



# Growth, Age Validation, Mortality, and other Population Characteristics of the Red Emperor Snapper, *Lutjanus sebae* (Cuvier, 1828), off the Kimberley Coast of North-Western Australia

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Red emperor, *Lutjanus sebae*, were examined from commercial catches in the Northern Demersal Scalefish Fishery (NDSF) of north-western Australia from 1997 to 1999. Specimens ranged from 183 to 728 mm fork length (FL); males had a mean FL of 509 mm, and were significantly larger than females that had a mean FL of 451 mm. Ages were estimated from thin sections of sagittal otoliths. Marginal increment analysis of sagittal otoliths showed a single annual minimum during September and October and indicated that one annulus is formed each year. Male *L. sebae* ( $n=977$ ; 211–728 mm FL) ranged from age 2 to 30 years and females ( $n=1384$ ; 183–584 mm FL) ranged from age 1 to 34 years. Sagittal otolith weight and height were significantly correlated with age for each sex. There was significant differential growth between sexes. The relationship of observed fork length at age was described by the von Bertalanffy growth equation for males,  $L_t=627.8 \{1 - \exp[-0.151(t+0.595)]\}$  and females,  $L_t=482.6 \{1 - \exp[-0.271(t-0.065)]\}$ . The slow growth, long life span and large size and age at maturity of *L. sebae* indicate that this species has a low production potential and hence spatial area closures are vulnerable to over-exploitation. The instantaneous rate of natural mortality ( $M$ ) ranged from 0.104 to 0.122. The optimum rate of fishing mortality was estimated to be 0.052–0.061. The instantaneous rate of total mortality ( $Z$ ) estimated from catch at age data for fully recruited ages, was 0.374 in 1997/98 and 0.242 in 1998/99. Hence, the NDSF population of *L. sebae* is exploited above optimum levels. Given their low production potential, populations of *L. sebae* in north-western Australia and elsewhere in the Indo-Pacific region require prudent management. Furthermore, fishery managers need to consider as part of any harvest strategy for these fish to preserve significant levels of the spawning stock.

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## Introduction

Red emperor, *Lutjanus sebae* (Cuvier) are large valuable tropical demersal reef-associated fish in the Lutjanidae family. *L. sebae* is widely distributed throughout the Western Pacific and Indian Ocean region from Australia to southern Japan, and westwards to East Africa and the southern reaches of the Red Sea (Allen, 1985). They inhabit hard bottom areas and areas of vertical relief and/or large epibenthos from shallow near-shore waters (ca. 1 m) to depths of at least 150 m (Newman, unpublished data). In north-western Australia, *L. sebae* are a commercially important species from the Shark Bay area (26°S) northwards to the Northern Territory border and it is also a popular angling species throughout its

range (Kailola *et al.*, 1993; Newman, unpublished data).

In Western Australia, *L. sebae* is a highly valued food fish, that is marketed whole, usually fresh on ice, and is transported from regional centres in the north of the State to wholesale markets in the local capital city, Perth and to markets on the east coast of Australia. In the Northern Demersal Scalefish Fishery (NDSF) within the Kimberley region of Western Australia, *L. sebae* has comprised on average 23.6% of the total landed catch of demersal scalefish from 1995–1999, ca. 160 metric tonnes per year (Newman, 2001). It is the most valuable species landed in terms of the wholesale price and is second in landings only to the goldband snapper, *Pristipomoides multidens*.

Prior to 1999, published age estimates for *L. sebae* were derived from length frequency analysis, scales,

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vertebrae, or whole otoliths (Lablache & Carrara, 1988; Mees, 1992; Druzhinin & Filatova, 1980; Yeh *et al.*, 1986; Liu & Yeh, 1991; McPherson & Squire, 1992). Few of these studies attempted to validate age estimates, resulting in a plethora of divergent estimates of growth rates, mortality and longevity. Recently, Cappo *et al.* (2000) demonstrate that growth increments in the sectioned otoliths of *Lutjanus sebae* from the central Great Barrier Reef (GBR) are deposited on an annual basis. In addition, the validation of annuli in sectioned otoliths from the direct observation of individuals that were injected with oxytetracycline and recaptured after annulus deposition has now been established for 14 *Lutjanus* species (including *L. sebae*) from the GBR (Newman *et al.*, 1996; Hilomen, pers. comm.; Cappo *et al.*, 2000). The validation of annuli (alternating opaque and translucent growth increments) in the sectioned otoliths of reef fishes is now widespread (e.g. Ferreira & Russ, 1992, 1994; Fowler & Doherty, 1992; Fowler, 1995; Choat & Axe, 1996).

Newman *et al.* (2000a) showed that age estimates obtained from counts of increments on whole otoliths were consistently much lower and more imprecise, at all ages, compared with counts from sectioned otoliths. Furthermore, Newman *et al.* (2000a) demonstrated that underestimates of fish age derived from whole otolith counts caused serious over-estimation of natural mortality parameters and concluded that serious overfishing could occur if these estimates were applied for fishery management purposes. The accurate determination of fish age and growth information is essential to understanding the life history, growth rates, longevity and production potential of exploited reef fishes and is essential for the derivation of the demographic parameters fundamental to population dynamics models.

This study is the first detailed investigation of the age and growth characteristics of *L. sebae* in waters off the Kimberley coast of north-western Australia using sectioned sagittal otoliths. The objectives of this study are to validate the ageing technique, to determine the age, growth rate, size and age composition of *L. sebae*, and to elucidate the relationship between otolith dimensions and fish age. This study further seeks to describe exploitation patterns and mortality rates of the commercial fishery in offshore Kimberley waters.

## Materials and methods

Landings from commercial fishers in the Northern Demersal Scalefish Fishery (NDSF) were sampled on an *ad hoc* basis whenever possible from July 1995 to

November 1996, and subsequently on a monthly basis across all vessels in the fleet from May 1997 to December 1999. All fish sampled were caught with fish traps in waters 60 to 150 m depth, from 12°–20°S latitude (Figure 1). Specimens under the minimum legal size of 410 mm total length, were obtained directly from commercial catches with additional small fish obtained from both commercial fishers and research vessel cruises.

