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AGE, GROWTH AND MORTALITY OF THE TROPICAL GROUPER *EPINEPHELUS MERRA* (PISCES, SERRANIDAE) ON RÉUNION ISLAND, SW INDIAN OCEAN

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SERRANIDAE
OTOLITHS
VALIDATION
BACK-CALCULATION
SEMI-ARTIFICIAL BIOTA

ABSTRACT. – The growth, age, mortality rate and some aspects of the biology of a protogynous fish from the family Serranidae, *Epinephelus merra* Bloch, 1793, have been studied on the Réunion Island. This key species in the functioning of the Réunion coral reef ecosystem was sampled in a semi-artificial habitat. The log-transformed length-weight relationship was defined by: $\text{Ln}(W) = 3.015 \text{ LT} - 1.970$ and was not statistically different from that reported by other authors in natural habitats. Comparison between the total length of males and females revealed that sexual change occurred when fish were between 18 and 20 cm (TL), which corresponded to ages ranging from 3 to 5 years. A comparison between otolith reading methods for age assessment was done (*in toto* observations, assessment on digital photographs, and assessment by image analysis software). The von Bertalanffy growth curve provided low theoretical maximum length (L_{∞} ranging from 19.8 cm to 25.0 cm TL, depending on the method used) and relatively high growth rate (k ranging from 0.43 to 0.80, depending on the method used). Estimates of natural mortality (M) ranged from 0.90 to 1.67. These results could however be underestimated (L_{∞}) or overestimated (k and M), possibly due to Lee's phenomenon linked to sampling which mainly focused on medium and large sizes. Implications for fishery management are discussed.

SERRANIDAE
OTOLITHS
VALIDATION
RÉTROCALCUL
MILIEU SEMI-ARTIFICIEL

RÉSUMÉ. – L'âge, la croissance, la mortalité et certains aspects de la biologie d'un Serranidae protogyne de l'île de La Réunion, *Epinephelus merra* Bloch, 1793, ont été étudiés. Cette espèce-clé dans le fonctionnement de l'écosystème corallien réunionnais a été récoltée en milieu semi artificiel, et a présenté une relation taille-poids (transformation Log) définie par : $\text{Ln}(W) = 3,015 \text{ LT} - 1,970$ qui n'est pas significativement différente de la relation en milieu naturel définie par d'autres auteurs. La comparaison des longueurs totales des mâles et des femelles a révélé que le changement de sexe se fait pour des tailles comprises entre 18 et 20 cm, ce qui correspond à des âges compris entre 3 et 5 ans. Une comparaison entre différentes méthodes d'évaluation de l'âge à partir des otolithes a été réalisée (lectures *in toto*, évaluations par lectures sur photos numérisées, et par logiciel d'analyse d'image). La courbe de croissance établie avec le modèle de von Bertalanffy a donné une longueur maximale théorique faible (L_{∞} entre 19,8 et 25,0 cm selon la méthode utilisée) et un taux de croissance assez fort (k compris entre 0,43 et 0,80 selon la méthode utilisée). Les estimations de la mortalité naturelle (M) ont fluctué entre 0,90 et 1,67. Ces résultats sont cependant peut-être sous-estimés (L_{∞}) ou surestimés (k et M) de par un possible 'phénomène de Lee' lié à un échantillonnage centré sur des tailles moyennes et grandes. Les implications de ces résultats sur la gestion de l'espèce sont discutées.

INTRODUCTION

The age of individual fish can be estimated from the analysis of marks recorded in hard tissues such as scales (scalimetry), otoliths (otolithometry) or bony structures (skeletalochronology). Since Hederström

(1759) and Reibish (1899), otoliths have often been considered as the best hard structures on which to base age assessment in fish, which explains why otolithometry has been the most widely used ageing technique in fish science for more than two centuries. Temperate fish species were first studied because annuli are easier to distinguish when there

are marked seasonal differences in environmental factors such as temperature. In tropical waters, seasons are often not strongly marked and differences in seawater temperature slight, which can result in poorly visible seasonal and/or annual rings. This likely explains why age estimation in tropical fish was sometimes found to be less accurate than those observed in temperate fish (Samuel *et al.* 1987, Baillon 1991, Fowler *et al.* 1995, Machias *et al.* 1998, 2002, Massuti *et al.* 2000). However, and particularly since the discovery of daily increments on sagittae (Panella 1971), otolithometry has increasingly been used for tropical species (Morales-Nin 1988). Recent developments in otolith reading now allow reliable age assessments in tropical fish (Hood & Schlieder 1992, Sadovy *et al.* 1992, Lou 1993, Fowler *et al.* 1995, Gordo & Moli 1997, Szedlmayer 1998, Campana 1999, Newman *et al.* 2000a, b, Chale-Matsau *et al.* 2001, Newman 2002, Newman & Dunk 2002, Radebe *et al.* 2002, Yoneda *et al.* 2002).

