Demography of a large grouper, *Epinephelus fuscoguttatus*, from Australia's Great Barrier Reef: implications for fishery management

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ABSTRACT: *Epinephelus fuscoguttatus* is widespread throughout the Indo-Pacific and features strongly in regional fisheries, including the live reef fish trade. We investigated age-specific demographic and reproductive characteristics of *E. fuscoguttatus* from the Great Barrier Reef, Australia, and examined implications for resource management. Age, growth, longevity, and the relationships between size or age and female sexual maturity and the recruitment of males into the study population were examined. Age validation using both oxytetracycline marking and edge-type analysis demonstrated that a single annulus formed each year. This grouper is long-lived (>40 yr) and relatively slow-growing. The size and age distributions of the sexes strongly suggested protogynous hermaphroditism. Histological data suggested infrequent spawning in small mature females. Females contribute very little to reproductive output until about 566 mm fork length and 9 yr of age. Larger females make important reproductive contributions during their 30+ yr reproductive lifespan. Their relatively long lifespan, restriction of males to large size groups, and the disproportionate contribution of large females to reproduction have important implications for the harvest of *E. fuscoguttatus*. For example, current Queensland size regulations are poorly matched to the species' biology because they do not protect the reproductive elements of populations.

KEY WORDS: Age · Maturity · Great Barrier Reef · Reef fisheries management · Legal size limits · Epinepheline serranid · Longevity · Protogynous hermaphroditism

INTRODUCTION

Serranids, primarily members of the genera *Epinephelus* and *Plectropomus*, bear the brunt of subsistence and commercial reef fisheries in the southwestern Pacific (Heemstra & Randall 1993, Sadovy et al. 2003). Recent increases in catches are largely attributable to the live reef fish trade (Sadovy et al. 2003). Age-based demographic studies of *Plectropomus*, primarily *P. leopardus* and *P. maculatus* (coral trouts, e.g. Ferreira & Russ 1992, 1994) suggest relatively fast growth and moderate lifespans. While these features may provide some resilience in the face of increasing fishing pressure (but see Mamauag et al. 2000), the extent to which they are characteristic of other epine-

pheline serranids (groupers) is unclear. For example, some smaller epinephelines, such as *Cephalopholis cyanostigma* (bluespotted hind), achieve far greater lifespans (46 yr, Mosse 2002). The demographic characteristics of larger members of the genus *Epinephelus*, especially Pacific species, are poorly known (Manooch 1987).

Otolith-based age estimates were obtained for *Epinephelus morio* (red grouper) from sub-tropical waters in the 1960s (Moe 1969), and more recently for a number of topical species of *Epinephelus* (e.g. *E. itajara*, Bullock 1992; *E. flavolimbatus*, Manickchand-Heileman & Phillip 2000; *E. niveatus*, Wyanski et al. 2000). Although these studies have revealed that many *Epinephelus* spp. may live for 20 yr or more (Manooch

1987), there are still uncertainties regarding maximum ages within the genus. Age estimates to at least 41 yr have been recorded (*E. nigritus*, Manooch & Mason 1987), but may not reflect potential ages in the absence of fishing pressure (Huntsman et al. 1999). Epinepheline serranids have complex patterns of sexual development. Most species are protogynous hermaphrodites; however, schedules and patterns of female maturation and male recruitment into populations vary among the subfamily, especially in the diverse assemblages characteristic of coral reefs (e.g. Smith 1965, Shapiro 1987, Sadovy & Colin 1995, Adams 2002, Liu & Sadovy 2004). In the absence of information on lifespans, growth rates and maturation, it is difficult to predict their capacity to respond to fishing pressure. In this study we investigate the age-based demography of *E. fuscoguttatus* (brown marbled grouper or flowery cod), with a focus on longevity, pattern of growth and size- and age-specific reproductive features.

Epinephelus fuscoguttatus, which reaches approximately 1 m in length, is widely distributed in the Indo-Pacific (Heemstra & Randall 1993). Although abundance estimates from the Great Barrier Reef (GBR), Australia, indicate that *E. fuscoguttatus* is locally uncommon (<1 fish 1000 m^{-2}, Pears 2005b), this species is a valuable component of regional fisheries (Sadovy et al. 2003) and a favourite of the dive industry, due to its large size and iconic status (D. Miller pers. comm.). This species forms spawning aggregations that are reportedly targeted by fishers (Johannes 1981, Johannes et al. 1999, Robinson et al. 2004).

In north-eastern Australia, *Epinephelus fuscoguttatus* is caught as part of the reef line fishery by commercial and recreational fishers. Almost all (96% in 2003) of the commercial catch in this fishery is from the Great Barrier Reef Marine Park (Andersen et al. 2005). Total commercial catch peaked in 2001 at just >4800 t, and, since July 2004, has been subject to a total annual commercial quota of 3061 t for all species of reef fishes. Although species-specific catch data is not available for *E. fuscoguttatus*, species composition of commercial line fishing operations was documented during an observer program by the CRC Reef Research Centre's Effects of Line Fishing (ELF) Project from 1996 to 1998. *E. fuscoguttatus* made up 1.2% of the total number of fish caught in fishing operations for processed reef fish. Estimates of the total recreational catch were 2320 t in 1997 and 2460 t in 1999 (Williams 2002), an unknown, but relatively small, proportion of which was *E. fuscoguttatus*.

There were 2 aims to this study. Firstly, we sought to determine the age-specific size, growth and maturity characteristics of *Epinephelus fuscoguttatus*, as an example of a species in the upper size range of the genus, and secondly, to obtain demographic informa-

tion that is relevant to the management of a group of reef fishes subject to overfishing (e.g. Koslow et al. 1988, Sadovy 1994a, Huntsman et al. 1999, Wyanski et al. 2000, Pogonoski et al. 2002).

MATERIALS AND METHODS

Sample collection. *Epinephelus fuscoguttatus* were obtained from the GBR, Australia, with the majority collected from reefs between 18° 20' S and 21° 50' S (Fig. 1, Table 1). Pooling of these samples was necessary, and is reflective of the low abundance of this species in the GBR. Sampling was facilitated through commercial reef line fishers between April 2001 and January 2003, and supplemented by samples from research line fishing surveys conducted each austral spring (October to December) from 2000 to 2002 by the ELF Project (Mapstone et al. 2004). Some specimens of *E. fuscoguttatus* were also obtained from the Australian National Spearfishing Association annual competition held between 24 and 28 November 2001 at Centipede, Grub and Broadhurst Reefs. These samples were included because the spear fishers targeted large individuals of each fish species, including the study species, and large individuals were considered underrepresented by the ELF surveys due to selectivity characteristics of the gear used. Fork length (FL) of all individuals and total weight of whole fish were recorded to the nearest 1 mm and 10 g, respectively. As the caudal fin of this species is rounded, fork length and total length are equivalent. A length–weight relationship was determined by least squares regression and used to predict total weight of some samples from which the fillets had been removed. Whole gonads were preserved in FAACC (formaldehyde 4%, acetic acid 5%, calcium chloride 1.3%; Samoilys & Roelofs 2000) or 10% formalin (ELF samples) for histological processing. Sagittal otoliths were removed, cleaned and stored dry.

Ageing protocol and age validation. Age estimates were obtained from thin-sectioned sagittal otoliths (n = 242) (Fowler 1990), because whole otoliths were unreadable (Fig. 2A). One of each pair of otoliths was weighed to the nearest 0.1 mg, individually embedded in labelled resin blocks, sectioned through the nucleus using a low-speed diamond wafering saw, and the section was mounted on a glass slide (e.g. Choat & Axe 1996). All otolith readings were conducted on an image analysis system using transmitted light at 25× magnification. A reference collection of sections (n = 20) covering the full size range of *Epinephelus fuscoguttatus* sampled was produced to establish consensus of age estimates by experienced readers (Campana 2001). Alternating opaque and translucent bands

were visible (Fig. 2), so it was assumed that 1 pair of opaque and translucent bands was laid down each year and represented 1 annulus; opaque bands were counted along a consistent axis near the sulcus, where the bands were most visible.