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) and clean weight (CW). Clean weight is defined as the total weight after removal of the gills and viscera. Where possible, the sex was determined by 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 dry in envelopes prior to processing.

Measurements of fish length (TL, FL, SL) were used to derive length conversion equations using the following generalized linear regression models:  $TL=a+b$  (FL),  $FL=a+b$  (TL),  $FL=a+b$  (SL) and  $SL=a+b$  (FL). One-way analysis of variance ( $\alpha=0.05$ ) was used to compare mean age, size and weight between sexes. Trends in mean length and weight of fish over time were assessed using analysis of variance ( $\alpha=0.05$ ).

### Weight-length models

The relationship between length and weight was described by the power relationship:

$$W=aL^b$$

where W is weight (g) and L is 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.

Analysis of covariance ( $\alpha=0.05$ ) was used to determine if there were significant differences in the 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.

### Otolith preparation and analysis

Sagittae were weighed (to 0.01 mg), and measured along three axes (total length along the anterior–posterior axis including the rostrum, breadth along the

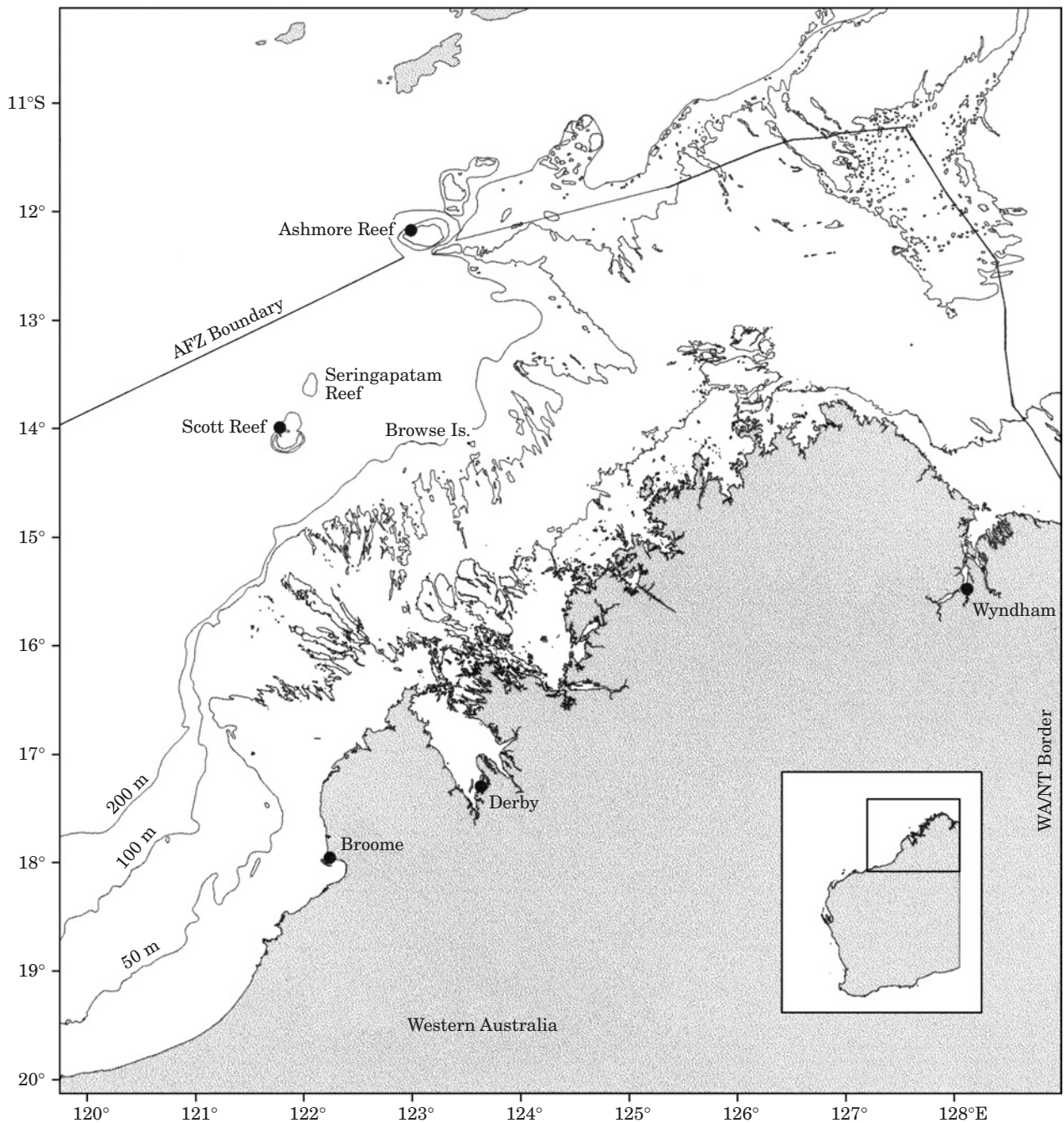


FIGURE 1. Location of the Northern Demersal Scalefish Fishery off the Kimberley coast of north-western Australia.

dorso-ventral axis and height (thickness) through the central core of the otolith to the outer edge of the otolith) to the nearest 0.01 mm using digital callipers. Only complete and intact otoliths were weighed and measured. These dimensions were related to the length and age of the fish using generalized linear regression techniques.

Analysis of fish age was based on examination of transverse sections of sagittal otoliths. Initially, 10

sagittal otolith pairs were examined to determine whether the number of opaque bands differed between left and right sagittae. The counts in each otolith pair were identical in all cases. Therefore, one sagitta per fish was randomly selected and embedded in epoxy resin. Thin transverse sections (250–300  $\mu\text{m}$ ) were made through the core of the otolith from the dorsal apex to the ventral apex with a low-speed jewellery saw containing a diamond-wafering blade.