Otolith growth is not uniform over time. A large translucent band generally forms during the high growth summer season while a narrow opaque band is generally formed during the slow winter season. This succession of a summer and a winter band forms a distinct yearly increment, or annulus, in the otoliths of most temperate and tropical fish species (Lecomte-Finiger 1999). Unfortunately, there are many exceptions to this rule so that it is necessary to validate the yearly frequency of otolith increment deposition as well as the timing of increment formation prior to using otoliths for ageing any new species under investigation. This thus avoids overestimation of age, due to 'false' annuli, or underestimation of age due to the absence of an annulus. The validation procedure then makes it possible to determine whether the observable annuli are really true or false annuli (Caillart & Morize 1989, Baillon 1991). There are three main techniques to validate age assessment. First, otoliths are analysed from fish of known age and the otolith age estimates are compared with real age. Second, marking individuals is accurate and is based on the incorporation of a determined chemical substance in hard tissues, resulting in a clear band on the otolith, most often red or violet, visible under UV magnification. The use of a marker has no detrimental effect and its presence in hard tissues is permanent (Campana & Neilson 1985, Baglinière *et al.* 1991). Third, it is also possible to monitor over time the marginal increment width and verify that its growth follows a one-year cycle.

Epinephelus merra is by far the most common Serranidae, and even the most common carnivorous fish species on shallow coral reef flats of Réunion Island (Letourneur 1996). Due to its abundance and high trophic level (Harmelin-Vivien & Bouchon 1976), this species may be considered as a key-species in the functioning of Réunion coral

reefs. However, Réunion coral reef flats are exposed to several types of anthropogenic disturbances mainly linked with urban development of the coastal areas. In particular, eutrophication leads to alterations in benthic habitat structure and changes in prey populations (Naïm 1993). Furthermore, *E. merra* is heavily targeted, even if the species is of relatively small size (maximum size about 27–30 cm, Randall & Heemstra 1993). Indeed, small fishes are very sought after by local fishermen, partly because larger individuals of other species are rare due to high fishing pressure (Taquet pers com). A marine protected area (MPA) including most coral reef areas on Réunion Island was set up in 1997, resulting rapidly in conflicts with fishermen and even with poachers (Barcello pers com). Despite its commercial and ecological importance, the biology *sensu lato* of *E. merra* remains poorly known. To our knowledge, no information on key demographic parameters such as age, growth, mortality and age at sex change has been published for specimens from the Indian Ocean, while only limited data exist on the growth of the species in New Caledonia (Loubens 1980) and Papua-New Guinea (Munro & Williams 1985), both in the SW Pacific Ocean. It thus appeared necessary to undertake such a study on this species which remains highly targeted in non-protected areas, but is also often poached due to its abundance and accessibility in shallow and relatively unexposed protected areas. Indeed, the 'failed' MPA experience demonstrated that successful reef management can not be implemented without prior knowledge on reef key species.

In the present study, we first validated the yearly frequency and timing of ring formation in the otoliths of *E. merra* by analysing otoliths of fish of known age and marking individuals with a fluorescent chemical compound. We then examined the otoliths of this serranid to estimate for the first time in Réunion Island its age and growth. To do so, three otolith reading methods (*in toto* direct reading, transverse section direct reading, and transverse section automatic reading) were used and their outcome compared. Finally, we used these estimates of age and growth to infer mortality rate and age at sexual change of *E. merra* from the Réunion Island.

MATERIALS AND METHODS

Study area: The Réunion Island is a young (< 5M years) volcanic mountainous island of 2512 km² located in the south-western Indian Ocean, approximately 800 km east of Madagascar. Along with Mauritius and Rodriguez Islands, it constitutes the Mascarene Archipelago (Fig. 1). The coral formations are all fringing reefs located along the dry west and south-west coasts of the island, where

