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THE EXTENDED LONGEVITY OF A SMALL CORAL REEF SERRANID; A LESSON FROM *CEPHALOPHOLIS CYANOSTIGMA* (BLUE SPOT ROCK COD) OF THE CENTRAL GREAT BARRIER REEF, AUSTRALIA

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ABSTRACT

The blue spot rock cod, *Cephalopholis cyanostigma,* is a small common coral reef serranid that forms a significant proportion of the discarded by-catch in the Great Barrier line fishery. Samples were obtained by spear and line fishing at Orpheus Island (range 114- 294 mm FL, mean = 226 mm, n = 137) and from Pelorus Island (range 120-285 mm FL, mean = 214 mm, n = 125). Sagittal otoliths were used to obtain age-based parameter estimates for the populations at each island. Analysis of marginal increments on monthly samples suggested that a single opaque band was deposited annually during November - December. Recaptures of three fishes (9,18, and 24 years old) in July and November 1997, five years after injection of oxytetracycline, further corroborated our conclusion that band formation was annual. The maximum age in our samples of 31 years suggested that the blue spotted rock cod was one of the longest lived serranids documented to date. The von Bertalanffy growth function provided the best description of the pattern of growth for populations at both islands with high coefficients of determination (R^2 = 0.86 and 0.82 for Orpheus and Pelorus islands, respectively). Female population of both sites grew relatively slow, not reaching asymptotic size until 7-10 yrs. Statistical comparisons on male and female growth patterns were not significant, however. There were significant differences in growth parameters between islands with C. *cyanostigma* on average growing larger at Orpheus Island ($L\infty$= 258 mm and *K*= 0.22) compared with Pelorus Island ($L\infty$=244 mm and K = 0.25). These age-based population parameter estimates indicated that C. *cyanostigma* was considerably longer lived than expected for a small coral reef serranid and further demonstrated the utility of age-based methods in studies of the demography of tropical reef fish. The implication for conservation and fisheries management of small tropical serranids is that species with similar population parameters are likely to sustain much lower levels of fishing mortality than previously thought.

Keywords: *Cephalopholis cyanostigma* (Serranidae), Growth, Longevity, Otolith, Validation

INTRODUCTION

Serranid fishes, collectively known as groupers and rock cods, are among the most important members of the predatory fish fauna on tropical and sub-tropical reefs (Shpiegel and Fishelson, 1991). Of the existing five subfamilies of Serranidae, the subfamily Epinephelinae is one of the greatest importance in fisheries (Heemstra and Randall, 1993). Members of this subfamily are distributed widely in all oceans with the greatest abundance and diversity occurring in the Indo-Pacific region (Heemstra and Randall, 1993; Munro, 1996). Ranging in size from a few centimeters to more than two meters long, they occupy a wide range of habitats, but are mostly often associated with rocky and coral reef habitats (Shpiegel and Fishelson, 1991; Heemstra and Randall, 1993). As one of the top predators in reef habitats, they are thought to play an important role in structuring fish communities (Thompson and Munro, 1978; Randall and Ben-Tuvia, 1983).

The genus *Cephalopholis,* which includes 22 species, is also distributed widely throughout all oceans (Heemstra and Randall, 1993). They are, however, most abundant in the Pacific Ocean and

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Red Sea (Randall and Ben-Tuvia, 1983; Heemstra and Randall, 1993). Being smaller in size on average (14-70 cm in total length) relative to other serranid genera, *Cephalopholis* tend to have a cryptic habit on coral reefs (Shpiegel and Fishelson, 1989). Despite their small size, this group of serranids is an important component of the reef fish catch for many coastal fisheries (Munro, 1996). In the past, *Cephalopholis* spp were considered to be less valuable and separated from the more highly regarded commercial species, such as *Plectropomus* and *Epinephelus* (Johannes and Riepen, 1995). The increase in demand for life reef fish, however, has seen members of this smaller sized genera become more widely marketed and sought after in tropical reef fisheries. This has become more evident following reduction of the larger, more valuable commercial species of groupers, such as *Plectropomus, Chromileptes* and *Epinephelus,* in the Indo-pacific regions (Munro, 1996; Froese and Pauly, 1998; Mosse and Hutubessy, 2004).

In the tropical Australia, *Cephalopholis cyanostigma,* also known as the blue spot rock cod, is commonly caught as by-catch in all regions of the Great Barrier Reef (GBR) by commercial and recreational fishermen in the Queensland Reef Line Fishery, which operates throughout the GBR (Mapstone *et al.,* 1998). The main target species of the fishery are *Plectropomus leopardus* and *Lethrinus miniatus* (Mapstone *et al.,* 1998). Despite being a by-catch species, the proportion of C. *cyanostigma* in the catch is reasonably high (~12%) although most is discarded (Davies, 1995, 2000). This relatively high proportion of *Cephalopholis* spp has been also reported in catches from other regions where fishing is a very important part of subsistence economies and such species are retained (Johannes and Riepen, 1995. It is reasonable to expect, therefore, that C. *cyanostigma,* as well as other species currently treated as by catch may become an important component of reef fish catches on the GBR and elsewhere around the Indo-Pacific region in the future.