Three thin sections were taken from each otolith to assist in determining fish age. The first section was as close as possible to the otolith core. Sections were washed by agitating in 2% HCl for up to 10 s to remove calcium build-up, rinsed twice in H<sub>2</sub>O, allowed to dry and mounted on microscope slides with casting resin. These sections were then examined under a dissecting microscope at 10–30 × magnification with reflected light on a black background.

#### *Age validation*

Marginal increment analysis (MIA) was used to validate the periodicity of ring formation. MIA relies on the assumption that if a translucent zone is laid down once per year, there should be a clear pattern of periodic growth on the edge of the otolith during the year. MIA is appropriate only if all fish in the population lay down the translucent zone at the same time. An annulus would then consist of a single opaque zone and a single translucent zone. The opaque zone is believed to form during periods of slow growth. [Beamish and MacFarlane \(1983\)](#) recommend that all age classes should be included in the analysis of MIA.

The marginal increment of each otolith was determined by the proportional method where the amount of otolith growth from the incomplete putative growth increment on the outer margin of the otolith is expressed as a fraction of the total growth in the preceding whole increment cycle (opaque and translucent zone). Measurements for MIA were undertaken in the ventral lobe of the otolith using an ocular micrometer and a dissecting microscope at 50 × magnification. Measurements were made as close as possible to the margin of the sulcus acousticus. Otolith sections were excluded from the analysis if the discrimination between the end of a translucent zone and the beginning of the subsequent opaque zone was unclear, in order to minimize measurement error. Mean marginal increments were plotted across all age classes in each month from April 1997 through to November 1998 to ascertain if they follow a consistent annual trend and thus be considered as true annuli.

Direct validation of annulus formation was attempted through the use of calcein marking. From April 1997 to September 1999, 1291 *L. sebae* were caught in fish traps off the Kimberley coast of north-western Australia in depths ranging from 40–115 m, tagged with large dart tags and injected with calcein (10 mg ml<sup>-1</sup>) before being released. Injection was carried out with a syringe and 26 gauge needle, which was inserted under the scales and through the skin into the coelomic cavity in close proximity to the

pelvic fin region. A minimum dosage of 15 mg of calcein per kg of fish was given. The otoliths of any recaptured fish were sectioned and viewed under ultra-violet light.

#### *Age determination*

By convention all fish were assigned an assumed 'birth date' of 1 January to assure proper year-class identification. Ages were assigned based on counts of annuli (alternating opaque and translucent bands) from sectioned otoliths. Annuli were counted without reference to fish length or date of capture. Each otolith was examined on three separate occasions. Annuli were counted in the ventral lobe of the otolith from the primordium to the proximal surface as close as was practicable to the ventral margin of the sulcus acousticus. All counts were made by one reader (SJM) to ensure consistency. If the three counts differed, otolith sections were re-examined. In most cases requiring resolution, 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 otolith structure. Otoliths with structural irregularities such as unusual calcification, deterioration of the ventral lobe, or poorly defined annuli were considered indecipherable. Indecipherable otoliths were excluded from analysis of fish age. Counts were compared and the precision of age estimates determined using the Index Average Percent Error (IAPE) of [Beamish and Fournier \(1981\)](#), in order to determine the level of confidence that can be placed in the interpretation of the otolith structure. Greater precision is attained as the IAPE is minimized.

#### *Growth and mortality models*

The von Bertalanffy growth function (VBGF) was fitted to observed length-at-age data using nonlinear least squares estimation procedures. The VBGF is defined by the equation:

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}$$

where  $L_t$  = length at age  $t$ ;  $L_\infty$  = asymptotic length;  $K$  = Brody growth coefficient and defines the growth rate towards  $L_\infty$ ;  $t$  = 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. The von Bertalanffy growth curves between sexes were compared using the likelihood ratio test of [Cerrato \(1990\)](#). The hypothesis under consideration is that there is a single underlying growth curve, regardless of the sex of the fish.

Estimates of the instantaneous rate of total mortality ( $Z$ ) were obtained from catch-at-age data of *L. sebae* from the NDSF. Annual catch in weight was converted to annual catch in numbers-at-age by the use of age frequency data standardized by fishing effort to obtain catch per age class. Catch in weight was converted to catch in numbers based on the mean weight of *L. sebae* observed in the sampled catch each year. Mortality estimates were then derived between successive years by obtaining the natural logarithm of the catch per age class (e.g. age 4) in year  $t$  and subtracting the natural logarithm of the catch per age class (e.g. age 5) in year  $t+1$  for all fully recruited age classes. Mean total  $Z$  was then calculated across all fully recruited age classes. Estimates of the survival rate of each species ( $S$ ) were then calculated by  $S=e^{-Z}$  (Ricker 1975). Instantaneous natural mortality rates ( $M$ ) were derived 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). Estimates of  $F$  were derived by subtraction, since  $F=Z-M$ . The annual harvest rate or percentage removal by the fishery was estimated by:  $\text{harvest rate} = [F/Z (1-e^{-Z})] \times 100\%$ . Exploitation rates ( $E$ ) were derived from the estimates of  $Z$  and  $F$  as defined by the equation  $E=F/Z$ .

#### Estimating optimum fishing mortality rates ( $F_{\text{opt}}$ )

Until the 1990s fishing mortality objectives such as  $F=M$  were often prescribed (e.g. Gulland, 1970). Adoption of harvest strategies such as setting  $F=F_{0.1}$  (which ignore stock-recruitment effects) were thought to be quite conservative, and usually resulted in  $F=M$  harvest strategies (Walters, 2000). Recently, the meta-analysis of Myers *et al.* (1999) synthesized information about stock-recruitment curve slopes expressed as maximum reproductive rates per spawner at low spawner biomass. When their results were substituted into age-structured population models and optimum equilibrium fishing rates  $F_{\text{opt}}$  calculated, the results implied that  $F_{\text{opt}}$  was substantially lower than  $M$  for most species and stocks (Walters, 2000; pers. comm.). The main exceptions were cases where regulation or natural phenomena resulted in age selectivity patterns where most fish have at least one chance to spawn before becoming vulnerable to high harvest rates (Walters, 2000; but see also Myers & Mertz, 1998).