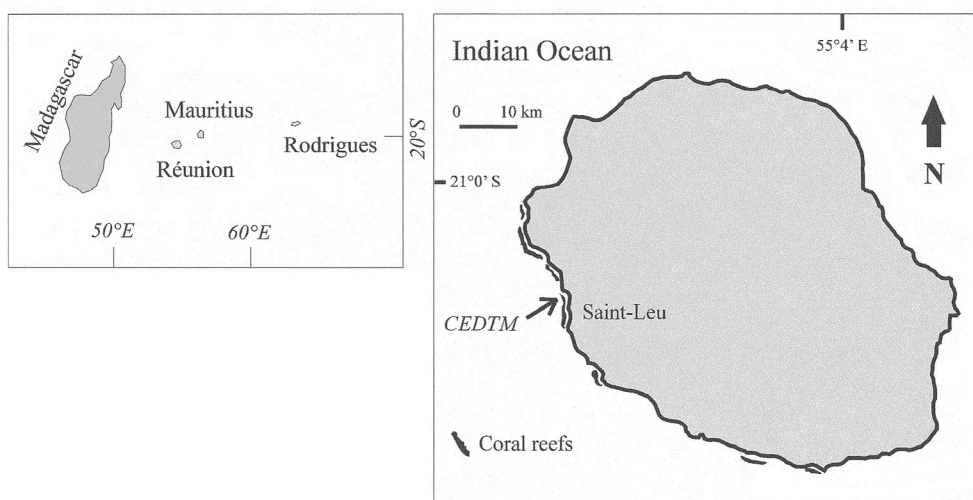


Fig. 1. – Location of Réunion Island in the south-western Indian Ocean, and of the CEDTM in front of the coral reef of Saint-Leu.

they form a discontinuous reef belt (Montaggioni & Faure 1980). Seawater temperature ranges from 23.3°C in austral winter to 27.7°C in austral summer (annual mean: 25.5°C) (Piton & Taquet 1992). Detailed environmental descriptions of Réunion Island have been given in previous studies (Montaggioni & Faure 1980, Naïm 1993, Letourneur 1996, Chabanet *et al.* 1997). The present work was carried out with fish collected in the artificial pools of the “Centre d’Études et de Découverte des Tortues Marines” (Sea Turtle Research and Display Center; hereafter CEDTM), which is located on land, close to one of the four Saint-Leu’ fringing reefs (Letourneur & Chabanet 1994) (Fig. 1). Until recently, CEDTM was a farm for juvenile marine turtles (*Chelonia mydas*) collected from isolated islets of the SW Indian Ocean and the Mozambique Channel, and comprised a total of thirty interconnected artificial pools (ten of 10 m³, ten of 40 m³, and ten of 100 m³). In 1996, the farm was converted into a research center coupled with a local museum for tropical sea turtles, with some specimens kept in captivity within some of the artificial pools alimented with seawater directly pumped from the shallow waters of the St-Leu fringing reef.

Species studied: The serranid *Epinephelus merra* Bloch, 1793 is widely distributed in the Indo-Pacific region (Randall & Heemstra 1993). Although this protogynous species mainly feeds on small invertebrates and fish (Harmelin-Vivien & Bouchon 1976, Harmelin-Vivien 1979), cannibalism can occur in particular circumstances (Letourneur *et al.* 1998). *Epinephelus* usually inhabits structurally complex coral reefs or rocky substrata (Chabanet 1994, Letourneur 1996) at depths of less than 10 m, but is occasionally found as deep as 50 m. In April 1994, a mass settlement of *Epinephelus merra* occurred on all Réunion coasts (Letourneur *et al.* 1998). During this event, hundreds of settlers were aspirated by the water lift pumps of the CEDTM and then remained in the artificial pools where they could shelter in artificial blocks of various sizes. They most likely fed on the numerous invertebrates and small fish continuously aspirated by the lift pumps and also possibly on marine turtle food debris which, however, did not include growth hor-

mones (Ciccione pers com). The individuals of *Epinephelus merra* remained hidden among the artificial blocks in the pools, displaying behaviour similar to that usually observed in the natural environment (Ciccione pers com). Although most of the fish present in the pools belong to the April 1994 mass settlers’ cohort, a few individuals were also more or less regularly aspirated by the water lift pumps over the years, but in much lesser abundance.

Sampling and marking procedure: An age assessment study must be complemented by a validation of increment periodicity in order to verify the determination of age with increments, thus avoiding over- or under-estimation of age. To validate the yearly frequency of otolith increment deposition, we analysed otoliths of fish of known age, and then compared the age estimates from otoliths with the real age. In addition, we used tetracycline marking to assess the timing of otolith formation, thus determining whether the large summer band was indeed formed in summer. A total of 38 individuals of *Epinephelus merra* from the CEDTM were marked with tetracycline injection at the beginning of summer (December 1999) and immediately released in the artificial pools. Tetracycline solution was prepared with tetracycline powder mixed with physiological liquid in order to avoid a strong difference with the blood pH. The solution was injected into the dorsal muscles with a syringe at a concentration of 50 mg of tetracycline per kg of fresh fish weight (Caillart & Morize 1989). Tagged fish were recaptured and sacrificed for otolith analysis on 1 February (26 fish), and 5 May 2000 (12 fish). Standard (SL) and total length (TL) were measured to the nearest millimeter and total weight to the nearest gram. Sex was also determined macroscopically, after the opening of the abdominal cavity.