Three established validation methods were utilised to test the assumption that increments were annuli (e.g. Choat & Axe 1996, Cappo et al. 2000, Manickchand-Heileman & Phillip 2000). Firstly, oxytetracycline (OTC) injection was used to mark the otolith to determine the periodicity of increment formation. Because capture rates of *Epinephelus fuscoguttatus* are very low (0.17 fish per fishing-day by commercial line fishers on the GBR) and field tagging and release would have resulted in unacceptably low recapture probabilities, the OTC validation was done using captive individuals (Cappo et al. 2000). Two wild-caught adult *E. fuscoguttatus* were individually tagged, injected with 50 mg kg^{-1} total weight OTC in saline (McFarlane & Beamish 1987), and then maintained in an outdoor aquarium for a growth period of >1 yr (see Table 3). They were fed a diet of discarded reef fish or commercial bait (fish and crustaceans) 3 times wk^{-1}, and could prey on small reef fish in the aquarium. After the growth period, the fish's otoliths were removed and examined for the presence of an OTC mark using a Leica microscope with ultraviolet illumination and an image capture facility. Each otolith was also examined at the same magnification using bright field (transmitted) light. The increments formed outside of the OTC mark were counted and measured. The following formula, modified from Cappo et al. (2000), was used to determine the periodicity: the distance from the OTC mark to the edge of the otolith (x) is:

$$x = y \cdot G \cdot P$$

where y is the distance between increments (presumed annuli) in millimeters, G is the growth period (yr), and P is the periodicity of increment formation (yr^{-1}), so that:

$$P = \frac{x}{y \cdot G}$$

Secondly, edge-type analysis (Manickchand-Heileman & Phillip 2000) was also used. In this analysis, the monthly frequency of occurrence of otoliths with an
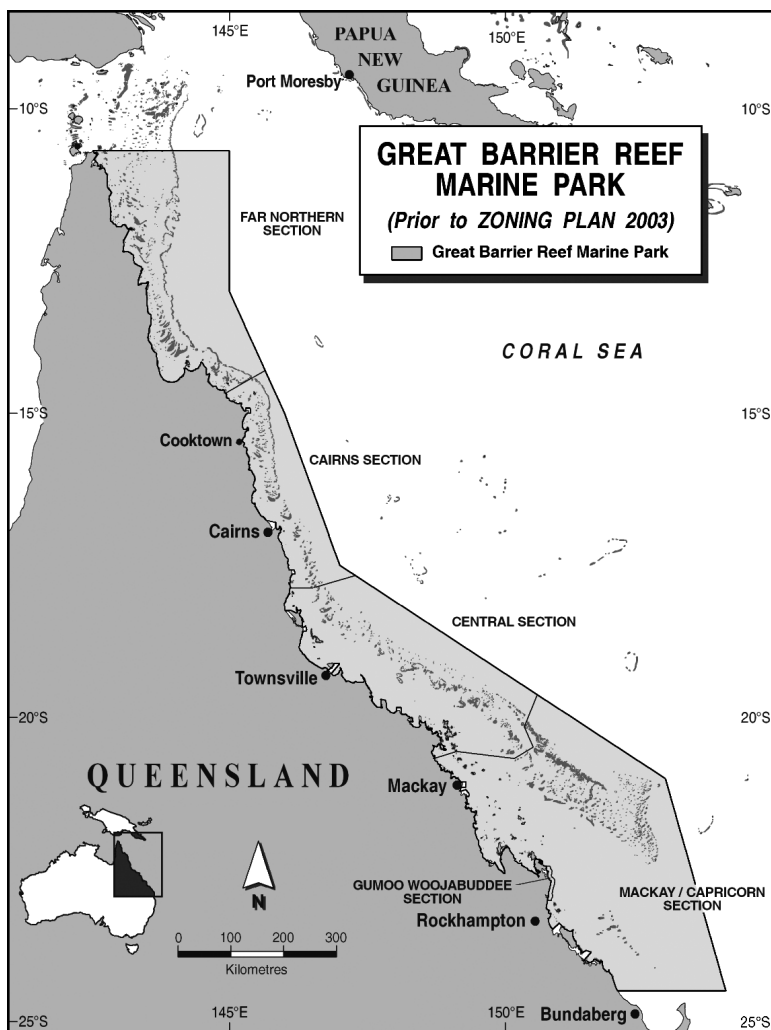

Fig. 1. Map of north-eastern Australia showing the Great Barrier Reef. Specimens of *Epinephelus fuscoguttatus* were obtained from the Cairns (n = 5), Central (n = 108) and Mackay / Capricorn (northern half, n = 129) sections of the Great Barier Reef Marine Park

Table 1. *Epinephelus fuscoguttatus*. Details of samples by collection method, month and year (collection method in brackets—1: research line fishing; 2: commercial line fishing; 3: recreational spear fishing)

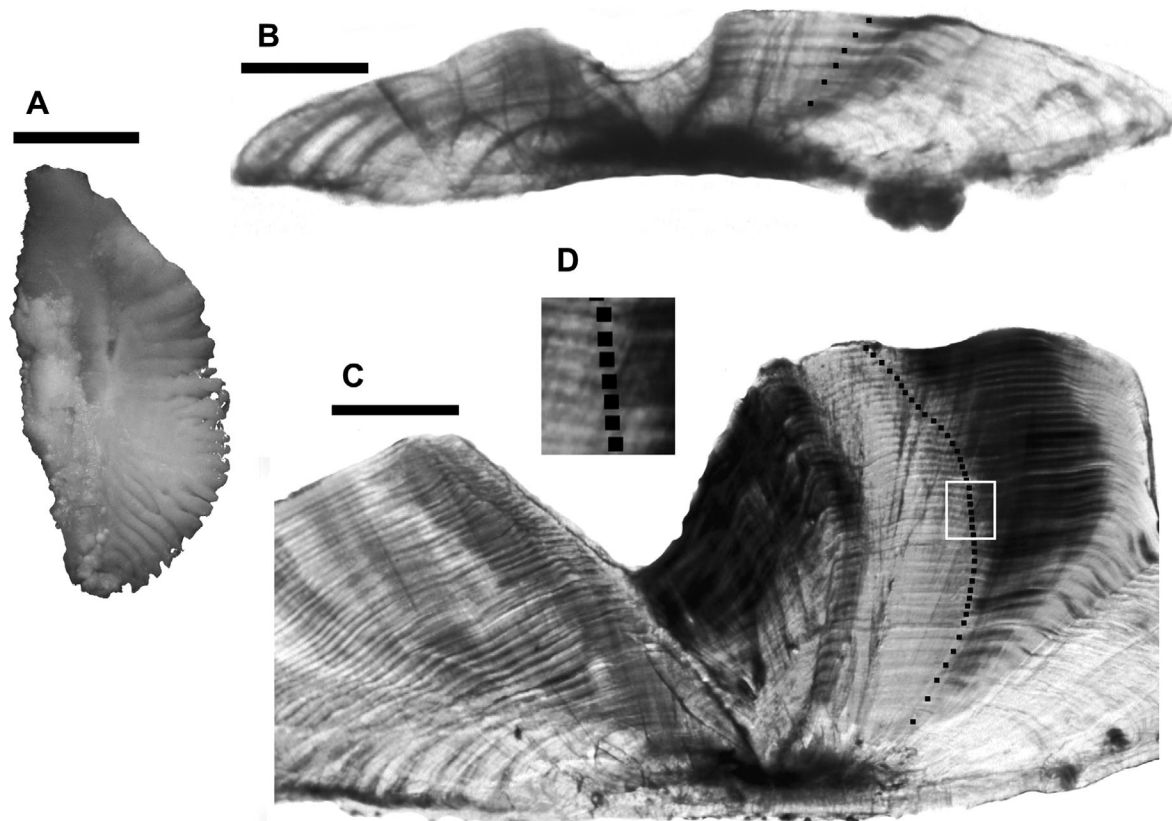| Month	2000 [1]	2001 [1]	2001 [2]	2001 [3]	2002 [1]	2002 [2]	2003 [2]	Total
Jan						7	11	18
Feb						5		5
Mar						4		4
Apr			7			3		10
May			12			2		14
Jun						5		5
Jul			11					11
Aug			9					9
Sep			9					9
Oct	5	3	7			1		16
Nov	27	25	6	25	20	2		105
Dec		23	8		4	1		36
Total	32	51	69	25	24	27	14	242