The harvest strategy of  $F_{\text{opt}}=0.5 M$  (Walters, 2000) was adopted in this study as the optimum fishing mortality rate for the sustainable exploitation of *L. sebae* in the NDSF. This harvest strategy seeks to ensure adequate egg production and hence the maintenance of recruitment such that the current

TABLE 1. Length conversion equations for *L. sebae* off the Kimberley coast of north-western Australia. Estimates were obtained of 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=(1.0654 × FL)+3.5947	1658	0.9984
FL=(0.9371 × TL) - 2.6297	1658	0.9984
FL=(1.1521 × SL)+11.8230	1577	0.9890
SL=(0.8584 × FL) - 5.7307	1577	0.9890

exploitation rate of fishers in the NDSF should not compromise the ability of future generations to harvest the resource. Walters (2000) reported that any fishery assessment that results in levels of  $F_{\text{opt}}$  above  $0.5 M$  needs to be very carefully justified, either by clear demonstration that higher fishing mortality rates have been sustained for several fish generations or that the age-selectivity schedule permits virtually full replacement of recruits (by the fish that survive to spawn) prior to the age at first capture.

Furthermore, Patterson (1992) reported that fishing mortality rates above  $2/3 M$  are often associated with stock declines, whereas fishing mortality rates below this level have resulted in stock recovery. Therefore, we consider that fishing mortality rates above  $2/3 M$  to represent an undesirable state for the resource, and a situation which management action should avoid, in essence a limit reference point ( $F_{\text{limit}}$ ) for fishery managers. Calculation of  $F_{\text{opt}}$  and  $F_{\text{limit}}$  for *L. sebae* requires an estimate of the natural mortality ( $M$ ), since  $F_{\text{opt}}=0.5 M$  and  $F_{\text{limit}}=2/3 M$  (Walters, 2000; Patterson, 1992).

## Results

A total of 2386 *L. sebae* were examined for age analysis from the NDSF ranging in size from 183–728 mm FL (189–7204 g TW). Of the fish collected, 977 were identified as males ranging from 211–728 mm FL and 274–7204 g TW, while 1384 were female ranging from 183–584 mm FL and 205–3938 g TW. Length conversion equations were derived for total length, fork length and standard length (Table 1).

#### Length-weight models

Length-weight relationships were calculated separately for males, females and for both sexes combined (Table 2). The relationship between TW and FL is presented in Figure 2. Weight-at-length was

TABLE 2. Length–weight relationships for *L. sebae* off the Kimberley coast of north-western Australia. Estimates were obtained of 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 in mm and the weight is TW or CW in g)

Group	$a$	$b$	$n$	$R^2$
<i>L. sebae</i> (all fish—TW)	$2.051 \times 10^{-5}$	3.0147	2242	0.9811
<i>L. sebae</i> (all fish—CW)	$1.553 \times 10^{-5}$	3.0379	2233	0.9849
<i>L. sebae</i> (male—TW)	$1.524 \times 10^{-5}$	3.0614	899	0.9831
<i>L. sebae</i> (female—TW)	$2.227 \times 10^{-5}$	3.0020	1317	0.9594

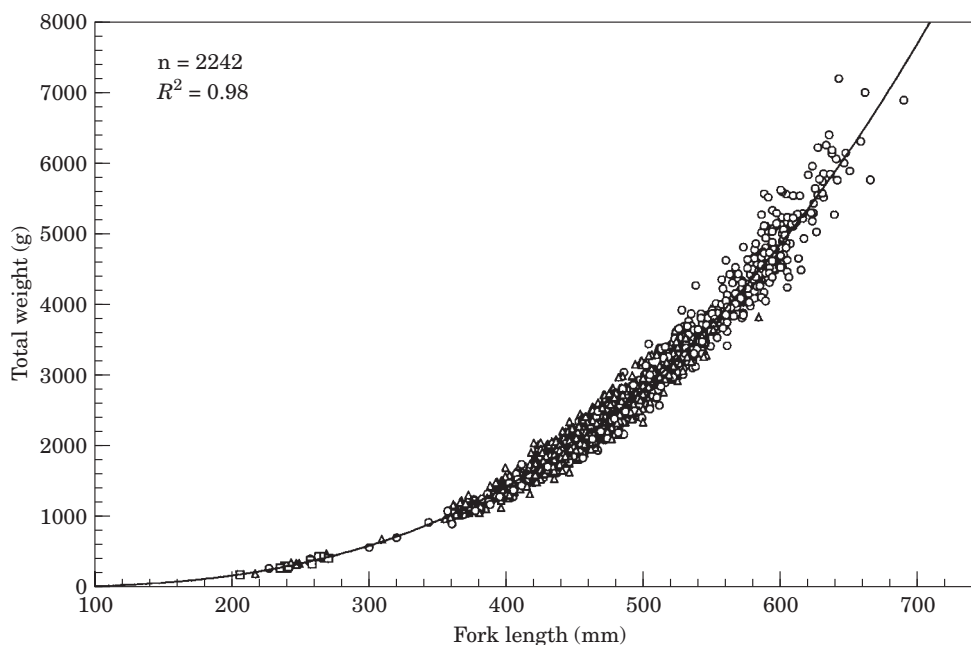


FIGURE 2. Relationship between fork length and total weight for *L. sebae* off the Kimberley coast of north-western Australia. (○) male; (△) female; (□) unknown.

significantly different between sexes for *L. sebae* (TW:  $F=22.16$ ;  $df: 1, 2213$ ;  $P<0.001$ ; CW:  $F=32.75$ ;  $df: 1, 2204$ ;  $P<0.001$ ), with males larger than females. Mean weights (TW:  $F=579.96$ ;  $df: 1, 2215$ ,  $P<0.001$ ) and mean lengths (FL:  $F=566.48$ ;  $df: 1, 2595$ ,  $P<0.001$ ) of *L. sebae* between sexes were both significantly different, with males larger than females (see also Figure 3). Mean age ( $F=23.78$ ;  $df: 1, 2359$ ,  $P<0.001$ ) of *L. sebae* females was significantly higher than males.

