

# Life-history characteristics of coral reef gobies. II. Mortality rate, mating system and timing of maturation

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**ABSTRACT:** High adult mortality rate is expected to select for early maturation. However, physiological constraints or size-related reproductive benefits might select for delayed maturation, especially in small-bodied species. Additionally, the mating system and the relative intensity of mate competition can modify the timing of maturation. Here, we investigate the influence of mortality rate and mating system on the timing of maturation in 5 species of small coral reef goby that are either polygynous (*Asterropteryx semipunctatus* and *Istigobius goldmanni*) or monogamous pair-spawners (*Amblygobius bynoensis*, *Amblygobius phalaena* and *Valenciennea muralis*). All 5 species experienced high annual adult mortality rates with annual survivorship of  $\leq 2.3\%$ . The mean size at maturity, compared to maximum adult size, was smaller than is typical for fishes, indicating selection for early maturity in all of these species. The season of growth had little effect on size at maturity, but had a considerable effect on age at maturity, with summer-growing individuals exhibiting a younger mean age at maturity than winter-growing individuals. As predicted, males of the 3 monogamous pair-spawning species matured earlier and smaller than females (*A. bynoensis* and *A. phalaena*) or at the same time as females (*V. muralis*), but contrary to expectation, males of the 2 polygynous species (*A. semipunctatus* and *I. goldmanni*) did not mature later and at a larger size than females. Overall, the timing of maturation in these species is consistent with predictions from general life-history theory, however, the sex-specific timing of maturation may be influenced by body size constraints and the mating system.

**KEY WORDS:** Maturity · Mortality · Life history · Body size · Gobiidae · Mating system

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## INTRODUCTION

Life-history theory predicts that the life stage upon which mortality exerts most influence will shape the timing of sexual maturation. High and unpredictable density-independent adult mortality is predicted to select for early maturation and high reproductive effort early in life (Schaffer 1974, Begon & Mortimer 1981, Stearns 1992). In contrast, high juvenile mortality, but low adult mortality, will favour late maturation with the production of many small young and the reproductive effort spread over many reproductive events (Begon & Mortimer 1981, Stearns 1992). Because mortality rate

is often strongly correlated with body size (Roff 1992), the timing of maturation is also expected to vary in relation to an organism's size. Small-bodied species often experience high rates of mortality throughout life and, consequently, are predicted to exhibit early maturation and high reproductive effort. Early maturation confers several benefits, such as a higher probability of survival to maturity, shorter generation times and a higher instantaneous rate of natural increase (Stearns 1992).

Selection for early maturity in small species may be offset, however, by selection to delay maturity to obtain size-related reproductive benefits. For example,

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in fishes the number of eggs produced at each spawning is limited by the volume of the body cavity available to accommodate the ripe ovaries (Wootton 1998). Thus, the size of the body cavity can impose a substantial constraint on batch fecundity of small-bodied species. Assuming a growth cost of reproduction, females could maximise both initial and future fecundity by delaying reproduction until a larger size is attained (Stearns 1992). Selection may also favour delayed reproduction in males if mate choice and reproductive success are linked to body size. In situations where a large body size confers a competitive advantage in contests over mates, nest sites or breeding territory, male reproductive success may be increased by delaying reproduction to attain a larger body size at maturation (Emlen & Oring 1977).

For coral reef fishes, mortality rates are typically highest during the early life history (Meekan 1988, Hixon 1991, Jones 1991, Caley 1998). However, for many small-bodied species, adult mortality may also be considerable because their small size renders them vulnerable to predation throughout life (Munday & Jones 1998). Consequently, early maturity and high reproductive effort is predicted for most small coral-reef fishes. Here, we investigate the timing of maturation for 5 species of coral reef goby (Gobiidae), a diverse and abundant group of small fishes found in a wide range of coral reef habitats (Leis & Rennis 1983, Randall et al. 1997, Greenfield & Johnson 1999, Ackerman & Bellwood 2000). The coral reef gobies in our study are all small species (<130 mm total length), with relatively short maximum life-spans (11 to 16 mo, depending on species; Hernaman & Munday 2005, this volume). The relatively short life-span of these species might select for early maturation to increase the probability of survival to maturity, and this may be facilitated by a phylogenetic capacity for maturation at a small absolute body size (Miller 1984). Conversely, reproductive constraints associated with a small body size might favour delayed maturation to gain size-related reproductive benefits.

The mating system and the intensity of competition for mates or resources can also influence the relative timing of maturation. Two of the study species (*Asterropteryx semipunctatus* and *Istigobius goldmanni*) are polygynous and 3 (*Amblygobius bynoensis*, *Amblygobius phalaena* and *Valenciennea muralis*) are monogamous pair-spawners (Hernaman 2003). Generally in fishes, males might be expected to mature smaller and younger than females because females gain fecundity with size at a higher rate than males (Stearns 1992). However, males tend to mature later and larger than females in mating systems where there is strong competition for females or for resources that may affect reproductive success (Warner 1984, Stearns 1992).

Competition among males is expected to be most intense in polygamous mating systems and relatively slight in monogamous and pair-spawning species (Emlen & Oring 1977, Stearns 1992). Therefore, males of the 2 polygynous species should delay reproduction to attain a larger size, and consequently, mature later and larger than females. In contrast, males of the 3 monogamous pair-spawning species would not be predicted to mature later or at a larger size than females. In fact, males of pair-spawners might mature at a smaller size than females because they do not suffer the same size-related constraints on fecundity as females. However, body size has been found to influence mate selection in some monogamous pair-spawning gobies, with both males and females preferring larger partners (Reavis 1997b, Takegaki & Nakazono 1999). Therefore, males of the pair-spawning species should mature at either the same size or smaller than females.

To investigate the timing of maturation and determine how it is influenced by mortality rate and the mating system, we first determined the annual mortality rate of each species. We then estimated the absolute size and age at maturity of males and females, and tested for sex-specific differences in the mean size and age at maturity. If the mating system influenced the timing of maturation, we predicted that males of the 2 polygynous species would mature later and larger than females, whereas in the 3 monogamous pair-spawning species, males would mature at the same size or smaller than females. Finally, to compare the timing of maturation with predictions from general life-history theory, we compared the observed size at maturity for the 5 species considered here with the size at maturity reported for a range of other fishes by Charnov (1993).

## MATERIALS AND METHODS

**Sample collection and preparation.** Fish were collected using a clove oil/alcohol mixture and euthanased by immersion in an ice slurry. Total length, standard length (nearest 0.1 mm) and weight (nearest 0.001 g) were recorded, and the otoliths removed for estimating age. The gonads, or body midsections containing the gonads, were dissected from each fish and preserved 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.

Histological preparations of the gonads and body midsections were used to determine the maturity stage of each fish. Body midsections were decalcified in 10% formic acid for 24 h prior to histological processing. After embedding in paraffin wax, midsections and gonads were serially sectioned at 6  $\mu$ m at 3 positions of the go-

nad (anterior, middle and posterior). Thin sections were mounted on microscope slides, stained with Mayer's alum haematoxylin and Young's eosin-erythrosin, and examined under a high-power compound microscope.

Female maturity was classified on the basis of the most advanced oocyte stage present. The terminology and description of each oocyte stage followed Yamamoto et al. (1965), West (1990), and Takashima & Hibiya (1995). Ovaries comprised of previtellogenic oocytes in the chromatin nucleolus and perinucleolus stages, with no evidence of prior spawning, were categorised as 'immature'. Ovaries were categorised as 'developing' when cortical alveoli stage oocytes were present (Takashima & Hibiya 1995). Ovaries were categorised as 'mature, ripening' when the most advanced oocyte stage was in the vitellogenic stage, and as 'mature ripe' when maturation stage oocytes dominated the ovary. An ovary was classified as 'mature spawned' when post-ovulatory follicles were present, the gonad walls were thick (50 to 80  $\mu\text{m}$ ) and the ovary exhibited a disorganised internal structure. An ovary was termed 'mature resting' when it was comprised only of previtellogenic oocytes, had thin gonad walls and an organised internal structure, and the gonad area was larger than found in immature females.

