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DEMOGRAPHIC CHARACTERISTICS OF SELECTED EPINEPHELINE GROUPERS (FAMILY: SERRANIDAE; SUBFAMILY: EPINEPHELINAE) FROM ALDABRA ATOLL, SEYCHELLES

BY

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ABSTRACT

Sagittal otoliths were extracted from samples of six species of groupers (Serranidae: Epinephelinae) caught with hand lines around the periphery of Aldabra atoll (southwest Indian Ocean) in December 2000: *Epinephelus fuscoguttatus* (*n*=26), *Epinephelus multinotatus* (*n*=33), *Epinephelus polyphekadion* (*n*=77), *Epinephelus tukula* (*n*=62)*, Plectropomus laevis* (*n*=22) and *Variola louti* (*n*=101). Growth increments consisting of alternating translucent and opaque bands were observed in transverse sections of sagittae. The von Bertalanffy growth function was fit to size and increment number data, values of the growth coefficient (*k*) ranged from 0.13 for *E. tukula* to 0.48 for *V. louti*, with a mean value of 0.24 for all species. Estimates of the annual instantaneous rate of natural mortality ranged from 0.13 yr^{-1} for *E*. *polyphekadion* to 0.28 yr^{-1} for *V. louti*. The maximum number of putative annuli observed in transverse sections of sagittae ranged from 15 for *V. louti* to 31 for *E*. *polyphekadion*. While the study demonstrates the utility of structural increments in sagittal otoliths for establishing key demographic characteristics, parameters derived from age estimates are preliminary given the need to validate the periodicity of increment formation. Nevertheless, the results suggest that groupers in general are long-lived, slow-growing species that have low rates of natural mortality. The findings are important to fisheries management and conservation authorities as they support the contention that these species have a low resilience to exploitation and their populations may be particularly vulnerable to overfishing.

INTRODUCTION

Progress in understanding the dynamics of tropical fish populations has been hindered by the misconception that banding patterns do not form in the otoliths or other hard parts of reef fish due to a lack of seasonality in the tropics (Longhurst and Pauly, 1987). As a result, fisheries resource assessments in the southwest Indian Ocean region have been based predominantly on the analysis of length frequency data (eg., Sanders *et al*., 1988). A principal constraint of length-based techniques is the inability of modal analyses to discriminate older age classes, especially for long-lived, slow-growing species, resulting in unreliable growth rate and longevity estimates (eg., Goeden, 1978; Langi, 1990).

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The assumptions that tropical fish have rapid continuous growth and short life spans has been dispelled by studies that have shown annual banding patterns in sagittal otoliths (see Fowler, 1995 for review). The utility of seasonally deposited increments for deriving growth rates, longevity and other key demographic characteristics has been demonstrated for representative species of families important in reef fisheries, eg: Lethrinidae (Pilling *et al*., 2000); Lutjanidae (Newman *et al*., 1996); Serranidae (Ferreira and Russ, 1992; Ferreira and Russ, 1994); and Scaridae (Lou, 1992; Choat *et al*., 1996). While growth has been investigated for *Epinephelus fuscoguttatus* and *Variola louti* by Wright *et al*. (1985), longevity, natural mortality and other fundamental life history characteristics have yet to be established for some of the larger groupers such as *Epinephelus tukula*.

The Epinepheline groupers, family Serranidae and subfamily Epinephelinae, occur in shallow tropical and subtropical seas of the Indo-Pacific region. They are usually at the top of food chains playing a major role in the structure of coral-reef communities (Randall, 1987) and are relatively abundant on the reefs of Aldabra atoll (Teleki *et al*., 2000). Since groupers are favored for consumption or sale in commercial and subsistence fisheries, they are commonly targeted by fishermen (Munro, 1983). Their aggressive nature and relatively large size make them more vulnerable to fishing gears (Munro and Williams, 1985) and aspects of their reproductive biology and demography predispose them to overexploitation (see Sadovy, 1996 for review). These factors may explain the sequential reduction in abundance of groupers on the Seychelles Bank to the northeast of Aldabra atoll over the last decade (Grandcourt and Cesar, 2002).

Reliable estimates of demographic characteristics such as growth and mortality rates are vital to the evaluation of fisheries resources. Given the declining status of these species and problems associated with the use of size-frequency data, age-based investigations are required in order to improve the integrity of stock assessments. In this context, objectives of this study were to establish age-based demographic parameters including size at age-specific growth rates, natural mortality rates, longevities, otolith growth rates and parameters of the von Bertalanffy growth function, assuming an annual pattern of growth increment formation. The absence of any significant fishery in the waters around Aldabra atoll presents a unique opportunity for the collection of these data, much of which is unavailable for the majority of the selected study species.