Otolith analysis: Pairs of sagittae were removed under a binocular microscope, cleaned with distilled water, and stored dry in tubes placed in the dark (Vigliola 1997). Three reading methods were used to read the otoliths. The first method consisted of reading sagittae directly *in toto* under a binocular microscope. Observations were

performed using a bath of camomile essential oil in order to increase light transmission (Loubens 1978, Campana & Neilson 1985, Panfili 1992). For 'n' annual increments, the fish is hereafter aged 'n+'. The other two reading techniques required otoliths sectioning. Right sagittae were embedded in auto-polymerizing resin and, after 24 h of drying, sectioned transversally with a diamond wire saw coupled to a binocular microscope to choose the best section plane. The sectioned blocks were then fixed to a glass slide with a thermoplastic glue and polished using successively 1000 and 600 grit sandpapers, and a mix of alumina polishing compounds until a thin otolith section passing through the core was observed (Secor *et al.* 1991). The surface of this section was lightly decalcified to increase the optical contrast of growth increments (Campana & Neilson 1985). Each otolith section was then photographed. Depending on otolith size, several photos were necessary to cover each section. Photographs were then digitalized and reassembled into a large picture representing the entire otolith of each fish. The second otolith reading method consisted of a direct examination of those photos, while the third method consisted of automatically examining the photos using an image analysis software (Vigliola 1998). For each of the three reading techniques, each otolith was read several times until three consistent increment counts were obtained. A reading consisted of counting the number of increments from the core to the edge of the otolith, measuring the radius R of each increment, and locating the tetracycline mark. For the latter, we used a fluorescent microscope equipped with a Leitz filter combination (I2) which included a BP 450-490 nm exciter filter, a RKP 510 nm chromatic beam-splitter, and a LP 515 nm barrier filter.

Data analysis: A length-weight relationship was estimated by least square linear regression after log-transformation of both variables. This relationship obtained from 38 fish collected in artificial pools was then compared with the L-W relationship obtained in natural environments with 229 *E. merra* from Réunion Island (Letourneur 1998). In order to validate the yearly frequency of increment formation in otoliths of *E. merra* which entered the artificial pools at the time of the April 1994 mass settlement event, we expected that most fish collected in February 2000 would be 5+ years old, while those collected in May 2000 would be 6 years old. The tetracycline mark was used to further understand the process of increment formation in *E. merra*. Indeed, the location of the tetracycline mark induced in otolith at the beginning of the summer should correspond with the formation of a large translucent summer band, while the growth of the marginal increment measured between February and May should correspond to the period of fastest otolith growth. For each reading method and for each fish, size at age was back-calculated using the Lea (1910) growth back-calculation model:

$$L_t = (L_c \times R_t) / R_c ; \text{ where } L_c = \text{total length at time of capture, } L_t = \text{total length at time of } t\text{th annulus formation, } R_c = \text{radius at time of capture, and } R_t = \text{radius at time of } t\text{th annulus formation.}$$

A von Bertalanffy (1938) growth model was then fitted to this data set by non-linear regression:

$$L_t = L_\infty(1 - \exp^{-K(t-t_0)}) ; \text{ where } L_t \text{ is the fish length at age } t, L_\infty \text{ the theoretical asymptotic length, } K \text{ the body growth coefficient, and } t_0 \text{ the age when fish length is 0. This model, hereafter called model (1), is by far the most}$$

commonly used to estimate growth in fishes. However, we also used a modified von Bertalanffy growth model without considering t_0 , due to its non-significance from a biological point of view. This model, hereafter called model (2), assumes in fact that fish are of length 0 at hatching ($L_t = L_\infty(1 - \exp^{-Kt})$). We also looked at the coefficient of correlations between the data and the models, in order to determine whether model (2) could be considered better than model (1).

Assessment of mortality: The instantaneous rate of natural mortality (M) was inferred from the growth parameters using the methods of Pauly (1980), Hoenig (1983) & Ralston (1987). We are aware that these methods are not very powerful, but they are widely used in fisheries and then could allow useful comparisons. Conversely, we were not able to use the model of Ault *et al.* (1998) usually considered as more powerful, because it is based on the parameter of longevity St (i.e. the survivor rate of a cohort reaching the maximum age reported in a virgin stock) for which any estimate can be made in our case.