Classifications of male reproductive development followed Nagahama (1983), Cinquetti & Rinaldi (1987), and Takashima & Hibiya (1995). A male was classified as 'immature' if it had a small testis comprised of cysts of primary and secondary spermatogonia and spermatozoa, but no spermatozoa and no evidence of prior spawning. The classification 'developing' was given to a small testis comprised of all stages of spermatogenesis, but where the spermatozoa cysts comprised <25% of the gonad area with no evidence of prior spawning. The classification 'mature' was given to a testis comprised predominantly of cysts containing spermatids and spermatozoa and where spermatozoa cysts accounted for >25% of the gonad area, or where there was evidence of prior spawning (e.g. empty cysts, cysts with only a few spermatozoa remaining and a large number of spermatogonia cysts).

To determine criteria specific to the study species that could be used to identify an immature gonad versus a recently spawned gonad, aquaria-maintained fish that had recently spawned, and for whom the spawning date was known (Hernaman 2003), were sacrificed and the gonads processed histologically as described above. The histological sections were examined under a high-power compound microscope and the presence of each stage of gametogenesis, and any other distinguishing features that would indicate a recent spawning event, were noted.

**Estimation of adult mortality rates.** Age- and length-based catch curves were used to provide direct

estimates of instantaneous mortality rate ( $Z$ ) (for this study  $Z$  equals the natural mortality rate,  $M$ , because of the absence of fishing mortality,  $F$ ). For age-based catch curves, fish were grouped into monthly age-class intervals, where age was estimated by counts of otolith growth increments (Hernaman & Munday 2005). The natural logarithm of the number of fish in each age class was plotted against the corresponding age class and a linear regression fitted:

$$\ln(\text{no. of fish in age class}) = b(\text{age class}) + a$$

The absolute value of parameter  $b$  is equivalent to  $Z$ . An estimate of the monthly survival rate ( $S$ ) was calculated by  $S = e^{-Z}$  (Ricker 1975).  $Z$  was also estimated using length-based catch curves that have an age-based element (described in King 1995) and the general regression equation of Hoenig (1983) based on observed maximum age. Hoenig's equation was used as an indirect method of estimating  $Z$  because the key assumptions associated with the age- and length-based catch curve methods, that all age and size groups had a similar abundance at recruitment and have been subjected to the same total mortality rate after recruitment (King 1995), were not tested. Hoenig's (1983) equation is:

$$\ln Z = 1.44 - 0.982 \ln t_{\max}$$

where  $t_{\max}$  is the maximum observed age (yr). For each of the 5 study species,  $t_{\max}$  was defined as the age (expressed as a fraction of a year) of the oldest individual sampled, estimated from counts of otolith growth increments (Hernaman & Munday 2005).

**Size and age at maturity.** Size at maturity was estimated using the size-class frequency distribution of staged males and females. The estimated age of fish was obtained from counts of otolith growth increments (Hernaman & Munday 2005), and the age at maturity investigated using the age-class frequency distribution of staged males and females. Mean size and age at maturity were defined as the size or age at which 50% of the sample was mature (King 1995). To determine the mean size and age at maturity, the following logistic model was fitted to the data:

$$P_i = \frac{1}{1 + e^{-B(X_i - C)}}$$

where  $P_i$  is the proportion of mature fish in each age or size class,  $X_i$  is the corresponding age class or the midpoint of the size class,  $B$  is the instantaneous rate of fish maturation and  $C$  is the size or age at which 50% of the sample were mature (Chen & Paloheimo 1994).

**Sex-specific differences in the mean size/age at maturity.** A multiple logistic model (Lam & Hernaman unpubl.) was used to determine whether mean size (or age) at maturity differed between males and females.

Briefly, this method entails applying a multiple logistic model to the size (or age) at maturity data, and testing the null hypothesis of no sex-specific difference in the estimated regression coefficients for females and males ( $\beta_F$  and  $\beta_M$ , respectively). After the model was fitted, the values of the estimates and their estimated variance–covariance matrix were outputted for the construction of the 95% confidence interval for the ratio  $R$  (where  $R = \beta_F/\beta_M$ ). The Hosmer & Lemeshow (2000) goodness-of-fit test was used to determine how well the multiple logistic model fitted the data.

This analysis requires a binary classification (i.e. males vs females, immature vs mature), thus developing individuals had to be included in either the immature or mature category. Because of the occasional difficulty in accurately distinguishing developing males from recently spawned males, all developing individuals (both males and females) were included in the 'mature' category. Whilst this has the potential of underestimating the timing of maturation, the actual effect on the estimated mean size/age at maturity was negligible because there were very few individuals classified as 'developing' and, consequently, combining these 2 categories produced very little change in the actual values of mean size/age at maturity (i.e. 0 to 4.2 mm difference, depending on species/sex, in mean size at maturity between using developing/mature combination and mature-only; 0 to 0.6 mo difference in mean age at maturity) and absolutely no change in the results of statistical analyses testing for sex-specific or seasonal differences in size/age at maturity.

**The effect of seasonal growth rate on mean size and age at maturity.** Examination of the size- and age-class frequency distributions indicated that, for some gobies in this study, maturity occurred over a relatively large size and/or age range. Because both growth rate and the proportion of reproductively active fish differed between cool and warm periods of the year (Hernaman 2003), and fish were caught during both periods, the question arose as to whether the variation in size and/or age at maturity was due to seasonal effects. To test for significant seasonal differences in mean size and age at maturity, a multiple logistic model was used in a similar manner to that described above. Each fish was classified according to its maturation stage and whether it had experienced post-settlement growth predominantly through the summer months of increasing seawater temperature (September to February) or through the winter months of decreasing seawater temperature (March to August). The date of settlement was estimated by subtracting the fish's estimated age from its date of capture and adding the pelagic larval duration. The pelagic larval duration was estimated by enumeration of the growth increments from the otolith core to the presumed settlement mark. All 5 gobies

exhibited a distinctive transition in growth increment structure (width and optical properties) that was assumed to coincide with settlement (Sponaugle & Cowen 1994, Wilson & McCormick 1999).

For valid statistical analysis using the multiple logistic model, a sample size  $\geq 5$  was needed in each of the 4 cells (i.e. maturity stage  $\times$  season). The question of seasonal effects on size/age at maturity arose only after the fish had been caught, and so the sampling regime had not been designed to specifically test this question. Consequently, statistical analysis of seasonal effects on size/age at maturity could not be conducted for any of the males nor for female *Istigobius goldmanni* because of low sample sizes of immature winter-growing individuals. To ensure that sex-specific differences in the timing of maturation did not reflect differential seasonal sampling (e.g. having more winter-growing females than males), sex-specific differences in the timing of maturation were also examined for summer-growing males and females only, and these patterns and values of mean size/age at maturity compared with those obtained using the whole data set.

**Comparison of size at maturity with life-history patterns.** To determine whether the size at maturity of the 5 coral reef gobies was consistent with general life-history theory, the timing of maturation was compared with the pattern reported by Charnov (1993), i.e. average size at maturity occurs at 65% of mean asymptotic size. For each species, the 'mean asymptotic size' was taken as the mean size of the largest 10% of individuals sampled (hereafter termed  $L_{10}$ ) for each sex separately. To examine the timing of maturation relative to the mean asymptotic size, the mean size at maturity was divided by the value of  $L_{10}$  and expressed as a percentage.

## RESULTS

### Mortality rates

Age-based estimates of  $Z$  gave monthly adult survivorship values ranging from 65.5 to 73.1% depending on species (Table 1). Monthly survivorships equated to very low annual survivorships for all 5 species, with  $\leq 2.3\%$  of adults surviving annually.

Age-based catch curves predicted annual adult mortality rates of 97.7 to 99.4% depending on species and sex (Table 1). All 5 species showed relatively little variation in annual mortality rate between sexes (Table 1). Annual mortality estimates obtained from length-based catch curves and from the indirect method of Hoenig (1983) were very similar to the age-based results (Table 1), with all 3 methods predicting annual mortality rates  $\geq 95.8\%$ .