MATERIALS AND METHODS

Study Site and Species Selection

Aldabra is situated in the southwest of the exclusive economic zone of the Republic of Seychelles (9^{o}24' S, 46^{o}20' E), 420 km to the north of Madagascar (Fig. 1). Samples were obtained from locations around the perimeter of the atoll during a research cruise in December 2000. Representatives of the family Serranidae selected for sampling based on their relative abundance in the catch included: *Epinephelus fuscoguttatus*, *Epinephelus multinotatus*, *Epinephelus polyphekadion*, *Epinephelus tukula*, *Plectropomus laevis* and *Variola louti*.

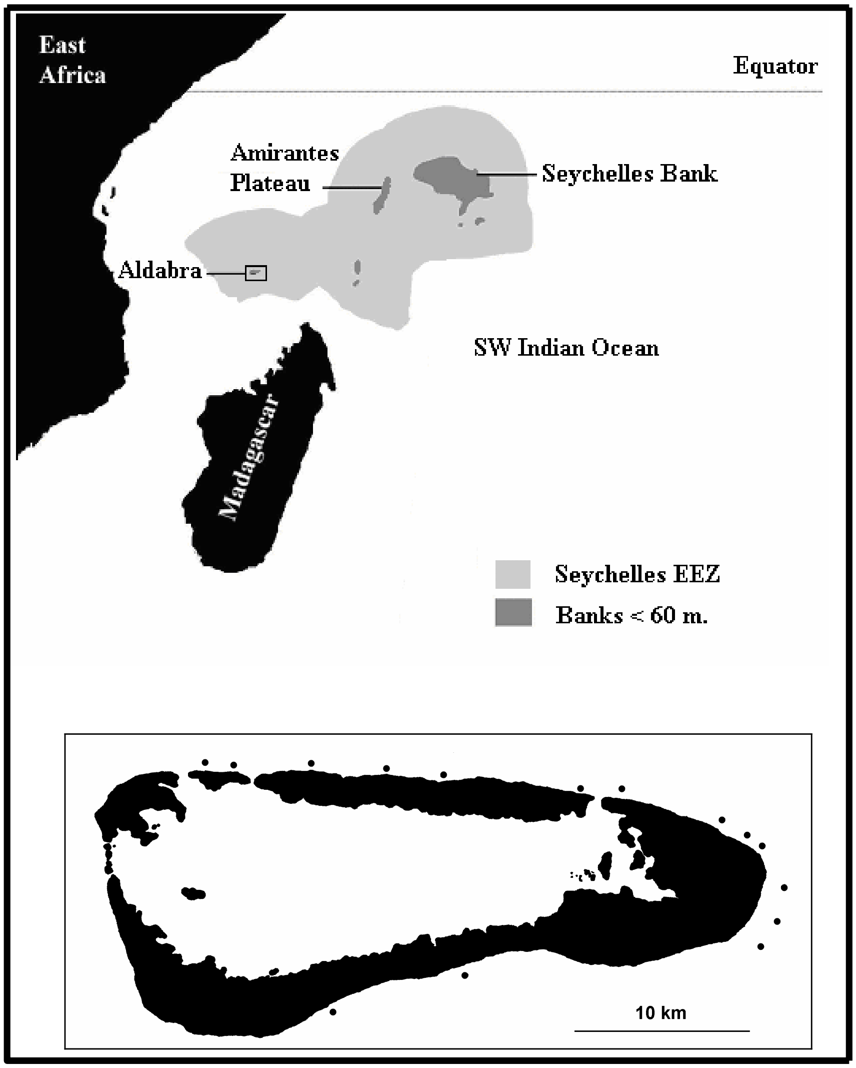

Figure 1. The position of Aldabra atoll in the southwest Indian Ocean, showing locations (●) from which fish were caught (insert).

Sampling and Otolith Processing

Fish were caught during December 2000 using hand lines with baited hooks set between 30 m. and 70 m. Total (L_T) and fork length (L_F) measurements were obtained using a measuring board and recorded to the nearest mm. As all samples were taken on completion of the research cruise when fish were landed, sex could not be determined as fish had been gutted and cleaned. Eviscerated weight was determined using an electronic balance and recorded to the nearest *g*. Sagittal otoliths were removed from samples, cleaned in water and stored dry in paper envelopes.

One of each pair of sagittae was weighed to the nearest 0.1 mg. The nucleus was then marked and the otolith embedded in epoxy resin. Resin blocks were mounted on glass slides using thermoplastic glue. Transverse sections 200 to 300 μm thick were made through the core using a low speed Buehler Isomet jewelry saw. Sagittal sections were ground using 400 grit wet and dry abrasive paper. Processing of otoliths was based on methods of Secor *et al*. (1991).

