Abstract.— Otoliths were used to determine the age and growth of the coral trout *Plectropomus leopardus* from Lizard Island area, Northern Great Barrier Reef, Australia. An alternating pattern of opaque (annulus) and translucent zones was visible in whole and sectioned otoliths. However, compared to sectioned otoliths, whole readings tended to underestimate age of older fish. Otoliths of mark-recaptured fishes treated with tetracycline showed that one annulus is formed per year during the winter and spring. The oldest individual examined was 14 years of age. Schnute's growth formula was used to determine the best model to describe the growth of the coral trout. The von Bertalanffy model for fork length (FL) fitted the data well and the resulting model was $L_t = 52.2(1 - e^{-0.354(t + 0.766)})$. Line-fishing usually does not capture fishes smaller than 25 cm FL, thereby excluding most 0+ and 1+ year old fish and probably the slower growing 2+ year old fish. These first three years of life represent the period of fastest growth, so, if the growth curve is fitted only to the line fishing data, the growth rate of the population is underestimated. Multiple regression was used to predict age from otolith weight and fish length and weight. Otolith weight was the best predictor of age in the linear model and explained as much variation in age as fish size in the von Bertalanffy model.

Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus,* (Lacepede 1802) from Lizard Island, Northern Great Barrier Reef

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The coral trouts of the genus *Plectropomus* Oken are members of the serranid subfamily Epinephelinae, commonly known as groupers. These fishes occur in shallow tropical and subtropical seas of the Indo-Pacific region (Randall and Hoese, 1986) where they usually are at the top of food chains and thus play a major role in the structure of coral reef communities (Randall, 1987).

Groupers typically represent an important fishery resource throughout the tropical and subtropical regions of the world (Ralston, 1987). On the Great Barrier Reef, the common coral trout *Plectropomus leopardus* (Lacepede 1802) is the most abundant species of the genus (Randall and Hoese, 1986) and usually the primary target of recreational and commercial fishermen. The Queensland commercial line-fishing fleet takes a total annual catch of about 4,000 metric tons (t) of reef and pelagic species. The coral trout composes the largest single component of this catch (over 30%) with around 1200 t caught annually (Trainor, 1991). The recreational sector of this fishery is estimated to catch two to three times the commercial catch of reef fish (Craik, 1989[1]).

Worldwide studies on age and growth of Epinephelinae indicate that they are long lived, slow growing, and have relatively low rates of natural mortality (Manooch, 1987). Fishes with these characteristics are susceptible to overfishing. Only by obtaining validated estimates of growth is it possible to determine population dynamics, estimate potential yield, monitor the responses of populations to fishing pressure, and properly manage the fishery.

Some information on age, growth, and longevity is available for the common coral trout. On the Great Barrier Reef, Goeden (1978) estimated the growth rate of this species at Heron Island from length-frequency data. Mcpherson et al. (1988), determined age and growth of the common coral trout in the Cairns region by counts of annuli in whole otoliths. Loubens (1980) estimated age and growth for *P. leopardus* from New Caledonia from counts of annuli in broken and burnt otoliths. The periodicity of formation of annual rings in the latter two studies was verified through observation of marginal

[1] Craik, G. J. S. 1989. Management of recreational fishing in the Great Barrier Reef Marine Park Tech. Memo. GBRMPA-TM-23, 35p.

increments in otoliths. Direct validation of age has not yet been attempted for *P. leopardus*.

Fish population models usually require a general description of the growth process by means of an appropriate mathematical function. The von Bertalanffy (1938) growth model is the most studied and the most frequently used, since its application by Beverton and Holt (1957) to the yield-per-recruit problem (Kimura, 1980; Gallucci and Quinn, 1979). Many alternative growth curves have been proposed (see Moreau, 1987) as well as the use of polynomial functions (Chen et al., 1992). In this work, Schnute's (1981) formula was used to find the model that best described the growth of *P. leopardus*.

For several species of fishes, otolith growth has been found to continue with age, independent of fish size (Boehlert, 1985; Casselman, 1990; Beckman et al., 1991). Boehlert (1985) suggested the use of otolith weight as a non-subjective, cost-effective methodology for age determination that would decrease variability among age estimates.

The aims of this study were to obtain direct validation of age-at-length information and to find the model that best described the growth of the common coral trout from Lizard Island, Northern Great Barrier Reef, Australia. In addition, the relationship between otolith weight, body size, and age of the coral trout was studied to understand the mode of growth of the otolith and to assess the usefulness of otolith dimensions in predicting age.

