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Growth rate, age determination, natural mortality and production potential of the scarlet seaperch, *Lutjanus malabaricus* Schneider 1801, off the Pilbara coast of north-western Australia

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Abstract

The age of scarlet seaperch, *Lutjanus malabaricus*, from deep waters (>100 m depth) on the continental shelf of north-western Australia was estimated by examining transverse sections of their sagittal otoliths. Ages were assigned based on counts of alternating opaque and translucent zones (annuli). The consistency of the readings showed that the otolith increments can be used for age determination. Otolith weight was strongly correlated with fish age providing confirmation that the opaque and translucent zones used to estimate age in this study are formed on an annual basis. Growth was found to be moderately slow. The maximum observed age for a male was 31 years corresponding to 802 mm FL. There was significant differential growth between the sexes in observed length-at-age, with males growing larger than females. The von Bertalanffy growth parameters were: $L_\infty = 686.4$ mm FL, $K = 0.180\,\text{yr}^{-1}$, $t_0 = -0.33$ for males, and $L_\infty = 565.8$ mm FL, $K = 0.262\,\text{yr}^{-1}$, $t_0 = -0.09$ for females. The annual instantaneous rate of natural mortality (*M*) was estimated to be 0.112. The life history characteristics of *L. malabaricus* indicate that this species has a low-production potential and hence is vulnerable to overfishing. Harvest strategies should, therefore, be conservative and fishery managers need to consider harvest refugia in those fisheries where size at first capture cannot be manipulated by modifications to fishing gear, such as the demersal fish trawl and fish trap fisheries of Western Australia.

Keywords: Lutjanidae; Sectioned otoliths; Age; Growth; Natural mortality; Otolith weight; Limit reference point; Production potential; Fisheries management

1. Introduction

Tropical snappers (Lutjanidae) are widely distributed throughout the tropical and subtropical seas of the world (Allen, 1985). The scarlet seaperch or saddletail seaperch, *Lutjanus malabaricus* Schneider (1801), is widespread throughout the Indo-Pacific region from the Fiji Islands to the Persian Gulf, and from Australia to southern Japan (Allen, 1985). In Western Australia, *L. malabaricus* is found from Shark Bay (25°S) northwards to the Indonesian archipelago. It is found along the continental shelf associated with both coastal and offshore reef areas, shoal grounds and areas of flat bottom with occasional epibenthos or vertical relief in depths to at least 140 m. Juveniles are often associated

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with seagrass beds and are found in the by-catch of prawn trawlers working nearshore. *L. malabaricus* is of major commercial importance to the trap, line and fish trawl fisheries of Western Australia, with landings in 1996–1997 of more than 168 t (Fisheries, 1999). *L. malabaricus* also forms a common component of the catch of recreational fishers and is considered a valuable angling species, although the magnitude of the recreational catch within Western Australia is not known.

The age of *L. malabaricus* has previously been estimated by modes in length–frequency distributions and from counts of rings visible on scales, vertebrae and whole otoliths (Druzhinin, 1970; Yeh, 1988; Lai and Liu, 1974, 1979; McPherson and Squire, 1992). These methods were not validated. Newman et al. (2000a) used sectioned otoliths to estimate age of *L. malabaricus* on the Great Barrier Reef at comparable latitudes to the present study. Tetracycline labelling of tagged fish by Cappo et al. (2000) provided direct validation of these age estimates. Furthermore, the validation of annuli in otoliths from the direct observation of individuals injected with oxytetracycline and recaptured after annulus deposition has now been established for 13 *Lutjanus* species from the Great Barrier Reef (Newman et al., 1996; Cappo et al., 2000). These studies also indicated that there is a functional linear relationship between otolith weight and age, independent of fish size, suggesting that otolith weight can be used as a non-subjective methodology for determining age (Worthington et al., 1995a,b). The number of increments in sectioned otoliths is one of the more robust and reliable estimators of fish age in tropical reef fish (e.g. Choat and Axe, 1996; Hart and Russ, 1996; Newman et al., 1996; Cappo et al., 2000).

There is a need to better understand the population dynamics of *L. malabaricus* and robust estimators of age and growth rate. Studies of the age, growth and mortality rates of *L. malabaricus* from sectioned otoliths have not been undertaken off the Pilbara coast of Western Australia. Knowledge of the demographic parameters of *L. malabaricus* will assist in developing management models for the sustainable exploitation of these fishes. The objectives of this study were to determine the age, rates of growth, and natural mortality of *L. malabaricus* off the Pilbara coast of Western Australia and to investigate the relationship between sagittal otolith dimensions and the age and length of each species.