The Pauly method estimates M through log-transformations:

$$\text{Log}_{10}M = 0.0066 - 0.279\text{Log}_{10}L_\infty + 0.6543\text{Log}_{10}K + 0.4634\text{Log}_{10}T \text{ (parameters as above, and } T \text{ is the mean seawater temperature).}$$

The Hoenig method is a longevity-mortality relation, adjusted for sample size, based on the principle that with a larger sample size there is a greater probability of encountering the true maximum age of the fish:

$$M = (\text{Ln}(2n+1)) / (t_{\max} - t_c); \text{ where } n \text{ is the sample size, } t_{\max} \text{ the highest age represented in the catches, and } t_c \text{ the first age fully represented in the catches. Here, } t_{\max} = 7, \text{ and } t_c = 4 \text{ (see result section). Finally, the Ralston method uses the following formula: } M = 0.0189 + 2.06K.$$

RESULTS

Length-weight relationship

The TL-SL relationship (size range of individuals: 16.8 to 24.0 cm SL) was the following: $SL = 0.75TL + 26.84$ ($n = 38$, $r = 0.94$).

In artificial pools, the length-weight relationship of *E. merra* was:

$$\text{Ln}(W) = 3.015 \text{ LT} - 1.970 \text{ (} n = 38, r = 0.99\text{); while in the natural environment it was: } \text{Ln}(W) = 3.196 \text{ LT} - 2.018 \text{ (} n = 229, r = 0.99\text{) (Letourneur 1998). Both relationships had similar slopes (} F_{0.01(1,116)} = 6.76; p < 0.01\text{) and intercepts (} F_{0.01(1,117)} = 6.76; p < 0.01\text{). The length-weight relationships in natural and semi-artificial habitats were thus not statistically different.}$$

Timing of otolith increment formation

All fish survived and were in good health after injection of tetracycline in December. The tetracycline mark induced was not clearly visible and was

most often diffuse under the fluorescent microscope in otoliths of individuals sampled in February, about one month after injection. However, a clear and distinct red mark was present near the edge of the otolith of individuals sampled at the beginning of May, a little more than four months after injection. No thin "white opaque" band was observed between the tetracycline mark and the edge of the otolith, suggesting that the large translucent band that characterizes fast growth was formed in summer in *E. merra*.

Validation of otolith increments

The number of increments counted in the otoliths of the 38 *E. merra* ranged between four (thus, a 4+ aged fish) and seven (thus, a 7+ aged fish), all reading methods confounded. Readings were consistent among methods for 31 of the 38 fish. Among these 31 individuals, age estimate from otolith analysis indicated that fish were 5+ (25 fish) or 4+ and 6+ (3 fish) years old (Table I), which is consistent with the mass settlement of April 1994 and demonstrates the yearly periodicity of increment deposition in the otoliths of *E. merra* from Réunion Island.

Table I. – Observed age, size (TL cm) and weight (g) data for *Epinephelus merra* from Réunion Island. Individuals with age differing according to the otolith reading used were not considered here.

Age	N	Size		Weight	
		Mean (sd)	Min-max	Mean (sd)	Min-max
4+	3	23.3 (3.7)	19.7 - 27.2	253 (81)	158 - 300
5+	25	23.6 (2.5)	19.5 - 27.6	260 (84)	110 - 400
6+	3	26.2 (1.7)	24.7 - 28.0	323 (64)	250 - 370

Age, growth and mortality

Estimates of the growth parameters resulting from the von Bertalanffy equation (models (1) and (2)) varied between the methods and the models used (Table II). Asymptotic length ranged between 19.8 and 25.0 cm (TL), k varied between 0.43 and 0.80, whereas t_0 (model (1)) was the less variable parameter, and ranged between -0.009 and -0.010 . The asymptotic weight derived from these estimates ranged between 146 and 295 g.

The coefficients of correlation between data and models (Table II) were slightly higher with model (2) than with model (1), indicating that model (2) could be considered as better than model (1). If we thus consider model (2), the theoretical asymptotic length (L_∞) indicated a relatively low maximum size of *Epinephelus merra*, ranging from 21.8 to 25.0 cm (TL) (corresponding respectively to values of W_∞ ranging from 195 to 295 g). The values of k , ranging from 0.43 to 0.8 indicated a rapid growth.