Materials and methods

Coral trout (*n*=310) were sampled in the Lizard Island area (lat. 14° 40' S, long. 154° 28' E) from March 1990 to February 1992. Fishes were caught by recreational and commercial fishermen using hook and line (*n*=184) and by recreational spearfishermen (*n*=94). Individuals smaller than 20–cm total length are usually not vulnerable to line fishing, so they were caught around Lizard Island by scuba divers using fence nets (*n*=32). Fork length (FL, cm), standard length (SL, cm) and total weight (TW, g) were measured for each fish. FL is defined as the length from the front of the snout to the caudal fork, and SL is defined as the length from the front of the upper lip to the posterior end of the vertebral column. A simple linear regression of the form FL= *a* + *b**SL was used to describe the relationship between FL and SL. To describe the relationship between FL and TW the variables were logarithmically transformed and the linearized version of the power function $TW(g)= a*FL(cm)b$ was fitted to the data.
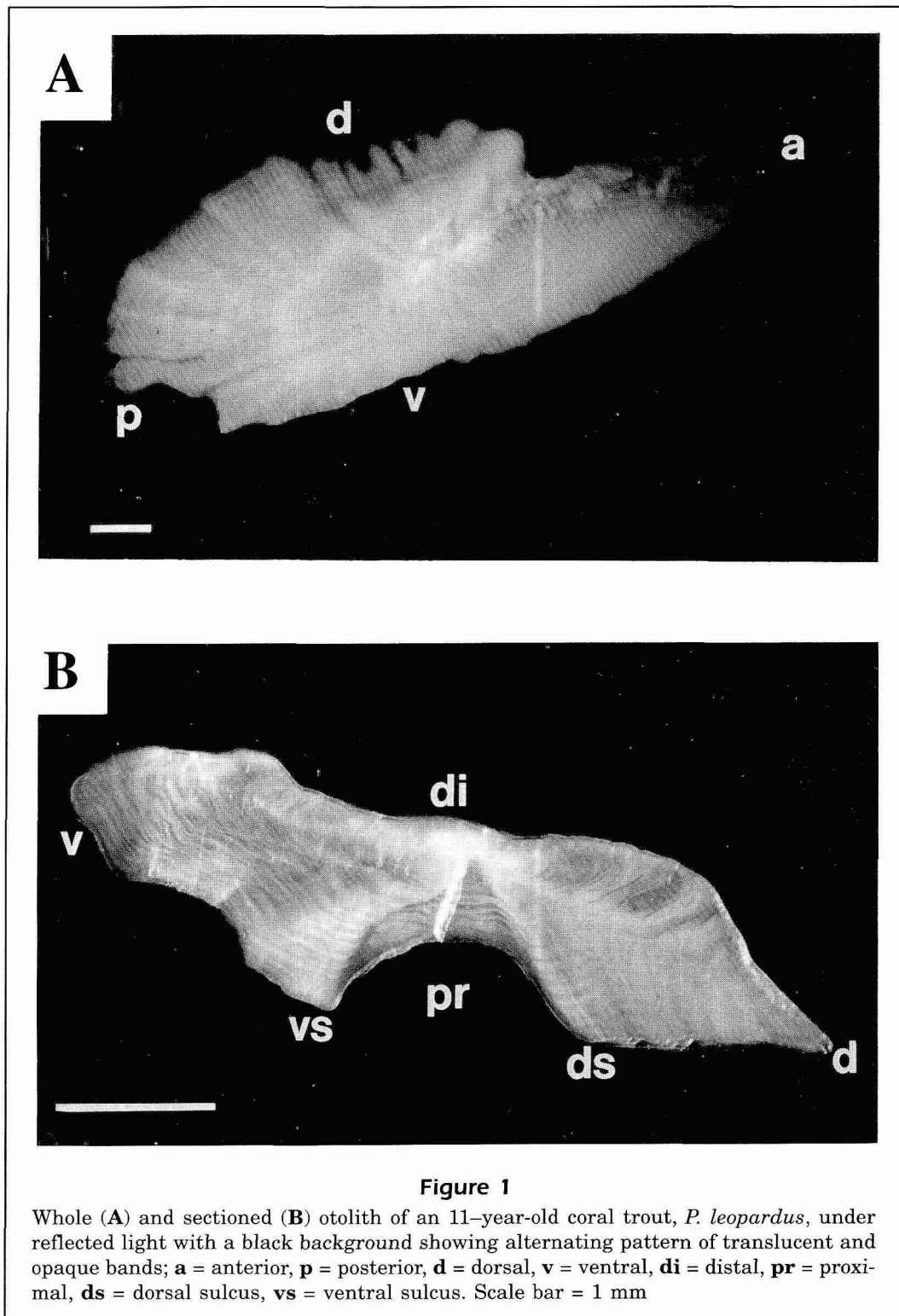
In the coral trout, the sagittae are the largest of the three pairs of otoliths and were used for readings. Sagittae were removed, cleaned, weighed, and stored dry. Left and right sagittae, when intact, were weighed to the nearest milligram. Otoliths were prepared and read as described by Ferreira and Russ (1992). To increase contrast between bands, whole otoliths were burned lightly on a hot plate at 180°C (Christensen, 1964). Both right and left sagitta were read whole under reflected light with a dissecting microscope at 16× magnification. The otoliths, with the concave side up, were placed in a black container filled with immersion oil. Subsequently, the left sagittae was prepared for reading by embedding in epoxy resin (Spurr, 1969) and sectioning transversely through the core with a Buehler Isomet low-speed saw. Sections were mounted on glass slides with Crystal Bond 509 adhesive, ground on 600– and 1200–grade sand paper, polished with 0.3–μ alumina micropolish and then examined under a dissecting microscope at 40× magnification with reflected light and a black background (Fig. 1). Annuli were counted from the nucleus to the proximal surface of the sagitta along the ventral margin of the sulcus acousticus.

Terminology for otolith readings followed definitions of Wilson et al. (1987). Two experienced readers independently counted opaque zones (annuli) in each whole and sectioned otolith of a random subsample (*n*=136) to assess the precision and accuracy of countings obtained by the two methods. The precision of age estimates was calculated with the Index of Average Percent Error (IAPE), (Beamish and Fournier, 1981). Results obtained from whole and sectioned otoliths were compared by plotting the difference between readings obtained from whole and sectioned otoliths (Section Age-Whole age) against Section Age. The results of this comparison indicated that whole otolith readings tended to be lower than readings from sectioned otoliths when more than six rings occurred in the otolith. Therefore, remaining otoliths were read whole first and, if the number of rings was higher than six or the whole otolith was considered unreadable, the otolith was sectioned and counts were repeated. The results were accepted and used in the analysis when the counts of the two readers agreed. If the counts differed, the readings were repeated once and if the counts still differed, the fish was excluded from the analysis.

Ages were assigned based on annulus counts and knowledge of spawning season. The periodicity of annulus formation was determined with the use of tetracycline labelling. From August 1990 to February 1992, 80 fishes were caught in a trapping program at Lizard Island fringing reef (Davis, 1992[2]),

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[2] C. Davies. 1992. James Cook University. Townsville. Q4811, Australia, unpubl. data.

Figure 1

Whole (**A**) and sectioned (**B**) otolith of an 11–year-old coral trout, *P. leopardus*, under reflected light with a black background showing alternating pattern of translucent and opaque bands; **a** = anterior, **p** = posterior, **d** = dorsal, **v** = ventral, **di** = distal, **pr** = proximal, **ds** = dorsal sulcus, **vs** = ventral sulcus. Scale bar = 1 mm

tagged with T-bar anchor tags and injected with tetracycline hydrochloride before being released. The fish were injected in the coelomic cavity under the pelvic fin with a dosage of 50 mg of tetracycline per kg of fish (McFarlane and Beamish, 1987), in a concentration of 50 mg per mL of sterile saline solution.

