolith

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### INTRODUCTION

Body size and maximum life-span are correlated for a broad range of organisms, including mammals, birds and invertebrates, and in general maximum life-span increases with increasing body size (Blueweiss et al. 1978, Stearns 1992). Additionally, Charnov (1993) observed that, as an important invariant of life history, growth rate is inversely related to asymptotic size. Therefore, small species are typically expected to exhibit short life-spans and fast growth rates, whereas large species are expected to have greater life-spans and slow growth. Whilst many small species of fish are indeed short-lived, some small temperate and tropical species are actually relatively long-lived (Miller 1996, Munday & Jones 1998), therefore the applicability of

general life-history predictions to small reef fish requires further investigation.

The available data suggest that a positive relationship between size and maximum age may not be universally applicable to coral reef fishes (Choat & Robertson 2002). Firstly, many small species, especially some pomacentrids (e.g. Hill & Radtke 1988, Worthington et al. 1995, Meekan et al. 2001) and small acanthurids (e.g. Choat & Axe 1996, Hart & Russ 1996), are long-lived. Secondly, species with similar maximum ages can differ in maximum size by an order of magnitude (Choat & Robertson 2002). Lastly, within-taxon comparisons indicate that a positive relationship between size and maximum life-span may not always apply. For example, several small species of acanthurids have greater maximum ages than much larger species in the

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same family (Choat & Robertson 2002), and 3 closely related species of lutjanids that have similar maximum size differ in maximum age by 12 to 19 yr (Newman et al. 1996, 2000). Therefore, size–age relationships may be very complex for coral reef fishes, and more information is required on the growth and life-span of small species to determine to what extent they conform to life-history predictions and generalisations (Munday & Jones 1998).

An ideal group in which to test life-history predictions for small reef fishes is the family Gobiidae (gobies), which is dominated by species with a maximum total length of less than 100 mm. Despite being among the most diverse and abundant group of coral reef fishes (Leis & Rennis 1983, Randall et al. 1997, Ackerman & Bellwood 2000), very little is known about growth rates, patterns of growth and life-span of tropical gobies. Available data suggest that coral reef gobies inhabiting burrows or living in sand/rock habitats may be relatively short-lived (<2 yr; Yanagisawa 1982, Reavis & Barlow 1998, Kritzer 2002). However, more cryptic species, such as coral-dwelling gobies, appear to have longer life-spans (e.g. >4 yr; Munday 2001). Therefore, the type of habitat utilised and its associated predation risk might make an important contribution to the relationship between life-span and body size, as has been highlighted for temperate gobies (Miller 1984) and suggested for tropical gobies (Munday & Jones 1998).

We investigated growth rates and life-span of 5 common coral reef gobies (*Asterropteryx semipunctatus*, *Istigobius goldmanni*, *Amblygobius bynoensis*, *Amblygobius phalaena* and *Valenciennes muralis*) and compared them with predictions from life-history theory. The coral reef gobies in our study are all small species, but the maximum size differs between species, ranging from 45 to 120 mm total length. These species also differ in their patterns of habitat use, being found amongst coral rubble, in sand/rock habitats or in burrows. Thus, these 5 species provided an ideal opportunity to compare patterns of growth and maximum life-span in relation to both body size and habitat use.

Growth models are often used to describe patterns of growth, and consideration must be given to choosing an appropriate model. Although often subject to criticism (e.g. Roff 1980), the von Bertalanffy growth function (VBGF), which describes a growth pattern characterised by rapid initial growth that slows towards an asymptotic size, is the most widely used growth curve in the fisheries literature (Chen et al. 1992). The VBGF has been commonly used to describe the growth patterns of long-lived coral reef fishes (e.g. Hart & Russ 1996, Newman et al. 1996, Gust et al. 2002) that tend to have a relatively brief period of rapid growth followed by an extended period at asymptotic size. However,

short-lived fishes might tend to have a prolonged period of rapid growth with relatively little time spent at asymptotic size, and therefore models other than the VBGF might best describe their pattern of growth. For this reason we used a range of growth models to determine the most appropriate descriptor of growth in each of the 5 goby species. Furthermore, males and females often grow at different rates (e.g. Gladstone & Westoby 1988, Newman et al. 1996, McCormick 1998) and their patterns of growth may be best described by different growth models. Therefore, growth rates, life-span and growth models are examined separately for males and females.

Specifically, we addressed 3 questions for each of the 5 coral reef gobies considered here: (1) What is the maximum life-span, (2) what is the pattern of growth and which is the most appropriate growth model for describing that growth pattern, and (3) are there sex-specific differences in growth rates?

## MATERIALS AND METHODS

**Collections.** Specimens of each species were collected at intervals from August 1997 to December 1998 from the reef flat at Pioneer Bay, Orpheus Island, Australia (18°35' S, 146°29' E). Fish were caught using handnets and a clove oil/alcohol mixture (Munday & Wilson 1997) that caused short-term anaesthesia. Fish were sacrificed by immersion in an ice slurry, blotted dry, measured (total length [TL] and standard length [SL] to the nearest 0.1 mm) and weighed (wet weight to the nearest 0.001 g). The head was severed from the body and stored in 70% ethanol. The body, including the reproductive organs, was placed in a solution of 4% formaldehyde, 5% glacial acetic acid and 1.3% calcium chloride (FAACC) for at least 1 wk and then transferred to 70% ethanol.

**Length–weight relationship.** To enable sex-specific and interspecific comparisons of growth properties, the relationship between fish length and fish weight was estimated by a power curve,  $W = aL^b$ , where  $W$  is weight (g),  $L$  is length (TL, mm) and  $a$  and  $b$  are constants.

**Estimation of age using counts of otolith growth increments.** Sagittal otoliths were extracted from the brain cavity, cleaned, and stored dry in multiwell culture plates until required. To enable enumeration of growth increments, a transverse section of each otolith was prepared. Using thermoplastic glue (crystalbond) as the mounting medium, the otolith was positioned on the end of a glass slide, with the otolith core on the inner edge of the slide. Holding the slide perpendicular to the sand paper, the otolith was then hand-ground using 800 grit sand paper. The crystal-

bond was softened by reheating on a hotplate and the otolith was repositioned to the middle of a slide with the ground side facing down. The otolith was then hand-ground using 800 grit sand paper and 12  $\mu\text{m}$  lapping film until a thin section was obtained that allowed the growth increments to be counted from the core to the edge.

Otolith increments have a daily periodicity in each of the study species (Hernaman et al. 2000), therefore counts of increments provided an estimate of age in days. Counts were conducted using a compound microscope fitted with a polarizing filter. Counts were made on 3 separate occasions, with each count being conducted without reference to previous counts, and the average of the 3 counts used as the age estimate. The otolith was not used if the counts differed by >10%. To minimise interpretation error (Campana 2001), 2 additional experienced readers counted growth increments on a subset of the sample, including those of *Asterropteryx semipunctatus* which were the most difficult to read. To examine the precision of age estimates, the coefficient of variation (CV) was determined for each individual, from which a mean CV was calculated for each species (Campana 2001).

**Maximum life-span.** The maximum life-span was defined as the age of the oldest fish collected.

**Growth pattern.** To examine patterns and rates of growth, size-at-age plots were constructed for each species where the age estimate (d) for each individual was plotted against its total length (mm). Two approaches were taken to examine the pattern of growth for each species. Firstly, 4 different growth models were fitted to the size-at-age data, and 3 measures of goodness-of-fit compared for each model: (1) values of the residual sum of squares (RSS), (2) coefficient of determination ( $r^2$ ) calculated from the residual and explained sums of squares, and (3) plots of the residuals against age. Secondly, Schnute's (1981) model was fitted to the size-at-age data, and the most appropriate growth model selected according to the estimated values of the model parameters,  $a$  and  $b$ . For each species, the value of parameter  $a$  was a small positive or negative value. Whether the value was interpreted as being equal to zero affected the selection of the most appropriate model. To test the null hypothesis that  $a = 0$ , Schnute (1981) suggests fitting a second growth model (which does not incorporate the parameter  $a$ ) to the data and examining the variance ratio defined by the residual sum of squares for Model 2 divided by the sum of squares for Model 1. The variance ratio is approximately  $F$ -distributed with the appropriate degrees of freedom under the null hypothesis that  $a = 0$ . Therefore, if the  $F$ -statistic is greater than the variance ratio, the null hypothesis is retained.