Fig. 2. *Epinephelus fuscoguttatus.* (A) Whole otolith (scale bar = 5 mm). (B,C) Sectioned otoliths with annuli indicated by dots: (B) 6+ year old female (fork length [FL] = 468 mm, total weight = 1.89 kg) and (C) 42+ year old female (FL = 855 mm, total weight = 9.80 kg). Scale bars for B & C are 1 mm. (D) Detail from C

opaque or translucent edge was determined to provide further independent evidence of periodicity of increment formation. It was difficult to determine the edge-type for some otoliths because of their inherent variability. These otoliths were classified as uncertain edge-types. The proportion of uncertain edges increased with the putative age of fish, and so fish >12 yr were excluded from the analysis (n = 65). The percent of otoliths with opaque edge-types was plotted by month, and the monthly frequency of occurrence of opaque edges was compared to a uniform distribution by a chi-squared goodness-of-fit test for circular distributions (Zar 1999). Samples were pooled across years by month, due to low sample sizes for some months. This assumes that temporal patterns in increment formation were broadly similar among years, as found for other reef fish taxa (e.g. Williams 2003).

Thirdly, the relationship between otolith weight and number of increments was examined using correlation analysis (Choat & Axe 1996). A strong correlation between otolith weight and putative age (number of increments) was expected if otoliths accreted calcium carbonate throughout the life of the fish.

Counts of opaque bands for each section were made on 3 separate occasions by the senior author

(R.J.P.) without prior knowledge of the fish's characteristics. Age estimates that coincided for at least 2 counts, or the median value if the range of age estimates did not differ by more than ±5% of the median age estimate (e.g. not more than ±1 yr for fish 20 yr of age) were accepted and used to plot size-at-age. An index of average percent error (Beamish & Fournier 1981) was calculated to assess reproducibility of the age estimates.

Demography. The size and age data were used to estimate mean size, age and age of the oldest 10% of the sample (termed 10% longevity) (e.g. Gust et al. 2002). A von Bertalanffy growth function (VBGF) was fitted by non-linear least-squares regression of FL on age data, to estimate the growth characteristics of the species. As no fish under 2 yr of age were collected, the intercept of the curve was constrained to the approximate size at settlement for *Epinephelus* (25 mm FL, Leis 1987) so that the von Bertalanffy parameter t_0 was −0.20. Differences in size of the sexes in the overlapping age ranges were examined using analysis of covariance (ANCOVA), with age as the covariate and sex as a fixed factor. Hoenig's (1983) method, which estimates total instantaneous mortality from

maximum observed age using data from 134 stocks, was used to predict mortality.

Reproductive biology. Gonads were blotted dry and weighed to the nearest 0.1 g. All sex assignment and maturity staging was done from histological sections of gonads under a high-power microscope using the criteria in Table 2; these include criteria used in combination to indicate female spawning history in inactive ovaries, in order to distinguish between immature and mature individuals (Shapiro et al. 1993, Sadovy & Colin 1995, Samoilys & Roelofs 2000). For 13.1% of females, the spawning history could not be determined, and these individuals were excluded from the estimation of maturity. Males were considered mature if spermatozoa filled major sperm ducts, or if collapsed ducts were evident, indicating prior functioning as a male.

The size and age structures for females and males were obtained, as were the mean sizes and ages of the sexes. To identify potentially important female breeders, ovary weight data were used as a proxy for female fecundity and mapped onto the growth curve for mature active females. Estimates of size and age at 50% sexual maturity were determined for females by 2 methods: (1) assessing the percent of all ovaries with signs of current or past spawning activity (i.e. mature active and mature inactive females, Table 2) by size or age groups and (2) assessing the percent of females that were sexually active (i.e. mature active, Table 2) during the spawning period (November, December and January; Pears 2005b) by size or age groups (termed *effective maturity*). *Effective maturity* recognises that despite maturity, only some females were sexually active. The relationships between gonad weight of inactive females and size and age were examined, and were expected to show disproportionate increases during the size and age intervals of first maturity (Adams 2002). To determine if females that were inactive during spawning months were taken between spawning episodes, the percent coincidence of mature resting females being sampled from the same reef and day as ripe or near spawning females was examined for ELF research samples (which have highly accurate location and time data for each specimen). The pattern of male recruitment into the sampled population by size and age was examined. The overlaps in the size and age frequencies of mature females and males were determined, and the median values of these ranges were calculated to give an indication of the size and age range over which sex change can occur (Shapiro 1987).

RESULTS

Ageing protocol and validation

Otoliths of *Epinephelus fuscoguttatus* had visually distinct increments when examined microscopically (Fig. 2B, C) that enabled age to be estimated in 98.8%

Table 2. *Epinephelus fuscoguttatus*. Histological criteria used in classifying gonads into sex and maturity stages (modified from Smith 1965, Moe 1969, West 1990, Shapiro et al. 1993, Ferreira 1995, Samoilys & Roelofs 2000, Adams 2002)

Developmental stage	Histological description
Immature female	No evidence of prior spawning, ovary small and lamellae well packed with gonia and pre-vitellogenic oocytes (chromatin nucleolar and perinucleolar stage).
Mature inactive female	Ovary dominated by pre-vitellogenic oocytes. Perinucleolar oocytes are the most advanced healthy oocytes present. Prior spawning indicated by the presence of muscle bundles and/or occasional atretic vitellogenic oocytes. May have brown bodies. Ovary generally larger in diameter than those of immature females, and may be vacuolated.
Undetermined inactive female	Ovary contains gonia and pre-vitellogenic oocytes, but it is impossible to determine if fish has spawned previously (mature) and is in a resting state or is an immature female.
Mature active female (i.e. ripening, ripe, near spawning & spent)	Ripening (yolk vesicle or cortical alveoli) or vitellogenic (yolk stage) oocytes present or indications of recent prior spawning (i.e. spent). May contain hydrated oocytes and/or post-ovulatory follicles (i.e. near spawning ovaries). Early stages of oocytes may also be present in varying numbers. May contain signs of prior spawning. Ovaries of spent females are generally disorganised and undergoing atresia, with muscle bundles and extensive vascularization.
Transitional	Proliferating testicular tissue in a gonad that has evidence of prior spawning as a female (as above) and/or degenerating ovarian material, where spermatozoa have not yet proceeded to fill the dorsal sperm sinuses. Spermatogenesis has progressed at least to the secondary spermatocyte stage. Ovarian tissue dominates and perinucleolar cells are the most advanced healthy female germ cells. Atretic and fragmenting oocytes may be present.
Mature male	Testes dominated by testicular tissue, which may contain crypts of gonia and germinal stages at various stages of development. Well-developed major sperm sinuses and peripheral ducts. Includes inactive and active males.