Five fish were recaptured after periods of at least one year at large. Two of those fish were reinjected at the time of recapture and kept in captivity for periods of three to four months.

To determine the time of formation of the first annulus, five young of the year were captured with

fence nets. Three of these fishes were injected with tetracycline at the time of capture, and all five fish were kept in captivity for periods of 3 to 17 months. The otoliths of the fishes treated with tetracycline were removed, sectioned, and observed under fluorescent light. To determine time of formation of the translucent and opaque zones, the distances between events for which time of occurrence was known (i.e., between two tetracycline bands or between a tetracycline band and the margin of the otolith) were measured on otolith sections and plotted against the corresponding time interval. The relative positions of the translucent and opaque zones to these marks were then measured and plotted on the same scale. While this method does not provide real distances, it standardizes the measurements allowing for comparison between fish of different ages.

The relation between otolith weight, fish size (length and weight), and age was analyzed. Otolith weight was plotted against FL for each age class separately. A multiple linear regression model was fitted in a step-wise manner to predict age from otolith weight and fish size and to predict otolith weight from age and fish size. The inclusion level for the independent variables was set at $P=0.10$. The assumptions of normality and homoscedasticity were tested by plotting the residuals from the regression models.

The growth models were fitted to the data and their coefficients and standard errors estimated by means of standard non-linear optimization methods (Wilkinson, 1989). As the plot of the length-at-age data indicated, some form of asymptotic growth, Schnute's (1981) reformulation of the von Bertalanffy growth equation for length in which $a \neq 0$ was fitted to the data:

$$L_t = y1^b + (y2^b - y1^b)\left\{\frac{1-e^{-a(t-t1)}}{1-e^{-a(t2-t1)}}\right\}^{\frac{1}{b}}$$

where L_t is length at age; $t1$ and $t2$ are ages fixed as 1 and 14 respectively; $y1$ and $y2$ are estimated sizes at these ages; and a and b are the parameters which indicate if the appropriate growth curve lies closer to a three or two parameter sub-model. By limiting parameter values, the data were used directly in selecting the appropriate sub-model, namely the generalized von Bertalanffy, Richards, Gompertz, Logistic, or Linear growth models. Subsequently, the original von Bertalanffy (1938) growth equation for length $L_t = L_\infty (1 - e^{-K(t-to)})$ was fitted to the data. L^t is length at age; L_∞ is the asymptotic length, K is the growth coefficient, t is age, and t_0 is the hypothetical age at which length is zero.

To evaluate the effects of gear selectivity (and consequently varying size and age composition) on the estimates of growth parameters, the von Bertalanffy growth equation was fitted first to data collected by line and spear fishing only and then to the same data combined with the fence-net sample composed of younger fish.

Results

Otolith reading

In the coral trout, the sagittae presented a pattern of alternating translucent zones and wide opaque zones (annuli) with no sharp contrast between zones (Fig. 1). The first two annuli were notably wider and less well defined than the subsequent ones in sectioned otoliths. Whole sagittae were used to confirm the presence of these first annuli.

In whole otoliths, annuli were clearly distinguishable and easy to count along the dorsal side of the otolith, where up to 12 rings were counted in some otoliths. However, readings from whole otoliths tended to be lower than readings from sectioned otoliths when more than six rings were present, and this tendency increased with the mean number of rings, particularly after ten rings. (Fig. 2). Tetracycline-labelled otoliths validated the periodicity of annuli in sectioned otoliths, indicating that whole otolith readings tend to underestimate age of >10-year-old fishes. A comparison between results of
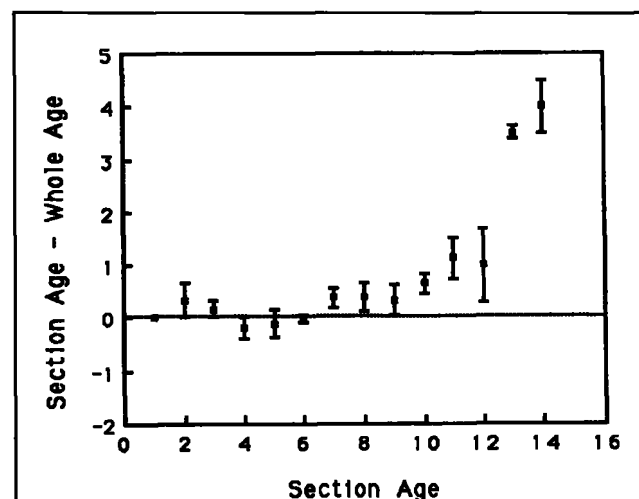

Figure 2

Average difference between counts obtained from sectioned and whole otoliths (Section Age-Whole Age) of coral trout, *P. Leopardus*, plotted against Section Age. Error bars show standard error.

countings performed on whole and sectioned otoliths showed that, in the sub-sample analysed, the Index Average Percent Error (IAPE) of Beamish and Fournier (1981), was lower for counts performed on whole (6.7%) than for counts performed on sectioned otoliths (12.1%). For the total sample, where readings from whole and sectioned otoliths were integrated, the IAPE was reduced to 5.1%.