2. Materials and methods

Samples of *L. malabaricus* ($n = 214$) were obtained between July 1997 and September 1999 principally from a fish trawl research program off the Pilbara coast of Western Australia (116–120°E) in depths from 100 to 200 m. Additional samples ($n = 42$) for age and growth analysis were also collected from the commercial fish trawl fishery off the Pilbara coast in depths of 50–100 m.

All fish were measured to the nearest millimetre total length (TL), fork length (FL) and standard length (SL), and weighed to the nearest gram total weight (TW). All individuals were measured on the left side, with the body flattened and the jaw closed. Where possible, the sex was determined by macroscopic examination of the gonads. The sagittal otoliths were removed by opening the otic bulla under the operculum. Otoliths were then washed in freshwater and stored in envelopes prior to processing.

2.1. Otolith preparation and age determination

Left and right sagittae were weighed (to 0.01 mg) and measured along three axes (total length, breadth and height through the central core of the otolith) to the nearest 0.01 mm using digital callipers. These dimensions were related to the length and age of the fish using linear regression techniques.

All ageing work was based on the analysis of transverse sections of otoliths. One sagitta per fish was randomly selected and embedded in epoxy resin. A thin transverse section (250–350 μm) was made through the core of the otolith from the dorsal apex to the ventral apex with a Buehler Isomet low-speed jewellery saw. These sections were then examined under a dissecting microscope at 20–50× magnification on a black background with reflected light.

Ages were assigned based on counts of annuli (alternating opaque and translucent bands) from sectioned otoliths. Alternating opaque and translucent bands (annuli) in sectioned otoliths of *L. malabaricus* have been shown to form once per year by direct (tetracycline labelling) age validation techniques (Cappo et al., 2000). To establish the level of confidence placed in the interpretation of the otolith structure, the precision of counts from the sectioned otoliths was assessed. Each otolith was examined on three separate occasions. For those fish whose three counts differed, the third count was used for analysis of age and growth, since by this time more experience had been gained in the interpretation of the otolith structure of these fishes. The counts were compared and the precision of age estimates was calculated using the index average percent error (IAPE) of Beamish and Fournier (1981). Greater precision is achieved as the IAPE is minimised.

2.2. Length–weight models

The relationship between length and weight was described by the power relationship: $W = aL^b$ where W is the total weight (g), and L the fork length (mm). The relationship between length and weight was fitted to a log-transformed set of data, and the parameters were back-transformed (with correction for bias) to the above form. Measurements of fish length (TL, FL, SL) were used to derive length conversion equations: $\mathrm{TL} = a + b(\mathrm{FL})$, $\mathrm{FL} = a + b(\mathrm{TL})$, $\mathrm{FL} = a + b(\mathrm{SL})$ and $\mathrm{SL} = a + b(\mathrm{FL})$.

Analysis of covariance ($\alpha = 0.05$) was used to determine if there were significant differences in the total weight-at-length (FL) relationships between sexes. Length and weight data were transformed to a natural logarithm function ($\log_e x$) to satisfy assumptions of normality and homogeneity. Multiple comparisons were performed using Tukey's honestly significant difference (HSD) test. One-way analysis of variance ($\alpha = 0.05$) was used to compare mean age, size and weight between sexes.

2.3. Growth and mortality models

The von Bertalanffy growth function (VBGF) was fitted to estimates of length-at-age using non-linear least squares estimation procedures. The VBGF is defined by the equation: $L_t = L_\infty\{1 - \exp[-K(t - t_0)]\}$, where L_t is the length at age t, L_∞ the asymptotic length, K the growth coefficient which defines the growth rate towards L_∞, t the age of the fish, and t_0 the hypothetical age at which fish would have zero length if it had always grown in a manner described by the equation. A modified analysis of the residual sum of squares (ARSS) was used to compare the VBGF's between sexes (Chen et al., 1992). The hypothesis being tested is that there is a single underlying growth curve between each sex.

Estimates of the instantaneous rate of total mortality (Z) were obtained using the age based catch-curve method of Beverton and Holt (1957) and Ricker (1975). The natural logarithm of the number of fish in each age class (N_t) was plotted against their corresponding age (t) and Z estimated from the descending slope b. Estimates of the survival rate (S) were then calculated by $S = e^{-Z}$ (Ricker, 1975). The use of catch curves implies a relatively constant mortality rate across time periods when fish age from t to $t + 1$ and is appropriate here as *L. malabaricus* displays an asymptotic growth pattern.

The samples of *L. malabaricus* obtained from the 100 to 200 m depth zone off the Pilbara coast are considered to represent an unfished stock as fishing activity in this zone has been negligible and it is somewhat remote from the inshore fishing grounds. The catch curve for *L. malabaricus*, therefore, provides an excellent estimate of M for this species.