(239) of the otoliths examined. Two age estimates were in agreement for 87.5% of otoliths, and the index of average percent error was low (1.9%), thus indicating that reproducibility of the age estimations was high.

The OTC-marking experiment and the edge-type analysis revealed an annual periodicity of increment formation (see Table 3, Figs. 3, 4 & 5). The number of full and partial increment cycles formed on the outside of the OTC mark indicated that a single opaque band and a single translucent band were formed each year (Fig. 4). This agreed with the calculated periodicity from measurements (1.02 to 1.04 yr, Table 3). Inference from the coincidence of known dates (marking and end dates) with type of band (opaque or translucent) indicated that the opaque bands formed between September and November. *Epinephelus fuscoguttatus* showed a significant difference among monthly frequencies of otoliths with opaque margins ($\chi^2 = 176.00$, $p < 0.0005$), with elevated values ($>50\%$) occurring from August to November (Fig. 5). The findings from the edge-type analysis confirmed the results of the OTC-marking experiment that increment periodicity is annual. Furthermore, both techniques were in close agreement on the seasonality (austral spring) of formation of opaque bands. The edge-type of 28% of the sections was uncertain for the age range examined. These uncertain edge-types were present in all but one month (March). There was a strong correlation ($r^2 = 0.94$) between otolith weight and fish age (Fig. 6).

Table 3. *Epinephelus fuscoguttatus*. Details of age validation experiment of 2 wild-caught adults marked with OTC (T: translucent zone; O: opaque zone)

|	Fish 1	Fish 2
Specimen code	RP150	RP786
Sample location	Eyrie Reef	Centipede Reef
Date of OTC marking	10 Nov 2000	22 Aug 2001
End date	20 Jun 2002	12 Dec 2002
Growth period (d)	587	477
Growth period (yr)	1.6	1.3
Fork length at start	343	420
Fork length at end	470	526
Growth in length (mm)	127	97
Growth in length (mm yr^{-1})	79.4	81.5
Location of OTC mark	Start of T-zone	Near end of T-zone
Number of zones outside of OTC mark	T + O + T	O + T + O
Margin type	Thick T-zone	Start of T-zone
Age at end (yr)	4+	7+
Calculated periodicity of 'annuli' formation (yr)	1.02	1.04
Suggested timing of opaque zone formation	Sep to Oct	Sep to Nov
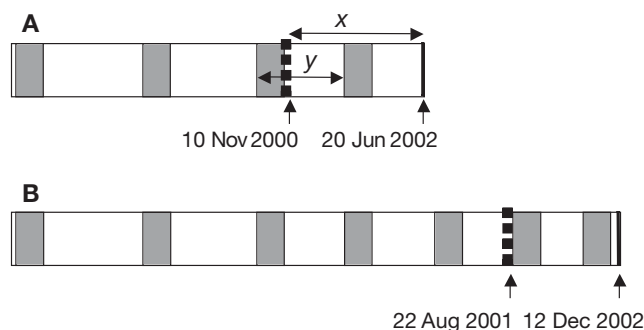
Fig. 3. *Epinephelus fuscoguttatus*. Diagram representing sections through otoliths from the first annulus (left) to outer edge of the otolith (right) from the oxytetracycline (OTC)-marking experiment (dashed lines: OTC; shaded areas: opaque zones; clear areas: translucent zones). The distance from the OTC mark to the outer edge (x), and from the start of the penultimate opaque band to the start of the last opaque band (y) are indicated on Panel A
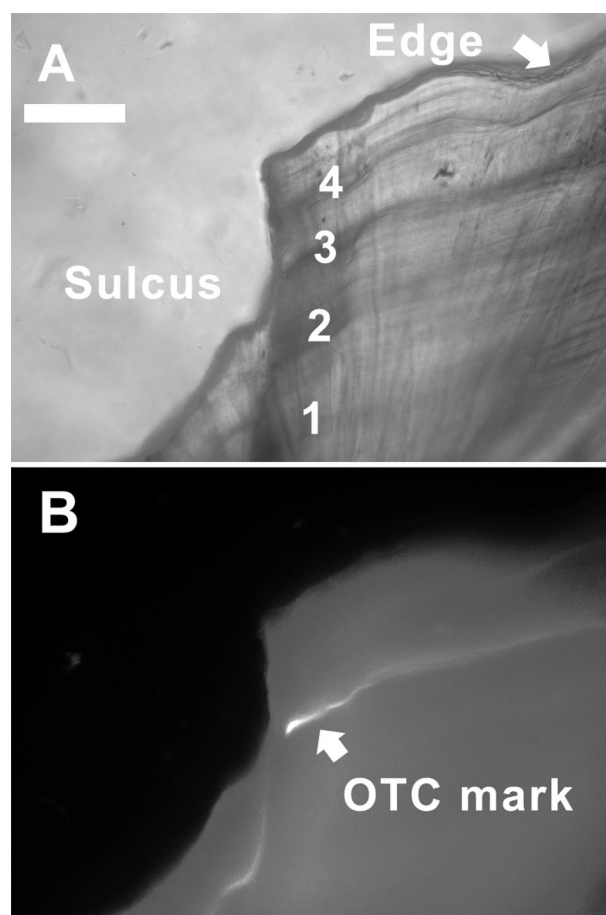

Fig. 4. *Epinephelus fuscoguttatus*. Details of OTC-marked otolith showing: (A) 4 annual bands and (B) OTC mark on same area under ultraviolet light. Scale bar = 0.2 mm
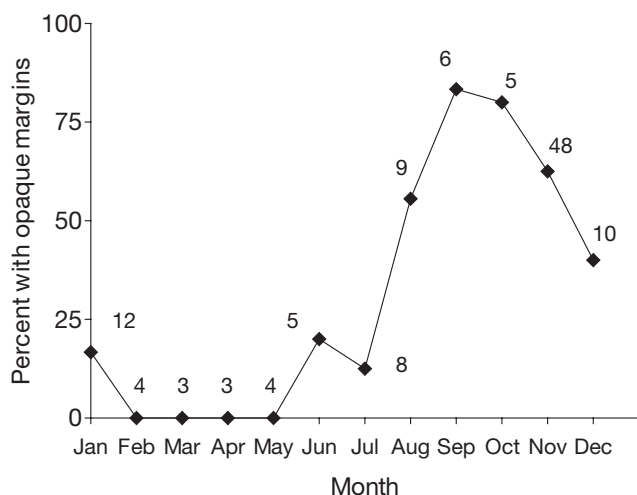
Fig. 5. *Epinephelus fuscoguttatus.* Edge-type analysis for sectioned otoliths from the Great Barrier Reef, showing percentage of otoliths with opaque margins. Numbers above data points indicate sample sizes
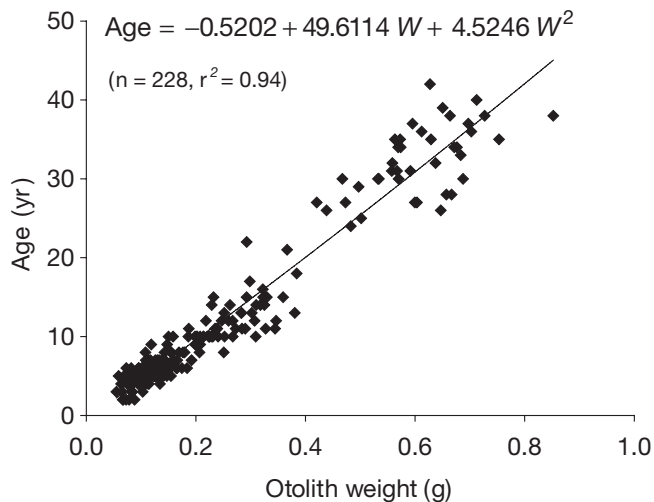