Otolith growth

Otolith weight was directly related to age and an exponential function of fish length (Fig. 3). Within each age class, otolith weight was positively correlated with fork length for most classes (Table 1), indicating a tendency for larger fish to have larger
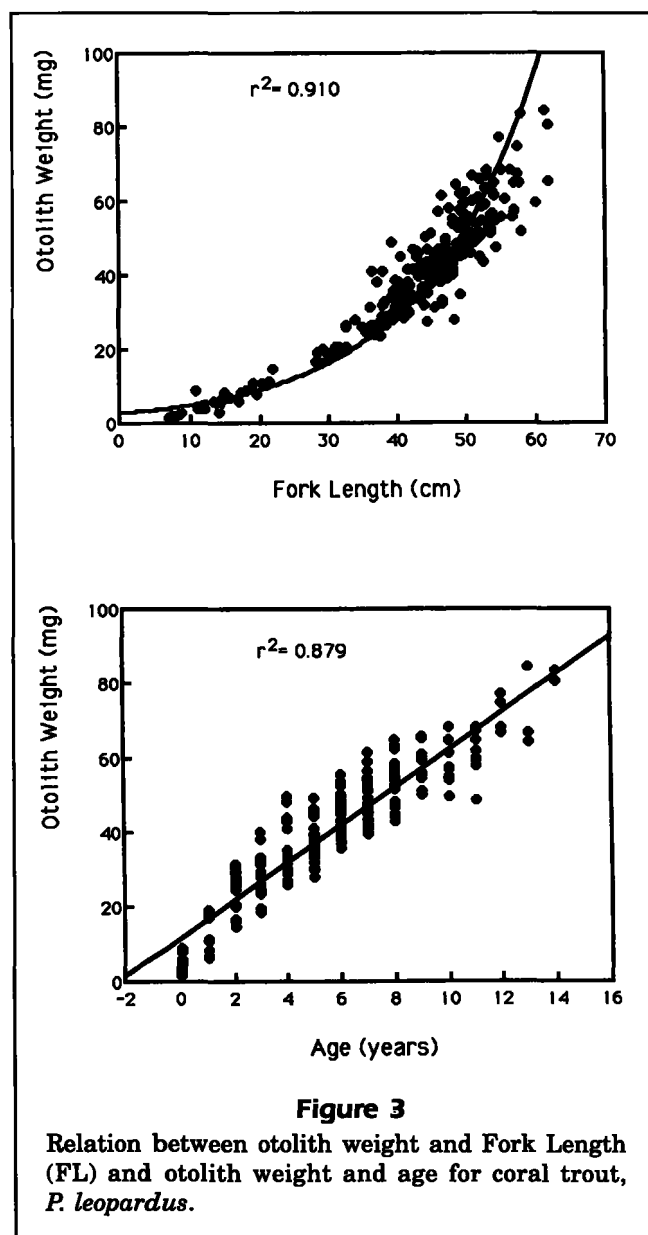
otoliths than smaller fish of the same age. The weight of the otolith was a good predictor of age and accounted alone for 89% of the variability in age of the coral trout (r^2=0.889, P<0.0001), with fork length accounting for 1.5% (partial r^2= 0.015). Otolith weight was a function of age and fish size, as indicated by the results of the multiple regression fitting. The interaction between age and fork length alone accounted for 89% of the variability (r^2=0.892, P<0.0001)
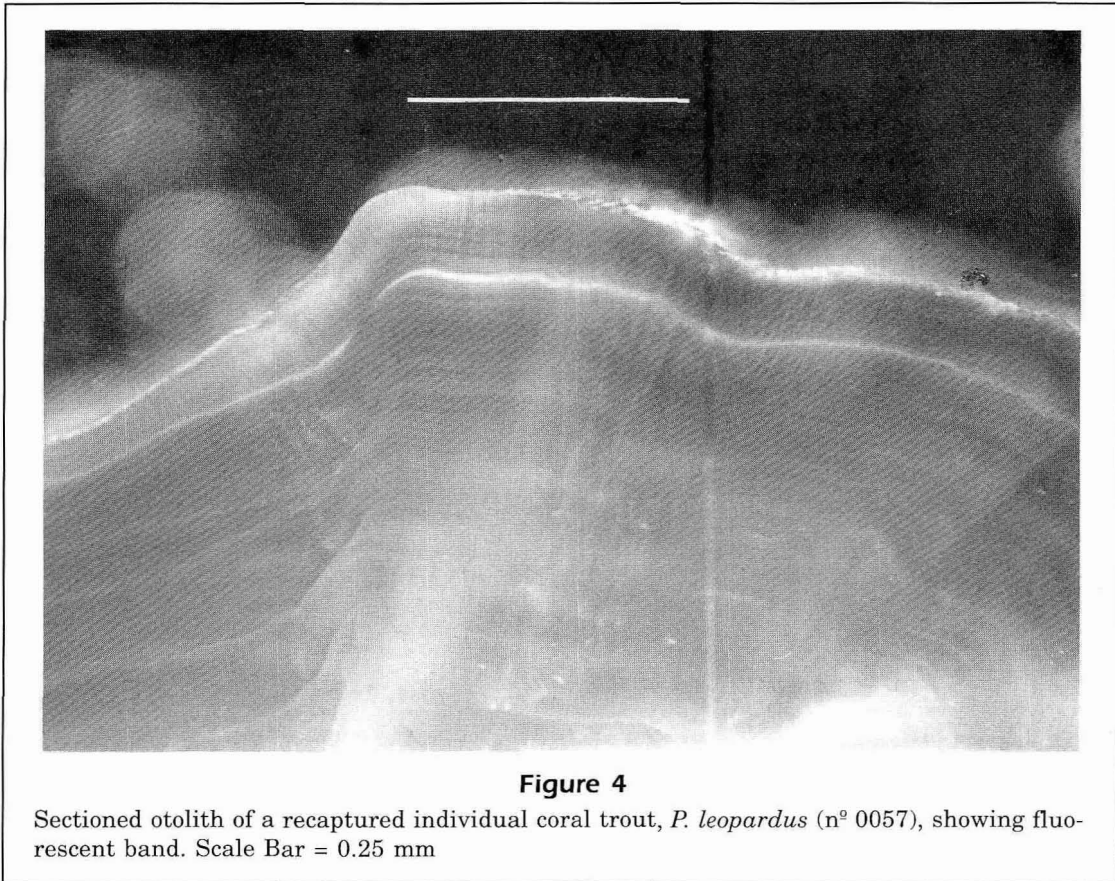
Validation of annulus formation

All fishes treated with tetracycline displayed clear fluorescent marks in their otoliths (Fig. 4). The results obtained for recaptured and captive fish, ranging in age from one to eight years, showed that annuli are formed once per year (Fig. 5). The first annulus is formed in the otoliths of the juvenile coral trout during their first year of life (Fig. 6). The relative positions of the fluorescent bands, in relation to the otolith margin and the translucent and opaque zones (annuli), indicated that the formation of the annulus occurred mainly during winter and early spring (Figs. 5 and 6).