Information about population biology of small serranids, and species of *Cephalopholis* in particular, is sparse. Off the 22 species of *Cephalopholis* around the world, only 9 species have been studied on their biology. These studies examine age at sexual maturity (Shapiro, 1987), spawning behaviour (Donaldson, 1989), habitat partitioning, food and feeding habits (Shpiegel and Fishelson, 1989), ecology and territoriality (Shpiegel and Fishelson, 1991;Mackie, 1993), and population structure and sex change (Siau, 1994). However, none of these published accounts have provided information on critical population parameters such as longevity, rates of growth and mortality.

The objective of this study was to determine reliable method of ageing individual fish. This is the first requirement in the process of obtaining reliable estimates of population parameters. Age was determined by the examination of sagittal otoliths for annual bands. These have been shown to exist in a wide range of reef fish in GBR (eg. Ferreira and Russ, 1992; Fowler, 1990;Lou, 1992; Choat *et al.,* 1996; Newman *et al.,* 1996). We validated the periodicity of bands using direct (oxytetracycline marking) and indirect (marginal increment) techniques. Both techniques indicated that the opaque bands were deposited on the annual basis with timing of band deposition corresponding to November-December. Based on counts of sectioned otoliths we constructed age structures and estimated population parameters for C. *cyanostigma* from fringing reefs on two coastal continental islands in the central GBR. The results indicate that *C. cyanostigma* is unexpectedly long lived (> 30 years) for such a relatively small fish (mean FL=240 mm) and raises questions about the generality of conventional ecological theory on the relationship between body size and longevity.

METHODS

Study sites

The study was conducted on the fringing reefs of two continental islands, Orpheus and Pelorus Islands that form part of the Palm Island group, central GBR, Australia (18°30'S and longitude 146°E). The locations provided three main advantages: (a) a previously initiated study provided the basis for oxytetracycline validation; (b) C *cyanostigma* is abundant on the fringing reefs surrounding the islands; (c) the close proximity of the islands to the main-land meant that regular monthly sampling was both logistically feasible and affordable.

Sample collection

Samples were collected in monthly bases between April 1997-November 1998. Research surveys covered depths ranging from 3 to 15m using spear and hook and line on a monthly basis from the fringing reefs of both islands. Upon retrieval from the water, the catch was placed on ice and transported to the field station laboratory for processing. In the laboratory, fish were measured (total length = TL, and standard length = SL) to the nearest millimetre and weighed (total weight = TW and gutted weight = GW) to the nearest gram. Both left and right sagittal otoliths were extracted, cleaned with fresh water, dried and stored for further processing. The total number of fish sampled for the study was 262.

Otolith processing and age determination

Length and width of the left and right sagitta were measured to the nearest 0.01 mm using an image analysis system and then weighed to the nearest 0.001 g. A paired t-test was performed to examine whether there was a consistent difference in weight between the left and right sagitta. There was no significant difference *(t* = 0.11, *df*= 17, *P* = 0.9141 for Orpheus and *t* = 1.8, *df*= 19, *P* = 0.0862 for Pelorus Island), so the right otolith was used consistently for convenience.

To determine the age from otoliths, we first examined a sub-sample of 150 otoliths. The protocol involved: first, placing the whole otolith in a container with a black background filled with immersion oil. Second, counts were done by two readers using a dissecting microscope and reflected light at 25x magnification without knowledge of the results of the other reader or details of fish size or location of capture; Thirdly, the same sub-sample of otoliths were embedded in epoxy resin, sectioned using low speed circular diamond, attached to glass slides and ground with wet carborundum paper of 800 and 1200 grit and then polished using alumina powder of 12.5 µm grit on a cloth pad. At least two independent readings of the whole and section otoliths were made by each reader and the results were accepted based on the agreement between at least two of the readings. Counts obtained from sectioned otoliths were then compared with the results from the whole otolith counts.

For the majority of otoliths, which have more than 6 opaque bands, counts were on the axis along the ventral sulcus (vs.), from the nucleus to the margin. For otoliths with less than 6 bands, counts were made along the distal (di) axis towards the ventral end of otoliths. This was necessary, as the early bands in these otoliths were broad and diffuse and difficult to count reliably along the ventral sulcus.

Timing of annulus formation

The timing of formation of annuli was determined based on marginal incremental index analyses (Barger, 1985). Distances were measured from the last opaque ring to the otolith edge along the ventral side of the sulcus using an image analysis system. The average increment widths were then plotted by month and the pattern examined. The monthly changes in the mean and standard error of marginal increments were estimated and plotted for each age class between 7 and 15 years old and for age classes 3 to 6 as a group (due to insufficient sample sizes in the lower age classes).

Validation experiment

Our study took advantage of an earlier study of the ecology and reproductive behaviour of C *cyanostigma* done at Orpheus Island (Mackie, 1993). As part of the field component of the study, an attempt was made in April 1993 to validate periodicity of otolith bands by injecting 75 individuals (50 mg/g of body weight into the coelomic cavity) of *C. cyanostigma* with oxytetracycline (OTC) and releasing them. Two of these previously injected fish were recaptured from Orpheus Island in June 1997 and one in November 1997. These three recaptured individuals provided the basis to directly validate the periodicity of the banding over a five-year period at liberty in the field based on the number of complete bands on the marginal side of the location of the OTC mark.