We used 2 models that can describe asymptotic growth, the VBGF:

$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

and the Richards growth model:

$$L_t = L_\infty (1 + [1/p] e^{-k(t-t_0)})^{-p}$$

where  $L_t$  is mean length at age  $t$ ,  $L_\infty$  is the mean asymptotic length,  $k$  is the growth coefficient that describes the rate at which the asymptotic size ( $L_\infty$ ) is approached, and  $p$  is the shape parameter for the Richards model. For the VBGF,  $t_0$  is the theoretical age at which length is zero, but for the S-shaped Richards growth model  $t_0$  corresponds to an inflection point on the curve. These 2 models were chosen because they describe different patterns of growth in the early life stages. The VBGF describes an initial period of rapid growth that then reaches an asymptote, whereas the Richards model describes an S-shaped growth curve with the most rapid growth appearing in the middle of the growth pattern. This type of growth could occur when newly settled fish have a period of slow growth following settlement.

We also used 2 non-asymptotic growth models, the Power curve (described as:  $L_t = a[t^b]$ , where  $a$  and  $b$  are constants, and  $L_t$  is mean length at age  $t$ ), and the Broken Stick regression (sometimes referred to as Breakpoint regression) which fits 2 linear models to the data by determining a breakpoint,  $x_0$ . All fish aged  $<x_0$  have the equation  $y = a + bx$  fitted to the size-at-age data, whilst all fish aged  $>x_0$  have the equation  $y = c + dx$  fitted. The parameters  $a$  and  $c$  are points on the  $y$ -axis where the 2 linear models cross the  $y$ -axis,  $b$  and  $d$  describe the slope of each linear regression. The breakpoint,  $x_0$ , is defined as:  $x_0 = (a - c)/(d - b)$ . The Broken Stick regression was selected in place of a linear model because, even for species that had indeterminate adult growth, the rate of adult growth was slower than for the early life-stages, meaning that 1 linear model could not adequately describe both juvenile and adult growth. The Broken Stick regression was fitted to the size-at-age data using an SAS programme written by Brian Niven (Department of Maths and Statistics, University of Otago, New Zealand). The remaining models were fitted using least-squares non-linear regression with the Gauss-Newton algorithm in the statistical package SYSTAT 10.

Initially, the 4 growth models were fitted separately to male and female size-at-age data for each species, and their goodness-of-fit examined. We then tested for sex-specific differences in growth and, where none were found, fitted the 4 growth models to combined-sex data. For brevity and clarity, we present growth models fitted only to combined-sex data for species where analysis indicated there were no sex-specific differences in rates or patterns of growth. Fish were

sexed by the shape and size of the genital papilla (short and blunt in females, long and tapered in males) and/or by macroscopic and histological examination of the gonads. It was sometimes difficult to sex small juveniles, even using histological techniques, and these individuals were included in both male-only and female-only data when fitting growth models to the size-at-age data. Specifically, this meant individuals aged <120 d for *Asterropteryx semipunctatus*, <141 d for *Istigobius goldmanni*, <100 d for *Amblygobius bynoensis*, <72 d for *Amblygobius phalaena*, and <76 d for *Valenciennes muralis*.

To test the null hypothesis of no significant difference between male and female growth patterns, 1 of 2 methods was employed depending on the pattern of growth. (1) Analysis of covariance (ANCOVA) was used for species with linear adult growth. Using this method, we compared the slopes of linear regressions fitted separately to adult male and female size-at-age data. (2) For species with attenuating adult growth, a comparison of growth curves between sexes was made using the methods of Chen et al. (1992) and Kimura (1980). Firstly, analysis of residual sum of squares (ARSS) (Chen et al. 1992) was used to determine whether the use of separate growth curves for females and males provided a better fit than 1 common growth curve. Secondly, to examine differences in specific growth characteristics, 95% confidence ellipses were generated around the parameter estimates of  $k$  and  $L_{\infty}$  (parameters of the VBGF) for each sex, with  $t_0$  constrained to a common value (Kimura 1980). Non-overlapping confidence ellipses were considered to indicate a significant difference between sexes in these 2 parameters (Kimura 1980). To estimate a common value for  $t_0$ , the VBGF was fitted to the size-at-age data for males and females separately, allowing the model to provide estimates for all 3 parameters ( $L_{\infty}$ ,  $k$  and  $t_0$ ). The  $t_0$  of males and females was then averaged to provide a common value. Using an average value ensured equal bias in deviation from the original  $t_0$  for both sexes. The value of  $t_0$  obtained for males and females was often very similar (i.e. within 0.01 and 8.57 of each other depending on species) and, therefore, the impact of using an average  $t_0$  value calculated in this manner was minimal.

**Seasonal comparison of growth.** Inspection of the size-at-age data suggested a possible seasonal influence on growth rate for some species. To test this possibility, the techniques of Kimura (1980) were used to compare growth curves between seasons. The year was divided into periods of increasing (September to February) and decreasing (March to August) seawater temperatures based on average monthly seawater temperatures at Pioneer Bay recorded by the Great Barrier Reef Marine Park Authority ([www.gbrmpa.gov.au/corp\\_site/info\\_services/science/](http://www.gbrmpa.gov.au/corp_site/info_services/science/)

seatemp). Average monthly seawater temperature varied annually by 7.5 to 9.0°C (maximum average monthly temperature 30.3°C, minimum 21.3°C) over the study period. The months over which each individual had grown were determined by subtracting its estimated age (minus the period from hatching to settlement) from its date of capture. Individuals were then classified according to whether their growth had occurred predominantly or wholly through either summer or winter. Older individuals that had experienced growth in both seasons were categorised according to the season in which most of their initial growth had occurred, as the faster growth rates experienced by juveniles and small adults were presumed to have a larger effect on final size-at-age than growth experienced later in life.

## RESULTS

### Length–weight relationship

The maximum size of male and female *Asterropteryx semipunctatus* and *Istigobius goldmanni* were more dissimilar than the maximum size of male and female *Amblygobius bynoensis*, *Amblygobius phalaena* and *Valenciennes muralis* (Table 1). The largest male *A. semipunctatus* and *I. goldmanni* were 24 and 16% larger respectively than the largest females. In contrast, the largest male *A. bynoensis* and *V. muralis* were only 4 and 3% larger respectively than the largest females. The largest female *A. phalaena* was 2% larger than the largest male.

Table 1. Maximum body size (total length, mm) and length–weight relationships of male and female coral reef gobies. Provided are the coefficient of determination ( $r^2$ ) and estimates of the parameters  $a$  and  $b$  from the relationship  $W = aL^b$ , where  $W$  is weight and  $L$  is length. M: male; F: female; n: number

Species	Sex	Max. size (mm)	n	Length–weight relationship		
				$a$	$b$	$r^2$
<i>Asterropteryx semipunctatus</i>	M	56	138	0.95	3.10	0.989
	F	45	139	0.32	3.42	0.974
<i>Istigobius goldmanni</i>	M	64	99	1.07	2.99	0.991
	F	55	86	0.61	3.15	0.969
<i>Amblygobius bynoensis</i>	M	98	64	0.96	3.01	0.988
	F	94	64	0.82	3.06	0.991
<i>Amblygobius phalaena</i>	M	102	58	1.33	2.96	0.989
	F	105	57	1.07	3.01	0.996
<i>Valenciennes muralis</i>	M	116	71	1.32	2.84	0.989
	F	113	98	0.73	3.00	0.932

Length–weight relationships displayed predictable values, with  $b$  (where  $W = aL^b$ ) ranging from 2.84 to 3.42 (Table 1). Females tended to be heavier than males (Table 1), although the difference was least for both *Amblygobius* species, intermediate for *Istigobius goldmanni* and *V. muralis*, and most pronounced for *Asterropteryx semipunctatus*.