Growth model

The samples obtained from line-fishing and spearfishing were selective towards individuals larger than 25 cm FL. Consequently, the 0+ age class was not represented in this sample and the age-1 year class was represented by only four individuals (Fig. 7). The sample collected with fence nets, composed of individuals from the smaller size classes, consisted totally of individuals of the 0+ and 1+ year classes (Fig. 7). Table 2 shows the results obtained when fitting the growth model to the data including all age classes and to the data including only age ≥2+.

Figure 3
Relation between otolith weight and Fork Length (FL) and otolith weight and age for coral trout, *P. leopardus*.

Table 1
Correlation between otolith weight (mg) and fork length (cm) for each age class of the coral trout *P. leopardus*.

Age	r^2	$P<$	df	Age	r^2	$P<$	df
0	0.826	0.0001	18	8	0.481	0.0001	19
1	0.972	0.0001	10	9	0.405	0.0001	12
2	0.829	0.0001	27	10	0.120	no sig.	8
3	0.747	0.0001	19	11	0.937	0.0001	7
4	0.652	0.0001	18	12	0.526	no sig.	3
5	0.650	0.0001	30	13	0.993	0.05	2
6	0.489	0.0001	43	14	0.049	no sig.	2
7	0.514	0.0001	30				

Figure 4
Sectioned otolith of a recaptured individual coral trout, *P. leopardus* (n° 0057), showing fluorescent band. Scale Bar = 0.25 mm

When fitting Schnute's model to both sets of data, the value of the parameter b was very close to 1. In the boundary where $b = 1$, the curve was reduced to a three parameter model that corresponds to the von Bertalanffy curve for length (Schnute, 1981). The resulting growth model for all age classes, in the form of a von Bertalanffy model, was

$$L_t = 52.2 \left(1 - e - 0.354 \left(t + 0.766\right)\right) \ r^2 = 0.895 \ \text{(Fig. 8)}.$$

The results obtained when fitting the growth curve to all data and to the data for fish ≥2+ years old only were quite different (Table 2). From age-2 onwards, the growth rate is much slower than the one estimated by using all age classes, as indicated by the growth coefficient K. Consequently, the estimated L_∞ is larger and the estimated t_o is a very large, negative value. The resulting growth model was

$$L_t = 61.29 \left(1 - e - 0.132 \left(t + 4.66\right)\right) \ r^2 = 0.622 \ \text{(Fig. 9)}.$$

No systematic trend in the residuals was observed (normality test $P>0.1$) (Figs. 8 and 9).

The relation between fork length (FL) and the standard length (SL) was

$$SL = -0.308 + 0.852 * FL, r^2 = 0.994,$$

and the relationship between FL and Total Weight (TW) was

$$TW = 0.0079 * FL^{3.157}, r^2 = 0.967.$$

Discussion

While some comparisons between readings of whole and sectioned otoliths have indicated good agree-

Table 2

Von Bertalanffy growth parameters V.B. and respective standard errors (SE), correlation coefficients (r^2) and degrees of freedom (df) for the growth curve fitted to all data and to the data for coral trout, *P. Leopardus*, ≥2 year old only.

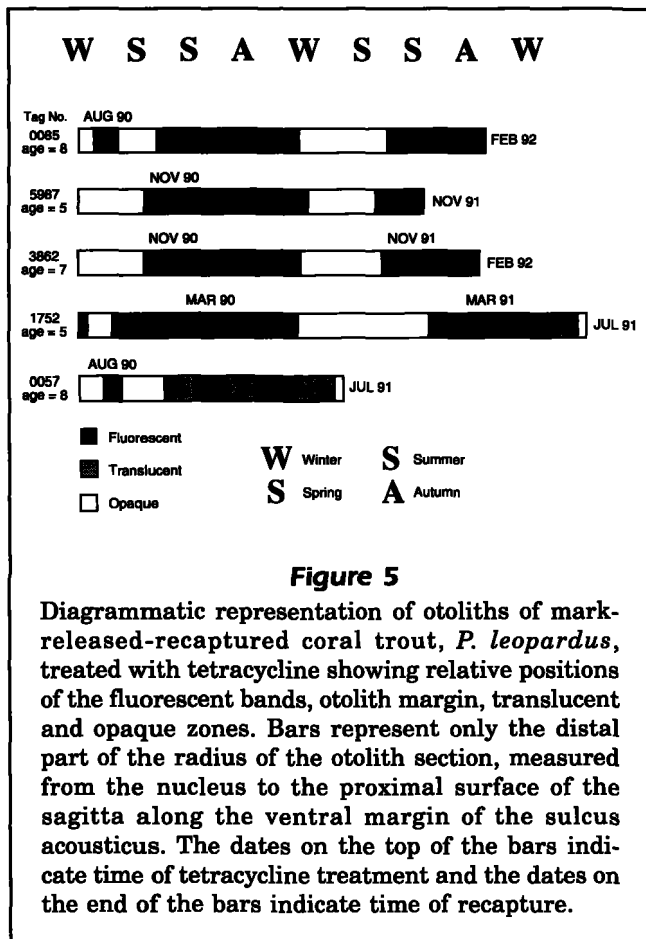|	L_∞ (SE)	K (SE)	t_o (SE)	r^2	df
V.B. all ages	52.20 (0.768)	0.354 (0.024)	−0.766 (0.097)	0.895	310
V.B. age ≥2+	61.29 (3.483)	0.132 (0.030)	−4.660 (1.024)	0.622	272