Temporal trends were evident in the mean length and weight of *L. sebae* over the duration of the study. Mean FL was significantly different among years from 1997 to 1999 (ANOVA:  $F=6.24$ ;  $df: 1, 2226$ ,  $P<0.01$ ), with 1997=1998, 1998=1999, 1997 > 1999. Mean TW was also significantly different among years from 1997 to 1999 (ANOVA:  $F=10.37$ ;  $df: 1, 1930$ ,  $P<0.001$ ), with 1997=1998, 1997=1999, 1998>1999.

#### Age validation

Otoliths displayed alternating opaque and translucent zones. A cyclical trend in the marginal increment state is evident (Figure 4). The mean monthly marginal increment was lowest in September–October and highest in July–August in each of two consecutive years (Figure 4). A transition in the predominance of opaque zones to translucent zones at the otolith margin occurs during the period of May–June to August inclusively, with the opaque zone being deposited at the otolith margin for the greater part of the cycle. The month of September is characterized by a high frequency of opaque margins and a corresponding low marginal increment ratio (MIR). As the MIR increases from September the frequency of opaque otolith margins also increases. The annulus is completed by the end of August in each year, with the new increment beginning to form in September–October.

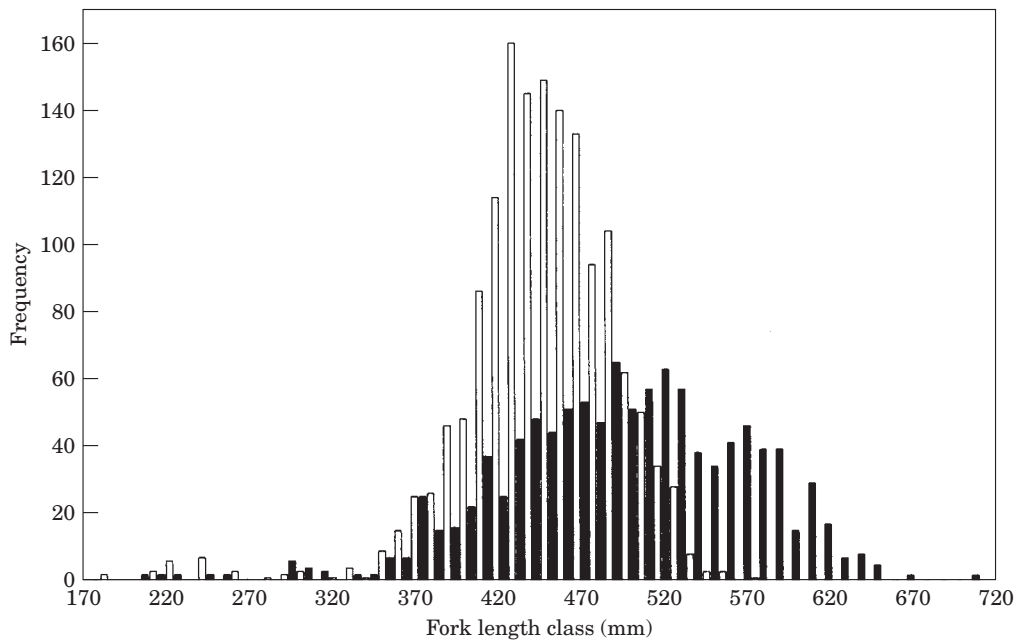


FIGURE 3. Length frequency distribution (10 mm length classes) of male and female *L. sebae* sampled for age determination. (■) male; (□) female.

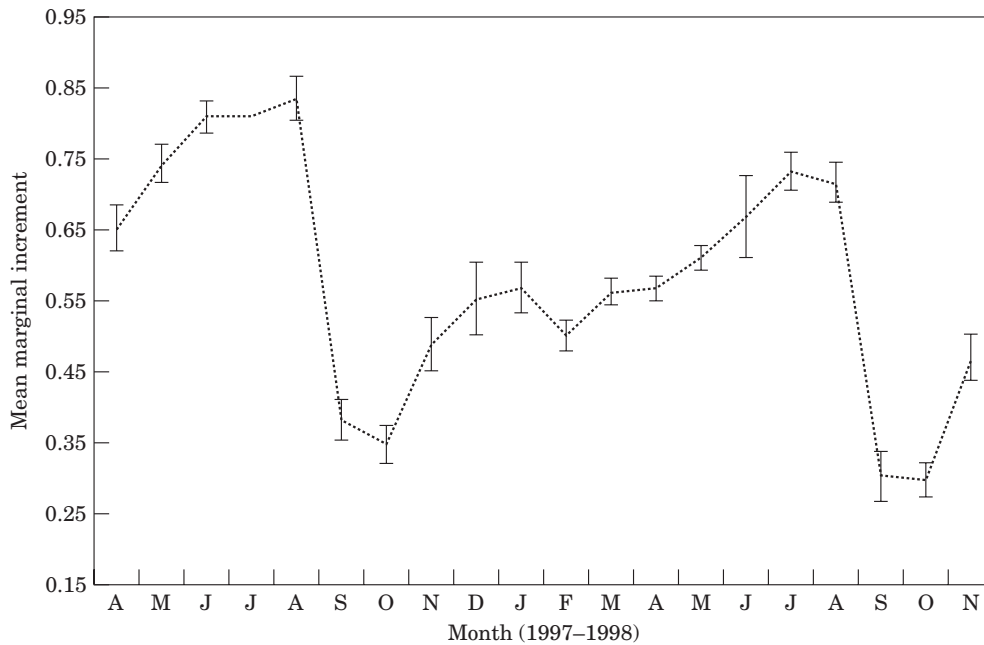


FIGURE 4. Mean monthly marginal increment for red emperor, *Lutjanus sebae* from April 1997 to November 1998. Error bars represent  $\pm 1$  SE.