Growth

We based our final estimation of growth parameters on the counts of sectioned otoliths. We fitted Schnute general growth model (Schnute, 1981) to determine the most appropriate growth model to estimate growth parameters. The von Bertalanffy growth function provided the best fit to the length-at-age-data. This model has the form

$$L_{t=} L_\infty(1\text{-}e\text{-}k(t\text{-}to))$$

Which,

L_t = length at age t

L_∞ = mean asymptotic length

K = growth coefficient; and

t_0 = age at which fish length would be zero if it always grew according to the model.

The model was fitted to data from the two locations (Orpheus and Pelorus Islands) separately and the resulting model fits compared. The likelihood ratio test (x^2) (Kimura, 1980) was used to examine whether the pattern of growth differed significantly between the sample populations from the two islands. These differences were then presented by plotting the 95% confidence regions around the asymptotic length (L_∞) and the growth coefficient (K). Other statistical analysis including Chi-square contingency tables were used to compare the frequency of age and size classes between the two Islands.

RESULTS

Otolith Structure and Growth

Of the three-otolith pairs of the C. *cyanostigma,* the sagittae are the largest and oval in shape, as the rostrum and antirostrum almost join anteriorly. Annuli in whole otoliths have a white milky appearance. The bands appear dark, however, if viewed under transmitted light. The best area for counting the bands on sagittal otoliths was along the ventral side of the sulcus acusticus, from the core to the proximal surface. The percentage agreement in counts between readers was 94% and 96% for Pelorus and Orpheus samples, respectively, demonstrating the counts were highly repeatable.

For both whole and sectioned otoliths the first few bands (3-5) appear thicker and more diffuse relative to latter bands. This often made interpretation of latter bands difficult when counts were done on whole otoliths. This is not the case, however, for sectioned of otoliths, especially along the ventral side of the sulcus towards the distal surface (Fig. 1). The sequence of alternating opaque and translucent bands is quite distinct making interpretation easier and more consistent. Figure 2 provides a comparison of age data obtained from counting whole and sectioned otoliths. It is evident that for fish of less than 13 years, reading whole otoliths provide relatively similar results to counts of sectioned otoliths. As the age of fish increases, however, whole otoliths became more difficult to read and less precise. At this point, counts of sectioned otolith are more likely to provide accurate counts.

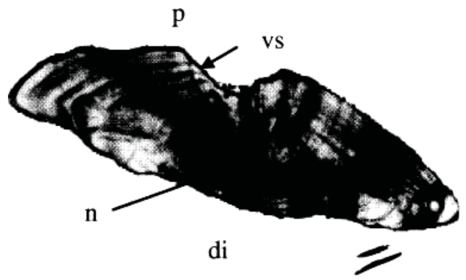


Figure 1. Photo of sectioned sagittal otolith of C. *cyanostigma* showing clear annual rings with nucleus (n), proximal (p), distal (di) surface, ventral sulcus (vs), ventral (v), and dorsal **(d)**

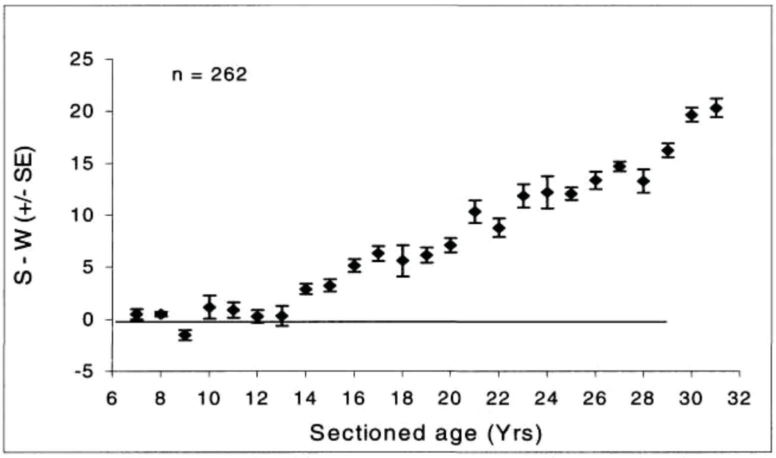


Figure 2. Plot of mean difference (±SE of the mean) between sectioned and whole (S-W) otolith ages against sectioned age

Validation and timing of ring formation

The two validation techniques provided consistent evidence that the observed bands in C. *cyanostigma* were deposited on an annual basis. The otoliths of the three individuals fish marked with OTC were recaptured after 5 years living in their natural habitats. These otoliths exhibited five consecutive rings outside the clearly defined fluorescent OTC towards the edge otolith edge (Fig. 3). This provided very strong evidence of the annual periodicity of the increments over a 5 years period in the wild for three individual fish of estimated age 9, 18, 24.