Fig. 6. *Epinephelus fuscoguttatus.* Relationship between otolith weight (*W*) and presumed age

Size and age structures

The sampled *Epinephelus fuscoguttatus* ranged from 320 to 970 mm FL, 550 g to 17.75 kg total weight and 2 to 42+ yr of age. The mean (±SE) size, weight and age were 580 ± 9.6 mm FL, 5.76 ± 0.3 kg and 11.8 ± 0.7 yr, respectively. Size distributions revealed that males had a larger mean size than females and the largest individuals were male (Fig. 7A). Conversely, age–frequency distributions indicated that the oldest individual sampled was a female (Fig. 7B). Recruitment of *E. fuscoguttatus* to commercial line fishing

gear begins at 2 yr old, and is complete by the modal age of 5 to 6 yr.

For 232 individuals from which gonads were examined histologically, 203 were females (87.5%) and 29 were males (12.5%). Females ranged from 320 to 855 mm FL, 550 g to 11.40 kg total weight and 2 to 42 yr (mean ± SE: 542 ± 8.3 mm FL, 3.46 ± 0.11 kg, 8.8 ± 0.5 yr, respectively). Males ranged from 683 to 925 mm FL, 5.95 to 15.40 kg total weight and 11 to 40 yr (mean ± SE: 820 ± 9.7 mm FL, 10.60 ± 0.47 kg, 29.7 ± 1.5 yr, respectively). Reproductive organs were not available for the largest fish (970 mm FL). The bimodal male and
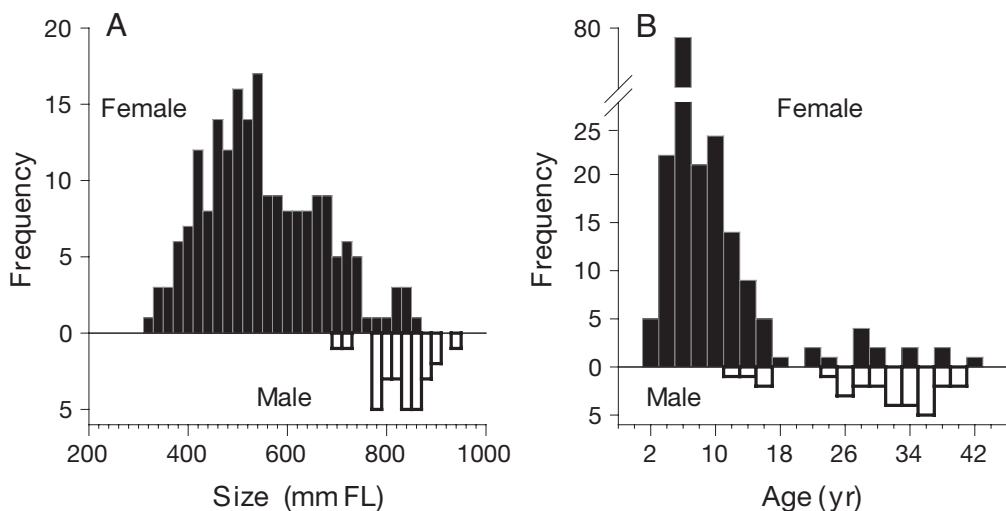

Fig. 7. *Epinephelus fuscoguttatus.* (A) Size–frequency and (B) age–frequency distributions for females (n = 203) and males (n =29). Size groups are 20 mm fork length; age groups are 2 yr

female size and age distributions (mode of females is less than mode of males) are shown in Fig. 7. Females persisted in large size and age groups, suggesting that not all females change sex. Females were on average significantly smaller and younger than males (t-test$_{Size}$: $t_{0.05(1),\ 78.5}$ = –21.72, p < 0.0001; t-test$_{Age}$: $t_{0.05(1),\ 221}$ = –14.95, p < 0.0001). The slopes of the relationship between length and age for females and males were not significantly different ($F_{1,66}$ = 2.203, p = 0.143), satisfying the assumption of homogeneity of slopes. Also, the ANCOVA indicated that males were significantly larger than females for the age range examined (11 to 40 yr, $F_{1,67}$ = 15.281, p < 0.001).

Longevity, growth and mortality

Epinephelus fuscoguttatus is a relatively long-lived reef fish; the oldest fish examined was 42 yr old (female, 855 mm FL, 9.80 kg, Fig. 2C), and the 10% longevity estimate (±SE) was 36 ± 0.5 yr. *E. fuscoguttatus* exhibited an asymptotic pattern of growth. Fitting the VBGF to observed length at age data (Fig. 8A) for both sexes combined gave a mean asymptotic fork length, L_∞, of 806.9 mm and a coefficient of growth, K, of 0.16 (n = 239, r² = 0.84). Most somatic growth occurred in the first 10 to 15 yr: 80% of L_∞ is achieved by about 10 yr on average. The predicted total mortality rate was 0.11 yr^{-1}. The length–weight relationship was: $W = 1.16 \times 10^{-5}$ FL$^{3.075}$ (n = 127, r² = 0.98).

Reproductive biology

The sample comprised 6.9% immature females, 11.2% undetermined inactive females (of uncertain maturity status), 41.4% mature inactive females, 28.0% mature active females (includes ripening, ripe, near spawning and spent) and 12.5% mature males (definitions in Table 2). The plotting of ovary weight data (as a proxy for female fecundity) onto the growth curve indicated large old females (>600 mm FL and >10 yr) were important breeders over a 30+ yr reproductive lifespan (Fig. 8B). Ovary weight increased by 2 to 3 orders of magnitude as size increased from approximately 400 to 700+ mm FL (from ~1 g up to 940 g, Fig. 9A). This increase of ovary weight was largely achieved by about 10 yr of age, and then maintained for the remainder of the lifespan (Fig. 9B).

Female maturity and male recruitment

The size and age at 50% sexual maturity for females were estimated to be 408 mm FL and 3.7 yr, respec-
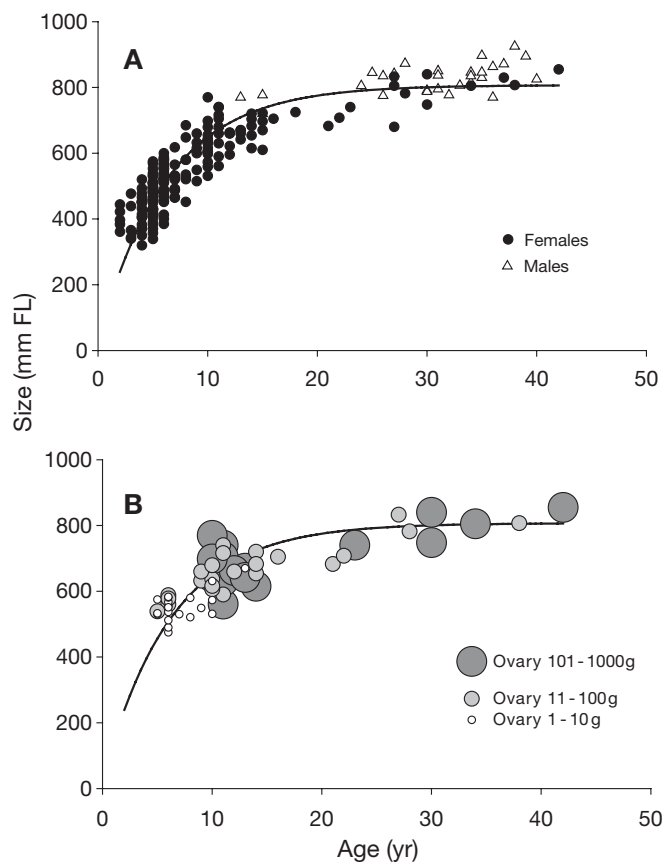