Figure 5
Diagrammatic representation of otoliths of mark-released-recaptured coral trout, *P. leopardus*, treated with tetracycline showing relative positions of the fluorescent bands, otolith margin, translucent and opaque zones. Bars represent only the distal part of the radius of the otolith section, measured from the nucleus to the proximal surface of the sagitta along the ventral margin of the sulcus acousticus. The dates on the top of the bars indicate time of tetracycline treatment and the dates on the end of the bars indicate time of recapture.

ment (Boehlert, 1985; Maceina and Betsill, 1987), others have suggested that reading whole otoliths underestimates true age and that this problem becomes worse with fish age (Boehlert, 1985; Hoyer et al., 1985). This is mainly due to the fact that in many species, sagittae growth is asymmetrical (Irie, 1960). Growth appears to be linear only up to a certain age or size, after which additions occur mainly on the interior proximal surface, along the sulcus region (Boehlert, 1985; Brothers, 1987; Beamish and McFarlane, 1987). That seems to be the case for the coral trout, as comparison of results of whole and sectioned otoliths indicated that lateral views did not reveal many of the annual growth zones in older individuals. However, whole otoliths require much less time for analysis than sectioned ones and seem to provide more precise readings. Therefore, it is useful to know the limit of reliability of whole readings and to define the conditions appropriate for its use.

Like the inshore coral trout *Plectropomus maculatus* (Ferreira and Russ, 1992), the common coral trout *P. leopardus* is a relatively long-lived, slow-growing species. The results on growth and

longevity obtained here differ somewhat from those of previous studies. Goeden (1978), using the Petersen method, identified age cohorts up to age 5+ for *P. leopardus*. However, the limitations of the use of length-frequency data to estimate age of long-lived fish are well known (Manooch, 1987; Ferreira and Vooren, 1991). Mcpherson et al. (1988), using counts of annuli in whole otoliths, were able to age fish up to seven years old. Longevity was probably underestimated in their study as counts were performed only on whole otoliths. More recently, Brown et al. (1992)[3] analyzed whole and sectioned otoliths of coral trout from the same area as Mcpherson et al. (1988) and were able to count up to 14 rings. Loubens (1980) counted annuli from burnt and broken otoliths and estimated a maximum longevity for

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[3] Brown, I. W., L. C. Squire, and L. Mikula. 1992. Effect of zoning changes on the fish populations of unexploited reefs. Stage 1: pre-opening assessment. Draft interim report to the Great Barrier Reef Marine Park Authority, Townsville, Australia, 27 p.
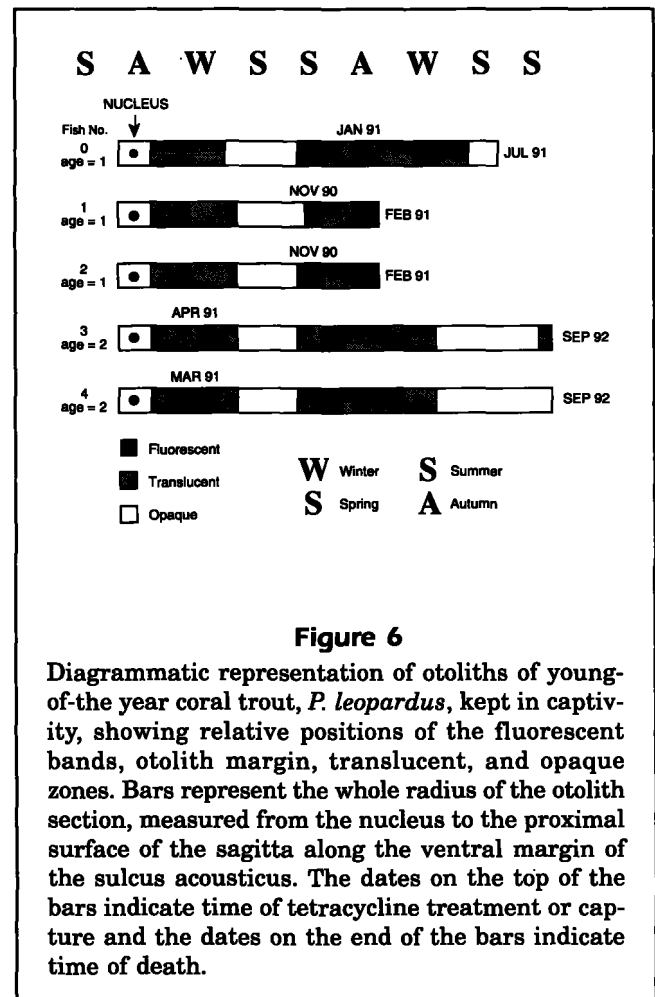

Figure 6
Diagrammatic representation of otoliths of young-of-the year coral trout, *P. leopardus*, kept in captivity, showing relative positions of the fluorescent bands, otolith margin, translucent, and opaque zones. Bars represent the whole radius of the otolith section, measured from the nucleus to the proximal surface of the sagitta along the ventral margin of the sulcus acousticus. The dates on the top of the bars indicate time of tetracycline treatment or capture and the dates on the end of the bars indicate time of death.

P. leopardus of 19 years in New Caledonia. These higher estimates of longevity suggest that coral trout at Lizard Island could also attain older ages. In this case, the absence of fishes older than 14 years of age in the sample collected at Lizard Island could be related to local levels of fishing pressure.