### Precision of age estimates

The age estimates for all species generally had a very high level of precision. The CV for each individual ranged from 0 to 16%, but was generally  $\leq 4\%$ . The value of the CV was not related to fish age nor fish size in any of the species. The mean CV per species ranged from 1.95 to 2.79%, depending on species, with the highest CV associated with *Asterropteryx semipunctatus* and *Istigobius goldmanni*.

### Maximum life-span

All 5 species were relatively short-lived, with the oldest individual in the sample ranging from 11 to 16 mo depending on species and sex (Table 2).

### Growth patterns

All 5 gobies invested a large proportion of their life-span in somatic growth, with growth occurring over much of their size range, and relatively little or no time

Table 2. Maximum life-span of 5 coral reef gobies (defined as the age of the oldest individual sampled), and the average proportion of the maximum size attained by half of the maximum life-span. M: male; F: female; n: number

Species	Sex	n	Age of oldest individual d (mo)	% of maximum size attained by half of maximum life-span
<i>Asterropteryx semipunctatus</i>	M	92	457 (16)	63
	F	70	419 (14)	73
<i>Istigobius goldmanni</i>	M	80	375 (13)	55
	F	66	323 (11)	60
<i>Amblygobius bynoensis</i>	M	75	377 (13)	65
	F	78	349 (12)	60
<i>Amblygobius phalaena</i>	M	64	400 (14)	64
	F	70	414 (14)	66
<i>Valenciennea muralis</i>	M	68	345 (12)	64
	F	87	363 (12)	63

spent at asymptotic size (Figs. 1 to 5: note that separate-sex data are presented for *Asterropteryx semipunctatus* and *Istigobius goldmanni*, because a sex-specific difference in growth was evident for these 2 species, see below). The 5 species showed similar growth rates in relation to their maximum life-span with generally about 2/3 of their maximum size attained by half of their maximum life-span (Table 2).

Adult growth was linear for *Istigobius goldmanni* (Fig. 2), and the Broken Stick regression was clearly the best descriptor of growth for both sexes (Fig. 2, Tables 3 & 4). Growth of *Asterropteryx semipunctatus*, *Amblygobius bynoensis*, *Amblygobius phalaena* and *Valenciennea muralis* attenuated near the maximum size of each species (Figs. 1 & 3 to 5). Consequently, growth patterns were neither completely linear nor asymptotic, and both the Broken Stick regression and the VBGF adequately described the growth pattern of these 4 species (Figs. 1 & 3 to 5, Tables 3 & 4).

### *Asterropteryx semipunctatus*

The size-at-age relationship showed a period of rapid juvenile growth followed by a decrease in growth rate in fish over 150 d old, and growth attenuating at ca. 330 d (females) or 350 d (males) (Fig. 1). The VBGF was the best descriptor of growth for females, with an even distribution of residuals throughout the life-span and the lowest RSS (Table 4, Fig. 1). All models gave a poorer description of male growth. In particular, all models tended to overestimate the size of males aged 200 to 300 d and >400 d, and tended to underestimate the size of males aged 300 to 400 d (Fig. 1). The Broken Stick regression and VBGF had the best combinations of low RSS, high  $r^2$  and most even distribution of residuals (Table 4, Fig. 1). It was difficult to distinguish between these models; however, fitting Schnute's (1981) model to the size-at-age data suggested that the VBGF was likely to be the best descriptor of growth for both males and females (Table 3).

### *Istigobius goldmanni*

This species exhibited a 2-phase, linear pattern of growth (Fig. 2a), with a period of rapid growth from settlement to ca. 125 d old, followed by a second period of slower linear growth. Consequently, the best descriptor of growth for both sexes was the Broken Stick regression (Fig. 2, Tables 3 & 4). The other 3 models first over- then underestimated the size of individuals <110 d old (Fig. 2). For both sexes, fitting the Broken Stick regression to the size-at-age data resulted in

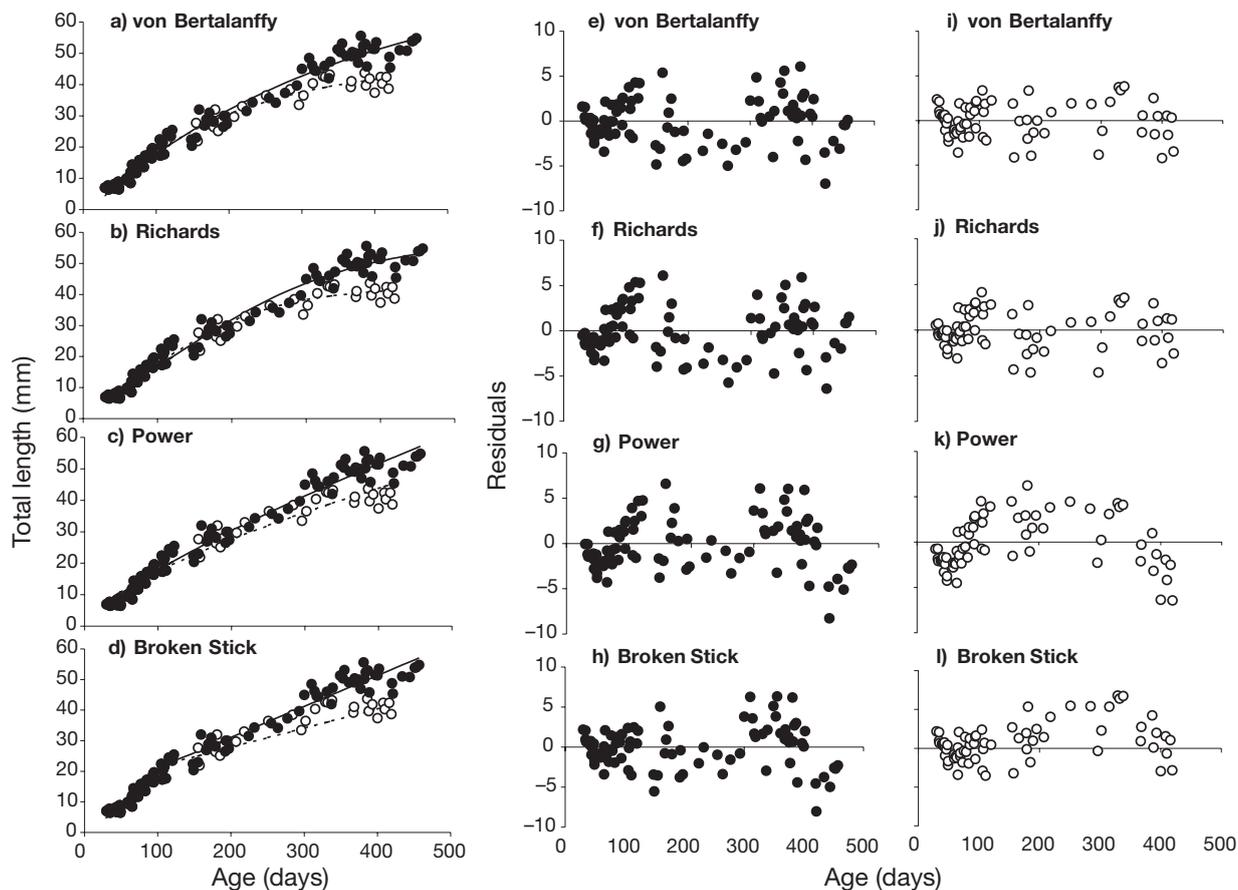


Fig. 1. *Asterropteryx semipunctatus*. Growth models (a–d) fitted to male (●) and female (○) size-at-age data, and resulting residuals (e–l). Unsexed juveniles used in both male and female data sets

the lowest RSS (Table 4). The RSS obtained from fitting the VBGF was not dramatically higher than that obtained from fitting the Broken Stick regression. However, the VBGF was only able to provide a reasonable description of growth for *Istigobius goldmani* by using unreasonably large predicted values of  $L_{\infty}$  (98.1 and 64.8 mm TL for males and females respectively), which were much greater than the maximum size of this species at Orpheus Island (64 and 56 mm TL for males and females, respectively). Fitting Schnute's model to the size-at-age data confirmed that a non-asymptotic growth model was likely to be the best descriptor of growth, with an exponential and a linear model suggested for males and females respectively (Table 3).