Fig. 8. *Epinephelus fuscoguttatus*. (A) Growth curve. Von Bertalanffy growth function (VBGF) fitted to size-at-age data. The *y*-intercept of the VBGF is constrained to the approximate size at settlement for *Epinephelus* spp. (25 mm FL, Leis 1987). (B) Ovary weights (as a proxy for fecundity) of mature active females mapped onto the growth curve

tively, using Method 1 (Fig. 10A,B). In contrast, Method 2 (*effective maturity*) gave higher estimates of 566 mm FL and 9.2 yr, respectively (Fig. 10C,D). The plots of ovary weight of *inactive* females with size and age showed a disproportionate increase at ca. 550 mm FL and 9 to 10 yr that supported the effective maturity estimates (Fig. 11). Analysis of ELF research samples found that during spawning months 72% of the mature inactive females were taken from the same reef and day as mature active females, 57% of which were taken from the same reef and day as females in near spawning condition (ovaries contained hydrating or hydrated oocytes). Mature inactive females were collected throughout the sampling range during the spawning months. Mature inactive females (mean ± SE: 498 ± 54.2 mm FL and 6.2 ± 1.8 yr) were on average smaller and younger than mature active females (645 ± 95.6 mm FL and 13.6 ± 9.2 yr) during the spawning period (t-test$_{Size}$: $t_{0.05(2),\ 83.9}$ = –9.825, p < 0.0001; t-test$_{Age}$: $t_{0.05(2),\ 57.3}$ = –7.32, p < 0.0001, Fig. 12).
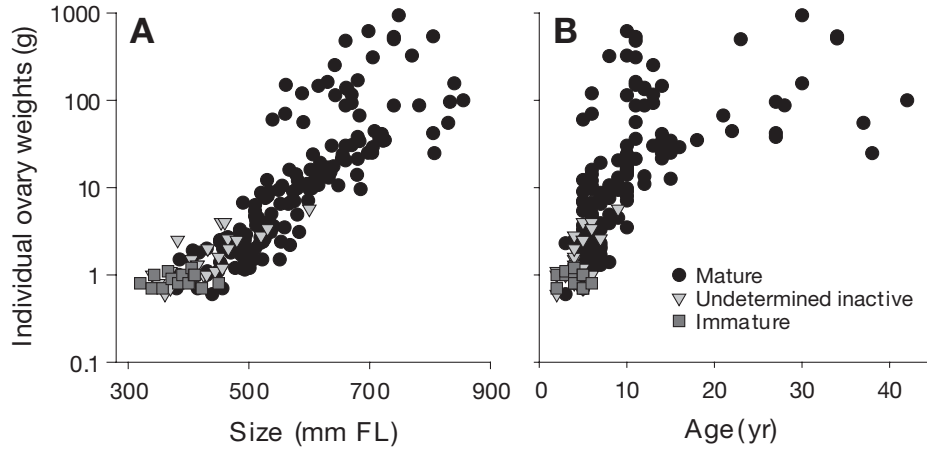
Fig. 9. *Epinephelus fuscoguttatus*. Ovary weights for females from the Great Barrier Reef using a $\log_{10}$ scale by (A) size and (B) age. 'Mature' indicates mature inactive and mature active females (for definitions, see Table 2)
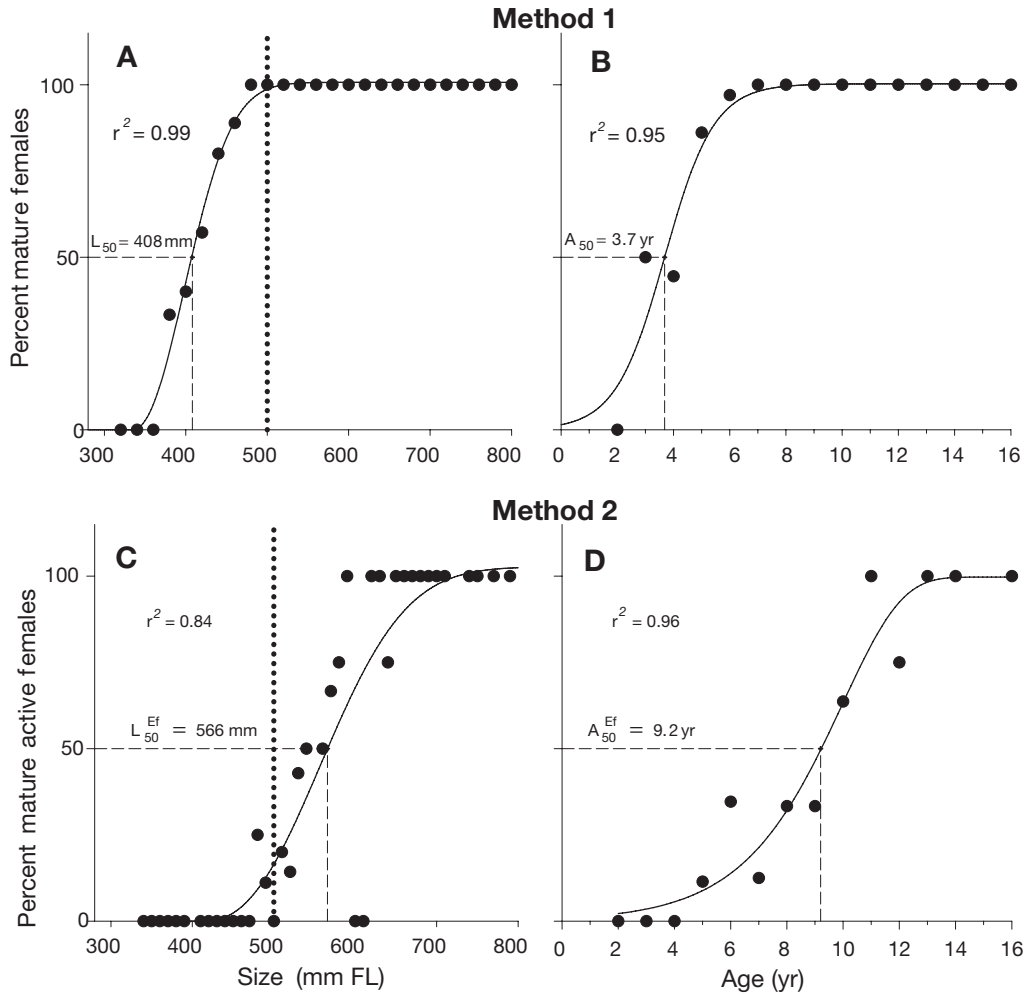