In the present work, the results of tetracycline labelling indicated that in the otoliths of *P. leopardus* the opaque zone (annulus) was formed during the winter and spring months whereas the translucent zone was formed during summer and autumn. Though the physiological basis for the formation of optically distinct zones in calcified structures has not been directly established, their presence has been commonly associated with varying growth rates, influenced by temperature, photoperiod, feeding rate, or reproductive cycle (see Casselman, 1983, and Longhurst and Pauly, 1987, for review). On a daily basis, it has been demonstrated that the translucent zone, or accretion zone, is formed during the phase of more active otolith growth, and the opaque or discontinuous
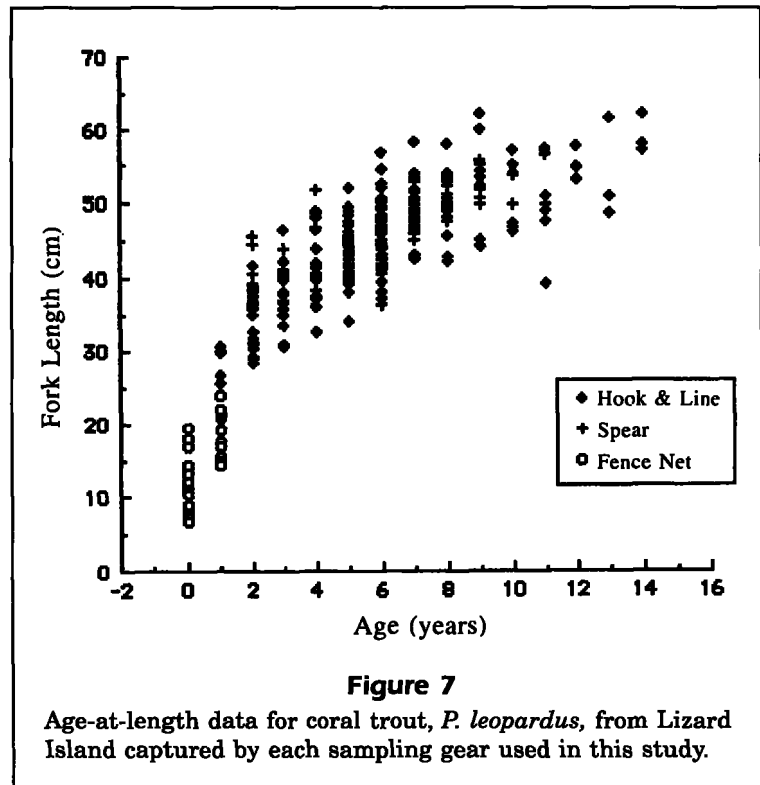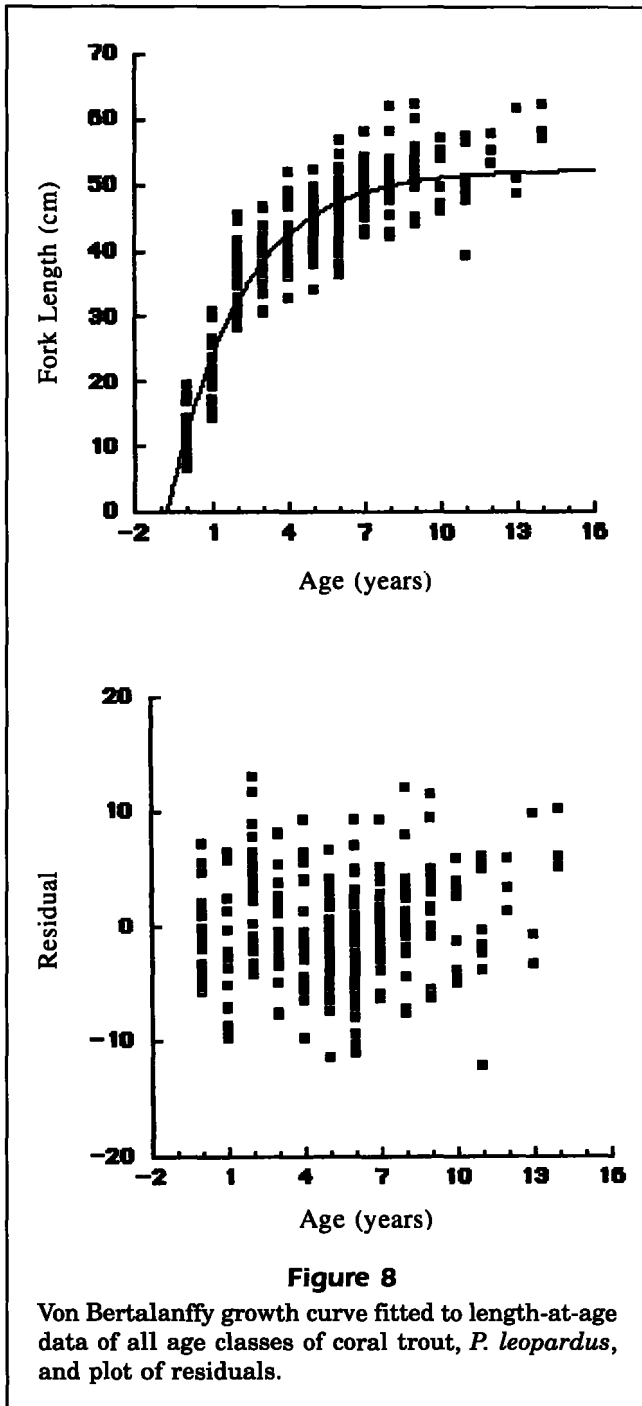

Figure 7

Age-at-length data for coral trout, *P. leopardus*, from Lizard Island captured by each sampling gear used in this study.

zone is formed during growth stagnation (Mugiya et al., 1981; Watabe et al., 1982). Mosegaard et al. (1988) examined the effect of temperature, fish size, and somatic growth rate on otolith growth rate and suggested that metabolic activity, not necessarily somatic growth rate, governs otolith growth. Thus, if the formation of the opaque zone in the coral trout otoliths is associated with a period of reduced metabolic activity, an external determining factor could be temperature, as the lowest values for water temperature around Lizard Island are observed during winter and early spring.[4] Annulus formation occurred in otoliths of juveniles and adults of coral trout during the same period, suggesting that reproduction is not a determining factor.

The growth of the otolith was continuous with age but apparently related to somatic growth. A similar pattern has been observed for other species of fish (Beckman et al., 1991). Otolith weight was the best predictor of age in the linear model, explaining as much variation in age as fork length in the von Bertalanffy model.