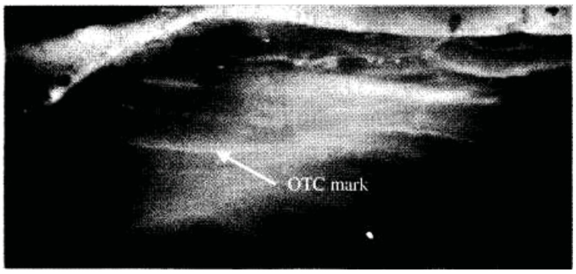


Figure 3. Photo of transverse sections of sagittal otolith showing mark of Oxytetracycline lines (OTC) injected into the fish and naturally lived for 5 years in the water.

Generally, the mean increment widths were high during autumn and throughout winter period (June - September) and decreased dramatically during summer, reaching a minimum during December - January. This pattern was consistent for all age classes except the eight year old age class. The mean increment averaged across all age classes was presented in Figure 4. The distance between the last opaque band observed in the otoliths of the recaptured OTC marked fish was also wider and there was no sign of new ring formation. These trends further supported our assertion that band formation occurred once a year during December-January, as they were recaptured in June and November, which would be well before and immediately before the expected time of ring formation, respectively.

Size and age structures

Fish sampled from Orpheus and Pelorus Islands, ranged in size between 114 to 294 mm FL and 120 to 285 mm FL, respectively. The overall size distribution between the two study sites was significantly different ($X^2 = 140.07$, df=7,$0.025 < P < 0.05$) (Fig. 5). Mean FL of the two populations was compared using t-test after testing the assumption of normality and homogeneity. The result showed that the mean size was significantly larger at Orpheus Island location (mean FL = 230.8±2.83 SE) than at Pelorus Island (mean FL = 218.95±2.42SE).

There was a large proportion offish of greater than 15 years of age in the age structures of samples from both locations (Orpheus and Pelorus Islands). The age ranged 2 to 31 years for Orpheus and 3 to 23 years for Pelorus (Fig. 6).

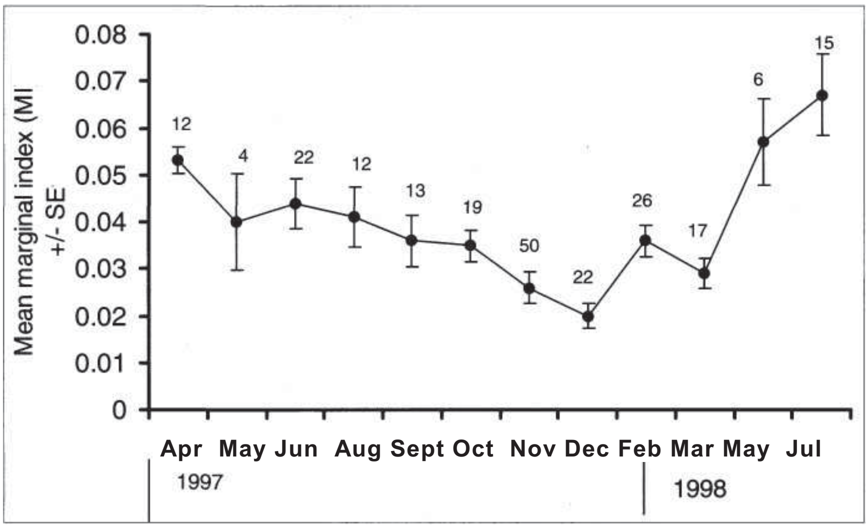


Figure 4. Monthly mean of marginal incremental index (MI) of the latest opaque ring to the otolith edge of *C. cyanostigma.* Numbers indicate sample size and vertical bars indicate ± SE

