Asian Fisheries Society, Manila, Philippines

Growth, Age Estimation and Preliminary Estimates of Longevity and Mortality in the Moses Perch, *Lutjanus russelli* (Indian Ocean form), from Continental Shelf Waters off North-Western Australia

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Abstract

Moses perch, Lutjanus russelli were sampled in continental shelf waters off the Pilbara coast of North-Western Australia from July 1997 to September 1999. Ages were determined by examining the thin transverse sections of their sagittal otoliths and were based on counts of alternating opaque and translucent zones (annual growth increments). Otolith length and breadth (width) increased linearly with fish length, whereas otolith weight was strongly correlated with fish age. The continuous growth of the otoliths provides additional evidence that the opaque and translucent zones used to estimate age in this study are formed on a yearly basis. Growth was rapid during the first 5 years of life, after which growth in length was much reduced. No significant differential growth between the sexes was evident in observed length-atage. Parameters of the von Bertalanffy growth curve (fork length-at-age) were L_{∞} = 330.1, K = 0.347 and t_0 = -0.27. Preliminary estimates of longevity between sexes were similar with a maximum observed age of 21 years for male and 20 years for female. The preliminary estimate of the annual instantaneous rate of natural mortality (M) was 0.152. The life history characteristics of L. russelli indicate that this species is potentially vulnerable to overfishing despite its small size. The existing fisheries management arrangements and control mechanisms within the trap, line and trawl fisheries of North-Western Australia are likely to maintain adequate levels of the spawning stock biomass of these fish as long as each fishing sector does not expand beyond current boundaries.

Introduction

Tropical snappers (Lutjanidae) are widely distributed throughout the tropical and subtropical seas of the world (Allen 1985). The Moses perch, *L. russelli* (Bleeker 1849, Pisces: Lutjanidae) is widespread throughout the Indo-West Pacific region from the Fiji Islands to East Africa, and from Australia to southern Japan (Allen 1985). Allen (1985) describes a Pacific Ocean

form and an Indian Ocean form of *L. russelli*. This paper relates to the Indian Ocean form of *L. russelli*. Within Western Australia, *L. russelli* is found in Shark Bay (25°S) northwards 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 frequent mangrove estuaries and nearshore rocky reef areas and are sometimes found near seagrass beds.

Along North-Western Australia, *L. russelli* is a moderately important component of the commercial catch of the fish trap and fish trawl fisheries, with total landings in 1998 to 1999 exceeding 62 tons (Penn 2001). In addition, *L. russelli* is a valuable component of the recreational catch in the Pilbara region of Western Australia, where it is the 8th most important finfish species landed (Williamson pers. comm.). Furthermore, ongoing market development and value-adding of the landed catch by commercial fishers is increasing the representation of many of the smaller lutjanid species in commercial landings.

The validation of annual growth increments in thin otolith sections from the direct observation of individuals that have been injected with oxytetracycline and recaptured after the deposition of the annual growth increment has now been established for 14 *Lutjanus* species from the Great Barrier Reef (Newman et al. 1996, Hilomen 1997, Cappo et al. 2000). These studies have also indicated that there is a functional linear relationship between otolith weight and age. Fish otoliths provide reliable estimates of age because they are not subject to resorption, remodelling or regeneration (Secor et al. 1995).

Studies of the age, growth and mortality rates of *L. russelli* have not previously been undertaken off the Pilbara coast of Western Australia. The determination of fish age and the age structure of fish populations is the key to estimating rates of growth and mortality. Knowledge of these demographic parameters will assist in the development of management models for the sustainable exploitation of these demersal fish resources. The objectives of this study were to determine the age, rates of growth, and natural mortality of *L. russelli* off the Pilbara coast of Western Australia and to investigate the relationship between sagittal otolith dimensions and fish age and length.

Materials and Methods

Samples of *L. russelli* (n=136) were obtained between July 1997 and September 1999 principally from a fish trawl research program off the Pilbara coast of Western Australia (116°E to 120°E) in depths of 100 to 200 m. Additional samples for age and growth analysis were also collected from the commercial fish trawl fishery off the Pilbara coast in depths of 50 to 100 m. Individual *L. russelli* less than 23 cm fork length (FL) were not available or vulnerable to fish trawl fishing and none was obtained for analysis. All fish were measured to the nearest mm total length (TL), fork length (FL) and standard length (SL), and weighed to the nearest g total weight (TW). Where possible, sex was determined through macroscopic examination of the gonads. The sagittal otoliths were removed by opening the otic bulla from under the operculum. Otoliths were then washed in freshwater and stored in envelopes prior to processing.