Increment counts in sectioned otoliths were made using a dissecting microscope and reflected light with a black field. Otoliths were read once by the author. Sections were smeared in immersion oil prior to examination in order to reduce scatter and improve contrast. In order to reduce bias, slides were coded so that no information relating to the size of the fish was available when increment counts were made.

Data Analyses

Growth. Growth was investigated by fitting the von Bertalanffy growth function (von Bertalanffy, 1938) to size and increment number data from otoliths. The von Bertalanffy growth function is defined as follows:

$$L_t = L_\infty \ (1 - e^{-k\,(t-t0)})$$

Where L_t is length at time t, L_∞ is the asymptotic length, k is the growth coefficient and t_0 is the hypothetical time at which length is equal to 0. Because juvenile fish were under-sampled, the growth model was constrained through the origin ($t_0 = 0$) in order to obtain biologically tenable parameters.

Natural Mortality. Estimates of the annual instantaneous rate of natural mortality (M) were obtained for each species using the empirical equation derived by Hoenig (1983):

$$ln(Z) = 1.46 - 1.01\ ln(t_{\text{max}})$$

Where Z is the total mortality rate, which is analogous to M in an unexploited population, and t_{max} is the age of the oldest fish, taken as the maximum number of increment counts in sagittal otolith sections.

Sagittal Weight-increment Number Relationships. Relationships between sagittal weights and numbers of increments observed were determined using least-squares linear regression with sagittal weight as the independent variable and increment number as the dependent variable. The regression equation ($y = b.x + a$) was fitted to sagittal weight and increment number data.

Length-weight Relationships. Parameters of the length-weight relationship were obtained by fitting the power function $W = a.L^b$ to length and weight data where: W is the weight, a is a constant determined empirically, L is the length and b is close to 3.0 for species with isometric growth. Because fish were sampled in a gutted state, the weight was raised by a factor of 1.15 to represent the ungutted condition. This value was derived from a subjective estimation of the weight of organs removed from the body cavity during gutting which occurred directly after capture.

RESULTS

Catch

A total of 5,390 kg of fish were caught on patch reefs around the periphery of Aldabra atoll. The catch was composed of nine species from six genera and four families (Table 1). While *Lutjanus bohar* was the most abundant species in terms of weight, representatives of the family Serranidae made up 61% of the total catch, 54% of which was sampled for length-weight measurements and otoliths. Sample sizes and size ranges for the study species were: *Epinephelus fuscoguttatus* (*n*=26, 49.5-76.7 *cm* L_T); *Epinephelus multinotatus* (*n*=33, 44.8-62.0 *cm* L_T); *Epinephelus polyphekadion* (*n*=77, 37.6-62.0 *cm* L_T); *Epinephelus tukula* (*n*=62, 72.3-128.4 *cm* L_T), *Plectropomus laevis* (*n*=22, 72.2-108.1 *cm* L_F); and *Variola louti* (*n*=101, 33.9-57.8 *cm* L_F).

Table 1. Total catch weights, sample weights and numbers for species caught around Aldabra atoll, December 2000.

Species	Catch (*kg*)	Sample weight (*kg*)	Number sampled
Cheilinus undulatus	88	0	0
Epinephelus fuscoguttatus	414	130	26
Epinephelus multinotatus	131	84	33
Epinephelus polyphekadion	613	193	77
Epinephelus tukula	1,486	875	62
Lethrinus nebulosus	67	0	0
Lutjanus bohar	1,941	0	0
Plectropomus laevis	383	272	22
Variola louti	267	228	101
Total	5,390	1,782	321

Otolith Structure

Transverse sections of sagittal otoliths showed defined structural increments consisting of alternating opaque and translucent bands when viewed with reflected light under low-power magnification (Fig. 2). Distances between bands became smaller from the core towards the outer edge of the otolith. The contrast of the banding pattern was variable between species. Opaque increments were most distinct in sagittal sections from representatives of the genus *Epinephelus*: *E. fuscoguttatus*, *E. multinotatus*, *E. polyphekadion*, *E. tukula* and less well defined in sections from *Plectropomus laevis* and *Variola louti*. The maximum number of opaque increments observed in sagittal otolith sections (considered to represent longevity) ranged from 15 for *V. louti* to 31 for *E.*

polyphekadion; other values obtained were 30 (*E. fuscoguttatus*), 27 (*E. multinotatus*), 26 (*E. tukula*) and 20 (*P. laevis*).