**Size and age at maturity**

*Asterropteryx semipunctatus* matured over an 8 mm size range for females (22 to 30 mm total length [TL]) and over a 12 mm size range (18 to 30 mm TL) for males (Fig. 1a,b). The mean size at maturity of males

was significantly smaller than that of females (Table 2a, Fig. 2a), although the difference was only 2.2 mm (males 25.5 mm TL; females 27.7 mm TL). Maturation occurred over a 3 mo age range for females and a 2 mo age range for males (Fig. 1c,d). There was no significant difference in the mean age at maturity

Table 1. Age-based catch curve estimates of the instantaneous mortality rate,  $Z$ , and the corresponding monthly survivorship ( $S$ , %  $\text{mo}^{-1}$ ) and annual mortality ( $M$ , %  $\text{yr}^{-1}$ ). Also given are the annual mortality rates estimated from  $Z$  obtained using a second direct method (length-based catch curves) and an indirect method (Hoenig's 1983 general equation).  $n$ : number

Species	Sex	n	Age-based catch curves			Length-based catch curves $M$ (% $\text{yr}^{-1}$ )	Hoenig (1983) $M$ (% $\text{yr}^{-1}$ )
			$Z$	$S$ (% $\text{mo}^{-1}$ )	$M$ (% $\text{yr}^{-1}$ )		
<i>Asterropteryx semipunctatus</i>	M	92	0.3587	69.9	98.7	97.6	95.8
	F	70	0.4079	66.5	99.3	99.4	97.3
<i>Istigobius goldmanni</i>	M	80	0.3568	70.0	98.6	98.8	98.0
	F	66	0.4225	65.5	99.4	99.6	99.0
<i>Amblygobius bynoensis</i>	M	75	0.3466	70.7	98.4	98.9	98.0
	F	78	0.3283	72.0	98.1	98.9	98.5
<i>Amblygobius phalaena</i>	M	64	0.3132	73.1	97.7	98.9	97.3
	F	70	0.3234	72.4	97.9	98.6	97.3
<i>Valenciennea muralis</i>	M	68	0.3981	67.2	99.2	98.0	98.5
	F	87	0.4137	66.1	99.3	98.0	98.5

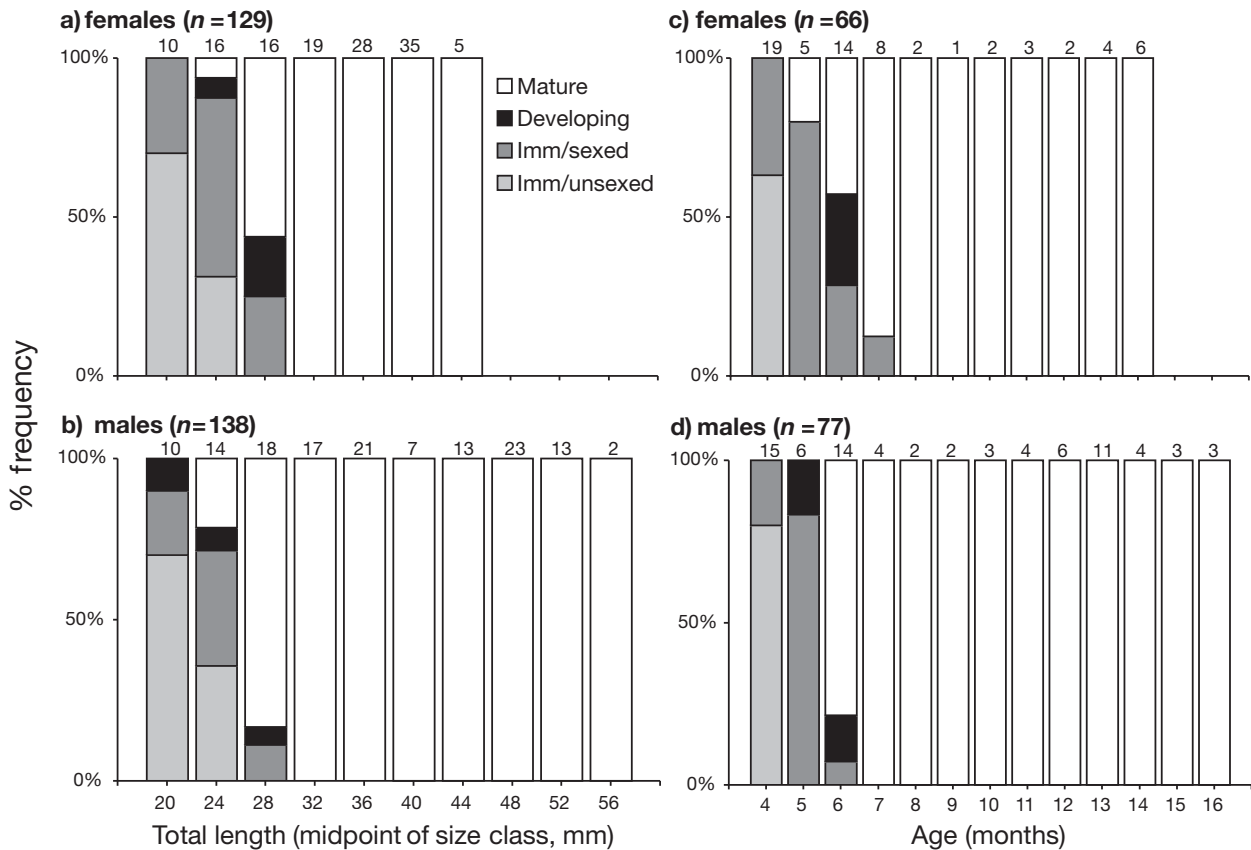


Fig. 1. *Asterropteryx semipunctatus*. Size and age at maturity. Numbers above bars indicate number of individuals in size or age class