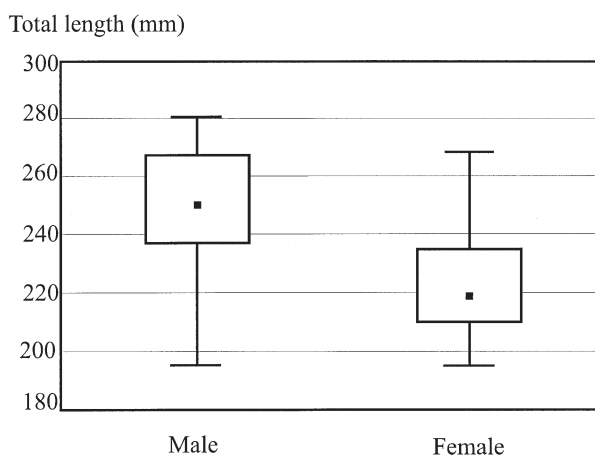


Fig. 2. – Comparison of total length between males ($n=16$) and females ($n=22$) of *Epinephelus merra* from the CEDTM, Réunion Island. Black-spot is mean, white box is the 25%-75%, range of data, and vertical bars are min and max values.

These estimates of growth rate were used to assess mortality rates for *Epinephelus merra* using the Pauly' and Ralston equations. Mortality estimates for *E. merra* from Réunion Island ranged between 0.90 and 1.67 (Table II). The Hoenig equation estimated a mortality of 1.45.

Table II. – Top, Parameters of the von Bertalanffy growth curve of *Epinephelus merra* obtained with the three otolith reading methods. $N = 132$ (otolith increments and back-calculation pooled together). R is the coefficient of correlation. W_∞ calculated from the LW relationship. Bottom, estimates of the rate of natural mortality for *Epinephelus merra* from Réunion island obtained from the Pauly & Ralston equations for the two models and three different otolith reading methods.

	<i>In toto</i>	Numerized pictures	Image analysis software
Model (1)			
L_∞ (TL, cm)	21,2	19,8	20,2
k	0,5	0,7	0,6
t_0	-0,009	-0,01	-0,009
R	0,93	0,88	0,88
W_∞ (g)	180	146	155
Model (2)			
L_∞ (TL, cm)	25,0	21,8	22,0
k	0,43	0,7	0,8
R	0,94	0,90	0,89
W_∞ (g)	295	195	201
	<i>In toto</i>	Numerized photographs	Image analysis software
Model (1)			
Pauly equation	1,23	1,57	1,41
Ralston equation	1,05	1,46	1,25
Model (2)			
Pauly equation	1,07	1,53	1,66
Ralston equation	0,90	1,46	1,67

Male-female comparison

Our sampled individuals confirmed the protogynous state of the species, which is first female, then male (Table III). Indeed, 75% of females were smaller than 23.5 cm (TL) and 75% of males were larger than 23.7 cm (Fig. 2). The mean length (TL) of males was 24.7 cm and 22.3 cm for females. As variances were the same between males and females ($F_{0,01(22, 14)} = 4.07$; $p < 0.01$), a SNK-test (or t -test) of comparison of means was applied. The SNK-test indicated a significant difference between mean size of the sexes ($t = 2.704$; $p < 0.01$).

Table III. – Size (TL cm) and weight (g) of females and males of *Epinephelus merra* in our sample (N = 38). Values in parentheses are confidence intervals at $\alpha = 0.05$.

	N	Size		Weight	
		Min-max	Mean	Min-max	Mean
Females	16	16.5 - 26.8	22.3 (1.1)	110 - 350	216 (41)
Males	22	19.5 - 28.0	24.7 (1.0)	140 - 400	297 (29)

Similarly, the mean weight of males was 297 g and 216 g for females. As variances were the same between males and females ($F_{0,01(22, 14)} = 10.77$; $p < 0.01$), a SNK-test of comparison of means was applied. The SNK-test indicated a significant difference between mean weight of the sexes ($t = 3.283$; $p < 0.005$).

DISCUSSION

Age, growth and mortality are important assessment parameters for fish biology. For the Serranidae, most research on these aspects has been conducted on large species (Manooch & Mason 1987, Mathews & Samuel 1987, Chauvet 1988, Bullock *et al.* 1992, Sadovy *et al.* 1992, Johnson & Collins 1994, Vaughan & Burton 1994, Potts & Manooch 1995, Sadovy & Eklund 1999) and comparisons with *E. merra* were thus impossible. Only a few studies have been conducted on small sized species (Mathews & Samuel 1987, Chan & Sadovy 2002). Except for the works of Loubens (1980) and Munro & Williams (1985) who provided some data on growth for *E. merra* in the SW Pacific Ocean, the present work thus represents the first attempt to elucidate these aspects for that species. We have shown that otoliths of *E. merra* were easy to read and interpret, with annuli appearing to form during the austral summer, and the yearly frequency of otolith increment deposition was validated.