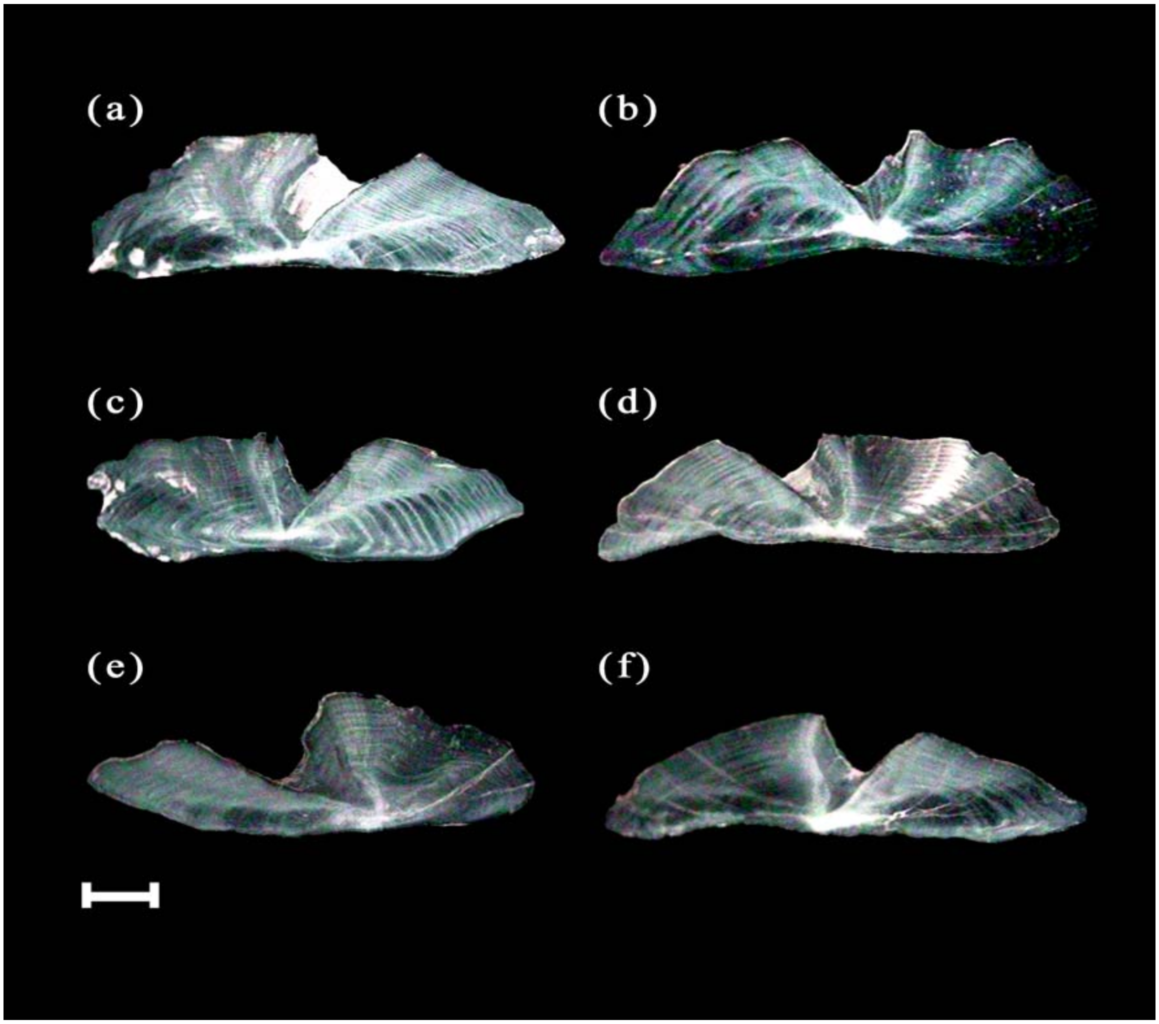

Figure 2. Photomicrographs of transverse sections through sagittal otoliths of six species of groupers collected at Aldabra atoll, December 2000: (a) *Epinephelus fuscoguttatus* (69.7 *cm* L_T); (b) *Epinephelus multinotatus* (49.6 *cm* L_T); (c) *Epinephelus polyphekadion* (52.6 *cm* L_T); (d) *Epinephelus tukula* (88.7 *cm* L_T); (e) *Plectropomus laevis* (102 *cm* L_T); (f) *Variola louti* (56.9 *cm* L_T). (Scale bar = 1 mm).

Growth

Relationships between fish size and number of increments in otolith sections were predominantly asymptotic in form (Fig. 3). The von Bertalanffy growth function provided a good fit to the data with coefficients of determination ranging from 0.74 for *E. tukula* and *V. louti* to 0.95 for *E. fuscoguttatus*. Parameter estimates of the growth coefficient (*k*) ranged from 0.13 for *E. tukula* to 0.48 for *V. louti*, with a mean of 0.24 for all species. Parameters of the von Bertalanffy growth function are summarized in Table 2.