Length-weight models

The relationship between length and weight was described by the power relationship: $W = aL^b$, where W is total weight (g) and L is 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:

TL = a + b (FL), FL = a + b (TL), FL = a + b (SL) and SL = a + b (FL).

Analysis of covariance (a = 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, with multiple comparisons performed using Tukey's honestly significant difference (HSD) test.

Otolith preparation and age determination

Otolith removal, measurement and preparation followed the procedures and protocols described in Newman et al. (1996), Newman et al. (2000) and Newman and Dunk (2002). Otolith dimensions were related to the length and age of the fish using linear regression techniques. All age estimates were based on the analysis of thin transverse sections of otoliths. These thin sections were examined under a dissecting microscope at 10 to 30' magnification with reflected light on a black background.

Ages were assigned based on counts of alternating opaque and translucent bands (annual growth increments) from the sectioned otoliths. Each otolith was examined on three independent occasions. For those fish whose counts differed, the third count was used for analysis of age and growth, since by this time considerable experience had been gained in the interpretation of the structure of the otoliths of *L. russelli*. The counts were compared and the precision of age estimates (agreement among counts) calculated using the Average Percent Error (APE) of Beamish and Fournier (1981).

Growth and mortality models

The von Bertalanffy growth function (VBGF) was fitted to estimates of length-at-age using nonlinear least squares estimation procedures. The VBGF is defined by the equation: $L_{t} = L_{\infty} \{ 1 - \exp [-K (t - t_{0})] \}$

where $L_t =$ mean length at age t; $L^{\infty} =$ asymptotic mean length; K = is a rate constant that determines the rate at which L_t approaches L^{∞} ; t = age of the fish; and $t_o =$ the hypothetical age at which the mean length is zero if it had always grown in a manner described by the VBGF. Minimum, maximum and mean lengths and ages were also recorded from the Pilbara population. A modified analysis of the residual sum of squares (ARSS) was used to compare VBGFs between sexes (Chen et al. 1992).

The samples of *L. russelli* collected from trawl surveys in the 100 to 200 meter depth zone off the Pilbara coast were considered to represent an unfished stock as fishing activity in this zone has been negligible and it is somewhat distant from the inshore fishing grounds. The age based catch curve for *L. russelli* was therefore expected to provide an opportunity to estimate M. Estimates of the instantaneous rate of natural mortality (M) 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. Estimates of the survival rate (S) were then calculated by S = e^{-Z} (Ricker 1975).

The estimate of M derived from the age-based catch curve were compared with the estimates of M derived from the empirical regression equations of Hoenig (1983) for fish, where: $\log_e Z = 1.46$ to 1.01 $\log_e t_{max}$ (t_{max} is the maximum age in years); and Pauly (1980) based on parameters of the VBGF and mean water temperature (in°C), where: $\log_{10} M = -0.0066$ to 0.279 $\log_{10} L^{\infty} + 0.6543 \log_{10} K + 0.4634 \log_{10} T$ (mean annual water temperature for the Pilbara coast (116°E to 120°E) is 26.9°C).

Results

Length-weight models

Length-weight relationships were calculated separately for males, females and for both sexes combined (Table 1). ANCOVA of weight-at-length was not significantly different between sexes (F = 0.269; df: 1,265; p > 0.5). The relationship between total weight and fork length is presented in figure 1. Length conversion equations were derived for total length, fork length and standard length (Table 2).

Otolith interpretation

The sagittae of *L. russelli* are laterally compressed, elliptical structures, with a concave distal surface, a pointed rostrum and a curved postrostrum. A curved sulcus crosses the proximal surface longitudinally. The depth of the sulcal groove increases with increasing fish age. Sagittae of *L. russelli* were found to have a distinct pattern of alternating translucent and opaque bands. Under light reflected off a black background, annual growth incre-

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ments appear opaque in contrast to surrounding translucent areas. The first few annual growth increments are usually broad and diffuse, with subsequent growth increments becoming progressively more compact towards the edge of the otolith. Annual growth increments were counted where possible in the region from the primordium to the proximal surface along the ventral margin of the sulcus acousticus. Annual growth increments in this region were usually well defined.