Methods

Asymptotic length was smaller than the size of most of our fish. This could be due to Lee's phe-

nomenon (Lee 1920). Indeed, we used a linear back-calculation model whereas it has been shown in several species that the length-weight relationship was allometric and our sample was constituted by medium and large sized individuals, which increases the likelihood of Lee's phenomenon (Francis 1990).

The assessment of timing of otolith formation with tetracycline injection (December) was efficient only with individuals sacrificed at the beginning of May, but not with those sacrificed in February. This suggests that, for *Epinephelus merra* (medium and large sizes), there was about a two month-lag between injection and the appearance of marks on otoliths, possibly due to physiological and/or biological processes. This particularity must be taken into account for further research on this species.

Length-weight relationship and size at sex change

We found that L-W relationship for our semi-artificial habitat did not differ from that found in a natural habitat by Letourneur (1998). Although we are aware that variation in length of fish over time is not necessarily always linked to L-W relationship, this result suggests however that the growth of *Epinephelus merra* could not have been affected by the characteristics of this semi-artificial habitat. This could be due to the characteristics of this species which is generally a sedentary ambushing predator. The CEDTM is run on the basis of research and museum requirements and is not at all concerned with production requirements, and this might explain why conditions in this semi-artificial habitat are so close to natural ones. Similar results and interpretations have been reported for *E. polyphkadion* which also has the typical behaviour of groupers and thus could be well suited to semi-artificial conditions (Caillart & Morize 1989). In the local context, but also possibly elsewhere in coral reef ecosystems, this result is particularly interesting because the wide range of types of degradation in reef health throughout the tropics (overfishing, urbanization, nutrient enrichment, etc.) could prevent a sufficient sampling range for individuals. Then, the use of a semi-artificial habitat could offer a valuable alternative if individuals are rare and/or difficult to catch, because it could allow the maintenance of individuals under growth conditions similar to those found in natural habitat, at least for groupers, until an adequate number of individuals is reached.

Possibly due to Lee's phenomenon, we recorded sizes at sex change higher than the L_{∞} calculated with von Bertalanffy growth curves. So theoretical sizes at sex change were recalculated with model (2) from the age of individuals. With these calculations, size at sex change ranged from 18 and 20 cm

(TL), corresponding to ages ranging from 3 to 5 years. Randall & Heemstra (1991, 1993) indicated that mean size of males is about 20 cm, and is thus consistent with our results. This information is important mainly because there is a clear ontogenetic shift in habitat use by this species, as found for other groupers (Shpigel & Fishelson 1989, Eggleston 1995, Sadovy & Eklund 1999), with small and medium sized individuals (immature and females) mainly inhabiting shallow coral reef flats (Letourneur 1996, Letourneur *et al.* 1998) and large sized individuals (males) inhabiting the outer reef slope (Chabanet 1994). Despite the recent (1997) protective measures on most coral reef areas in Réunion Island, poaching remains frequent. All poachers used line-and-hook (sometimes spear-gun) and mostly target *Epinephelus merra* on shallow reef flats. These practices could potentially cause disequilibrium in the sex-ratio, with possible effects on reproductive, recruitment and/or settlement processes as well as on demographic structures (Jennings & Lock 1996, Jennings & Kaiser 1998).

Possible implications for fishery management

To our knowledge, only Loubens (1980) and Munro & Williams (1985) provided some comparative data for this species, but only on growth for fish from the SW Pacific Ocean. They mentioned, respectively, L_{∞} of 18.0 cm SL and of 41.0 cm TL, and k values of 0.27 and 0.4. The L_{∞} value of Loubens (1980) was roughly similar to our results (TL), but he found a much lower growth rate, i.e. our k estimates were 2- or 3-fold higher, whereas the L_{∞} of Munro & Williams (1985) was almost twice our values, with a k' value 2-fold lower than ours. Such differences between our results and

those of these authors could be due to methodological problems, i.e. Lee's phenomenon in our case, the use of the graphical Petersen's method which is not very powerful for Munro & Williams (1985). Alternatively, they could be explained by spatial variation in growth parameters. Our results indicated rapid growth and a relatively high natural mortality rate. Estimates of M depending on the methods used were roughly equivalent, but we were not able to assess the fishing mortality (F), and thus the instantaneous rate of total mortality (Z). These assessments would require good evaluation of catches or landings (catch-at-age data), which were not available in Réunion for this species, mainly due to poaching and lack of organization of the local fishermen. In addition, various parameters of the reproductive processes (age at first maturity, fecundity etc.) are not known. Finally, the ontogenetic shift in the habitat use of *E. merra* (Letourneur 1996) could also generate higher fishing pressure on immature and female individuals than on males due to local practices, thus possibly affecting reproduction (Jennings & Lock 1996, Jennings & Kaiser 1998).