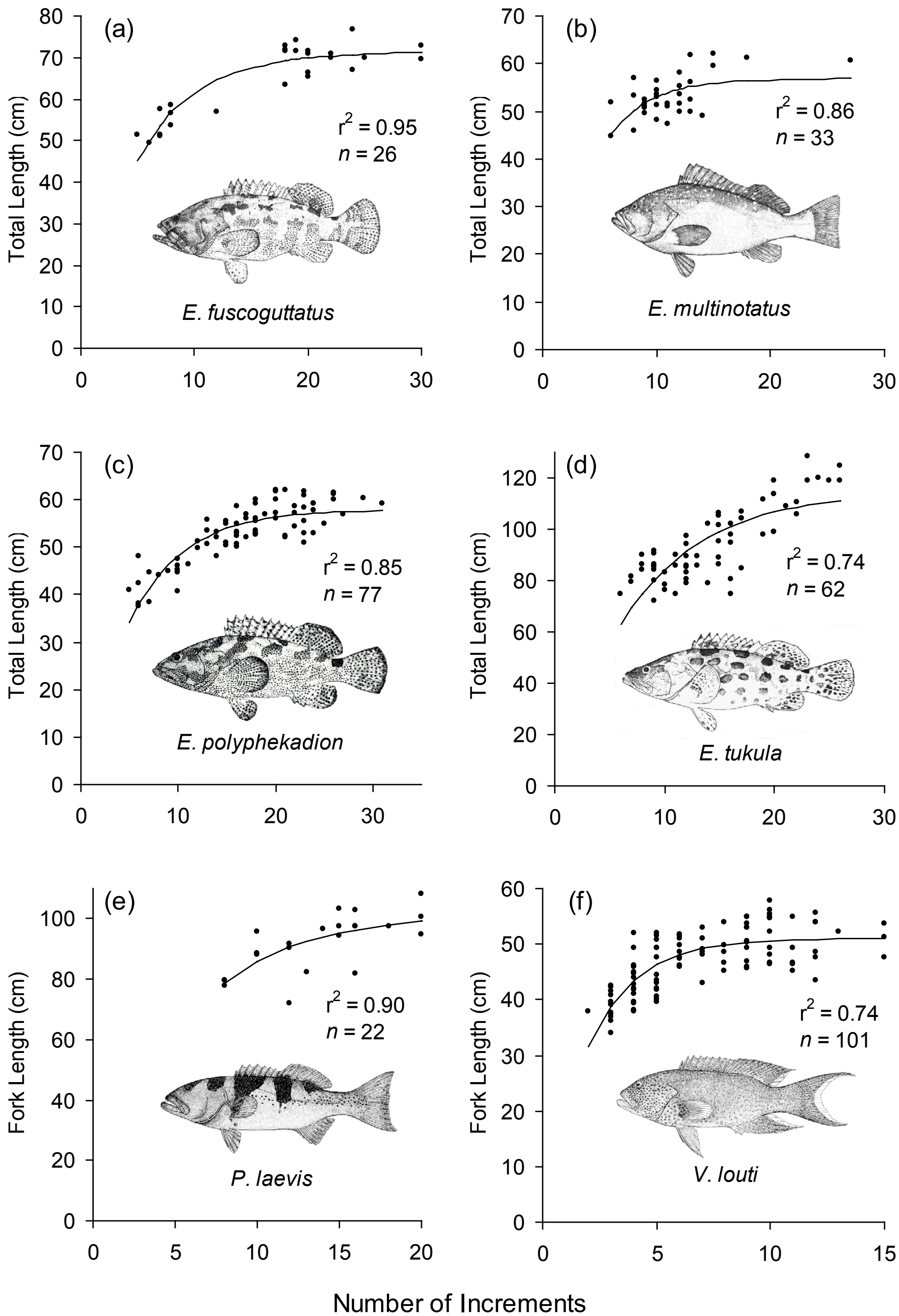

Figure 3. The von Bertalanffy growth function: $L_t = L_\infty \ (1 - e^{-k\,(t-t0)})$ fitted to the relationship between size and increment number, the model has been constrained through the origin ($t_o = 0$). (a) *Epinephelus fuscoguttatus*, (b) *Epinephelus multinotatus*, (c) *Epinephelus polyphekadion*, (d) *Epinephelus tukula*, (e) *Plectropomus laevis*, (f) *Variola louti*.