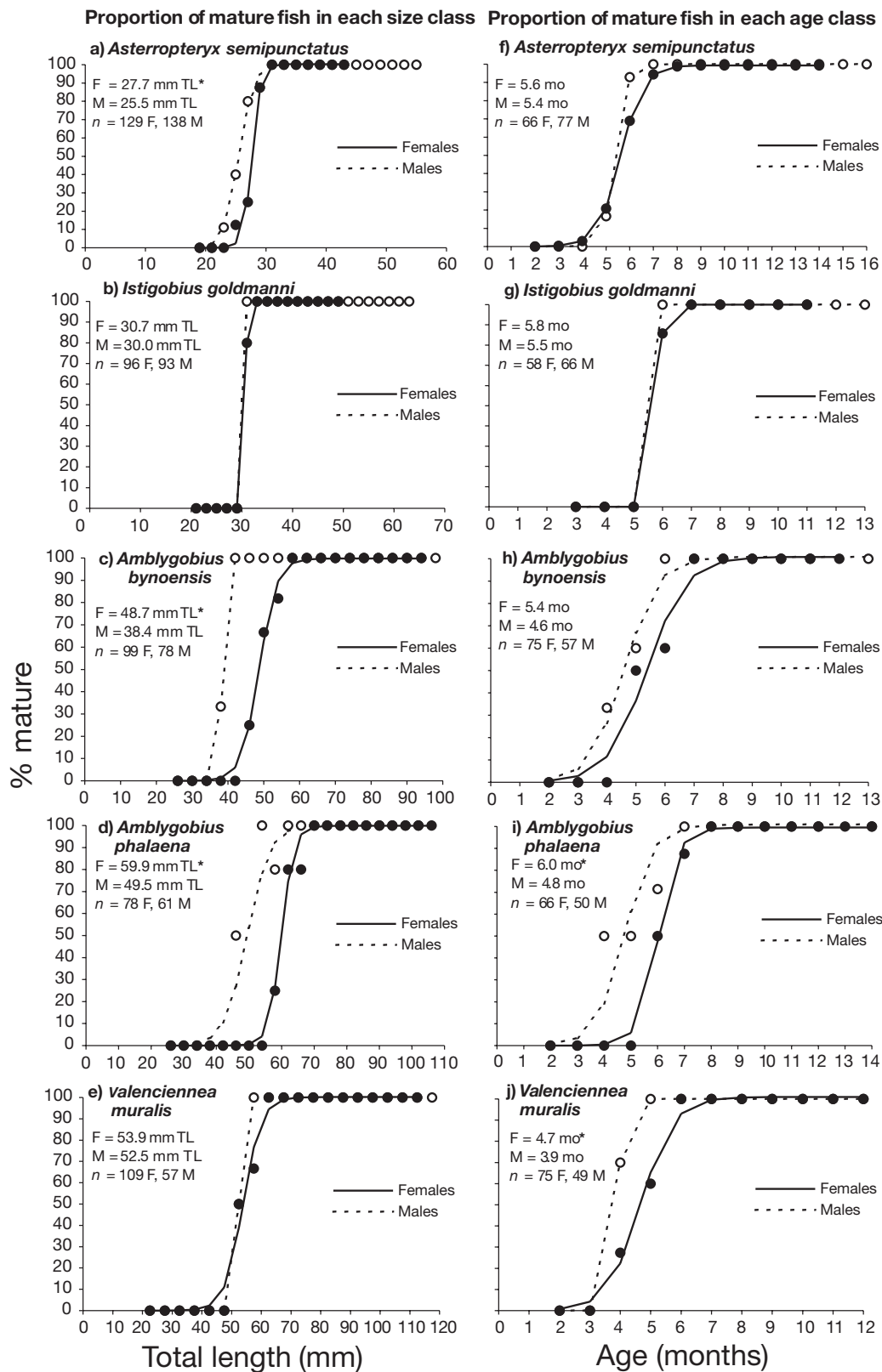


Fig. 2. Maturity ogives for size (a–e) and age (f–j) at maturity for 5 coral reef gobies. Values provided on graphs are the size/age at which 50% of the sampled fish were mature. \*: indicates a significant difference in mean size/age between sexes ( $p < 0.05$ ). Note different scales for x-axis. F: females; M: males; TL: total length; mo: months

between males (5.4 mo) and females (5.6 mo) (Table 2b, Fig. 2f).

*Istigobius goldmanni* matured over a relatively narrow size and age range for both sexes (Fig. 3). All indi-

viduals  $\geq 32$  mm TL were mature (Fig. 3a,b). There was no significant difference in the mean size at maturity between males (30.0 mm TL) and females (30.7 mm TL) (Table 2a, Fig. 2b). All females were mature by

Table 2. Results of multiple logistic models to test for sex-specific differences in size (a) or age (b) at maturity: Hosmer & Lemeshow goodness-of-fit test was used to determine how well the multiple logistic model fitted the data; results of testing the null hypothesis of no sex-specific difference in the estimated regression coefficients for females and males ( $\beta_F$  and  $\beta_M$ , respectively); ratio  $R$ , calculated using  $R = \beta_F/\beta_M$ , and its 95 % confidence intervals

	Hosmer & Lemeshow goodness-of-fit test			Null hypothesis $\beta_F = \beta_M$			$R (\beta_F/\beta_M) \pm 95\% \text{ CI}$		
	df	$\chi^2$	p	df	$\chi^2$	p	R	Lower	Upper
<b>(a) Size at maturity</b>									
<i>Asterropteryx semipunctatus</i>	5	1.456	0.918	1	4.685	0.030	0.933	0.877	0.992
<i>Istigobius goldmanni</i>	2	0.027	0.987	1	1.285	0.257	0.969	0.637	1.117
<i>Amblygobius bynoensis</i>	4	0.387	0.984	1	6.541	0.011	0.790	0.711	0.895
<i>Amblygobius phalaena</i>	7	3.442	0.841	1	5.753	0.017	0.839	0.746	0.954
<i>Valenciennesa muralis</i>	3	0.125	0.989	1	0.294	0.588	0.975	0.791	1.119
<b>(b) Age at maturity</b>									
<i>Asterropteryx semipunctatus</i>	6	1.466	0.962	1	3.074	0.080	0.910	0.824	1.015
<i>Istigobius goldmanni</i>	3	0.108	0.991	1	0.824	0.364	0.933	0.788	1.367
<i>Amblygobius bynoensis</i>	8	7.488	0.485	1	2.124	0.145	0.851	0.692	1.071
<i>Amblygobius phalaena</i>	7	2.426	0.933	1	3.992	0.046	0.844	0.707	0.996
<i>Valenciennesa muralis</i>	6	0.549	0.997	1	7.459	0.006	0.758	0.635	0.901

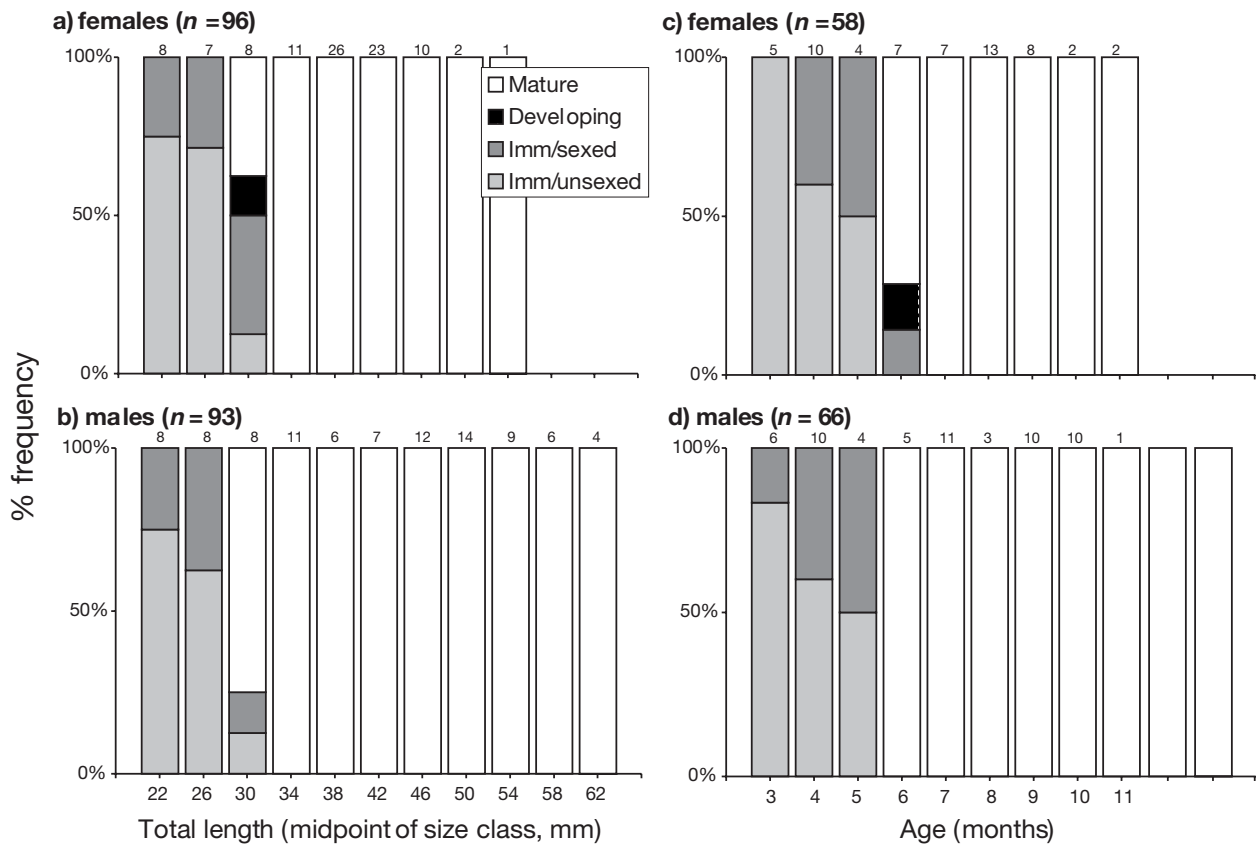


Fig. 3. *Istigobius goldmanni*. Size and age at maturity. Numbers above bars indicate number of individuals in size or age class