#### *Amblygobius bynoensis*

Both the Broken Stick regression and the VBGF adequately described growth in this species (Fig. 3, Tables 3 & 4). Both models gave a similar distribution

of residuals with age (Fig. 3). Although the Broken Stick regression gave the lowest RSS (Table 4) and fitting Schnute's model to the size-at-age data suggested a linear model would be best (Table 3), the VBGF was also considered an appropriate descriptor of growth because examination of the data points suggests an attenuation of growth for fish >250 d old (Fig. 3).

#### *Amblygobius phalaena*

Adult growth attenuated in the later stages (i.e. after ~300 d old) and, consequently, both the asymptotic models and the Broken Stick regression adequately described the pattern of growth from newly settled through to the largest/oldest individuals (Fig. 4). These models gave comparable  $r^2$  values (Table 4) and an even distribution of residuals (Fig. 4). The VBGF had the lowest RSS, and fitting Schnute's (1981) model to the size-at-age data suggested that the VBGF was likely to be the best descriptor of growth (Table 3).

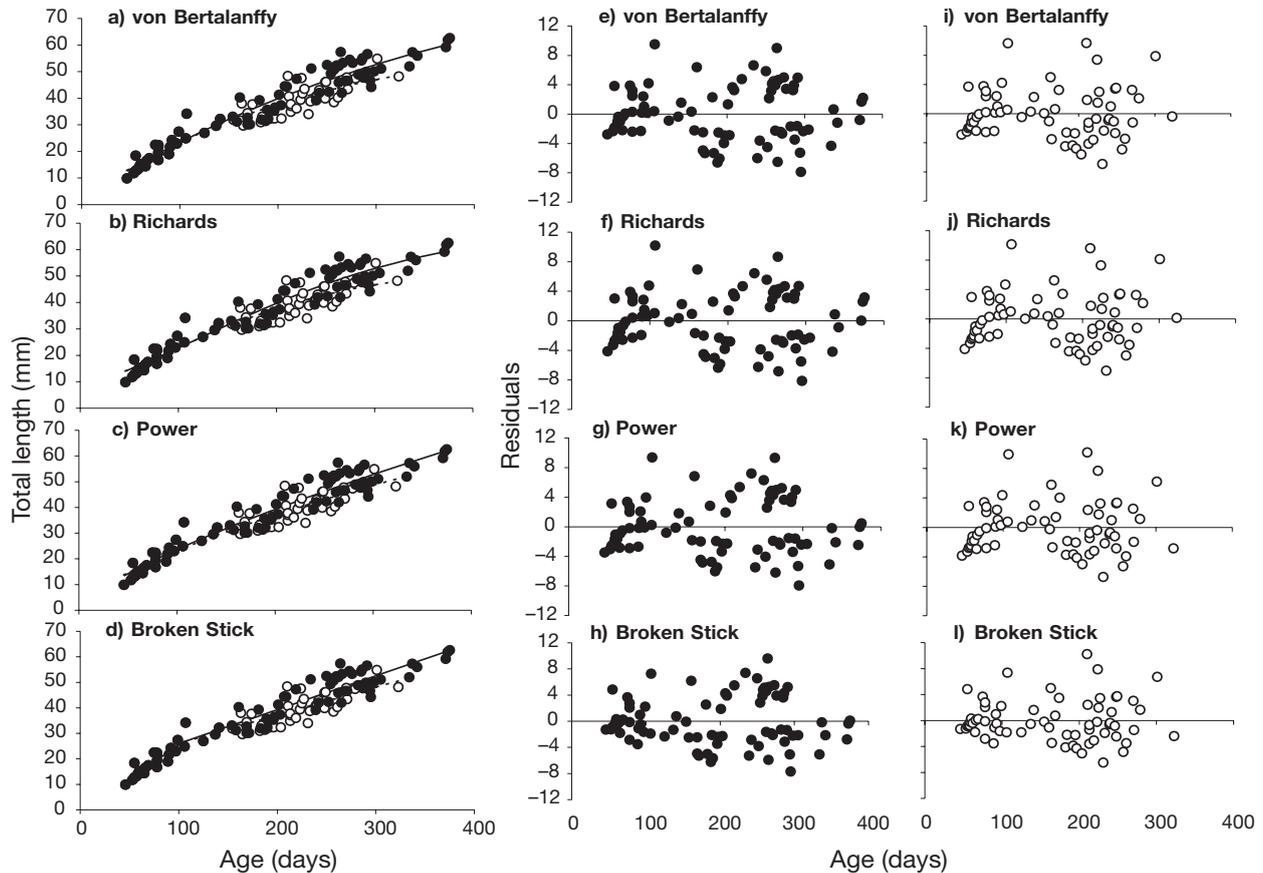


Fig. 2. *Istigobius goldmanni*. Growth models (a–d) fitted to male (●) and female (○) size-at-age data, and resulting residuals (e–l). Unsexed juveniles used in both male and female data sets

### *Valenciennesa muralis*

This species showed a period of linear growth from settlement to ca. 150 d old, followed by a period of slower growth (Fig. 5). All 4 models, and especially the Power curve, generally overestimated the size of young juveniles, but both the Broken Stick regression and the VBGF were equally able to describe growth throughout most of the life-span. These 2 models had a similar distribution of residuals (Fig. 5), and comparable RSS and  $r^2$  values (Table 4). In contrast to *Istigobius goldmanni*, the VBGF provided an adequate description of growth without assuming an unrealistic asymptotic size (Table 4). However, fitting Schnute's (1981) model to the size-at-age data suggested that a linear model would be the most appropriate descriptor of growth (Table 3).

### Limitations of the Power curve

The Power curve provided the poorest (for 3 species) or second poorest (remaining 2 species) fit to the size-

at-age data in terms of RSS and  $r^2$  values (Table 4). While it should be acknowledged that the Power curve has fewer parameters than the other models, and thus is at a disadvantage in terms of RSS and  $r^2$  values, the residual plots indicate that the Power curve was unable to adequately describe the growth throughout the entire life-span of any species. In particular, it often over-estimated the size of individuals at both ends of the life-span (i.e. the youngest and oldest individuals) resulting in a convex distribution of residuals (e.g. Figs. 1k, 3g & 4g).

### Sex-specific differences

A sex-specific difference in growth was evident for *Istigobius goldmanni* (ANCOVA;  $F_{1,87} = 9.71$ ,  $p = 0.002$ ) and *Asterropteryx semipunctatus* (ARSS;  $p < 0.0001$ ). Male *I. goldmanni* grew at a significantly faster rate (mean adult growth rate:  $0.13 \text{ mm d}^{-1}$ ) than females ( $0.11 \text{ mm d}^{-1}$ ) and attained a larger maximum size than females (Fig. 6). Similarly, male *A. semipunctatus* attained a larger maximum size than females,