Instantaneous natural mortality rates (M) were also obtained using the general regression equation of Hoenig (1983) for fish, where $\log_e Z = 1.46 - 1.01 \log_e t_{max}$ (t_{max} is the maximum age in years, since $Z = M$), and Pauly (1980) based on parameters of the VBGF and mean water temperature (°C), where $\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T$, and the mean annual water temperature for the Pilbara coast (116–120°E) is 26.9°C.

2.4. Estimating a limit reference point

A limit reference point represents a state of a fishery resource, which is considered to be undesirable and which management action should avoid (Caddy and Mahon, 1995). The LRP, F_{limit}, was calculated for *L. malabaricus*. Calculation of F_{limit} requires an estimate of M, since $F_{limit} = \frac{2}{3}M$ (Patterson, 1992). Patterson (1992) reports that exploitation rates above F_{limit} have been associated with stock declines, whereas exploitation rates below this level have resulted in stock recovery.

3. Results

A total of 214 *L. malabaricus* were examined for age analysis off the Pilbara coast of north-western Australia ranging in size from 167 to 802 mm FL, corresponding to a range in age of 1–31 years. Ninety-four fish were identified as males ranging from 214 to 802 mm FL and 2–31 years of age, while 86 were identified as female ranging from 286 to 617 mm FL and 3–26 years of age.

3.1. Otolith morphology and interpretation

The sagittae of *L. malabaricus* are laterally compressed, elliptical structures, with a concave distal surface, and a slightly pointed rostrum and post-rostrum. A curved sulcus crosses the proximal surface longitudinally. The depth of the sulcal groove increases with the increasing age. Annuli were usually counted in the region from the primordium to the proximal surface along the ventral margin of the sulcus acousticus. Annuli in this region were usually well-defined and more readily interpreted.

Sagittae of *L. malabaricus* were found to have a distinct pattern of alternating translucent and opaque bands (annuli). Under reflected light on a black background, annuli appear opaque in contrast to surrounding translucent areas. The first few annuli are somewhat broad and diffuse, with subsequent annuli becoming progressively more compact towards the edge of the otolith. Otoliths of *L. malabaricus* are readily interpretable, with a high level of precision among replicate counts of annuli, with the IAPE of 4.32%. This reflects a relatively high level of precision among otolith readings and indicates that otoliths were interpreted in a similar manner on each occasion.

All samples of *L. malabaricus* were obtained from fish trawl catches, which were selected against individuals less than 2+ years of age and less than 150 mm FL (Figs. 1 and 2). While few fish were retained in the 0+ and 1+ age classes, a number of individuals were caught from 150 to 450 mm, although they were not well represented in the catch (Fig. 2). Hence, fish less than 10+ years of age were not well represented in the catch (Fig. 1). A few large individuals (>700 mm FL) were obtained from the fish trawl fishery in depths of 50–100 m.

Otolith length and breadth were the good predictors of fish length in *L. malabaricus*, accounting for more than 91% of the variability (Table 1). In contrast, otolith weight and height were poor predictors of fish length (Table 1). Otolith weight was the best predictor of fish age for *L. malabaricus*, accounting for 91.7% of the variability in age (Table 1). Otolith length, breadth and height were poor predictors of age for *L. malabaricus* (Table 1).

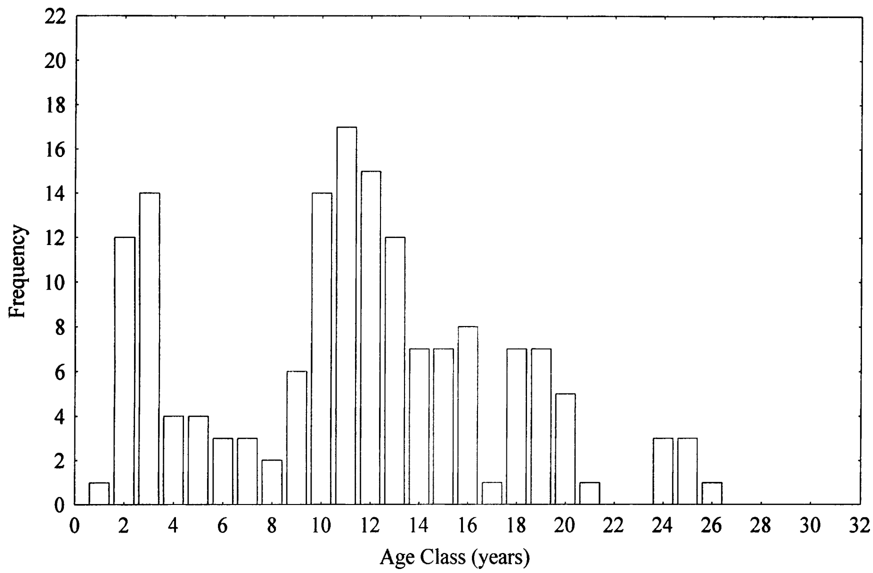

Fig. 1. Age–frequency distribution of *L. malabaricus* in the 100–200 m depth zone off the Pilbara coast of north-western Australia.