Table IV gives growth curve equations for some other Serranidae. Although far from being exhaustive, these examples simply highlight that most studies carried out on growth and/or mortality patterns of grouper concerned large species which often have a high commercial value. The current state of several coral reef areas throughout the world seems to indicate a clear danger of overfishing of various species (Roberts 1995, Jennings & Lock 1996). In this context, and as found for other marine ecosystems, the trend is to fish for smaller fish and/or smaller species (Jennings & Kaiser 1998, Pauly *et al.* 1998). The Réunion Island is not an exception to this general trend, as fishing pressure is high and large fishes are now scarce (Taquet &

Table IV. – Growth curve equations of some Epinephelinae. TL in mm.

Species	Area	von Bertalanffy growth curve	Source
<i>Cephalopholis miniata</i>	Kuwait	$TL = 341.1 \times (1 - e^{-0.1102(t+2.4160)})$	Mathews and Samuel, 1987
<i>Epinephelus adscensionis</i>	California, Florida	$TL = 499.4 \times (1 - e^{-0.167(t+2.495)})$	Potts and Manooch 1995
<i>E. aurealatus</i>	Kuwait	$TL = 391 \times (1 - e^{-0.288(t+1.023)})$	Mathews and Samuel 1987
<i>E. bonaci</i>	SE of USA	$TL = 1352 \times (1 - e^{-0.115(t+0.927)})$	Manooch and Mason 1987
<i>E. chlorostigma</i>	Kuwait	$TL = 648.3 \times (1 - e^{-0.195(t+3.723)})$	Mathews and Samuel 1987
<i>E. guttatus</i>	California, Florida	$TL = 471.4 \times (1 - e^{-0.2(t+2.397)})$	Potts and Manooch 1995
<i>E. guttatus</i>	Puerto Rico	$TL = 514.5 \times (1 - e^{-0.101(t+2.944)})$	Sadovy <i>et al.</i> 1992
<i>E. itajara</i>	Gulf of Mexico	$TL = 2006 \times (1 - e^{-0.126(t+0.491)})$	Bullock <i>et al.</i> 1992
<i>E. jayakari</i>	Kuwait	$TL = 726.5 \times (1 - e^{-0.293(t+1.208)})$	Mathews and Samuel 1987
<i>E. latifasciatus</i>	Kuwait	$TL = 821.1 \times (1 - e^{-0.328(t+0.205)})$	Mathews and Samuel 1987
<i>E. morio</i>	Gulf of Mexico	$TL = 789 \times (1 - e^{-0.178(t-0.826)})$	Johnson and Collins 1994
<i>E. morio</i>	USA	$TL = 1000 \times (1 - e^{-0.15t})$	Vaughan and Burton, 1994
<i>E. nigritus</i>	Cuba	$TL = 940 \times (1 - e^{-0.063(t+1.12)})$	Sadovy and Eklund 1999
<i>E. nigritus</i>	SE of USA	$TL = 2394 (1 - e^{-0.054t})$	Manooch and Mason 1987
<i>E. niveatus</i>	Florida Keys	$TL = 1320 \times (1 - e^{-0.087(t+1.013)})$	Moore and Labisky 1984
<i>E. striatus</i>	Cuba	$TL = 760 \times (1 - e^{-0.127(t+1.12)})$	Sadovy and Eklund 1999
<i>E. tauvina</i>	Kuwait	$TL = 991 \times (1 - e^{-0.15(t+0.34)})$	Lee and Al-Baz 1989
<i>E. tauvina</i>	Kuwait	$TL = 930 \times (1 - e^{-0.1655(t+0.3099)})$	Mathews and Samuel 1987
<i>Mycteroperca microlepis</i>	Florida	$TL = 1190 \times (1 - e^{-0.166(t+0.62)})$	Hood and Schlieder 1992

Teissier pers com). For these reasons, it is essential to have a better knowledge on the life history of small species, such as *E. merra*. This is probably the only reasonable way to better manage the fisheries and resolve conflicts between users of the protected coral reef areas of the island.

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