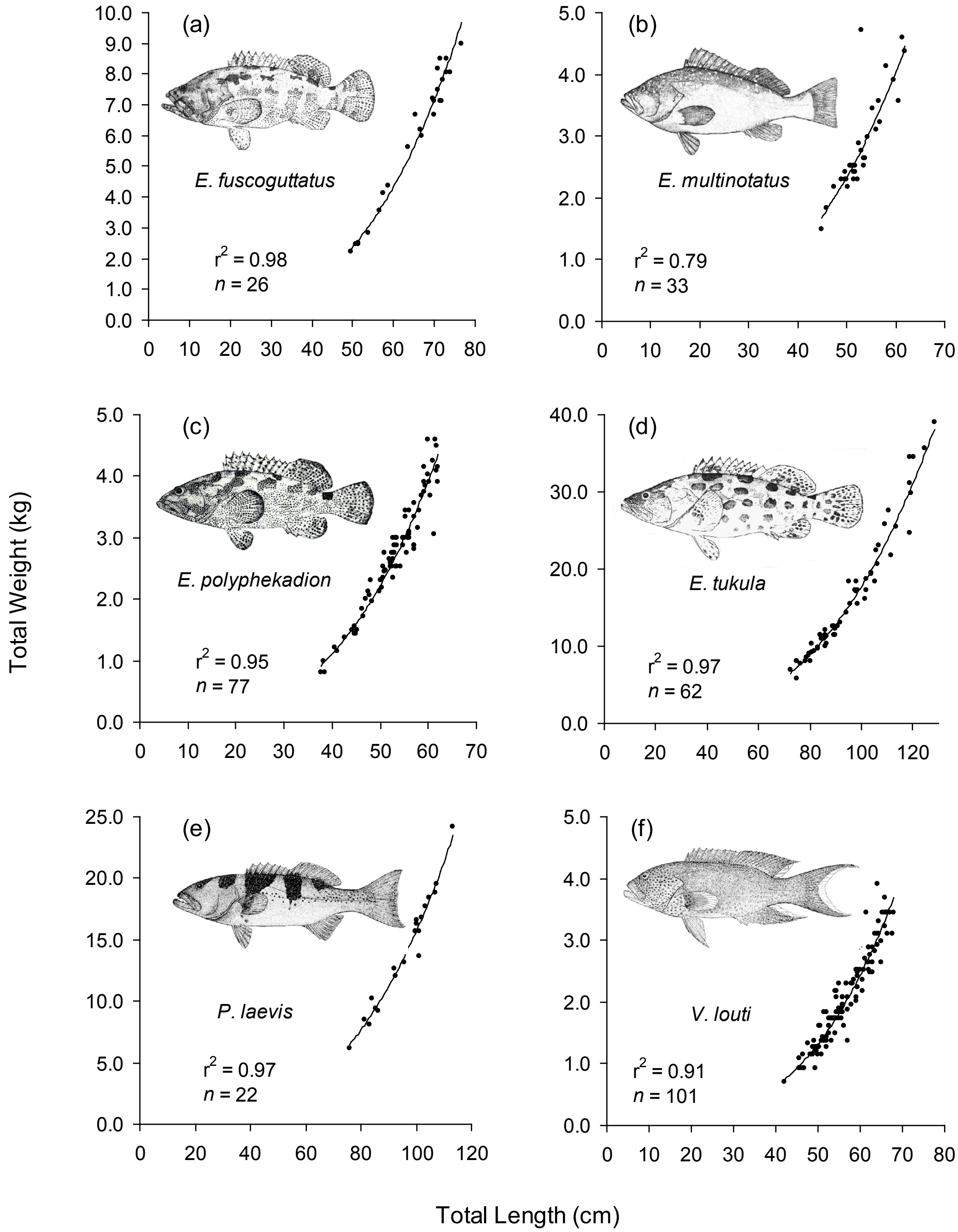

Figure 4. Length-weight relationships showing the power function: $y = a.x^b$ fitted to the data. (a) *Epinephelus fuscoguttatus:* $y = 6.0^{-6}.x^{3.28}$ (b) *Epinephelus multinotatus:* $y = 2.0^{-5}.x^{3.01}$ (c) *Epinephelus polyphekadion:* $y = 1.0^{-5}.x^{3.11}$ (d) *Epinephelus tukula:* $y = 1.0^{-5}.x^{3.07}$ (e) *Plectropomus laevis:* $y = 6.0^{-6}.x^{3.20}$ (f) *Variola louti:* $y = 3.0^{-6}.x^{3.35}$.

Table 2. Parameters of the von Bertalanffy growth function $L_t = L_\infty \ (1 - e^{-k\,(t-t0)})$ and maximum fish lengths (L_{max}) recorded for six species of groupers collected at Aldabra atoll, December 2000. Note: as the model has been constrained through the origin, $t_0 = 0$ for all species. All lengths are total (L_T) except those of *Plectropomus laevis* and *Variola louti* for which fork lengths (L_F) are given.