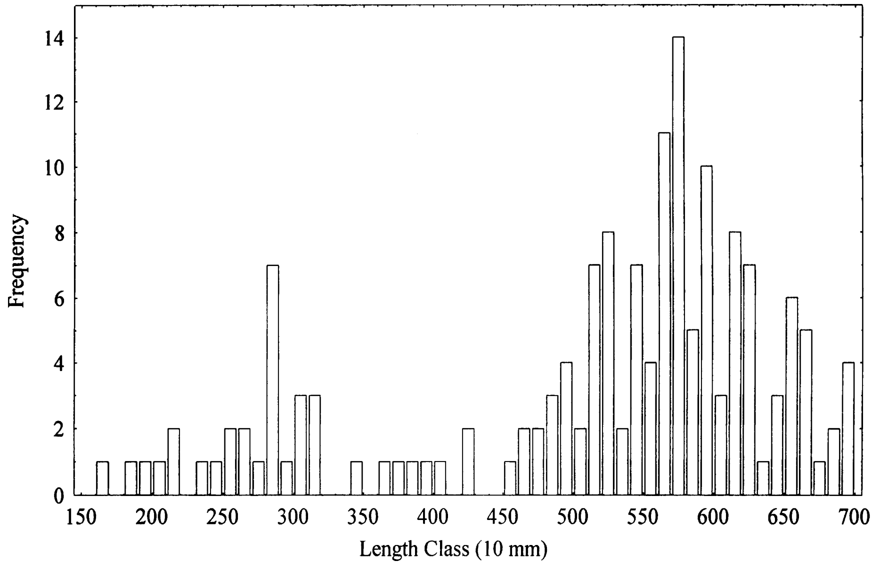

Fig. 2. Length–frequency distribution of *L. malabaricus* sampled for age determination (10 mm length classes).

3.2. Length–weight models

Length–weight relationships were calculated separately for males, females and for both sexes combined (Table 2). ANCOVA of weight-at-length was significantly different between sexes for *L. malabaricus* ($F = 18.57$; d.f. $= 1265$; $p < 0.0001$), with males larger than females. The relationship between TW and FL is presented in Fig. 3. Length conversion equations were derived for TL, FL and SL (Table 3).

Mean weight (TW) and mean lengths (FL) of *L. malabaricus* which were sampled differed significantly between sexes ($p < 0.001$ and $p < 0.01$, respectively), with males larger than females. Mean ages were also significantly different between sexes ($p < 0.05$); however, females were on average older than males.

3.3. Growth and mortality models

The von Bertalanffy growth curve was fitted to lengths-at-age for all specimens (Fig. 4), and separately for each sex (Table 4). Growth is slow, with growth in length much reduced beyond the 10+ age classes. The growth curves were significantly different

Table 1
Evaluation of the relationship between otolith dimensions and length and age of *L. malabaricus* off the Pilbara coast of north-western Australia. The predictive equations are of the simple linear regression form $y = a + bx$ (codes for the independent variables are described in the text). For regression analyses, fish length (FL) and age were used as the dependent variables (all regressions were significant at $p < 0.001$). The standard error (SE) of the estimate is a measure of the dispersion of the observed values about the regression line

Dependent variables	Independent variables	Sample	Equation	r^2	SE of estimate
FL	OW	213	FL = 301.3059 + (208.8818 × OW)	0.785	58.222
FL	OL	213	FL = −52.3823 + (27.6065 × OL)	0.942	30.149
FL	OB	214	FL = −140.986 + (49.990 × OB)	0.919	35.743
FL	OH	214	FL = 63.3324 + (135.7595 × OH)	0.753	62.244
Age	OW	213	Age = −0.47201 + (11.13266 × OW)	0.917	1.7846
Age	OL	213	Age = −13.4429 + (1.1784 × OL)	0.706	3.3542
Age	OB	214	Age = −18.1064 + (2.2017 × OB)	0.734	3.1859
Age	OH	214	Age = −12.7391 + (7.1030 × OH)	0.849	2.3998

Table 2
Length–weight relationships of *L. malabaricus* off the Pilbara coast from north-western Australia. Estimates were obtained from the parameters a and b of the relationship $W = aL^b$, the sample size (n) and the regression r^2 value (lengths used are FL (mm) and the weight is TW (g)