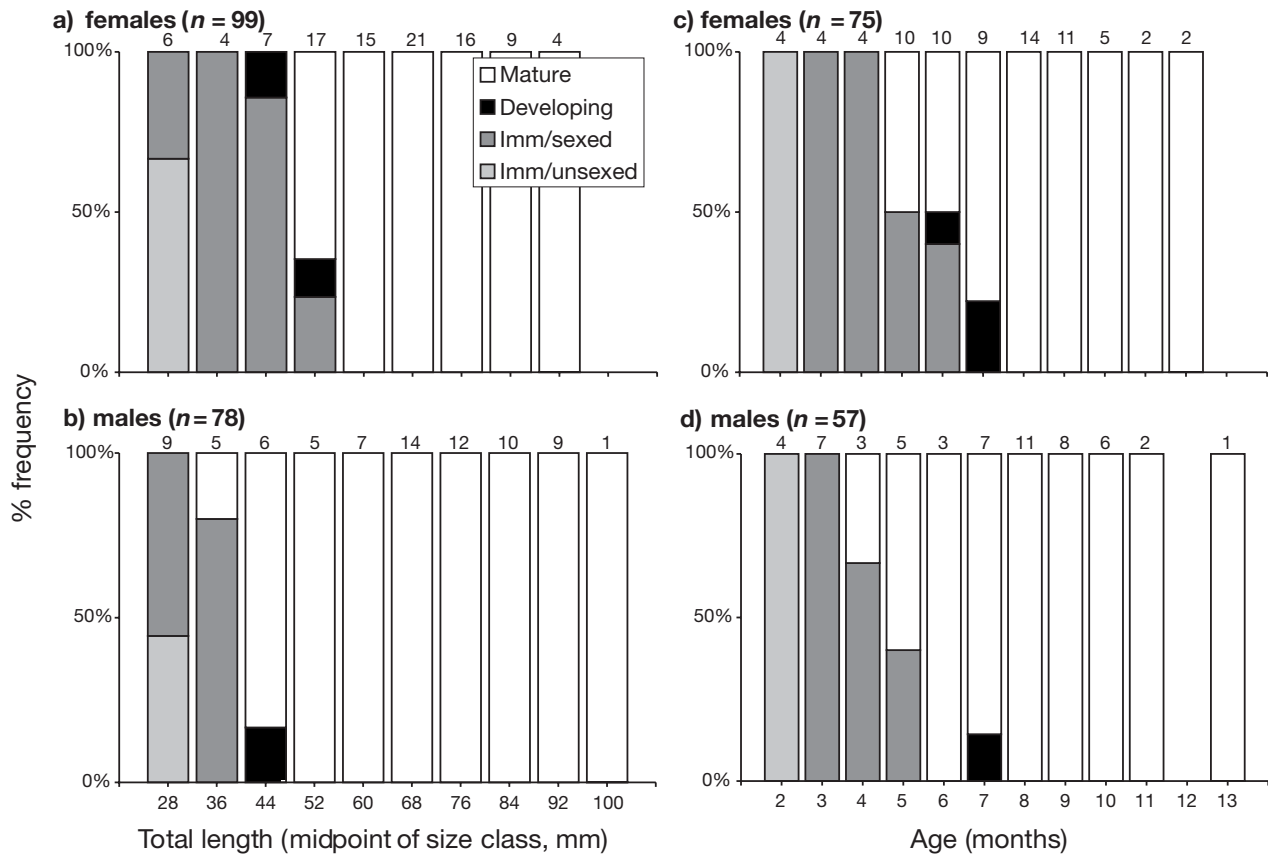


Fig. 4. *Amblygobius bynoensis*. Size and age at maturity. Numbers above bars indicate number of individuals in size or age class

7 mo of age and all males by 6 mo of age (Fig. 3c,d). There was no significant difference in the mean age at maturity between males (5.5 mo) and females (5.8 mo) (Table 2b, Fig. 2g).

For *Amblygobius bynoensis*, maturation of males and females occurred over a similar number of size and age classes, but mature males were present in smaller and younger size/age classes than females (Fig. 4). The mean size at maturity of males (38.4 mm TL) was significantly smaller than that of females (48.7 mm TL) (Table 2a, Fig. 2c). The youngest mature female was 5 mo old, the youngest mature male 4 mo, and all fish 8 mo were mature (Fig. 4c,d). Fitting a logistic model to the data resulted in a mean age at maturity of 5.4 mo for females and 4.6 mo for males (Fig. 2h). Despite this relatively large sex-specific difference in mean age at maturity, the parameters of the multiple logistic model,  $\beta_F$  and  $\beta_M$ , were not significantly different (Table 2b).

For *Amblygobius phalaena*, maturation of males and females occurred over a similar number of size and age classes, but mature males were present in smaller and younger size/age classes than females (Fig. 5). The mean size at maturity of males (49.5 mm TL) was significantly smaller than that of females (59.9 mm TL)

(Table 2a, Fig. 2d). The youngest mature female was 6 mo old and the youngest mature male 5 mo (Fig. 5c,d). The mean age at maturity of males (4.8 mo) was significantly younger than that of females (6 mo) (Table 2b, Fig. 2i).

For *Valencienna muralis*, maturation of males and females occurred over the same size and age range (Fig. 6). All fish  $\geq 60$  mm TL were mature (Fig. 6a,b). The mean size at maturity of males (52.5 mm TL) was not significantly different to that of females (53.9 mm TL) (Table 2a, Fig. 2e). All fish  $\geq 6$  mo old were mature (Fig. 6c,d). The mean age at maturity of males (3.9 mo) was significantly younger than that of females (4.7 mo) (Table 2b, Fig. 2j).

Additional analysis demonstrated that, in all but one case, the sex-specific patterns obtained using the whole data set were maintained when using the summer-only data. Therefore, sex-specific patterns of maturation obtained using the whole data were not the result of any potential differences in seasonal sampling between sexes. The one exception was mean age at maturity for *Valencienna muralis*. When using the whole data set, male *V. muralis* matured at the same mean size as females but at a significantly lower mean age than