Species	k	L_∞ (*cm*)	L_{max} (*cm*)
Epinephelus fuscoguttatus	0.20	71.3	76.7
Epinephelus multinotatus	0.27	57.0	62.0
Epinephelus polyphekadion	0.18	57.9	62.0
Epinephelus tukula	0.13	114.9	128.4
Plectropomus laevis	0.19	101.5	108.1
Variola louti	0.48	51.0	60.0

Natural Mortality

Annual instantaneous rates of natural mortality derived using the Hoenig (1983) empirical equation ranged from 0.13 yr^{-1} for *E. polyphekadion* to 0.28 yr^{-1} for *V. louti* (Table 3). The mean natural mortality rate for all species was 0.18 yr^{-1}.

Table 3. Estimates of annual instantaneous rates of natural mortality (*M*) derived from the Hoenig (1983) empirical equation for six species of groupers collected at Aldabra atoll, December 2000.

Species	Natural mortality rate ($M\ yr^{-1}$)
Epinephelus fuscoguttatus	0.14
Epinephelus multinotatus	0.15
Epinephelus polyphekadion	0.13
Epinephelus tukula	0.16
Plectropomus laevis	0.21
Variola louti	0.28

Length-Weight Relationships

The length-weight relationship ($W = a.L^b$) provided a good fit to length and weight data for all species (Fig. 4). Values of the coefficient of determination ranged from 0.79 for *E. multinotatus* to 0.98 for *E. fuscoguttatus*. Values of *b* ranged from 3.01

for *E. multinotatus* to 3.35 for *V. louti*, and were close to 3.0 for all species examined indicating that isometric growth occurs in these groupers.

Sagittal Weight-Increment Number Relationships

Linear relationships between sagittal weights and increment numbers indicated that otoliths increased in mass at a constant rate throughout the life of all species (Table 4).

Table 4. Parameters of the regression equation and coefficients of determination derived from the relationships between otolith weight and the number of increments observed in sagittal otolith sections for six species of groupers collected at Aldabra atoll, December 2000.

Species	*a*	*b*	r^2
Epinephelus fuscoguttatus	2.53	60.34	0.91
Epinephelus multinotatus	1.27	64.51	0.68
Epinephelus polyphekadion	0.06	54.23	0.76
Epinephelus tukula	3.71	38.29	0.80
Plectropomus laevis	2.76	95.21	0.57
Variola louti	0.67	85.32	0.72

DISCUSSION

Due to their importance in tropical fisheries around the world (Ralston, 1987), a number of studies have focused on the age and growth of representatives of the family Serranidae, in particular on members of the subfamily Epinephelinae, commonly known as groupers. These investigations have confirmed the utility of seasonally deposited increments in sagittal otoliths for estimating demographic parameters of these fishes. Age structures, growth rates, longevity estimates and other population characteristics have been established for a range of exploited grouper species (see Manooch, 1987; Munro and Williams, 1985 for reviews). This study extends the geographic and taxonomic range for which growth increments in sagittal otoliths have been observed for groupers and further demonstrates their utility in establishing key population parameters for the species examined.

Formation of alternating translucent and opaque growth increments in fish otoliths has been associated with a variety of factors including seasonal variations in water temperature, photoperiod, feeding, and reproduction (Manickchand-Heileman and Philip, 2000; Moe, 1969; Morales-Nin and Ralston, 1990; Panella, 1980; Reay, 1972). High amplitudes of seasonal growth oscillations observed for *Epinephelus chlorostigma* were attributed to the annual variation in water temperature of about 10 ^{o}C caused by the seasonal presence of a thermocline on the Seychelles Bank (Sanders *et al*., 1988). It is plausible that seasonal growth oscillations associated with rhythmic annual fluctuations in environmental conditions could be the causal factor of alternating opaque and translucent bands observed in sagittal otoliths of the Serranids examined in this study.

With exception of *V. louti*, all the study species had low values of *k*, with parameters of the growth coefficient of the von Bertalanffy growth function ranging from 0.13 for *E. tukula* to 0.27 for *E. multinotatus*. While the relationships between size and the number of increments were predominantly asymptotic in form, the growth of *E. tukula* was largely indeterminate as size increased with age throughout the lifespan, resulting in the large maximum size that was reached by this species. Conversely, the growth of *V. louti* was highly asymptotic in form with the majority of growth being achieved during the first six years of life. As the growth coefficient describes the rate at which the asymptotic length is approached, the high value of *k* by comparison with the other species was associated with its smaller asymptotic size and, in particular, reduced longevity, which is about half that of the other Serranids examined. The mean value of the growth coefficient (0.24) for all species in the present study compared well to the mean value of 0.22 reported by Manooch (1987) for 31 species of Serranidae.