Group	a	b	n	r^2
L. malabaricus (all fish)	2.348×10^{-5}	2.9279	289	0.9908
L. malabaricus (male)	2.516×10^{-5}	2.9156	128	0.9942
L. malabaricus (female)	2.507×10^{-5}	2.9187	183	0.9902

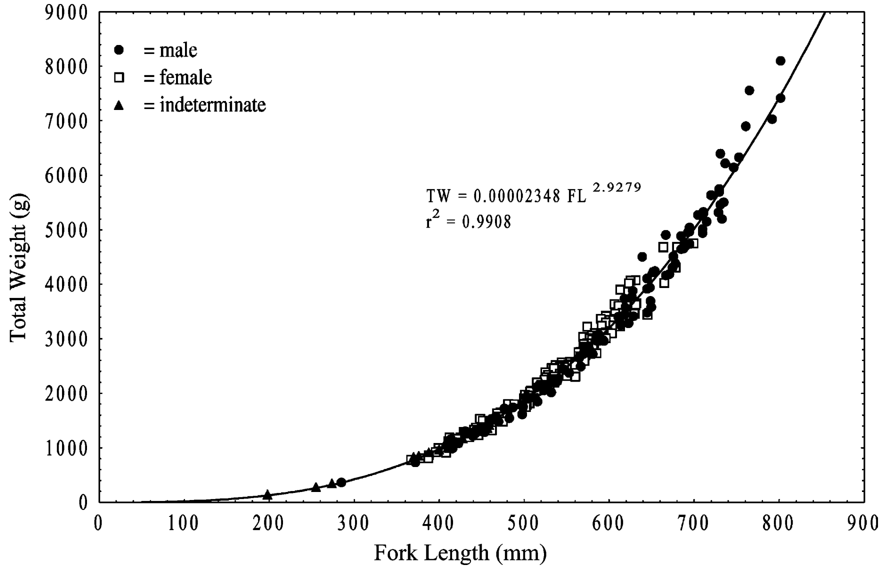

Fig. 3. Length–weight relationship for *L. malabaricus* off the Pilbara coast of north-western Australia.

between sexes ($p < 0.05$), with males reaching a larger size-at-age than females (Fig. 4).

L. malabaricus less than 11+ years of age were not fully recruited to the sampled population and were excluded from the mortality estimates derived from the catch curves (Fig. 5). The estimated M of the Pilbara population of *L. malabaricus* in the 100–200 m depth zone was 0.115 ($r^2 = 0.90$), representing an annual survivorship of ca. 89% yr^{-1} (Table 5). Examination of the catch curve data (Fig. 5) indicate that individuals in age classes 3+ to 9+ (that is, fish hatched between 1989 and 1995 from back-calculation of birth years) do not appear to have declined at the same rate as individuals in the 11+ to 26+ age classes (that is, fish hatched between 1972 and 1987). These data further indicate that the numbers of fish in the 2+ to 10+ age classes are not what might be expected from backward projection of the mortality schedule of fish aged 11 through 26 years (Fig. 5), and imply that the numbers of younger fish in each age cohort less than 10+ years of age (hatched in the 1990s) may be less than what was historically present in the 1970 and 1980s.

Table 3
Length conversion relationships for *L. malabaricus* off the Pilbara coast of north-western Australia. Estimates were obtained from the parameters a and b of the length–length relationships, sample size (n) and regression r^2 value (all lengths are in mm)

Length–length relationship	n	r^2
$TL = -2.5837700 + (1.03988241 \times FL)$	214	0.9993
$FL = 2.85164134 + (0.960940791 \times TL)$	214	0.9993
$FL = 16.2781754 + (1.19890058 \times SL)$	214	0.9940
$SL = -11.055256 + (0.829073473 \times FL)$	214	0.9940