In all months sampled no significant relationships between age estimates and marginal increment ratio were evident. Sample sizes used were adequate for the analysis. In general, the data within any month where a new increment was being formed within the sampled population approximated a normal

distribution (normal probability plots), while during transitional months two groups of points were evident, both approximately fitting parallel linear functions. Variability between age classes was greatest for younger fish, while older fish tended to have their MIR close to the mean.

TABLE 3. Comparisons among otolith dimensions and length and age of *L. sebae*. 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 (OW=otolith weight, OL=otolith length, OB=otolith breadth, OH=otolith height)

Depth variation	Independent variables	Sample size	Equation	R <sup>2</sup>	SE of estimate
FL	OW	2442	$FL=(135.609 \times OW)+318.077$	0.640	42.160
FL	OL	2268	$FL=(29.102 \times OL) - 108.684$	0.870	24.211
FL	OB	2422	$FL=(44.572 \times OB) - 131.607$	0.774	32.148
FL	OH	2429	$FL=(64.161 \times OH)+234.735$	0.387	53.174
Age	OW	2210	$Age=(11.118 \times OW) - 0.642$	0.786	2.3720
Age <sub>male</sub>	OW	902	$Age=(9.097 \times OW)+0.495$	0.883	1.4218
Age <sub>female</sub>	OW	1283	$Age=(13.742 \times OW) - 2.669$	0.847	2.1858
Age	OL	2129	$Age=(1388 \times OL) - 15.709$	0.340	4.1324
Age	OB	2281	$Age=(2.119 \times OB) - 16.828$	0.318	4.1367
Age	OH	2289	$Age=(7.015 \times OH) - 14.143$	0.861	1.8758
Age <sub>male</sub>	OH	950	$Age=(6.237 \times OW) - 11.604$	0.852	1.5843
Age <sub>female</sub>	OH	1330	$Age=(7.465 \times OW) - 15.613$	0.874	1.9591

The consistent annual cycle of the mean marginal increment indicates that one annulus is formed each year (Figure 4). As the marginal increment analysis involved random sampling across all age classes in the sampled population, the validation of annuli is expected to persist across all age classes. Two *L. sebae* were recaptured, with both fish at liberty for 314 days. Both recaptured fish were female with one fish growing 12 mm in length and the other 0 mm. These two calcein injected and tagged fish provide direct evidence of August being the time of transition from translucent to opaque zone formation at the otolith margin. Between the time of capture and recapture (314 days) all otolith growth was opaque. Although this does not demonstrate any annual cyclical pattern in deposition as only opaque material was deposited during the intervening period, the dominance of opaque deposition throughout the year is reinforced and indicates that a maximum of one opaque zone is deposited per year.

#### Otolith morphology, analysis and functionality

The sagittae of *L. sebae* are large elliptical structures that are somewhat laterally compressed with a slightly concave distal surface. A curved sulcus crosses the proximal surface longitudinally, with the depth of the sulcal groove increasing with fish age. The precision of otolith readings of *L. sebae* was high, with the Index Average Percent Error (IAPE), 4.7%. The low IAPE of *L. sebae* indicates a high level of precision among

otolith readings and indicate that otoliths were interpreted in a similar manner on each occasion they were examined.

Otolith length and breadth were useful predictors of fish length in *L. sebae*, accounting for more than 77% of the variability (Table 3). In contrast, otolith weight and in particular otolith height were both poor predictors of fish length accounting for less than 65% of the variability (Table 3). Conversely, otolith weight and otolith height were both useful predictors of fish age in *L. sebae*, whereas, otolith length and breadth were not (Table 3, Figure 5). When all fish were combined otolith height was a more robust predictor of fish age than otolith weight, accounting for 86% of the variability in age (Table 3). However, significant differential growth was evident between sexes (see below). Otolith weight and otolith height were both robust predictors of fish age for *L. sebae* when sex was known explaining 85–88% of the variability in age (Table 3, Figure 5).

#### Growth and mortality models

The von Bertalanffy growth curve was fitted to lengths-at-age for all *L. sebae*, and separately for each sex (Figure 6, Table 4). Growth of *L. sebae* is slow to age 8, with growth in length much reduced beyond the 8+ age cohorts. Length-at-age of *L. sebae* was significantly different between sexes (Log-likelihood=1.783, Test Statistic=1.002,  $P<0.01$ ; see also Figure 6). The estimated  $L_{\infty}$  and K values



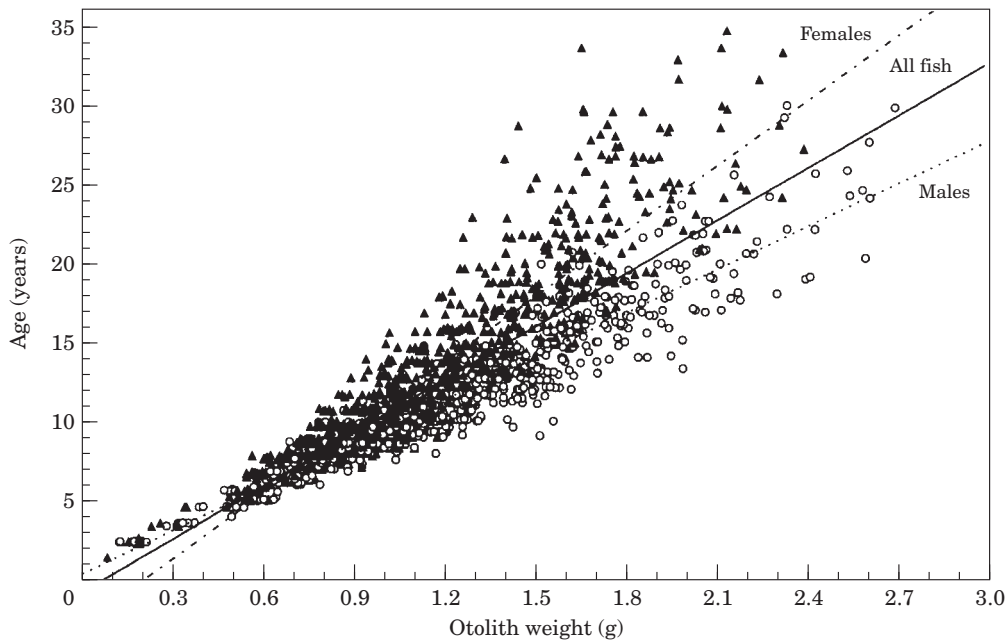


FIGURE 5. Relationship between otolith weight and age of *L. sebae* estimated from sectioned otoliths. (○) male; (▲) female.