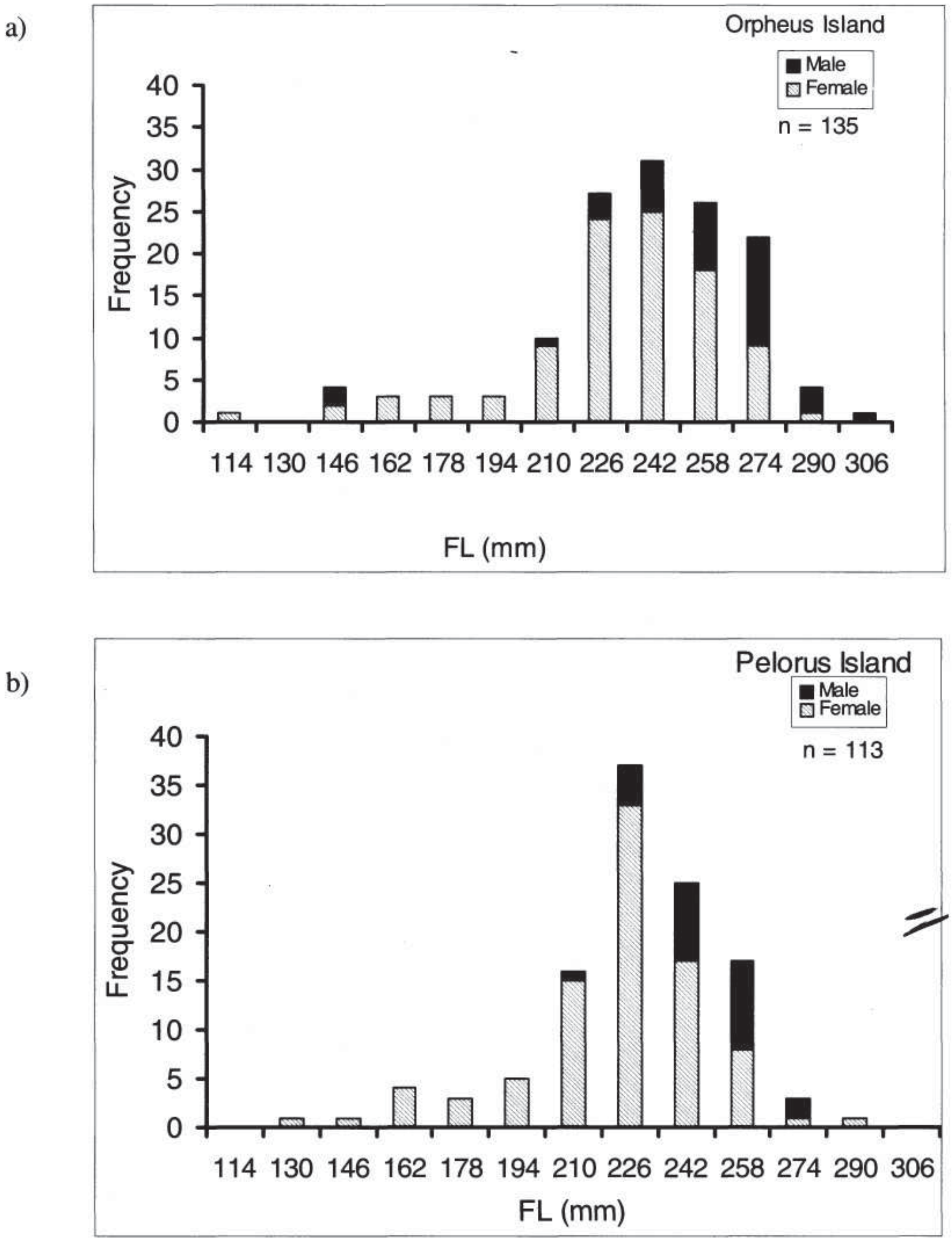
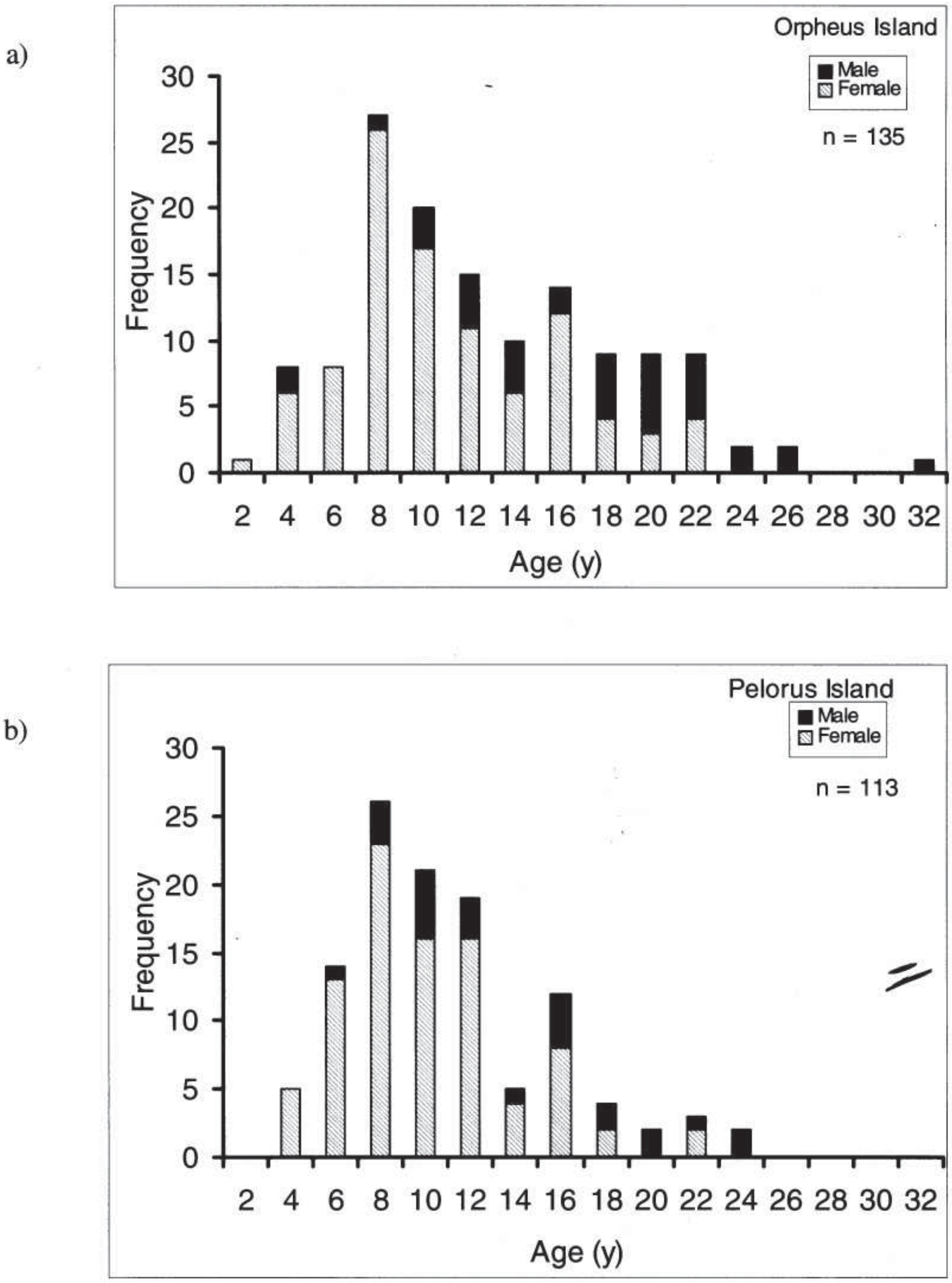