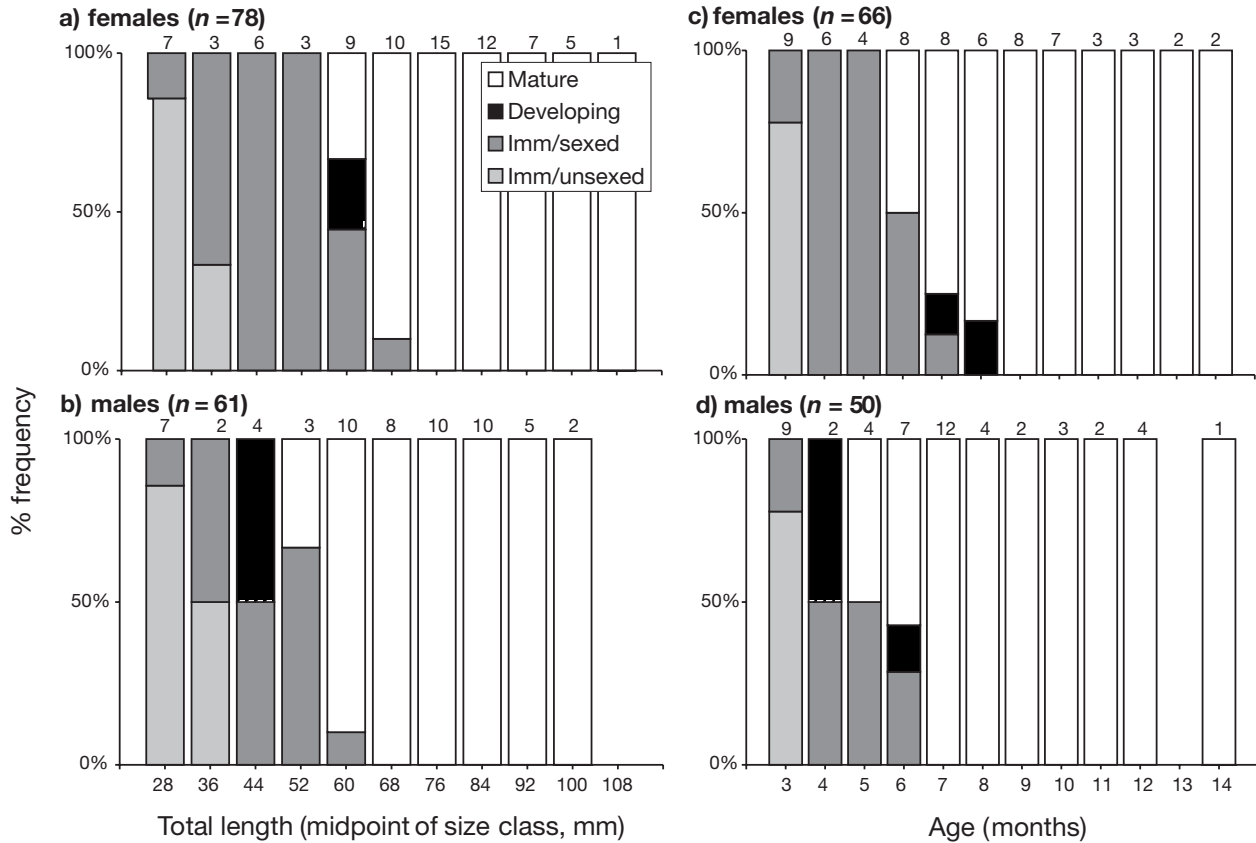


Fig. 5. *Amblygobius phalaena*. Size and age at maturity. Numbers above bars indicate number of individuals in size or age class

females. Using the summer-only data, there was no significant difference between sexes in either mean age or mean size at maturity. This outcome is consistent with the lack of a sex-specific difference in growth rate in this species (Hernaman & Munday 2005).

To summarise, males of the 3 monogamous pair-spawning species (*Amblygobius bynoensis*, *A. phalaena* and *Valenciennesa muralis*) matured at the same time or earlier than females. Contrary to expectations, males of the 2 polygynous species (*Asterropteryx semipunctatus* and *Istigobius goldmanni*) did not mature later and larger than females.

**Seasonal effects on size and age at maturity**

The predominant season of growth generally had little or no effect on size at maturity, but often had a considerable effect on age at maturity, with summer-growing individuals exhibiting a younger mean age at maturity than winter-growing individuals. Seasonal comparisons conducted for females of the 3 pair-spawning species indicated there was no significant difference in mean size at maturity between the 2 sea-

sons (multiple logistic model: *Amblygobius bynoensis*,  $\chi^2 = 0.411$ ,  $df = 1$ ,  $p = 0.522$ ; *Valenciennesa muralis*,  $\chi^2 = 0.090$ ,  $df = 1$ ,  $p = 0.764$ ; *A. phalaena*,  $\chi^2 = 0.537$ ,  $df = 1$ ,  $p = 0.464$ ). However, for both *A. bynoensis* and *V. muralis*, there was a significant difference in mean age at maturity between seasons (*A. bynoensis*,  $\chi^2 = 6.076$ ,  $df = 1$ ,  $p = 0.014$ ; *V. muralis*,  $\chi^2 = 4.946$ ,  $df = 1$ ,  $p = 0.026$ ). The mean age at maturity of summer-growing individuals was 1 mo younger than that of winter-growing individuals (*A. bynoensis*: 5.0 and 6.0 mo, *V. muralis*: 4.0 and 5.0 mo, summer- and winter-growing fish respectively). Both *A. bynoensis* and *V. muralis* exhibited marked seasonal differences in growth rates (Hernaman & Munday 2005), with fish growing predominantly through months of increasing seawater temperatures having higher growth rates than fish growing predominantly during decreasing seawater temperatures. Thus, for female *A. bynoensis* and *V. muralis*, winter- and summer-growing fish matured at the same mean size, but due to seasonal differences in growth rates, summer fish attained that size in a shorter time and thus matured at a significantly younger mean age than winter fish. Although the mean age at maturity of summer-growing *A. phalaena*

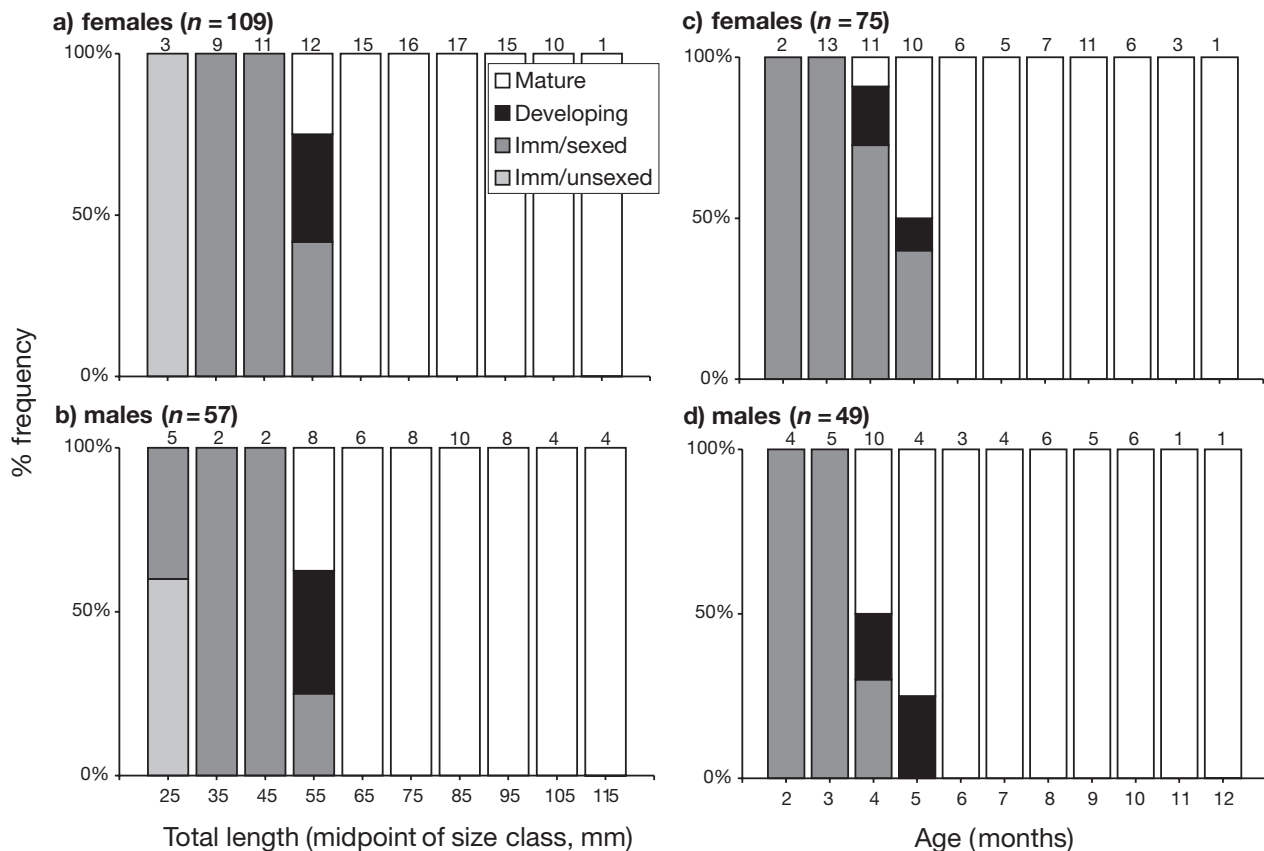


Fig. 6. *Valenciennaea muralis*. Size and age at maturity. Numbers above bars indicate number of individuals in size or age class

individuals was also younger than winter-growing individuals (5.5 and 6.1 mo respectively), the difference was not significant ( $\chi^2 = 0.240$ ,  $df = 1$ ,  $p = 0.624$ ).