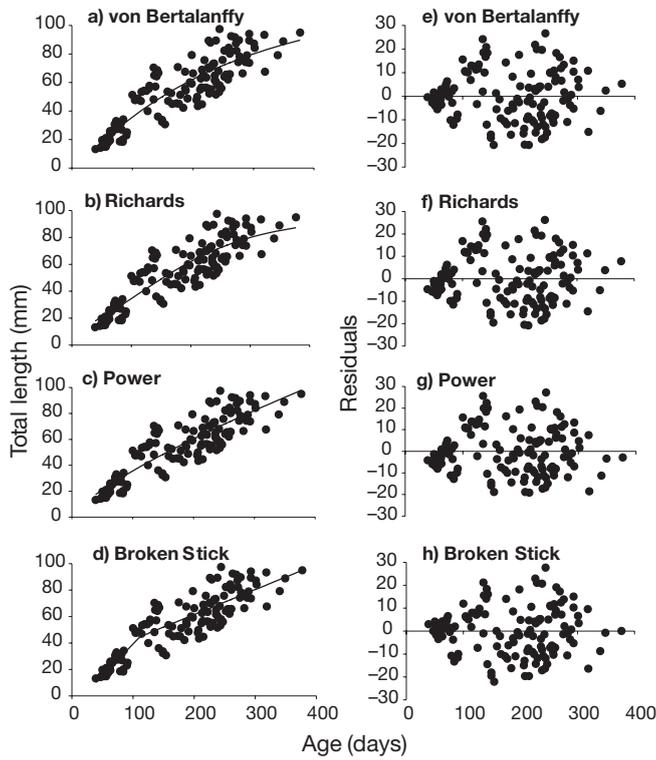


Fig. 3. *Amblygobius bynoensis*. Growth models (a–d) fitted to size-at-age data, and resulting residuals (e–h). Sexes are not differentiated because sex-specific differences in growth were not evident

and non-overlapping 95% confidence ellipses indicated significant sex-specific differences in the parameter estimates of  $k$  and  $L_{\infty}$  (Fig. 6). There was no significant difference between male and female growth for the 3 remaining species (ARSS: *Amblygobius bynoensis*,  $p = 0.668$ ; *Amblygobius phalaena*,  $p = 0.868$ ; *Valenciennaea muralis*,  $p = 0.729$ ) and overlapping 95% confidence ellipses generated for  $k$  and  $L_{\infty}$  indicated similar values of these 2 parameters for males and females (Fig. 6).

### Seasonal comparison of growth

*Amblygobius bynoensis* exhibited considerable variability in size-at-age (Fig. 3), and when counting otolith growth increments for this species, it was common to observe transitions from wide growth incre-

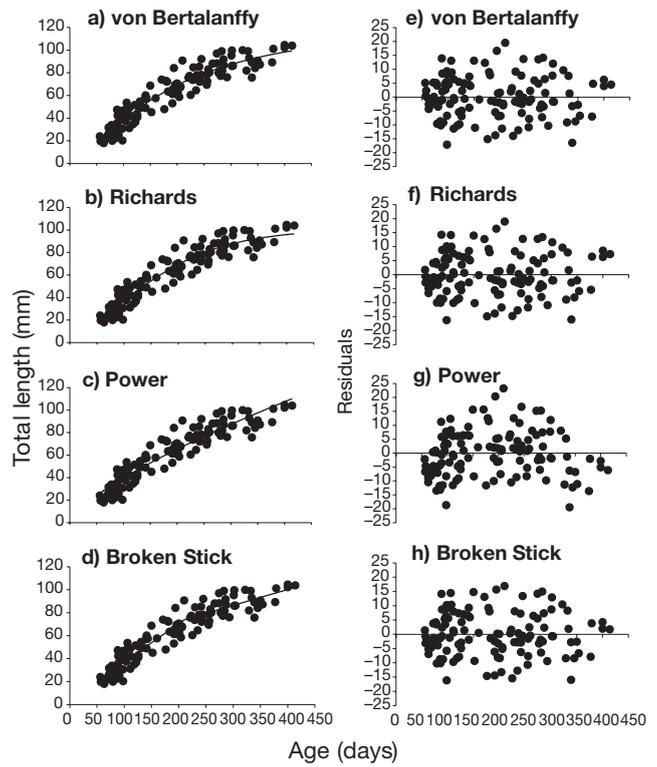


Fig. 4. *Amblygobius phalaena*. Growth models (a–d) fitted to size-at-age data, and resulting residuals (e–h). Sexes are not differentiated because sex-specific differences in growth were not evident

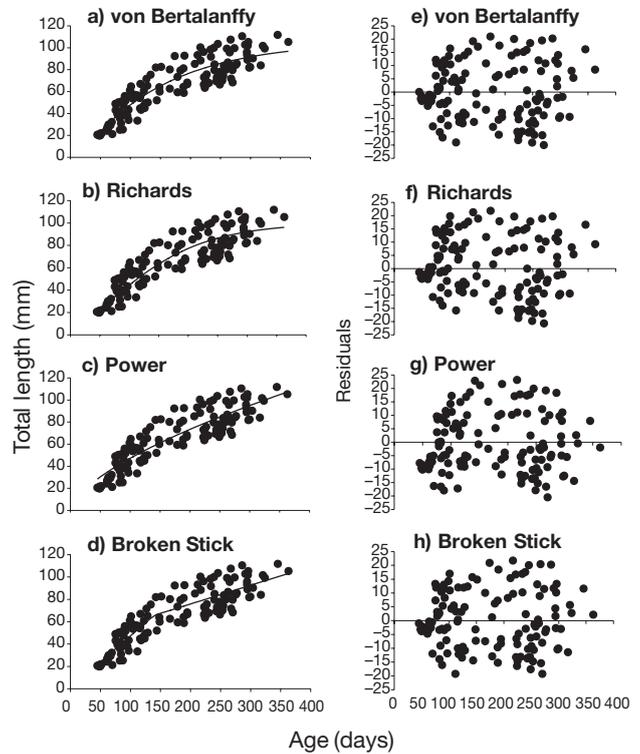


Fig. 5. *Valenciennaea muralis*. Growth models (a–d) fitted to size-at-age data, and resulting residuals (e–h). Sexes are not differentiated because sex-specific differences in growth were not evident

Table 3. Results of fitting Schnute's (1981) model to the size-at-age data for each of the 5 goby species, and the growth pattern suggested from fitting 4 growth models to the data. Separate sexes given for *Asterropteryx semipunctatus* and *Istigobius goldmanni* because sex-specific differences in growth were evident for these 2 species. VB: von Bertalanffy; BS: Broken Stick; Exp: Exponential; Lin: Linear. M: male; F: female

Species	Sex	Values of Schnute's (1981) model parameters		Test for significant deviation of <i>a</i> from zero	Growth model suggested by Schnute's (1981) model	Growth model suggested by model fit to the data
		<i>b</i>	<i>a</i>			
<i>Asterropteryx semipunctatus</i>	M	0.988	0.003	$a > 0$ ( $F_{1,88} = 5.26$ , $p = 0.021$ )	VB	VB or BS
	F	0.631	0.007	$a > 0$ ( $F_{1,66} = 32.32$ , $p < 0.001$ )	VB	VB
<i>Istigobius goldmanni</i>	M	3.480	-0.012	$a < 0$ ( $F_{1,76} = 4.70$ , $p = 0.033$ )	Exp	BS
	F	3.014	-0.005	$a = 0$ ( $F_{1,62} = 1.62$ , $p = 0.208$ )	Lin	BS
<i>Amblygobius bynoensis</i>	All data	1.979	-0.001	$a = 0$ ( $F_{1,139} = 1.15$ , $p = 0.285$ )	Lin	VB or BS
<i>Amblygobius phalaena</i>	All data	1.096	0.005	$a > 0$ ( $F_{1,118} = 4.08$ , $p = 0.046$ )	VB	VB or BS
<i>Valenciennesa muralis</i>	All data	1.065	0.009	$a = 0$ ( $F_{1,126} = 2.48$ , $p = 0.118$ )	Lin	VB or BS

Table 4. Comparison of 4 growth models fitted to the size-at-age data for 5 species of coral reef goby. Presented are the residual sum of squares (RSS), coefficient of determination ( $r^2$ ), and parameter estimates (see 'Materials and methods' for parameter definitions). VBGF: von Bertalanffy growth function; BS: Broken Stick.  $x_0$ : breakpoint