Figure 5. Length frequency distributions for *C. cyanostigma* from Orpheus (a) and Pelorus Islands (b) central Great Barrier Reef

The mean ages were 12 and 10 years, respectively and were significantly different (t- student = 2.99, df = 253; P = 0.0030). The overall age composition between the study sites also differed significantly (X^2 = 24.47, df = 7, P< 0.001).

Growth

Due to the apparent lack of difference in growth pattern between sexes for both locations, estimation and comparison of growth parameters were made using data for both sexes combined.



6. Age frequency distributions for *C. cyanostigma* from Orpheus (a) and Pelorus Islands (b) central Great Barrier Reef.

The general pattern of the von Bertalanffy growth model was similar among locations with steady growth towards the upper size limit up to about ages 5-7 after which growth slow considerably. Within these age ranges, C. *cyanostigma* achieved about 50-54% of its overall length (Figs. 7a and 7b). Analysis of the likelihood ratio (LR) indicated that there were significant differences in the asymptotic length (L∞) and the growth coefficient (K) between the two sites (Table 1) suggesting that a separate growth curves would best describe growth in both study sites. The 95% confidence regions (Kimura, 1980) around the von Bertalanffy growth parameters indicated that while the growth

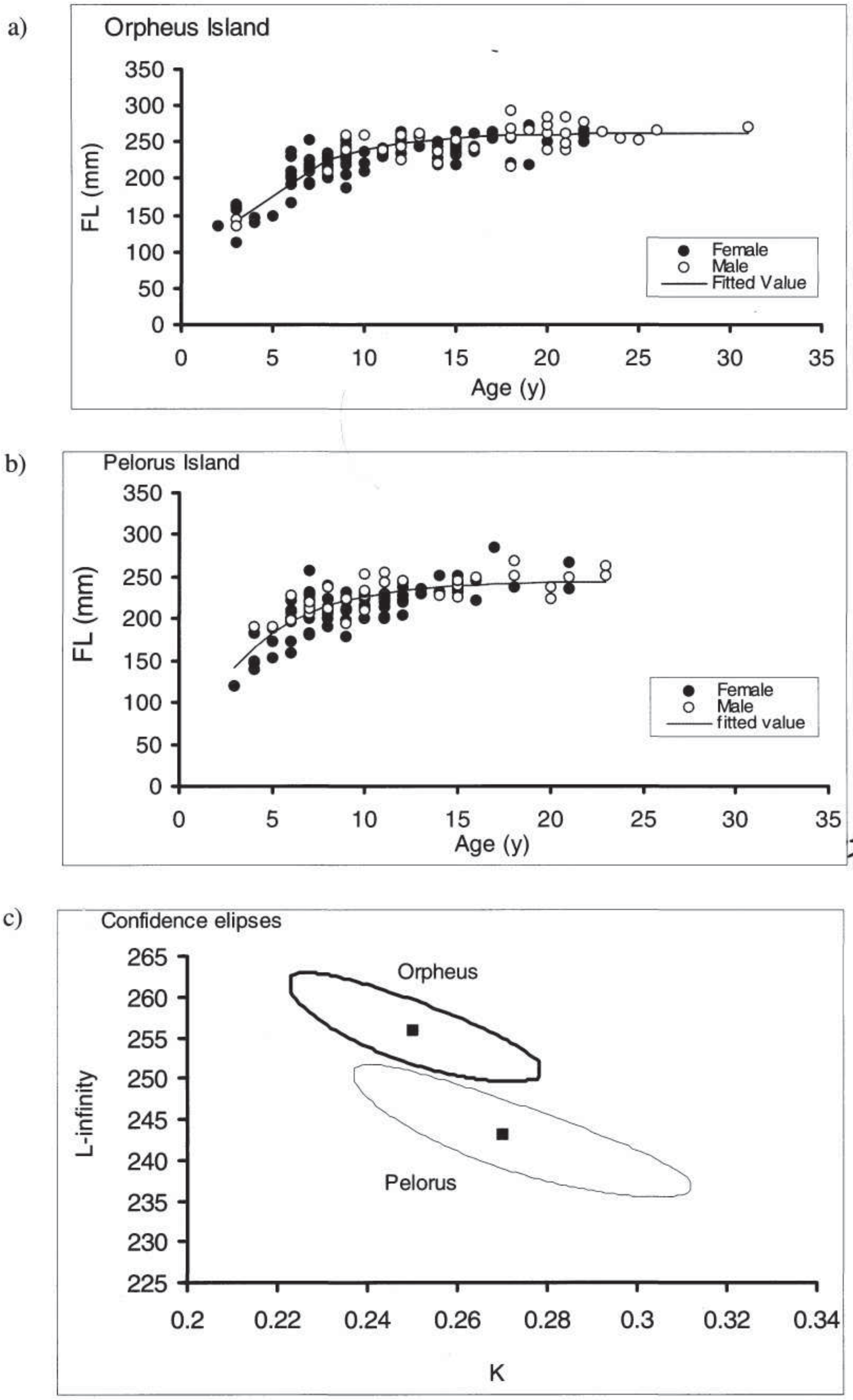


Figure 7. Von Bertalanffy growth curves (a,b) and the 95% confidence regions around the L∞ and K (c) parameters for female *C. cyanostigma* caught from Orpheus and Pelorus Island

Table 1. Comparison of the von Bertalanffy growth parameters for *C.cyanostigma* (both sexes combined) sampled from Orpheus and Pelorus Island, central Great Barrier Reef

	Sampling sites					
Parameters	Orpheus Island	Standard Error	Pelorus Island	Standard Error	*X2*	*P*-value
L	257.791	2.79	244.444	3.44	8.309	0004*
K	0.22	0.0134	0.25	0.0173	1.206	0.027*
To	-0.59	0.186	-0.41	0.187	0.135	0.713
R^2	0.86		0.82			
N	137		121			
FL range (mm)	114-294		120-285			
Mean FL	230.8	2.83	218.95	2.42		
Age range (y)	2-31		3-23			
Mean Age	12	0.499	10	0.401		

*.Significant **difference**

coefficients (K) may overlap, mean asymptotic size for the Orpheus Island population appears to be larger than for the Pelorus Island population (Fig. 7c). For both locations, females were distributed almost over the entire size and age range. The distribution of males was skewed towards the larger and older size classes with no males smaller than 114 and 120mm and younger than 2 and 3 years for Orpheus or Pelorus Island, respectively (Table 1 and Fig. 5).