Table 1. Length weight relationships of *L. russelli* from the Pilbara coast of North-Western Australia. Estimates of the parameters *a* and *b* of the relationship $W = aL^b$, sample size (*n*) and regression r^2 value were obtained. (Lengths are FL in mm and weight is TW in g)

Group	а	b	п	r ²
L. russelli (all fish)	1.867 ´ 10 ⁻⁵	2.9730	268	0.97
L. russelli (male)	2.100 ´ 10 ⁻⁵	2.9525	140	0.97
L. russelli(female)	$1.605 \cdot 10^{-5}$	2.9996	128	0.97

Table 2. Length conversion relationships for *L. russelli* from the Pilbara coast of North-Western Australia. Estimates of the parameters *a* and *b* of the length-length relationships, sample size (*n*) and regression r^2 values were obtained. (All lengths are in mm).

Length-length relationship	п	r ²	
TL = 3.3597 + (1.0675 fL)	124	0.995	
FL = -1.7085 + (0.9324 ´ TL)	124	0.995	
FL = 22.862 + (1.1368 ´ SL)	124	0.975	
SL = -13.487 + (0.8578 FL)	124	0.975	

Table 3. Correlations among otolith dimensions and the length and age of *L. russelli* from 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 SE of the estimate is a measure of the dispersion of the observed values about the regression line.

Dep. Var.	Ind. Var.	Sample Size	Equation	r ²	SE of Estimate
FL	OW	120	FL = 222.11 + (475.54' OW)	0.76	15.78
FL	OL	120	FL = 20.32 + (23.45' OL)	0.83	13.04
FL	OB	124	$FL = 12.61 + (45.03^{\circ} OB)$	0.79	14.56
FL	OH	124	FL = 177.12 + (71.28' OH)	0.46	23.06
Age	OW	119	Age = -3.56 + (75.11' OW)	0.93	1.22
Age	OL	119	Age = -29.03 + (3.17' OL)	0.77	2.15
Age	OB	123	Age = -31.94 + (6.38' OB)	0.78	2.08
Age	OH	123	Age = -12.91 + (12.53' OH)	0.70	2.45



Fig. 1. Length-weight relationship for *L. russelli* off the Pilbara coast of North-Western Australia

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The precision of otolith readings was relatively high, with the Index Average Percent Error (IAPE) at 5.96%. Hence, otoliths of *L. russelli* are readily interpretable, with a high level of agreement among replicate counts of annual growth increments. Otolith length was a good predictor of fish length in *L. russelli*, accounting for more than 83% of the variability (Table 3). In contrast, otolith breadth, weight and in particular otolith height were poor predictors of fish length (Table 3). Otolith weight was the best predictor of fish age for *L. russelli*, accounting for 92.6% of the variability in age (Table 3, Fig. 2). In contrast, otolith length, breadth and height were poor predictors of age for *L. russelli* (Table 3).

Growth and mortality models

All samples of *L. russelli* were obtained from fish trawl catches, which were selected against individuals less than 4+ years of age and less than 250 mm FL (Figs. 3 and 4). No fish in the 0+, 1+ and 2+ age classes was obtained for analysis. Lengths-at-age for the 1+ and 2+ age classes were established by back-calculating lengths-at-age of fish in the 3+ and 4+ age classes (Fig. 5). Back-calculation of lengths-at-age in the 1+ and 2+ age classes was undertaken in order to provide robust estimates of parameters of the von Bertalanffy growth curve. The back-calculated fork lengths-at-age were derived from fork length-otolith radius regressions.



Fig. 2. Relationship of fish age to otolith weight (g) for *L. russelli* off the Pilbara coast of North-Western Australia

Fig. 3. Age frequency distribution of *L. russelli* in the 100 to 200 m depth zone off the Pilbara coast of North-Western Australia



Fig. 4. Length frequency distribution of *L. russelli* sampled for age determination (10 mm length classes)



Fig. 5. von Bertalanffy length-at-age growth curve for *L. russelli* off the Pilbara coast of North-Western Australia

The von Bertalanffy growth curve was fitted to lengths-at-age for all *L. russelli* (Fig. 5), and separately for each sex (Table 4). The VBGF indicates that the rate of growth of *L. russelli* decreases rapidly with increasing age. Growth of *L. russelli* is rapid at age 5, with growth in length much reduced beyond the 5+ age classes. Length-at-age of *L. russelli* was not significantly different between sexes (p > 0.05; see also Fig. 5).