Fig. 10. *Epinephelus fuscoguttatus*. Two estimates of female maturity based on (Method 1) percentage of mature females by (A) size and (B) age and (Method 2) percentage of mature active females during the spawning months (November, December, January) by (C) size and (D) age. Dashed lines indicate 50% maturity estimates by size (Method 1: L_{50}, Method 2: L_{50}^{Ef}) and age (Method 1: A_{50}, Method 2: A_{50}^{Ef}), where ^{Ef} refers to 'effective' in effective maturity estimates of Method 2. Sample sizes: n = 173 for (A) and (B); n = 141 for (C) and (D). Dotted line shows minimum size limit for this species on the east coast of Queensland, Australia
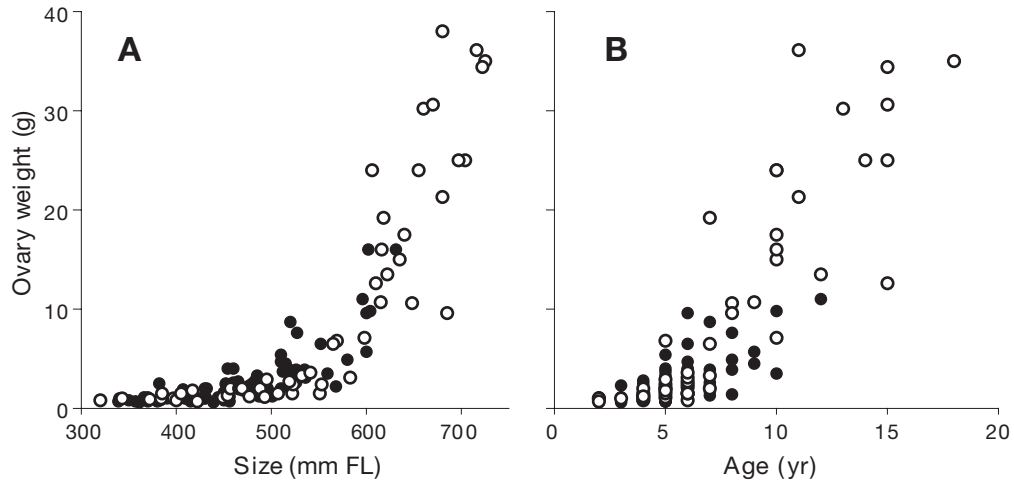
Fig. 11. *Epinephelus fuscoguttatus*. Ovary weight of inactive females by (A) size and (B) age (●: samples taken during the spawning period; ○: samples taken outside of the spawning period)
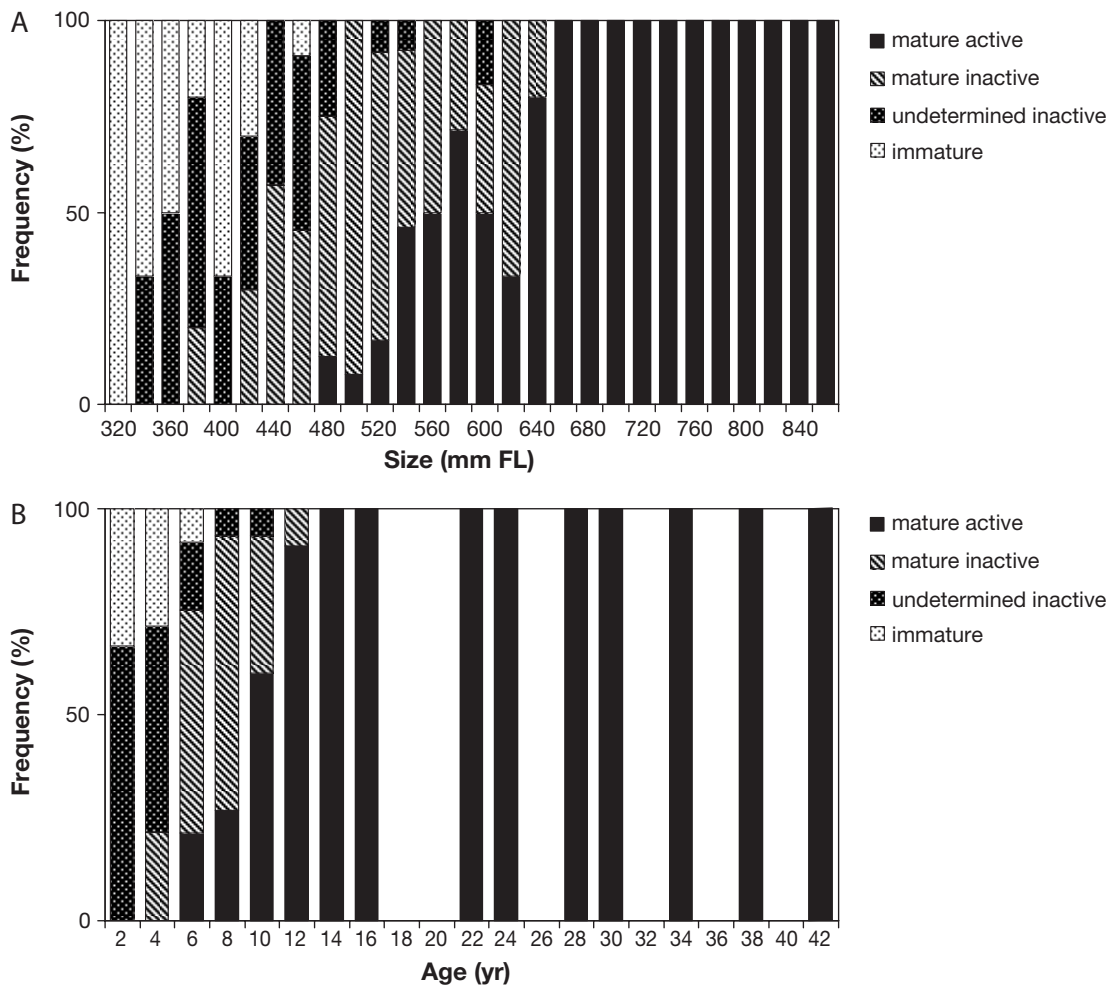

Fig. 12. *Epinephelus fuscoguttatus*. Proportion of each reproductive category for ovaries collected during the spawning period (November, December, January) by (A) 20 mm size groups and (B) 2 yr age groups. Reproductive categories defined in Table 2

Males did not occur in the samples until about 683 mm FL and 11 yr of age, above the size and age of 100% female maturity, providing no evidence of primary males (Fig. 7). Males made up 50% of most cohorts over 760 mm FL and 24 yr of age. From the overlap in size and age frequencies of mature females and males, sex change can occur from 683 to 855 mm FL and 11 to 40 yr. The size and age at sex change were estimated to be 791 mm FL and 25.5 yr (median values).

DISCUSSION

Epinephelus fuscoguttatus from north-eastern Australia are relatively long-lived, as the lifespan can exceed 40 yr and is at the upper end of published records for this genus. Although longevity can allow for greater cumulative reproductive success over time and may act as a buffer against occasional recruitment failure, it is also associated with greater vulnerability to fishing and lengthy recovery times after episodes of population depletion (Jennings et al. 1999). Unusual reproductive ecology of this large serranid included an extensive (>30 yr) reproductive lifespan, the likelihood that some females do not undergo sex change, late effective maturity, and the presence of inactive females with active females during the spawning period.

Growth is asymptotic, with most of the growth occurring within the first 30% of the lifespan. Thus, age and size are decoupled over much of the reproductive size range. This means that a combination of size- and age-specific biological data is needed to understand the life history of this species and also to determine which components of the population are vulnerable to capture under various harvest regimes.

The ageing protocol using thin-sectioned sagittal otoliths from *Epinephelus fuscoguttatus* gave reliable results that satisfied the 3 criteria needed to validate the relationship between periodicity of increments in otoliths and fish age (Fowler 1990). Namely, *E. fuscoguttatus* otoliths showed a positive relationship between number of increments in otoliths (presumed age) and otolith weight, indicating that otoliths grow throughout the life of individual fish, that the increment pattern in sectioned otoliths can be reliably interpreted, and that this pattern corresponds to an annual timescale. Although the analysis showed a strong unimodal pattern, larger monthly sample sizes and more representatives across a range of age groups would allow examination of individual variability within age groups. The annual timing of opaque band formation in austral spring agreed with findings for many other taxa (e.g. from the GBR see Fowler 1990, Choat & Axe 1996, Cappo et al. 2000).