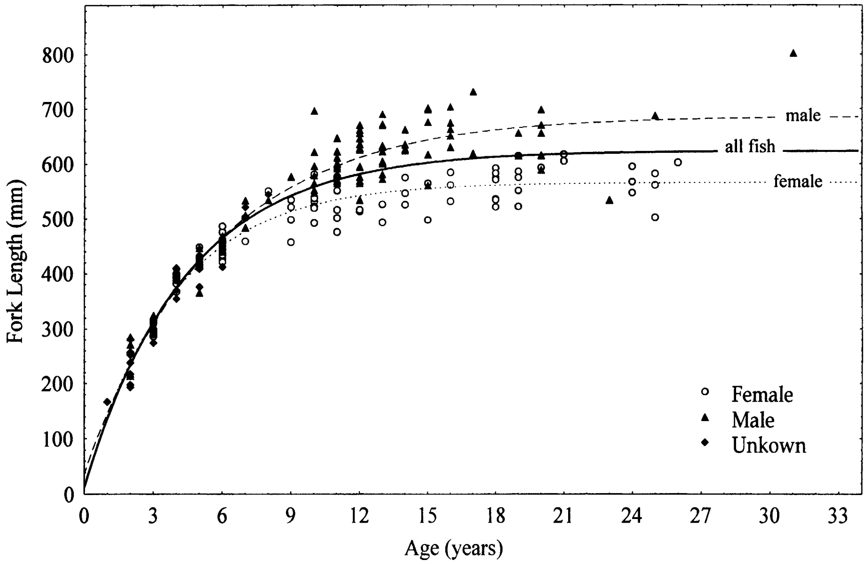

Fig. 4. von Bertalanffy length-at-age growth curve for *L. malabaricus* off the Pilbara coast of north-western Australia.

Estimates of M from the equation of Hoenig (1983) were slightly higher than those derived from catch curves and, therefore, predict a slightly lower survivorship rate (Table 5). Estimates of M from the equation of Pauly (1980) were much higher than those derived from both catch curves and the Hoenig equation and suggest a lower rate of survivorship (Table 5).

3.4. Limit reference point estimation

The LRP F_{limit} for *L. malabaricus* is estimated to be 0.0769 (Table 5). An F_{limit} of 0.0769 indicates that only approximately 7% of the available stock of *L. malabaricus* can be harvested on an annual basis.

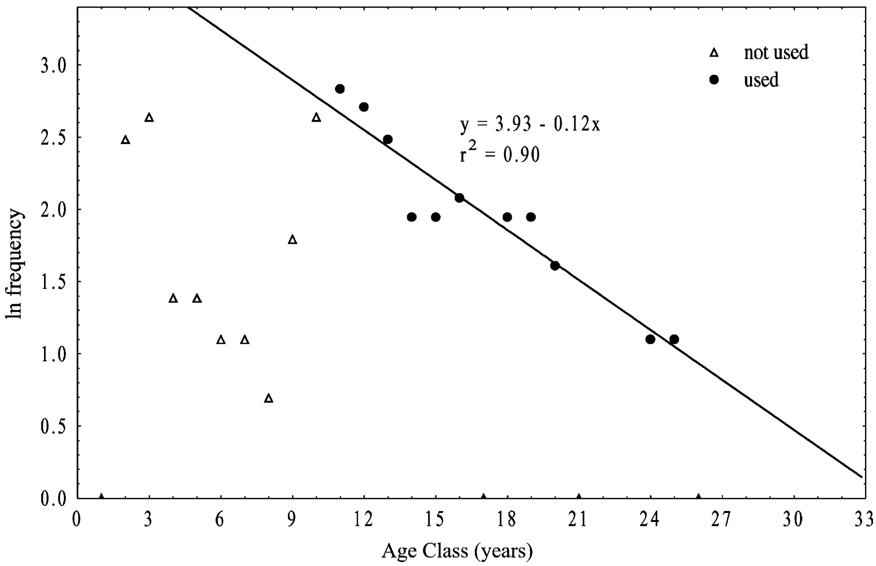

Fig. 5. Catch curve for *L. malabaricus* in the 100–200 m depth zone off the Pilbara coast of north-western Australia based on counts of annuli in sectioned otoliths (sagittae).

Table 4
Growth parameters and asymptotic standard errors (ASE) calculated from the von Bertalanffy growth function ($L_t = L_\infty\{1 - \exp[-K(t - t_0)]\}$) and means, minima and maxima of fork length and age, where the length FL is in mm, and age (t) is in years for *L. malabaricus* off the Pilbara coast of north-western Australia (n = sample size)

Parameters	Male	Female	Total
n	108	100	214
L_∞	686.4	565.8	622.8
ASE	12.55	5.399	7.347
K	0.180	0.262	0.225
ASE	0.015	0.016	0.015
t_0	−0.33	−0.09	−0.09
ASE	0.224	0.175	0.209
r^2	0.935	0.939	0.869
n	94	86	214
Fl_{mean}	568.6	490.9	502.1
Fl_{min}	214	286	167
Fl_{max}	802	617	802
n	94	86	214
t_{mean}	11.61	11.22	10.22
t_{min}	2	3	1
t_{max}	31	26	31

Table 5
Estimates of total mortality (Z), natural mortality (M) and survivorship (S) for *L. malabaricus* derived from catch curves based on ages determined from sectioned otoliths, and from the empirical regression equations of Hoenig (1983) and Pauly (1980). The limit reference point F_{limit} (Patterson, 1992) is derived based on estimates of M from catch curves