The main criteria for choosing a growth curve are quality of fit and convenience, differing according to whether the need is for a mathematical description of a detailed physiological growth process or for fishery management (Moreau, 1987). The results obtained here indicated clearly that the von Bertalanffy model adequately described the growth of the coral trout. Schnute's model was useful because of its flexibility and the stability of its parameters.

As most fishing gears are selective towards a certain size (Ricker, 1969), and smaller sizes are not usually available, it is common that growth curves are fitted to truncated data representing only part of the population. For the coral trout, because of gear selectivity and legal size restrictions (legal minimum=35 cm TL), only fish of 2+ years were captured by line- and spear-fishing. However, the first three years of life represent the period of fastest growth, after which the growth pattern changes considerably. As a result, much slower growth rates were obtained when the growth curve was fitted only to the age classes recruited to the fishery. The effects of different age ranges on estimated von Bertalanffy growth parameters have been recognized for many years (Knight, 1968; Hirschhorn, 1974) and greatly compromise comparisons of growth rates between populations (Mulligan and Leaman, 1992).

Furthermore, one effect of size-dependent mortality is the selective removal of fast-growing individuals (Ricker, 1969; Miranda et al., 1987). Thus, it is likely that the average size of the youngest age groups recruited to the fishery will be biased towards the largest, fast-growing individuals. This

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[4] Lizard Island Research Station. 1992. LIRS, PMB 37, Cairns, Queensland 4870, Australia. Unpubl. data.

Figure 8
Von Bertalanffy growth curve fitted to length-at-age data of all age classes of coral trout, *P. leopardus*, and plot of residuals.

Figure 9
Von Bertalanffy growth curve fitted to length-at-age data of ≥2+ years old coral trout, *P. leopardus*, and plot of residuals.

seems to be the case for age class 2+, the length of which is underestimated by the model including all data (Fig. 8). Exclusion of younger ages under these circumstances would further enhance the underestimation of K, as well as overestimation of L_∞ (Mulligan and Leaman, 1992).

Recent research has suggested the possibility of different growth processes within a population with associated selective fishing mortality (Parma and Deriso, 1990) and natural mortality (Mulligan and
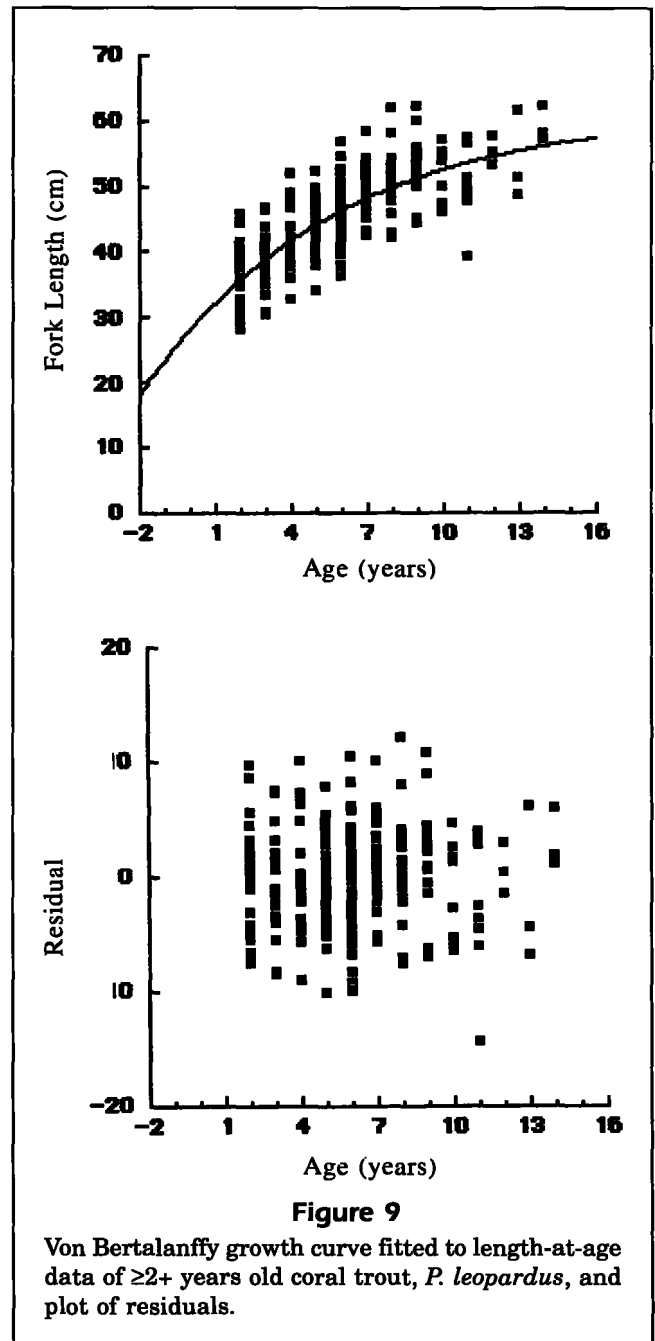
Leaman, 1992). The large variability in size at a given age observed for the coral trout suggests the occurrence of individual variability in growth. The reliability of methods of growth estimation like length-frequency analysis and growth increments from marking-recapture techniques, is greatly affected by this kind of variation (Sainsbury, 1980), further enhancing the importance of obtaining validated length-at-age estimates for exploited fish populations. The results of selective mortality are a direct effect of growth variability on the dynamics of abundance, and failure to consider the effects

of different growth potentials can result in gross overestimation of optimal fishing levels (Parma and Deriso, 1990).

The absence of marked seasonal changes in low latitudes has led to the general belief that tropical fishes do not form annual rings in their calcified structures (Pannella, 1974). Consequently, most of the studies of age determination of tropical fishes have concentrated on examination of daily rings. This technique, however, is time consuming and limited to younger ages (see Longhurst and Pauly, 1987, and Beamish and McFarlane, 1987, for review). The presence of annual marks in otoliths has been validated for an increasing number of species of tropical fishes (Samuel et al., 1987; Fowler, 1990; Ferreira and Russ, 1992; Lou, 1992) showing the potential of this technique to be used routinely in tropical fishery management.

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