L. russelli less than 6+ years of age were not fully recruited to the sampled population and were excluded from the mortality estimates derived from catch curves (Fig. 6). The estimated instantaneous rate of natural mortality of the Pilbara population of *L. russelli* in the 100 to 200 m depth zone

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

Parameters	Male	Female	Total	
n	85	64	136	
L¥	332.8	323.3	330.1	
(ASE)	3.25	5.23	3.01	
К	0.351	0.371	0.347	
(ASE)	0.02	0.03	0.02	
t _o	-0.21	-0.19	-0.27	
(ÅSE)	0.11	0.14	0.12	
r ²	0.95	0.92	0.90	
п	73	51	124	
FLmean	308.8	294.9	303.1	
FLmin	239	232	232	
FL _{max}	379	387	387	
п	72	51	123	
tmaan	9.71	8.45	9.17	
t _{min}	3	3	3	
t _{max}	21	20	21	

Table 5. Estimates of natural mortality (M) and survivorship (S) for *L. russelli* derived from catch curves based on ages determined from sectioned otoliths, and from the empirical regression equations of Hoenig (1983) and Pauly (1980)

Parameter	Catch Curve	Hoenig Estimate	Pauly Estimate	
М	0.152	0.199	0.454	
S	85.7%	82.0%	63.5%	



Fig. 6. Catch-curve for *L. russelli* in the 100 to 200 m depth zone off the Pilbara coast of North-Western Australia based on counts of annual growth increments in sectioned otoliths (sagittae)

was M = 0.152 (ages 6 to 21 years, SE = 0.02, $r^2 = 0.77$), representing an annual survivorship of ca. 86% yr⁻¹ (Table 5). Individuals in some age classes (eg. 8+) were not well represented in the catch and do not appear to be recruited in similar numbers to other cohorts (the equilibrium assumption). However, the descending right hand limb of the catch curve is somewhat similar across most ages and hence M is assumed to be constant.

Estimates of M from the equation of Hoenig (1983) were comparable to those derived from catch curves, predicting a somewhat similar survivorship rate (Table 5). In contrast, estimates of M derived from the equation of Pauly (1980) were substantially higher than those derived from either catch curves or the Hoenig equation (Table 5).

Discussion

This study is the first to establish the demographic parameters of age, growth rate and natural mortality of the Indian Ocean form of L. russelli. Evidence of the annual basis of ring formation is an integral component of any age and growth study. The presence of annual growth increments in L. russelli in this study has not been directly validated. Direct validation involving tetracycline labelling of tagged fishes has confirmed the presence of annual growth increments in sectioned otoliths of the Pacific Ocean form of L. russelli sampled in similar latitudes on the Great Barrier Reef (Sheaves 1995). Further evidence that the opaque bands represented annual growth increments came from growth rates obtained from tag-release-recapture programs (Sheaves 1995). 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 annual growth increments (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 demonstrated that the growth rings present in sectioned otoliths of lutjanid fishes represent less than annual growth increments.

The alternating bands of opaque and translucent zones considered as annual growth increments in this study are analogous to those reported as annual growth increments 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 ($r^2 = 0.926$) 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 reported in this study is similar to that reported by Newman et al. (1996), Newman et al. (2000) and Newman and Dunk (2002) in related lutjanid species and further supports the suggestion that the growth increments analyzed in this study are formed on an annual basis.

The oldest fish sampled in this study was a male 21 years of age. Sheaves (1995) estimated a maximum age of 17 years from similar latitudes on the Great Barrier Reef. The sample size in this study is relatively small

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(< 150 fish sampled and few fish over 330 mm were obtained). The maximum reported length of *L. russelli* is 450 mm (Allen 1985) hence, it is feasible that this species may live longer. Estimates of age of *L. russelli* have also been obtained by analysis of scales (Ye and Tang 1996, Chen 1997). However, these studies reported longevities of only 6 years for *L. russelli*. Analysis of scales has been shown to be a very imprecise structure for age determination in comparison to sectioned otoliths in *L. peru* (Rocha-Olivares 1998) and *L. johnii* (Marriott and Cappo 2000) providing considerable underestimates of fish age. Imprecision in the interpretation of scale structure is therefore likely to have resulted in the difference in maximum age reported by the studies of Ye and Tang (1996) and Chen (1997) in comparison to this study.

Fish were sampled from a relatively small size range (232 to 387 mm), yet the observed ages incorporated within this sample ranged from 3 to 21 years of age. Many age classes accumulate within a narrow size range. The lack of a relationship between age structure and length frequency distribution emphasizes the problems that will be associated with using length frequency analysis to identify age cohorts in this species. Estimates of demographic parameters derived from length frequency analysis of this species will be biased and caution must be applied if they are to be used for fishery management purposes.