Summer-growing female *Asterropteryx semipunctatus* also tended to mature at a younger mean age than winter-growing individuals (5.5 and 5.9 mo respectively), but the difference was not significant ( $\chi^2 = 0.296$ ,  $df = 1$ ,  $p = 0.587$ ). In contrast to the 3 pair-spawning species, a significant seasonal difference in mean size at maturity was evident for female *A. semipunctatus* ( $\chi^2 = 4.791$ ,  $df = 1$ ,  $p = 0.029$ ), although the difference was only 2.7 mm. Female *A. semipunctatus* growing predominantly through the winter months of decreasing seawater temperatures matured at a significantly smaller mean size (25.3 mm TL) than females growing predominantly through the summer months of increasing seawater temperatures (28.0 mm TL).

#### Comparison of size at maturity with life-history patterns

Female *Asterropteryx semipunctatus* and female *Istigobius goldmanni* matured at 64 to 65% of mean

asymptotic size, which is consistent with life-history patterns for fishes (65% of mean asymptotic size; Charnov 1993). In contrast, all other species/sexes matured at a smaller relative size than is typically found for fishes (Table 3). Female values ranged from 50 to 60%, and males ranged from 41 to 52% (Table 3). Thus, males of all 5 species not only matured at a considerably smaller relative size than expected from life-history patterns for fishes (65%; Charnov 1993), but also at or below the lowest threshold for organisms in general (50 to 80%, Charnov 1993).

Males of all species, except *Valenciennaea muralis*, matured at a considerably smaller relative size than females (Table 3). However, the way in which this occurred differed between the polygynous and the monogamous pair-spawning species. For the 2 pair-spawning *Amblygobius* species (for which there is no size dimorphism), it occurred because males matured at a significantly smaller mean size than females. However, for the 2 polygynous species, *Asterropteryx semipunctatus* and *Istigobius goldmanni* (for which sex-specific differences in mean size at maturity were small), it occurred primarily because males attained a larger maximum size than females.

Table 3. Relative size at maturity, defined as the percentage of the mean asymptotic size at which the mean size at maturity occurred, and calculated using: mean size at maturity/mean asymptotic size  $\times$  100. For fishes, mean size at maturity generally occurs at 65 % of mean asymptotic size (Charnov 1993). Mean asymptotic size ( $L_{10}$ ) taken as the mean size of the largest 10 % of individuals sampled for each sex separately. Also provided is the maximum size attained for each species from this study and as recorded from the literature (sex not provided). TL: total length

Species	Sex	Relative size at maturity (% of $L_{10}$ )	$L_{10}$ (TL, mm)	Maximum size (TL, mm)		
				This study	Recorded	Source
<i>Asterropteryx semipunctatus</i>	M	49	52.3	55.9	65	Randall et al. (1997)
	F	65	42.6	45.0		
<i>Istigobius goldmanni</i>	M	51	59.1	63.7	62	Randall et al. (1997)
	F	64	48.1	54.9		
<i>Amblygobius bynoensis</i>	M	41	92.9	97.5	120	Kuitert (1996)
	F	56	87.0	93.4		
<i>Amblygobius phalaena</i>	M	52	95.4	102.2	150	Randall et al. (1997)
	F	60	100.0	104.5		
<i>Valenciennea muralis</i>	M	48	109.4	116.1	130	Randall et al. (1997)
	F	50	107.4	113.0		

## DISCUSSION

### Mortality rate

All 5 goby species experienced high adult mortality rates with annual survivorship estimated to be  $\leq 2.3\%$ . The high annual adult mortality rates estimated for the study species are comparable to mortality rates estimated for other coral reef gobies. For example, the annual mortality rate of *Valenciennea strigata* at Moorea (French Polynesia) approached 100% (Reavis 1997a). Similarly, annual survivorship of *Istigobius decoratus* at Lizard Island (Great Barrier Reef) was estimated to be  $<1\%$  (Kritzer 2002). Predation is thought to be the primary agent of mortality in small reef fishes (Miller 1984, Munday & Jones 1998, Stewart & Jones 2001, Holbrook & Schmitt 2002) and is likely to be the main cause of mortality in the 5 study species. Coral reef gobies are consumed by a wide range of demersal and mobile piscivorous fishes, including scorpaenids, muraenids, pinguipedids, synodontids and serranids (Luckhurst & Luckhurst 1977, Sweatman 1984, Parrish et al. 1986, Norris & Parrish 1988, Kingsford 1992, Forrester 1995), all of which were commonly observed on the reef flat at Pioneer Bay.

Reproductive activities and the physiological demands of reproduction may contribute to the high mortality rates of the 5 species. Reproductive activities such as searching for a mate, courtship and spawning may increase exposure and vulnerability to predation (Smith & Wootton 1995). Reproduction may incur physiological costs that reduce life-span (Roff 1992). All 5 study species spawned at frequent intervals (Hernaman 2003) and, while their growth rate decreased following maturation, investment in somatic growth

continued for much or all of the adult life-span (Hernaman & Munday 2005). Therefore, they appear able to acquire sufficient energy to satisfy demands for both growth and reproduction, but this may come at a cost of reduced longevity. The acquisition of energy sufficient for both reproduction and growth could arise through an increase in foraging time, which may result in greater exposure to predation.

### Timing of maturation

Life-history theory predicts that high adult mortality will select for early maturation to maximise the probability of survival to first reproduction (Begon & Mortimer 1981, Stearns 1992). The 5 study species generally matured at a smaller size than observed for a range of other fishes (Charnov 1993), indicating selection for relatively early maturation. Nevertheless, physiological constraints or size-related reproductive benefits associated with a large body size may influence just how early maturation can occur. The minimum size threshold for maturation seems to be set by the fact that gametogenesis cannot generally be completed in a teleost frame of  $<10$  mm in length and weighing a few mg (Miller 1984). A large number of small goby species are capable of maturing at a very small body size that is at, or close to, this minimum size threshold, e.g. *Mistichthys luzonensis* mature at 11 mm; *Pandaka pygmaea* 7.5 to 10 mm; *Trimmatom* species at 8 mm; *Lythrypnus* species at 9 mm; *Risor ruber* at 10 mm; *Eviota* species at  $<15$  mm; *Paragobiodon* species at 10 to 14 mm (Smith & Tyler 1972, Miller 1984, Fishelson 1989, Taru & Sunobe 2000). While the size at maturity of the 5 study species was

generally smaller than is typically found for fishes, it was larger than the minimum threshold size suggested above. Therefore, it is likely that size-related reproductive benefits constrain the size of maturation and select against maturation at a very small absolute body size.

The 5 species exhibited a growth schedule characterised by rapid growth in the early life history, followed by an extended period of attenuating growth (Hernaman & Munday 2005). The onset of maturation might result in a reduction in growth if growth and reproduction compete directly for a limited amount of energy (Begon & Mortimer 1981, Stearns 1992). Accordingly, the Broken Stick growth model (Hernaman & Munday 2005) might be expected to break near the age at maturity. However, there was no consistent pattern with respect to the breakpoint ( $x_0$ ) of the Broken Stick regression (see Table 4 in Hernaman & Munday 2005) relative to the estimated mean age at maturity, suggesting that the point and rate at which growth slows following maturation differs among species, and that perhaps changes in growth rate are influenced by more than just maturation. The breakpoint was equivalent to the mean age at maturity for male and female *Valenciennesa muralis*, suggesting that growth attenuates soon after maturity. In contrast, the breakpoint in growth determined for male and female *Amblygobius phalaena* was 1 to 2 mo older than the estimated mean age at maturity. This suggests that sufficient energy is available at and soon after maturity to support maturation, as well as growth at the pre-maturity rate. Alternatively, the Broken Stick regression model might have fitted the breakpoint too late in the growth trajectory. Size-at-age plots for *A. phalaena* suggest a 3-phase pattern of growth for this species (Hernaman & Munday 2005). The Broken Stick regression model determined the breakpoint to be towards the end of the second growth phase. However, a breakpoint could also be envisaged at the end of the first growth phase, which would bring the estimated breakpoint much more in line with the estimated mean age at maturity.

The breakpoint occurred 1 to 2 mo younger than the estimated mean age at maturity for *Amblygobius bynoensis*, *Istigobius goldmanni* and *Asterropteryx semipunctatus*, suggesting that growth rate attenuated before maturation. That growth would slow prior to maturation seems counter-intuitive, but this pattern could be a result of a time lapse between resources being allocated to maturation and the subsequent visible evidence of gonad maturation. An alternative explanation is that mean age at maturity was overestimated from gonad analyses. Whilst this cannot be ruled out for *A. bynoensis* and *I. goldmanni*, it seems particularly unlikely for *A. semipunctatus* given the sample sizes for each age class.