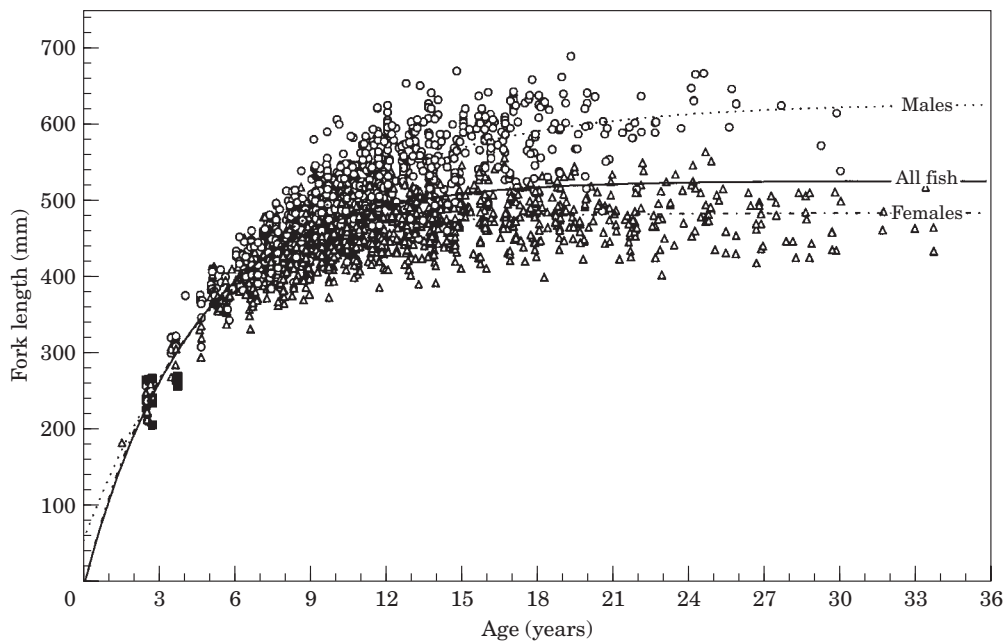


FIGURE 6. Length-at-age and von Bertalanffy growth curves for *L. sebae* off the Kimberley coast of north-western Australia. (○) male; (△) female; (■) unknown.

of *L. sebae* were also significantly different between sexes (Log-likelihood=1.178, Test Statistic=1.002,  $P < 0.05$  and Log-likelihood=1.008, Test Statistic=1.002,  $P < 0.05$ , respectively, Table 4).

The maximum observed age of *L. sebae* in the Kimberley region was 34+ years. The *L. sebae*

resource in the Kimberley region of north-western Australia has been exploited for over 20 years, therefore, it is possible that the longevity of *L. sebae* is in excess of 40 years. These two estimates of maximum age in *L. sebae* were applied to the Hoenig (1983) equation for fish in order to derive an estimate of  $M$ .

TABLE 4. Growth parameters derived from the von Bertalanffy growth function and population characteristics of *L. sebae* off the Kimberley coast of north-western Australia ( $n$ =sample size, FL is in mm, and age (t) is in years)

Parameters	Male	Female	Total
$n$	1001	1408	2384
$L_{\infty}$	627.79	482.62	524.77
$K$	0.1511	0.2710	0.2330
$t_0$	-0.5947	0.0650	0.0563
$R^2$	0.8044	0.8049	0.6179
$n$	1081	1516	2627
FL <sub>mean</sub>	508.5	450.5	472.4
FL <sub>min</sub>	211	183	183
FL <sub>max</sub>	728	584	728
$n$	977	1384	2386
$t_{\text{mean}}$	11.32	12.34	11.84
$t_{\text{min}}$	2	1	1
$t_{\text{max}}$	30	34	34

TABLE 5. Summary of total mortality (Z) estimates for *L. sebae* derived from catch curves based on ages determined from sectioned otoliths. Estimates of fishing mortality (F) are derived by subtraction since  $Z=F+M$  and are compared to estimates of optimum fishing mortality rates

Year	Z	F	$F_{\text{opt}}$	$F_{\text{limit}}$
1997/98	0.374	0.252–0.270	0.052–0.061	0.069–0.082
1998/99	0.242	0.120–0.138	0.052–0.061	0.069–0.082

Consequently, M is considered to be in the range of 0.1038–0.1223, representing an annual survivorship of 88–90% for an unfished population.

The age structures of *L. sebae* sampled among years were somewhat similar. The 1997 sample had a peak in year class 9 and a relatively strong 8+ year class, with abundance per age class declining rapidly to age 22 (Figure 7). In 1998 relatively strong year classes were present from age 8 through to age 10, with abundance per age class declining rapidly to age 22 (Figure 7). The strong 9+ year class present in 1997, was present as a strong 10+ year class in 1998 (Figure 7) and persisted as a strong 11+ year class in 1999 (Figure 7). The progression of this strong year class provides further evidence of the annual formation of growth increments. Relatively strong year classes were present from age 9 through to age 11 in the 1999 sample, with abundance per age class declining rapidly to age 22 (Figure 7). The strong 9+ year class present in 1998, was present as a strong 10+ year class in 1999 (Figure 7). In all years abundance per

age class declined rapidly to age 22, with fish older than 20 years not well represented in the catch. In all years fish less than 8 years of age were not well represented in the catch, inferring that these fish either do not enter traps or are present in areas not currently fished by operators in the NDSF.