The absence of small fish in the sampled population required back calculation of growth rates to determine length-at-age for 1 and 2 year old fish. Back-calculation of growth based on otoliths has the potential to underestimate length-at-age (Campana 1990). Hence, the growth rates derived from this study can be considered conservative. Growth of *L. russelli* under the above assumption appears to be rapid (K = 0.347) during the first 3 years of life and the growth curve is relatively 'square'. Approximately 68% of linear growth to L^{∞} is accomplished within the first 3 years of the lifespan, with growth in length much reduced after 5 years of age. The K observed in this study is higher than the K of 0.243 reported by both Ye and Tang (1996) and Chen (1997) using scales. Sheaves (1995) did not report parameters of the VBGF, but the observed length-at-age of the Great Barrier Reef fish was somewhat similar to that reported in this study.

Estimating mortality using age-based catch curves involves a number of assumptions. The catch curve of *L. russelli* suggests that the mortality rate across each age class is somewhat constant and therefore the natural mortality rate estimated from the catch curve of *L. russelli* is likely to be reasonable. *L. russelli* were fully recruited to the fish trawl fishery by age 6, and the instantaneous rate of natural mortality (M) above age 6 is low.

The M derived from the age structure of *L. russelli* was somewhat similar to the estimate of M derived from Hoenig's empirical equation, whereas the estimate of M obtained from the regression equation of Pauly (1980) was substantially higher. The Pauly (1980) equation does not provide reliable estimates of M in those fish species that have rapid initial growth followed by a relatively long life (Newman et al. 1996, Hart and Russ 1996). Care must be taken when applying empirical equations in population dynamics studies

as overestimates of M provide misleading impressions on the production potential of fish stocks. However, if there is a mismatch between the age at maturity and the age at full recruitment to the fishery, a lower estimate of M is likely to be the result. In this study, full recruitment to the fish trawl fishery does not occur until age 6. Although no information is available on the age at maturity of *L. russelli*, if maturity occurs prior to age 6, the estimate of M obtained in this study is likely to provide a lower estimate of M and therefore overestimate the impact of fishing.

There was a lack of small young fish and juveniles less than 4 years of age caught by the fish trawls and no fish less than 3 years of age were obtained for analysis. Juvenile *L. russelli* are known to frequent nearshore coastal habitats such as mangrove estuaries, headland areas and rocky shores (Newman and Williams 1996, Sheaves 1995). Furthermore, Sheaves (1995) reports that estuarine populations of *L. russelli* consist entirely of reproductively immature fish and that reproductively mature fish were only sampled from offshore waters well away from estuaries. The possibility therefore exists that juvenile *L. russelli* do not recruit in large numbers in the deepwater (> 100 m) continental shelf waters off the Pilbara coast and that the population size in more offshore waters is dependent upon cross-shelf movements of *L. russelli*. This hypothesis requires further investigation.

Assuming the above hypothesis is accurate, the life cycle of *L. russelli* is impacted by different fishing sectors as it undertakes ontogenetic movements from nearshore waters to deeper offshore waters. The nearshore waters of North-Western Australia comprising the estuarine and headland areas out to a depth of 30 m are restricted to recreational fishing activities. The commercial fish trap fishery boundary starts at the 30 m contour, while the inner boundary of the commercial fish trawl fishery commences at the 50 m depth contour. These management boundaries indicate that a high degree of natural protection is afforded L. russelli up to maturity. For example, assuming the age-at-maturity for these fish is approximately age 4 and as they are not catchable in the commercial sector until ages 6 to 8 onwards, indicates a number of post maturity age classes are not vulnerable to harvest. Therefore, the trap and trawl fisheries of North-Western Australia are likely to maintain adequate levels of the spawning stock biomass of these fish as long as each fishing sector does not expand beyond the current boundaries.

L. russelli off the Pilbara coast of Western Australia are long-lived (to at least 21 years of age), with rapid growth towards asymptotic length, and low rates of post maturity natural mortality. Thus, these fish are potentially vulnerable to overfishing despite their small size. However, in North-Western Australia, the likely natural protection of several age classes from harvest indicates that the productivity of this species will be maintained at adequate levels. Should the current management arrangements for this species be compromised, this situation will need to be re-assessed. Given the importance of *L. russelli* to both commercial fishers and recreational anglers, consideration should be given to establishing effective size limits for shallow water areas where successful releases can occur.

Acknowledgments

The Fisheries Research and Development Corporation (FRDC) provided financial support for this research as part of FRDC Project No. 97/138. Logistical support was provided by the Department of Fisheries, Government of Western Australia. This study would not have been possible without the invaluable contributions of D. Evans, R. Ashworth, B. Smith and I. Dunk. Ms. Peta Williamson kindly provided preliminary data on the recreational fish catch in the Pilbara region of North-Western Australia.

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