### Mating system and the timing of maturation

Sexual selection is expected to be intense in highly polygamous mating systems and relatively slight in monogamous and pair-spawning species (Emlen & Oring 1977, Stearns 1992). Males tend to mature later and larger than females in mating systems where there is strong competition for females or for resources that may affect reproductive success. Therefore, males might mature at a larger size than females in polygamous mating systems, but not in monogamous pair-spawning species.

Contrary to expectation, males of both polygynous species (*Asterropteryx semipunctatus* and *Istigobius goldmanni*) matured at approximately the same time as females. Three factors could potentially explain this: (1) competition for females or resources is not as intense as postulated; (2) alternative male reproductive tactics enable males to be reproductively competitive at a small size; and (3) male reproduction is energetically inexpensive and, therefore, males can continue to grow following maturation.

Competition for nest sites, and consequently females, appears to be strong in the 2 polygynous species, *Asterropteryx semipunctatus* and *Istigobius goldmanni* (Hernaman 2003). Intraspecific agonistic encounters were frequently recorded for both species and nest sites appeared to be in short supply (Hernaman 2003). Therefore, the first scenario does not appear to hold. Field and laboratory observations indicate that a large body size confers a competitive size advantage for males in contests over shelter sites and, consequently, females (Hernaman 2003). However, alternative male reproductive tactics, such as female mimicry or sneaking, could increase the spawning opportunity for small males and alleviate the pressure to delay maturation to gain size-related benefits. Alternative reproductive tactics by small males have been reported in other gobies (e.g. Miller 1984, Magnhagen 1992, 1998, Svensson et al. 1998), and sneaking by small males was observed in a Hawaiian population of *A. semipunctatus* (L. Privitera pers. comm.). Therefore, although not directly observed for *A. semipunctatus* and *I. goldmanni* in the current study, it is not unreasonable to assume that small males engage in alternative reproductive tactics, which may encourage maturation to occur earlier than expected. Finally, if male reproduction incurs little or no cost to growth, delaying maturation to gain a size advantage would be unnecessary. The growth rate of *A. semipunctatus* and *I. goldmanni* did decline following maturation, but adults maintained a linear pattern of growth for much (*A. semipunctatus*) or all (*I. goldmanni*) of their reproductive lives (Hernaman & Munday 2005), and high rates of growth coincided with high levels of reproduc-

tive activity (Hernaman 2003). Thus the difference between pre- and post-maturity growth rate may be sufficiently small that any growth benefits gained by delaying maturity are not worth the costs associated with the delay.

For the 3 monogamous pair-spawning coral reef gobies, the observed pattern of maturation conformed with the predicted pattern. Males of the 2 *Amblygobius* species matured earlier than females, and male *Valenciennes muralis* matured at the same time as females. For these 3 species, a balanced sex ratio, low mobility and moderate-low densities may help to stabilise pair-bonds and thus serve to alleviate mate competition.

While these factors may reduce the intensity of mate competition, it is incorrect to assume that mate competition does not occur following pair-formation in these gobies. Presumed mate defence was observed occasionally for all 3 pair-spawning species, and the size of the intruder relative to the existing partner may be an important factor in determining whether the pair-bond is maintained. For example, mate size was an important factor in the instability of *Valenciennes longipinnis* pairings (56% of pairs broke up after only 1 spawning), with desertion occurring when a mate became available that was larger than the current partner (Takegaki & Nakazono 1999). Thus, although monogamous pair-spawning may relax sexual selection under certain circumstances (Berglund 1997, Stearns 1992), there may still be competition for high-quality (e.g. large) partners following pair-formation.

### Seasonal effects on the timing of maturation

Seasonal differences in growth rate appear to have a considerable impact on the age at maturity, and thus the time to first reproduction, by influencing the time required to attain a size suitable for maturation. Although the mean size at maturity generally differed little between seasons, summer-growing individuals generally had a younger mean age at maturity than winter-growing individuals. This was clearly illustrated by female *Amblygobius bynoensis* and *Valenciennes muralis*. Winter- and summer-growing females matured at the same size, but due to seasonal differences in growth rates, summer fish attained that size in a shorter time (by 1 mo) and thus matured at a significantly younger age than winter fish.

The observation that seasonal growth effects can have a significant effect on the time taken to reach maturity has important implications for short-lived species, such as the gobies considered here, that experience high rates of mortality. The 5 study species have aseasonal spawning, with ripe females found in both summer and winter (Hernaman 2003). Larvae that

settle during early summer may have the best chance of surviving to maturity and producing offspring, because fast summer growth rates will enable a size sufficient for maturation to be attained in the shortest time possible. In contrast, larvae settling during late summer and winter will experience slower growth rates and take a longer time to reach maturity, and thus may have a lower chance of surviving to maturity. However, the extent to which mortality rates, and larval survival to maturity, differ between seasons is presently unknown. Density of the study gobies was significantly lower in winter than in summer (Hernaman 2003). How density-dependent processes and seasonal differences in environmental and physiological conditions influence mortality and survival to first reproduction in the 5 study species remains to be tested.

### Assumptions and caveats

Age- and length-based methods are often used to estimate mortality (e.g. King 1995, Newman et al. 1996, Gust et al. 2002), but both methods assume constant rates of recruitment and mortality. The assumption of constant rates of recruitment is unlikely to be met for the coral reef gobies. While reproductively active females were present in both summer and winter, the proportion of reproductively active females was substantially higher in summer than in winter (Hernaman 2003). Given the relatively small maximum size of the gobies, it is probable that a size-refuge from predation is not reached, suggesting that the assumption of constant adult mortality (through predation) may be met. However, other sources of mortality may increase with size/age, e.g. decreased survival due to costs associated with reproduction.

The general equation of Hoenig (1983), based on maximum age, produced mortality rates that were within 2.9% of the age-based values for all species, and therefore appears to provide a robust and relatively simple method of estimating mortality rate in small reef fishes. Hoenig's (1983) equation was based largely on unexploited stocks and may thus be particularly suited to the study gobies. Furthermore, 2 potential limitations of the equation (i.e. that [1] the maximum age observed depends on the number of animals in the sample, since rare old animals are more likely to be found in large samples, and [2] the age structure will change slowly following a decrease in mortality rate; Hoenig 1983) are unlikely to apply to the gobies in this study. Firstly, the sample sizes for each sex were relatively large, ranging from 64 to 92 individuals, depending on species (Table 1) and, with the exception of *Amblygobius phalaena*, were similar to (within 7 and 9 individuals) or larger than sample-size recom-

mentations based on the number of age-classes (Kritzer et al. 2001). Secondly, the short life-spans of these fish mean that the age structure is unlikely to change slowly following a decrease in mortality rate.

## CONCLUSIONS

Four main conclusions are drawn from this study: (1) annual mortality rates were high, with both direct and indirect methods predicting annual survival rates of  $\leq 2.3\%$ ; (2) the mean size at maturity, in relation to maximum size, was generally smaller than is typically found for fishes, indicating selection for early maturation, as predicted by life-history theory; (3) seasonal growth effects on the age at maturity may result in summer-growing individuals maturing earlier than winter-growing individuals; (4) as predicted, males of the 3 monogamous pair-spawning species matured earlier and smaller than females (*Amblygobius bynoensis* and *A. phalaena*) or at the same time as females (*Valenciennea muralis*), but contrary to expectation, males of the 2 polygamous species (*Asterropteryx semipunctatus* and *Istigobius goldmanni*) did not mature later and at a larger size than females.

In concert, these results demonstrate that a high rate of adult mortality selects for early maturity, but size-related reproductive benefits may limit exactly how early maturation will occur, thereby preventing maturation at a very small absolute size. Furthermore, the mating system and seasonal influences on growth can interact with the pattern of mortality to shape the precise timing of maturation in small reef fishes.

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