Parameter	Catch curve	Hoenig estimate	Pauly estimate
M	0.115	0.134	0.286
S (%)	89.1	87.4	75.1
F_{limit}	0.077		

4. Discussion

Evidence of the annual basis of ring formation is an integral component of any age and growth study using calcareous structures such as otoliths to determine age. The presence of annuli in *L. malabaricus* in this study has not been directly validated. Direct validation involving tetracycline labelling of tagged fishes has confirmed the presence of annuli in sectioned otoliths of *L. malabaricus* sampled in similar latitudes on the Great Barrier Reef (Cappo et al., 2000). In contrast, Milton et al. (1995) argued that the increments observed in the sectioned otoliths of *L. malabaricus* may not be annuli. This conclusion was based on radiometric techniques using disequilibria of Pb^{210}:Ra^{226} ratios of pooled otoliths. West and Gauldie (1994) reviewed the assumptions, biases and procedures underpinning radiometric techniques and concluded that the radiometric disequilibrium method is presently not sufficient to validate fish ages. Furthermore, direct validation in the form of tetracycline labelling of tagged fishes has clearly demonstrated that the alternating bands of opaque and translucent zones found in the sectioned otoliths of many species of reef fish represent annuli (Fowler and Doherty, 1992; Ferreira and Russ, 1992, 1994; Newman et al., 1996; Hart and Russ, 1996; Choat and Axe, 1996; Cappo et al., 2000). No studies have clearly disproved that growth rings in sectioned otoliths are not annuli.

Furthermore, evidence of the presence of annuli can be assessed by a number of criteria (Fowler and Doherty, 1992). Otoliths must display an internal structure of increments. Otoliths must grow throughout the lives of the fish at a perceptible rate and there must be a positive relationship between the size of fish caught and the size of the otoliths. The internal structure of increments must be formed periodically on a regular time scale (e.g. once per year). Several observations confirm the use of sectioned otoliths to age *L. malabaricus*. Transverse sections of sagittae showed a pattern of alternating translucent and opaque zones. The alternating bands of opaque and translucent zones considered as annuli in this study are analogous to those reported as annuli by Newman et al. (1996) and Cappo et al. (2000) in studies on lutjanids. There was a strong correlation between otolith weight and fish age ($r^2 = 0.917$) and the length-at-age of fish increased as the number of rings (ages) increased. The high correlation obtained between otolith weight and fish age further supports the suggestion that the bands reported in this study are formed on an annual basis.

The oldest fish sampled in this study was a male 31 years of age, and reflects the maximum observed longevity estimated by this study. Similarly, Mansour (1982) estimated a maximum age of 32 years from the sectioned otoliths of fish sampled in Kuwait.

The sample size is this study is relatively small (ca. 200 fish sampled and few fish over 800 mm were obtained) and the maximum length of *L. malabaricus* is reported to be 1000 mm (Allen, 1985), it is feasible that fish may live longer, possibly to 40+ years. Mathews and Samuel (1985) reported a maximum observed age of 46 years for *L. malabaricus* from the sectioned otoliths of fish sampled in Kuwait. A number of different methods have been used to estimate the age of *L. malabaricus*, including analysis of whole otoliths (McPherson and Squire, 1992), scales (Druzhinin, 1970), vertebrae (Lai and Liu, 1974, 1979; Edwards, 1985) and length–frequency analysis (Yeh and Chen, 1986; Ambak et al., 1987). These studies have reported longevities in the range 6–11 years, much less than those reported from studies involving analysis of sectioned otoliths.

The lack of a relationship between the age and length–frequency distribution (compare Figs. 1 and 2) emphasises the problems that will be associated with using length–frequency analysis to identify age cohorts in this species. For example, fish ranging in length from 500 to 600 mm FL vary in age from 7 to 25 years (see Fig. 4). Therefore, estimates of demographic parameters derived from length–frequency analysis of this species will be grossly biased and caution must be applied if they are to be used for fishery management purposes.

Growth of *L. malabaricus* in this study is slow ($K = 0.225$ from generalised growth curve). Approximately 50% of linear growth to L_∞ is accomplished within the first 3 years of the lifespan, with ca. 75% of linear growth to L_∞ accomplished within the first 6 years of the lifespan. Growth in length is much reduced after 10 years of age. The K observed in this study is similar to that derived by McPherson and Squire (1992, whole otoliths), Yeh (1988, length–frequency) and Chen et al. (1984, otolith sections). The observed K is higher than that estimated by Lai and Liu (1974, 1979) and Druzhinin (1970) which ranged from 0.12 to 0.15 using vertebrae and scales, respectively. The asymptotic FL is similar to that estimated by Mansour (1982).