DISCUSSION

Otolith analysis and interoperation

The comparison of counts of whole and sectioned otoliths demonstrated that whole counts were likely to significantly underestimate the age of *C. cyanostigma.* Under transmitted light, thin transverse sections of about 150 - 300 |µm exhibited distinct alternating opaque and translucent bands comparable to those documented for a number of large Serranid species (Ferreira and Russ, 1994. 1995; Crabtree and Bullock, 1998). The rings were clear and easily counted with a high level of precision within and among readers. The large discrepancy between the sectioned and whole counts is likely to result from the relatively small size of sagittae of *C. cyanostigma* and the number of bands. Many regular closely spaced bands follow the initial broad diffuse bands. While these regularly spaced bands were clearly discernible in sections they were too close to each other to be readily discriminated when viewing a whole otolith. Similar bias in counts of whole otoliths have been documented for other species of reef fish with small thin Otoliths *Plectropomus leopardus* (Ferreira and Russ, 1994, Acanthurids (Choat *et al.,* 1996), *Lutjanus quinquelinatus* (Newman *et al.,* 1996), *L. carponotatus* (Davies, 1995).

Our results also demonstrated that the sagittal otoliths of *C.cyanostigma* met the second criteria for use as a means to age fish, namely that bands were deposited consistently on an annual basis. This was strongly supported by i) the recovery from the wild of the three validated fish of ages 9. 18, and 24 five years after being injected with tetracycline and spending 5 years at large. Each fish had 5 consecutive rings between the OTC mark and the outer margin of their otoliths. ii) The pattern of growth of the otolith margin evident from analysis of marginal increments demonstrated a consistent pattern of the minimum monthly mean increment width in December—January. This pattern was consistent across a range of age classes and further corroborates the results from the OTC injected fish that the bands are deposited on an annual basis in the austral summer.

Choat *et al.* (1996) reported that annulus formation in *Scams rivulatus* also occurred in summer months, during which many reef fish undergoing spawning activity. *Epinephelus flavolimbatus* is another serranid species for which annual ring formation appears to coincide with time of peak spawning. Reports on other serranid species including those from the GBR of Australia showed that annual ring formation also occur out side of spawning period and during winter-spring (Newman *et al.,* 1996).