	Growth model	RSS	$r^2$	Parameter estimates:									
				VBGF/Richards			Power		BS				
				$L_\infty$	<i>k</i>	$t_0$	<i>a</i>	<i>b</i>	<i>b</i>	<i>d</i>	<i>a</i>	<i>c</i>	$x_0$
<i>Asterropteryx semipunctatus</i> males (n = 92)	VBGF	590	0.978	77.1	0.003	3.4	-	-	-	-	-	-	-
	Richards	651	0.975	58.6	0.007	132.1	-	-	-	-	-	-	-
	Power	715	0.973	-	-	-	0.519	0.767	-	-	-	-	-
	BStick	640	0.976	-	-	-	-	-	0.20	0.10	-1.25	10.88	121.3
<i>Asterropteryx semipunctatus</i> females (n = 70)	VBGF	269	0.976	47.2	0.006	11.2	-	-	-	-	-	-	-
	Richards	278	0.975	42.5	0.011	90.2	-	-	-	-	-	-	-
	Power	552	0.949	-	-	-	0.799	0.668	-	-	-	-	-
	BStick	447	0.955	-	-	-	-	-	0.20	0.06	-1.25	15.31	118.3
<i>Istigobius goldmanni</i> males (n = 80)	VBGF	1125	0.935	98.1	0.003	-9.6	-	-	-	-	-	-	-
	Richards	1156	0.934	70.8	0.007	123.5	-	-	-	-	-	-	-
	Power	1144	0.934	-	-	-	0.812	0.732	-	-	-	-	-
	BStick	1111	0.935	-	-	-	-	-	0.26	0.13	-0.94	12.72	104.4
<i>Istigobius goldmanni</i> females (n = 66)	VBGF	771	0.909	64.8	0.004	-6.1	-	-	-	-	-	-	-
	Richards	819	0.902	54.9	0.009	87.8	-	-	-	-	-	-	-
	Power	778	0.906	-	-	-	1.042	0.674	-	-	-	-	-
	BStick	685	0.919	-	-	-	-	-	0.26	0.11	-0.94	15.07	104.2
<i>Amblygobius bynoensis</i> (n = 143)	VBGF	15336	0.806	117.1	0.004	7.3	-	-	-	-	-	-	-
	Richards	16015	0.794	95.0	0.009	112.4	-	-	-	-	-	-	-
	Power	15662	0.796	-	-	-	1.071	0.761	-	-	-	-	-
	BStick	14324	0.819	-	-	-	-	-	0.48	0.19	-8.25	23.69	110.1
<i>Amblygobius phalaena</i> (n = 122)	VBGF	6820	0.908	114.4	0.005	21.1	-	-	-	-	-	-	-
	Richards	7006	0.905	101.1	0.010	102.8	-	-	-	-	-	-	-
	Power	8307	0.882	-	-	-	1.452	0.718	-	-	-	-	-
	BStick	7100	0.904	-	-	-	-	-	0.33	0.14	3.95	44.73	214.6
<i>Valenciennesa muralis</i> (n = 130)	VBGF	14856	0.806	106.1	0.007	14.1	-	-	-	-	-	-	-
	Richards	15303	0.798	100.1	0.012	81.3	-	-	-	-	-	-	-
	Power	15765	0.787	-	-	-	2.525	0.636	-	-	-	-	-
	BStick	14803	0.811	-	-	-	-	-	0.47	0.17	0.73	42.41	138.9

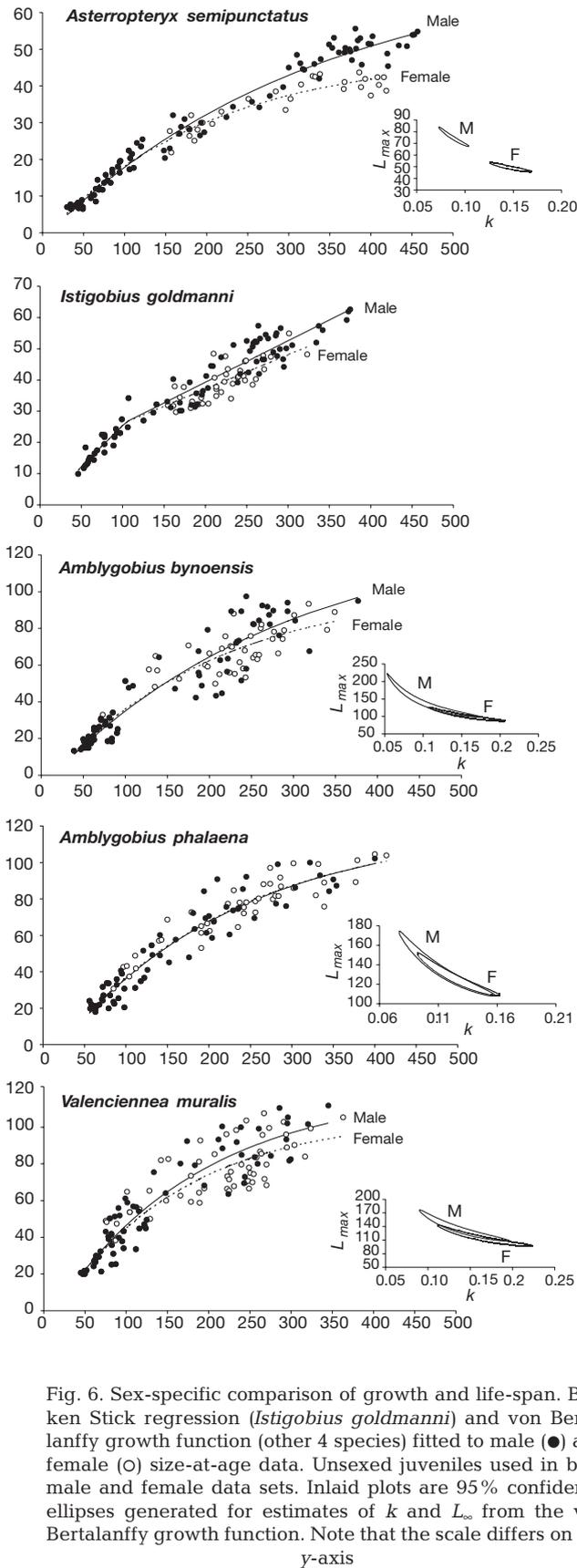


Fig. 6. Sex-specific comparison of growth and life-span. Broken Stick regression (*Istigobius goldmanni*) and von Bertalanffy growth function (other 4 species) fitted to male (●) and female (○) size-at-age data. Unsexed juveniles used in both male and female data sets. Inlaid plots are 95% confidence ellipses generated for estimates of  $k$  and  $L_{\infty}$  from the von Bertalanffy growth function. Note that the scale differs on the y-axis

ments to much narrower increments for an extended period of time, before the increments widened again. When the timing of the narrowing events was related to month of the year, they always occurred at the onset of the cooler, winter seawater temperatures. The extent to which the season of predominant growth affected growth rate and contributed to the large variability in size-at-age for this species was investigated. Although data for individuals >150 d old were limited for the summer season, non-overlapping 95% confidence ellipses generated for the parameters  $k$  and  $L_{\infty}$  (Fig. 7, inlaid plot) indicated significant between-season differences in the values of these 2 parameters.

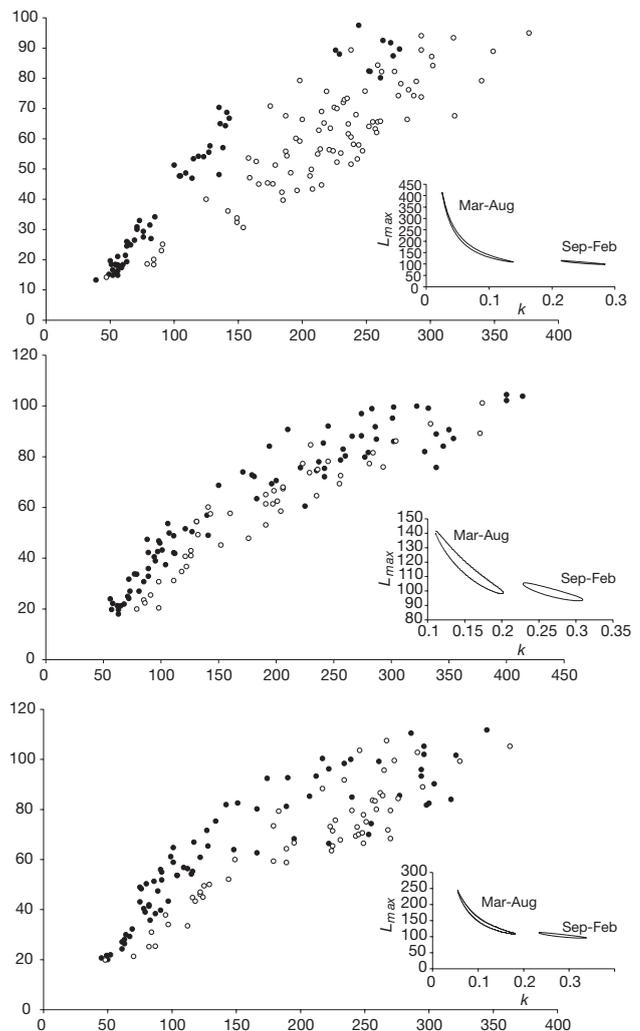


Fig. 7. Size-at-age for *Amblygobius bynoensis*, *A. phalaena* and *Valencienna muralis* that had grown wholly or predominantly through September to February (●) or March to August (○). Inlaid plots are 95% confidence ellipses generated for estimates of  $k$  and  $L_{\infty}$  from the von Bertalanffy growth function