Growth coefficients have previously been reported for *E. fuscoguttatus* and *V. louti* by Wright *et al*. (1985). Their value of *k* for *E. fuscoguttatus* (0.20) is the same as the estimate obtained here. Conversely, the growth coefficient for *V. louti* of 0.18 was considerably less than the estimate obtained here (0.48). The large difference in *k* for *V. louti* could be due to methodological differences as the previous estimate was derived using size frequency data. Given the inability of modal analyses to discriminate older age classes, especially for long-lived, slow-growing species, the growth parameter estimates obtained here are probably more reliable in this context. The growth coefficient estimate for *E. multinotatus* of 0.27 occurring in the northern Arabian Gulf (Mathews and Samuel, 1987), which was also derived from sections of sagittal otoliths, was the same as the estimate obtained in this study. Nevertheless, growth parameters could have been improved with larger sample sizes that covered the entire size range, especially those for *E. fuscoguttatus*, *E. multinotatus* and *P. laevis* for which sample sizes were small. Additionally, given the possibility that growth may differ among sexes, particularly as the species investigated are protogynous hermaphrodites, sex-specific growth characteristics should be determined in future studies.

Estimates of the annual instantaneous rates of natural mortality for *V. Louti* and *E. fuscoguttatus* of 0.48 yr^{-1} (Wright *et al*., 1985) were considerably greater than the estimates obtained here (0.28 and 0.14 yr^{-1} respectively). Nevertheless, the values estimated in the present study are in line with the trend for Serranids which in general have low rates of natural mortality (eg., Manooch, 1987).

Maximum ages for Serranid species determined using otolith microstructures range from 9 yrs. for *E. cruentatus* (Nagelkerken, 1979) to 41 yrs. for *Mycteroperca interstitialis* (Manickchand-Heileman and Philip, 2000). The provisional longevity estimates obtained in the present study, based on the maximum number of putative annuli (between 15 yrs. and 31 yrs.) are within the range estimated for groupers from other areas and suggest that the selected species examined from Aldabra atoll are generally long-lived. As with the growth rate, the maximum age of *E. multinotatus* in the northern

Arabian Gulf of 28 yrs. estimated by Mathews and Samuel (1987) compares well with the maximum obtained here (27 yrs.). Life history characteristics can be used to classify the resilience of a species to fishing pressure (Musick, 1999) and the level of productivity within the population. Growth parameters and longevity estimates derived here suggest that the Epinepheline groupers examined have low resilience to exploitation. This would explain the sequential reduction in abundance of groupers on the Seychelles bank that has occurred over the last decade (Grandcourt and Cesar, 2002) and demonstrates the need for a precautionary approach to the management of these species.

Parameters derived from length-weight relationships have utility in fishery independent methods of biomass estimation such as underwater visual census surveys (eg., Jennings *et al*., 1995). These methods improve assessments of reef-fishery resources (Connell *et al*., 1998) and reporting length-weight relationships is especially important for species for which no published parameter estimates exist (Manooch, 1987). Given the relative abundance of Serranid species on the reefs of Aldabra atoll (Teleki *et al*., 2000), it is anticipated that the parameters provided here will be used in biomass estimation and monitoring studies of these fishes in the future.

The relationships between otolith weights and increment numbers indicate that the otoliths of the species examined grow throughout the life of the fish, fulfilling one of the fundamental criteria required for aging (Fowler and Doherty, 1992). However, structures used for aging should be shown to correspond to a regular time scale of known duration (Beamish and McFarlane, 1983; Fowler and Doherty, 1992). Validation studies have confirmed the annual nature of increment formation in the otoliths of *Lethrinus mahsena* on the Seychelles Bank using oxytetracycline injection/mark-recapture (Grandcourt, 2002) and marginal increment/edge analysis (Pilling *et al*., 2000). While this study has confirmed the presence of discernible banding patterns, further work is required to authenticate the periodicity of increment formation. The results are nevertheless important in that they offer an insight into the demographic characteristics of these species from populations that have not been modified by intensive exploitation. Moreover, the patterns of age, growth, longevity and natural mortality observed adhere to the general trends for other Epinepheline groupers across the Indo-Pacific.

This study confirms the presence of banding patterns in the sagittal otoliths of a selection of Serranid species, extending the taxonomic and geographical range over which such observations have been made. Furthermore, evidence is provided suggesting that *Epinephelus fuscoguttatus*, *Epinephelus multinotatus*, *Epinephelus polyphekadion*, *Epinephelus tukula* and *Plectropomus laevis* are long-lived, slow-growing species that have low rates of natural mortality. These results are important to fisheries management and conservation authorities as they support the contention that groupers have a low resilience to exploitation and their populations may be particularly sensitive to fishing.

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