Differential growth between sexes was observed in this study, with males significantly longer than females of a similar age. This was evident only from age class 9 onwards. Using the VBGF for each sex, this corresponds to a mean length of 558 and 514 mm FL for males and females, respectively. This is somewhat similar to the length-at-maturity of 576 mm FL estimated for *L. malabaricus* from the Great Barrier Reef (McPherson et al., 1992). Therefore, the pattern of differential growth evident between sexes in *L. malabaricus* appears to be related to the onset of sexual maturity. This pattern of size differentiation between sexes within the *Lutjanus* genus on the Great Barrier Reef is consistent with all the studies to date indicating that males reach a larger size-at-age than females (McPherson and Squire, 1992; Newman et al., 1996, 2000b). Faster growth of males over females in older age classes has also been reported for *L. vitta* on the north-west shelf of Western Australia (Davis and West, 1992).

Estimating mortality using age-based catch curves involves a number of assumptions. These include the assumptions of constant recruitment and constant mortality for each age class. The steady state or equilibrium assumption of constant recruitment is likely to be violated for most species, as recruitment is generally extremely variable and inconsistent (e.g. Doherty and Fowler, 1994). Despite this, the catch curve of *L. malabaricus* suggests that the mortality rate across each fully recruited age class is relatively constant and, therefore, the natural mortality rate estimated from the catch curve of *L. malabaricus* is likely to be robust. *L. malabaricus* were fully recruited to the fish trawl fishery by age 11, and the instantaneous rate of natural mortality (M) is low (estimated to be 0.115). The abundance of fish in age classes 2–10 is less than what might be expected from the backward projection of the age structure of the sampled population. This infers that the numbers of younger fish (<10+ years of age) may now be much less than what was present in the 1970 and 1980s. The abundance of 'red snappers' (*L. malabaricus* is one of the three red snapper species) rapidly declined in the north-west shelf area in the 1980s as a consequence of high foreign fishing effort (Sainsbury, 1987; Ramm, 1994). Catches of 'red snappers' were much higher than estimates of sustainable yield obtained from production models (Sainsbury, 1987; Ramm, 1994). The decline in the abundance of valuable commercial fishes on the North-West Shelf and changes in community structure have also been linked with habitat modification and loss caused by fish trawlers (Sainsbury, 1987; Sainsbury et al., 1997). The low abundance of fish in the 2+ to 10+ age classes provides indirect evidence that current levels of recruitment (and possibly stock levels) across the Pilbara are possibly much less than historical levels prior to the resource being heavily exploited by both foreign and domestic trawl-based fisheries.

The *M* derived from the age structure of *L. malabaricus* was compared to those derived from the empirical regression techniques of Hoenig (1983) and Pauly (1980). Hoenig's empirical equation, based on maximum observed age, provided similar estimates of *M* to those derived from catch curves. The estimates of *M* obtained from the regression equation of Pauly (1980) provided a gross overestimate of *M* for these fishes and hence substantially underestimate survivorship. Errors in estimates of *M* have profound fisheries management implications as both yield and production models require estimates of *M*. Overestimates of *M* will provide overestimates of the potential yield of fish stocks and this may lead to overexploitation and ultimately recruitment overfishing (Newman et al., 2000a). The Hoenig (1983) equation has been shown to provide similar estimates of *M* to those derived from age-based catch curves (Hart and Russ, 1996; Newman et al., 1996, 2000a,b), hence use of the Hoenig (1983) equation based on the maximum age of fish sampled within a population will provide at least an upper limit for the estimate of *M*.

L. malabaricus off the Pilbara coast of Western Australia are long-lived (to at least 31 years of age), moderately slow growing fish, with low rates of natural mortality. Hence, these fish have a low-production potential and are vulnerable to overfishing. The apparent reduced abundance of fish in age classes less than 10 years of age needs to be investigated. Fishing pressure by both foreign and domestic fleets e.g. in nearshore waters may have substantially reduced the spawning stock biomass of *L. malabaricus*, resulting in reduced recruitment of fish in the 100–200 m depth zone. Furthermore, there is also the possibility that habitat loss as a consequence of fish trawl activities may have a negative impact on recruitment rates in the longer term by limiting the available habitat for these early life history stages.

Harvest strategies for this species will therefore need to be conservative, and fishery managers need to consider harvest refugia (large spatial area closures) in order to provide adequate protection of the spawning stock biomass of *L. malabaricus*, especially in deep-water areas where size at first capture cannot be manipulated by modifications to the fishing gear, such as the demersal fish trawl and fish trap fisheries of north-western Australia.

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