Generally, individuals that had grown wholly or predominantly through the summer months (September to February) had attained a significantly larger size at a given age than individuals that had grown wholly or predominantly through the winter months (March to August) (Fig. 7). However, there was still substantial within-season variation in size-at-age for individuals growing predominantly through the winter months (Fig. 7).

The data set for summer-growing adults of *Amblygobius phalaena* and *Valenciennesa muralis* was much larger than that for *A. bynoensis*, and seasonal differences in growth rates of the 2 former species were most apparent for individuals <130 and <150 d old, respectively (Fig. 7). Even so, non-overlapping 95% confidence ellipses generated for  $k$  and  $L_{\infty}$  indicated that seasonal differences in growth rate resulted in significant seasonal differences in these 2 growth parameters (Fig. 7, inlaid plots).

Seasonal differences in growth rates were clearly evident for juveniles of all 3 species. Juveniles growing through summer exhibited a significantly higher growth rate than winter-growing individuals (*Amblygobius bynoensis*, mean growth rate of 0.54 and 0.29 mm d<sup>-1</sup> for summer and winter growth respectively, ANCOVA:  $F_{1,61} = 102.14$ ,  $p < 0.001$ ; *A. phalaena*, 0.63 and 0.45 mm d<sup>-1</sup>,  $F_{1,37} = 95.22$ ,  $p < 0.001$ ; *Valenciennesa muralis*, 0.61 and 0.42 mm d<sup>-1</sup>,  $F_{1,57} = 107.64$ ,  $p < 0.001$ ). These seasonal differences in growth rates translate to an average of 25 mm (*A. bynoensis*), 18 mm (*A. phalaena*) and 19 mm (*V. muralis*) difference in size after a period of 100 d.

The data set for *Asterropteryx semipunctatus* and female *Istigobius goldmanni* was not conducive to detailed examination of seasonal differences in growth rates. Suitable data were available for male *I. goldmanni*, and ANCOVA indicated that males growing predominantly through summer had significantly higher growth rates than males growing predominantly through winter ( $F_{1,49} = 61.12$ ,  $p < 0.001$ ).

## DISCUSSION

The 5 coral reef gobies in this study were all small-bodied and all exhibited a relatively short maximum life-span and rapid growth rates. Maximum life-span was from 11 to 16 mo, and each species attained ca.  $\frac{2}{3}$  of its maximum size by half of its expected maximum life-span. Therefore, it appears that their patterns of growth and life-span conform to traditional concepts of life-history theory.

The pattern of growth of all 5 coral reef gobies differed considerably from that exhibited by other relatively small, but long-lived (up to 32+ yr old) coral

reef fishes, such as certain acanthurids (e.g. Choat & Axe 1996, Hart & Russ 1996) and pomacentrids (e.g. Meekan et al. 2001). These long-lived species tend to attain an asymptotic size very quickly (within 2 to 6 yr) and thus spend much of their life-span (often >75%) at that size. In contrast, all 5 coral reef gobies invested in somatic growth throughout much or all of their life-span and spent relatively little or no time at asymptotic size. While there was evidence that growth began to attenuate in the oldest individuals of 4 species, *Istigobius goldmanni* clearly exhibited linear adult growth with no signs of an asymptotic size. Rapid non-asymptotic growth has also been noted for *Istigobius decoratus*, a short-lived (<1 yr) goby collected from the lagoon at Lizard Island, Great Barrier Reef (Kritzer 2002). Similarly, the intertidal Hawaiian goby *Bathygobius coalitus* exhibited a linear pattern of growth for at least the first 9 mo of life, with no difference in growth rate between immature and mature gobies (Shafer 1998). Furthermore, size-at-age data presented for a range of temperate gobies also indicates non-asymptotic growth (Grossman 1979, Bouchereau & Guelorget 1998 and see Kritzer 2002). It seems, therefore, that non-asymptotic growth may be relatively common among both tropical and temperate water gobies.

Long-lived reef fishes often have a growth pattern characterised by rapid growth to asymptotic size and sexual maturity, followed by a relatively long period of reproductive activity, but little additional somatic growth (Choat & Robertson 2002). This growth pattern may reflect a physiological trade-off between growth and reproduction. Trade-offs play a central role in life-history theory, and a physiological trade-off between growth and reproduction is expected where these 2 processes compete directly for a limited amount of energy (Begon & Mortimer 1981, Partridge & Harvey 1988, Stearns 1992). However, circumstances may arise where a trade-off between growth and reproduction is minimised or does not occur. For example, energy allocated to reproduction may not entail a growth cost if there were limits to the rate at which energy can be diverted into the somatic tissues (Roff 1992). When fed the same rations, non-reproducing female guppies grew more than reproductively active females, but most of the growth was in the form of fat reserves and not somatic protein growth (Reznick 1983, cited by Wootton 1998). Alternatively, on reaching sexual maturity, a reproductive individual might be able to acquire sufficient additional energy to cover the energetic costs of reproduction, either by an ontogenetic shift in diet to a more profitable or higher quality food source (e.g. MacNeill & Brandt 1990, McCormick 1998), or by an increase in feeding rate. However, increased foraging time may result in increased predation risk, potentially resulting in a trade-

off between growth or reproduction and longevity. While the growth rate of the 5 study species decreased following maturation, investment in somatic growth continued for much or all of the adult life-span. Therefore, they appear able to acquire sufficient energy to satisfy demands for both growth and reproduction. This capacity to continue somatic growth may come at a cost of reduced longevity, as evidenced by their relatively short life-spans.

For the 5 study species, continued investment in somatic growth may potentially result in reproductive benefits for both sexes. A positive relationship between body size and fecundity (Hernaman 2003) means that females can maximise both current and future batch fecundity by continued somatic growth. While males do not need a large body size to accommodate testes capable of fertilising a large number of eggs, continued investment in somatic growth may increase their reproductive success through the competitive advantage of large body size in both intra- (Grossman 1980, Yanagisawa 1982, Breitburg 1987, Lindström 1992a,b, Forsgren et al. 1996) and interspecific (Breitburg 1987, Robertson 1996) competition for resources (e.g. nest sites, mates, food, territory). Intraspecific competition for nest sites and mates has been recorded for the polygynous *Asterropteryx semipunctatus* and *Istigobius goldmanni* (Hernaman 2003), with a large body size providing a competitive advantage in contests over those resources. Intraspecific competition for nest sites was not evident for the monogamous pair-spawning *Valenciennea muralis*, *Amblygobius bynoensis* and *Amblygobius phalaena* (Hernaman 2003). However, mate defence by both sexes was observed occasionally and continued investment in growth may provide a size benefit in contests over mates. Body size influences mate selection in other monogamous coral reef gobies, with both males and females preferring larger partners (Reavis 1997b, Takegaki & Nakazono 1999) and pair bonds being broken when a mate became available that was larger than the current partner (Takegaki & Nakazono 1999). Thus, investment of energy in somatic growth is likely to provide reproductive benefits for both sexes of all 5 study species.