Our finding is consistent with the conclusion of Moe (1969) who concluded that spawning and its physiological condition of the red grouper, *Epinephelus morio* is the main cause of the annual formation. Concurrence of the reproductive cycle of *C.cyanostigma,* which reaches its spawning peak in December, (Mosse *et al.,* 2002) and annual formation of the rings on the otolith, suggest that the condition of the fish may be more important (McPherson *et al.,* 1988). While this may not be the exclusive determinant of band formation, it is clear that some biological mechanism associated with low somatic growth plays a major role (Mosegaard *et al.,* 1988). It is believed that during reproductive season, allocation of energy for somatic growth may begin to be diverted to reproductive growth leading to decline in somatic growth rates. Sadovy and Severin (1992) proposed that this decline in somatic growth in the white grant *(Haemulon plumieri)* was responsible for the formation of the opaque bands.

Longevity

The estimate of maximum longevity provided here, places *Cephalopholis cyanostigma* among the longest-lived serranids reported to date. This result is particularly surprising given the diminutive maximum size of the species and conventional ecological theory relating maximum body size and longevity (Longhurst and Pauly, 1987). Maximum reported longevities for larger serranids, such as plectropomids and epinephelids, are on the order of 15-20 years (Ferreira and Russ, 1992; 1994; Sadovy *et al.,* 1994). The maximum longevity recorded for one of the largest serranids for which validated age estimates are available, *Myctoperca bonaci* (1.4 m, FL) from Florida waters, is 33 years (Crabtree and Bullock, 1998). The only comparable estimate of longevity for a cephalopholid is from a study by Matthews and Samuel (1987) for *Cephalopholis hemistiktos* from the Red Sea. They report a mean asymptotic length at 34.1l cm (TL) and the maximum life span is 26 years, which are comparable with both populations of C. *cyanostigma* in the present study. Recent work on *C. cyanostigma* from other geographic regions of the GBR including the Lizard Island region indicates that the results from this study are not unusual and that longevity may commonly exceed 40 years (Mosse *et al.,* 2002).

Pattern of growth

The growth pattern observed in this study indicated that *C. cyanostigma* had a low rate of growth and achieved a relatively small size in comparison to published growth estimates for other serranids (e.g. *P.leopardus, P.maculatus, E. labriformis, E. aerolatus, E. cruentatus, C.panamanensis).* It undergoes a period of relatively steady growth from 3 years approaching its asymptotic size at about 10-12 years after which growth is negligible. While the general pattern of growth was similar in each of the two locations studied, the comparison of growth curves suggested that they differed between locations. These differences in the asymptotic length (L_∞) may be the result of strong sedentary nature within the habitats for *C. cyanostigma* (MackigjJ993) and other *Cephalopholids* (Shpiegel and Fishelson, 1989; 1991). Differences in the relative quality of the local habitat (eg. food availability, presence of other predators or fishing pressure) are likely to affect their growth (Watson and Ormond, 1994).

In general, it has been postulated that the growth pattern of protogynous reef fish may be complicated by the change of sex from female to male (Matheson *et al.,* 1986). Given the lower amount of energy required to produce sperm relative to eggs, it may be expected that, on average, individuals will have more energy to allocate to somatic growth following sex change and that this may be evident as an increase in growth rate. If present, such an affect would be expected to be manifest as an increase in the average size at age of males relative to females. A number of reef fish have been reported to show differential growth pattern between sexes (e.g. Robertson and Warner, 1978; Choat *et al.,* 1996). Choat *et al.*(1996) found that growth rates in a number of terminal males of labroid species enhance after changing sex. We found no evidence of sex-specific growth rates in *C.cyanostigma.* While the oldest individuals in the sample were male for both locations, substantial proportions of the largest and oldest individuals were female suggesting that some females retain their initial sexual identities throughout life. Similar patterns have been found for Plectropomids (Adams *et al.*, 2000). In addition, similar growth patterns between females and males within each location indicates that the effect of hormonal stimulation on growth after changing sex may be not a general phenomenon. We suggest that the apparent growth spurt following sex change in Labroid fishes (Choat *et al.,* 1996) may be a feature of a particular life-taxon strategy and not a general feature of protogynous reef fish.

Furthermore, the validated age estimates from this study provide not just a sound basis for such studies for *C.cyanostigma* on the GBR, but also critically important for studying other coral reef fish population inhabiting the adjacent waters including Indonesia. This approach should be considered reliable for the similar study in Indonesia given the fact of low cost and minimal logistic requirement

This is one of the first investigations of the population parameters of a small tropical serranid using validated age-based methods. Our results demonstrate that the populations of *C.cyanostigma* from two islands in the central GBR can be characterised by high longevity and slow growth. While further work is required to substantiate the generality of these results, they are contrary ecological theory on the relationship between body-size, longevity and rate of natural mortality (Longhurst and Pauly, 1987). They are consistent, however, with findings from other age-based studies of a range of genera of small reef fish on the GBR. Small species of lutjanids (Davies 1995, Newman *et al,* 1996), acanthurids (Hart and Russ, 1994, Choat and Axe, 1996), scarids (Choat *et al,* 1996), labrids (Choat *et al,* 1996), pomacentrids (Doherty and Fowler, 1994) and lethrinids (Davies, *unpublished data)* have been found to have surprising longevities and correspondingly low estimates of rates of natural mortality relative to what would be predicted based on their average maximum size.

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