The dataset is adequate to support the demographic and reproductive conclusions, because the adult size ranges were well sampled and immature individuals were included. Individuals below 350 mm FL or 5 yr of age were under-represented, however. This may be due to selectivity of the sampling gear or the absence of habitat for small fish at the sampling localities, or a combination of both. Visual surveys for this species on many of the same reefs also failed to find small individuals (<300 mm FL, Pears 2005b), suggesting that the habitats of juvenile and sub-adult *Epinephelus fuscoguttatus* may differ from those sampled in this study. Habitat of young *E. fuscoguttatus* may be seagrass (Sommer et al. 1996), but other inshore habitats are also conceivable. It is also possible that sampling did not include the largest, and hence oldest, individuals in the population; however, we know of no confirmed records of *E. fuscoguttatus* on the GBR larger than those observed in the present study.

The observed distribution of the sexes by age and size strongly suggests that the sexual pattern of *Epinephelus fuscoguttatus* is monandric protogynous hermaphroditism, and individuals first function sexually as females, and, later, at least some of these mature females change to males. Sex change may potentially occur over a wide range of sizes and ages, although the oldest members of the population included females, indicating that not all individuals changed sex. Sex allocation theory indicates that individuals in hermaphroditic fishes should change sex whenever net future reproductive success would be higher for the opposite sex than for the existing sex (Charnov 1982). However, it may not always be advantageous for the largest female to change sex in protogynous species, due to the exponential relationship between fecundity and body size and the individual variability in this relationship (Munoz & Warner 2003). Confirming the sexual pattern and schedule of sex change of *E. fuscoguttatus* are research priorities.

There was a discrepancy between female maturity estimates obtained using 2 different methods. Estimates of size and age at 50% maturity using the proportion of females that were sexually active during the peak spawning months (*effective maturity*) were significantly higher than those determined from the proportion of all ovaries with signs of current or past spawning activity. For the latter technique, difficulty in determining female spawning history from some inactive ovaries arises, because the features used to indicate prior spawning (atretic oocytes, post-ovulatory follicles and muscle bundles) become harder to detect with increasing time since spawning and may eventually disappear (Shapiro et al. 1993, Sadovy & Colin 1995, Samoilys & Roelofs 2000, Adams 2002). A disproportionate increase in ovary weight at the size and age

corresponding to the former maturity estimates, the lack of ripe females among smaller-sized fish, and the possibility that undetermined inactive females were immature all support the effective maturity estimates.

The considerable proportion of mature inactive females during the spawning season in each year suggests several different scenarios. These include that not all females spawn in all years, or spawn only infrequently during the spawning period, or fish may not all spawn at the same times or locations. The presence of non-spawning mature females during the spawning season for 2 species of *Epinephelus* endemic to southern Africa was attributed to limited spawning near the edge of geographic ranges and/or to not all mature individuals spawning each year (Fennessy & Sadovy 2002). Non-spawning in female gag *Mycteroperca microlepis* has been attributed to a shortage of males (Coleman et al. 1996). Insufficient energy reserves, stress, or unsuitable environmental conditions may also cause fish to miss spawning in some years. For example, older females of an Australian sparid, *Acanthopargus australis*, had a low tendency to participate in seaward spawning migrations, possibly due to insufficient energy reserves to migrate and spawn (Pollock 1984).

This study found a strong pattern of female sexual activity with size and age. Despite histological signs indicating maturity, smaller and younger females were less sexually active than larger or older females. Non-spawning females should be regarded as effectively immature as they do not contribute to egg production in a given spawning event (Williams 2003). The apparent lack of reproductive activity and corresponding increase in the effective size and age of maturity may be a result of a trade-off between somatic growth and reproductive effort (e.g. Roff 1984). Support for this hypothesis is given by the size and age of effective maturity corresponding to the change from relatively fast to slower growth. The limited sexual activity of small young females suggests a life-history strategy for *Epinephelus fuscoguttatus* on the GBR in which energy is primarily invested in somatic growth for almost 10 yr; afterwards growth slows and energy is invested in reproduction. Research to understand spawning details for *E. fuscoguttatus*, including behaviour of inactive and active females during spawning episodes would be worthwhile.

The biological characteristics of *Epinephelus fuscoguttatus* (i.e. rarity, long lifespan, relatively slow growth, late effective maturity, protogynous sex change, spawning aggregation behaviour) and catchability indicate relatively low resilience to fishing pressure or other disturbances (Sadovy 1994b, Jennings et al. 1999, Pears 2005a). Protogynous species, particularly if sex change is fixed (i.e. occurs at a specific size

or age threshold), may be at risk of population collapse even at relatively low fishing mortality (Bannerot et al. 1987, Huntsman & Schaaf 1994, Alonzo & Mangel 2004). Large individuals are a rare, but important, part of the reproductive population, containing all of the males that are vital to maintain the sex ratio and prevent sperm limitation (Bannerot et al. 1987), as well as important female breeders that are highly fecund and contribute substantially to the reproductive output of the population for many years (Sadovy 1996).

Fishing typically selects for larger fish on reefs, and such size-selective fishing can overfish large individuals with profound effects upon reproductive output (Jennings et al. 1999, Alonzo & Mangel 2004). Recent studies indicate that reproductive success increases with maternal age and experience for some fish species (e.g. Hislop 1988, Trippel et al. 1997, Marteinsdottir & Steinarsson 1998, Berkeley et al. 2004a). Truncation of size and age structures by fisheries can, therefore, unduly reduce reproductive capacity (Berkeley et al. 2004b, Birkeland & Dayton 2005). In addition, large *Epinephelus fuscoguttatus* may be particularly vulnerable to fishing as anecdotal reports indicate post-release mortality is higher for large groupers. Marine protected areas (or no-take zones) are considered a valuable management option for protecting intact size and age structures and breeding populations of reef fish (Russ & Alcala 1996, Berkeley et al. 2004b). Expansion of the no-take zones on the GBR in 2004 (see www.gbrmpa.gov.au) is likely to provide some protection for *E. fuscoguttatus.*

Other recent changes to management regulations for the reef line fishery on Australia's GBR include slot size limits for *Epinephelus fuscoguttatus* (minimum 500 mm FL, maximum 1000 mm FL). Setting practical legal size limits in a multi-species fishery such as the GBR reef line fishery is complicated, particularly for taxa such as epinepheline serranids for several reasons (Hancock 1990), including that at least 40 species are captured, species identification is difficult, maximum body sizes and life-history traits vary widely and biological knowledge is limited for most species. The effectiveness of size limits will depend on whether they protect a reasonable proportion of the intended component of the population, the level of compliance with the regulation, the survival of released illegal-sized fish, and keeping fishing mortality to a low level.

The fished component of the GBR population of *Epinephelus fuscoguttatus* still includes most of the active spawning stock and all of the males. Although 500 mm FL is above the size of first reproduction in *E. fuscoguttatus*, females below approximately 566 mm FL contribute very little to the total reproductive output of the population. Consequently, the current minimum size limit on the GBR is not protecting the population's

breeding potential. A maximum size limit on the GBR is warranted, given the importance of large old individuals for reproduction; however, the current maximum size limit is too high, as few, if any, fish are afforded protection. Furthermore, large *E. fuscoguttatus* (>6 kg) can be difficult to sell due to concerns about potential ciguatera poisoning (R.J. Pears pers. obs.). To protect large female breeders, maintain the sex ratio, and prevent sperm limitation, the maximum size limit for this species should be revised based on the new biological data.

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