Female *Asterropteryx semipunctatus* and *Istigobius goldmanni* grew more slowly and attained smaller maximum sizes than males. One explanation is that females expend proportionally more energy on the production of gametes than males (e.g. Newman et al. 1996), and this extra energy requirement is at the expense of somatic growth. Egg production can constitute a considerable drain on energy reserves (Kamler 1992). For example, in female *Pomatoschistus microps*, 28 to 44 % of the dietary energy content is devoted to egg production (Rogers 1988, cited in Magnhagen

1993). Thus, for the 5 study species that spawn at frequent intervals over the summer months (authors' pers. obs.), sex-specific differences in the cost of gamete production could underlie differences in growth rate between sexes. However, sex-specific differences in growth were not apparent for *Valenciennea muralis*, *Amblygobius bynoensis* or *Amblygobius phalaena*. This disparity among species may be related to inter-specific differences in male egg-guarding behaviour. The eggs of *V. muralis*, *A. bynoensis* and *A. phalaena* are laid in 1 large cluster, and males appear to spend much of the egg-guarding period fanning the egg mass (Hernaman 2003). Males did not leave the nest site during egg-guarding and did not feed during this time. In contrast, *A. semipunctatus* and *I. goldmanni* eggs are deposited in a monolayer, extensive egg fanning was not observed, and males fed near the shelter site during egg-guarding (Hernaman 2003). Thus, the extensive and prolonged egg-fanning activities of *V. muralis*, *A. phalaena* and *A. bynoensis* males, combined with the absence of feeding during this time, may result in a relatively higher energetic cost of brood care, compared to that experienced by male *A. semipunctatus* and *I. goldmanni*, that is equivalent to the extra energetic cost of egg production in females.

The mating system may also contribute to sex-specific differences in growth rate and maximum size in some species. Sex-specific differences in growth rate were evident for the 2 polygamous species and absent for the 3 monogamous pair-spawning species. This pattern could be related to differences in mate competition associated with each of these mating systems. In monogamous gobies, body size of both males and females appears to be important in mate selection and the stability of the pair bond (Reavis & Barlow 1998). In contrast, for the 2 polygynous species, intra-sexual competition for mates and nest sites is likely to be much stronger among males than females (Emlen & Oring 1977, Warner 1984). Therefore, there may be a selective premium to rapid male growth and large size in the 2 polygynous species.

The fast growth rates and short life-span often exhibited by small fishes are thought to be the functional response of a high level of unpredictable mortality across the entire life-span (Miller 1996). Although there are a variety of causes of mortality in fish (e.g. reproductive demands, senescence and parasitism; Grossman 1979), predation is likely to be the primary agent of mortality in small species (Pauly 1980, Miller 1984, Munday & Jones 1998). Coral reef gobies are predated upon by a wide range of demersal and mobile piscivorous fishes (Sweatman 1984, Parrish et al. 1986, Norris & Parrish 1988, Kingsford 1992, Clark et al. 2000), and might also be vulnerable to predation by sea snakes, invertebrates (e.g. octopus) and shore

birds. Therefore, the short maximum life-span of all 5 study species is likely to reflect their vulnerability to predation by a wide range of predators.

Munday & Jones (1998) suggested that patterns of habitat use and predation risk might have a substantial influence on the maximum life-span of small fishes. Small temperate gobies show 2 divergent life-history strategies (Grossman 1979), which may be linked to the mortality rate associated with habitat type (Miller 1996). Nektonic species and those associated with open sandy habitats have a short life-span of <3 yr (Fig. 8), presumably because they experience a high risk of predation (Miller 1984). In contrast, cryptobenthic and burrow-dwelling species have relatively long lives of 7 to 11 yr (Fig. 8), presumably because they experience a lower risk of predation (Miller 1984). These differences in maximum life-span are often unrelated to differences in maximum size (Fig. 8, and see Miller 1979).

Although information for tropical gobies is limited, the available data suggest that gobies with similar patterns of habitat use to the 5 study species are also short-lived. For example, *Coryphopterus glaucofraenum* and *Istigobius decoratus*, that attain a similar maximum size and occur in similar habitats to *I. goldmanni*, have a maximum life-span of <1 yr (Forrester 1995, Kritzer 2002). Gobies that utilise burrows for shelter also have similar maximum life-spans to the 3 species in the current study that shelter in burrows. For example, *Amblyeleotris japonica* and *Valenciennesa strigata* both have a maximum life-span of <2 yr (Yanagisawa 1982, Reavis 1997a). In contrast, more

cryptic gobies such as obligate coral-dwelling gobies have longer maximum life-spans. For example, *Paragobiodon echinocephalus* can live for >2 yr (Kuwamura et al. 1996) and *Gobiodon histrio* can live at least 4 yr (Munday 2001).

A comparison between temperate and tropical gobies suggests that nektonic and open sand species have similarly short lives in both regions (Fig. 8), probably because high rates of predation drive the life-history traits of all these species. In contrast, temperate burrowing and cryptobenthic species tend to be longer-lived than similar sized tropical species with the same behaviour. This difference may reflect fundamental differences in life-history traits among latitudes. Choat & Robertson (2002) described, for 2 species of acanthurid fishes, a similar relationship between maximum age and latitude to that observed here, and concluded that this pattern may be linked to latitudinal variation in reproductive rates. The capacity to reproduce successfully throughout the year in the tropics may select for short life-spans, whereas the truncation of reproduction to just a few months in cooler waters may select for longer life-spans. Alternatively, there may be an intrinsic association between growth rates and longevity, such that slow growth in cool, high-latitude waters leads to a greater maximum age, whereas fast growth in warm, low latitude waters produces a shorter maximum age (Pauly 1980). However, further studies are required on a range of species in each geographic locale to examine interspecific variation and to separate phylogenetic relationships from latitudinal differences.

Seasonal variation in growth rate was evident for several of the study species. Individuals growing wholly or predominantly through the summer had attained a significantly larger size for a given age than individuals growing wholly or predominantly through the winter. This seasonal difference in growth rate was most pronounced in juveniles, suggesting that the season of settlement may have a significant impact on the timing of maturation, the probability of survival to maturation and reproductive output/success. Reproductive activity was highest during the summer months, but reproductively active females were also found in winter. Thus, recruitment to the adult habitat is likely to occur during both summer and winter. If the timing of maturation is dependent on size, juveniles settling during early summer will attain that size in a shorter time than juveniles settling during early winter. Thus, the time to first reproduction may be relatively shorter in summer-recruiting individuals. Faster growth, and thus a relatively larger body size, may also affect reproductive output because of the effects of body size on fecundity and contests over resources, such as nest sites and reproductive mates.

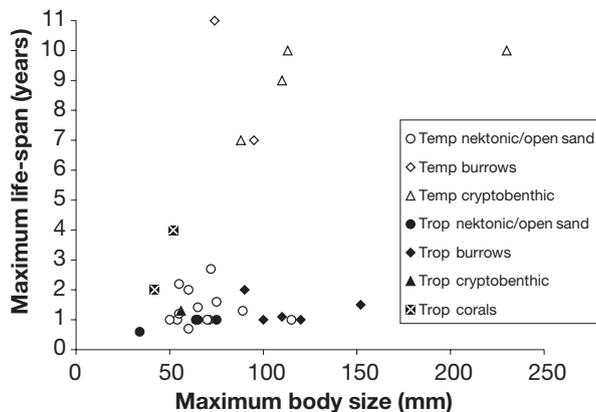


Fig. 8. Relationship between maximum body size and maximum life-span for a suite of tropical (Trop) and temperate (Temp) gobies with different patterns of habitat use. Data derived from: Miller (1961, 1979, 1984), Gibson (1970), Grossman (1979), Yanagisawa (1982), Moreira et al. (1991), Arruda et al. (1993), Magnhagen (1993), Forrester (1995), Gill et al. (1996), Kuwamura et al. (1996), Iglesias et al. (1997), Reavis (1997b), Sano (1997), Bouchereau & Guelorget (1998), Robertson & Kaufmann (1998), Kovacic (2001), Munday (2001), Kritzer (2002), and Mazzoldi et al. (2002) and present study

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