*Lutjanus sebae* less than age 8 were in general not fully recruited to the sampled population and were excluded from the mortality estimates derived from catch-at-age data. The year-specific total annual rate of mortality, Z, of *L. sebae* in the NDSF, was 0.374 for 1997/1998 (fish aged 8–25 years) and 0.242 for 1998/1999 (fish aged 8–25 years). Estimates of the rate of fishing mortality, F, were 0.25–0.27 for 1997/98 and 0.12–0.14 for 1998/99, representing an annual harvest rate of approximately 21–23% and 11–12% by the fishery in each year (Table 5). In addition, exploitation rates were in the range 0.67–0.72 for 1997/98 and 0.50–0.57 for 1998/99.

#### Estimation of optimum fishing mortality rates ( $F_{\text{opt}}$ )

The optimum fishing mortality rate,  $F_{\text{opt}}$  for *L. sebae* was estimated to be 0.0519–0.0611, with a limit reference point,  $F_{\text{limit}}$  of 0.069–0.082 (see Table 5). These results indicated that only approximately 6% of the available stock of *L. sebae* can be harvested on an annual basis in a sustainable manner, and that in order to prevent stock declines annual harvest rates should not exceed 10% of the stock size.

## Discussion

Annuli are deposited in the sagittal otoliths of *L. sebae* in June–August, when water temperatures are at a minimum (mean 26.4 °C). On the Great Barrier Reef annuli were completed on average 1–3 months after the minima in water temperature, in the austral spring–early summer period around late October for *L. sebae* (Cappo *et al.*, 2000). This coincides with the spring–summer peak in opaque zone formation in tropical fishes identified by Fowler (1995) and Beckman and Wilson (1995), but see also Newman *et al.* (1996) and Cappo *et al.* (2000). While the exact causal mechanism of opaque zone formation is poorly understood, data from this study and related studies on lutjanids suggest that water temperature minima (probably in association with other factors) influences the endolymph fluid chemistry of these fish resulting in opaque zone completion.

Annuli in sectioned otoliths have been shown to be valid indicators of age for 14 lutjanid species in the Indo-Pacific region through the use of direct age validation techniques, which involve tagging and

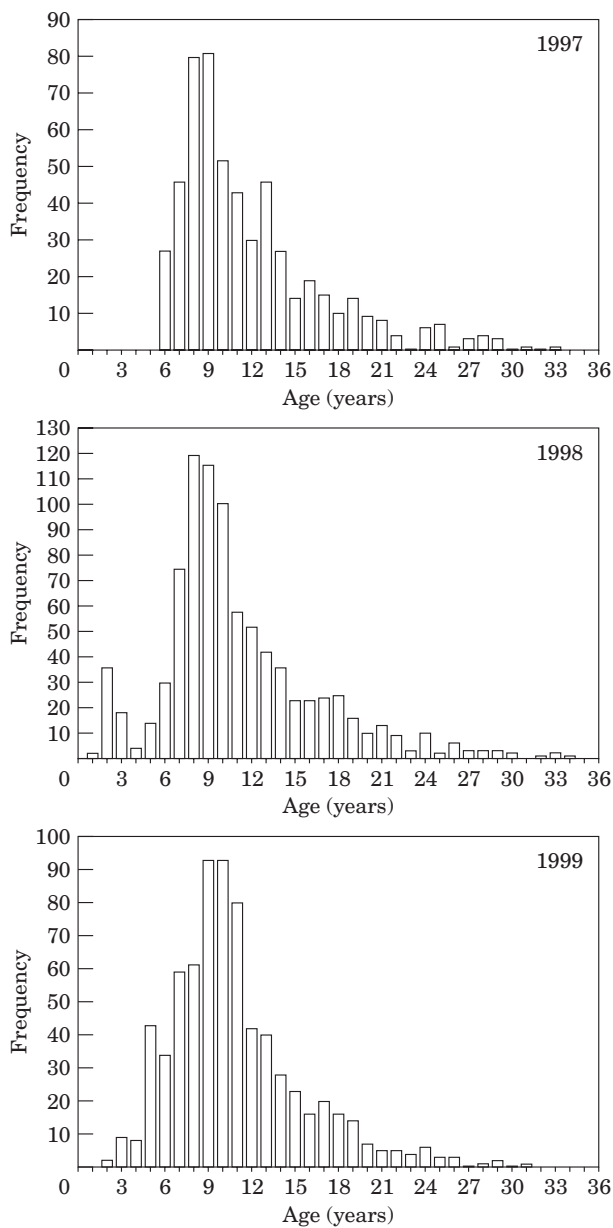


FIGURE 7. Age frequency distribution of *L. sebae* from the NDSF from 1997 to 1999.

injecting fish with tetracycline (Newman *et al.*, 1996; Cappo *et al.*, 2000). Validating the formation of annuli in sectioned otoliths for such a large number of lutjanid species indicates that the correspondence between annuli and age in years should be indisputable. Therefore, age validation for these species should no longer be considered essential if sectioned sagittal otoliths are used to derive age and growth parameters.

This study confirmed that *L. sebae* are long-lived. The oldest individual we aged was 34 years old, one

year younger than the sectioned otolith based age estimate 35 years reported for *L. sebae* in New Caledonia (Loubens, 1980). Those studies which have derived estimates of the age of *L. sebae*, based on the number of ‘annuli’ on scales (Druzhinin & Filatova, 1980), vertebrae (Yeh *et al.*, 1986; Liu & Yeh, 1991), and whole otoliths (McPherson & Squire, 1992), or inferred ages from modes in length frequency data (Lablache and Carrara, 1988; Mees, 1992) with little or no validation of fish age estimates are likely to be invalid.

The linear relationship between otolith weight and fish age (Figure 5) indicates that *L. sebae* otoliths continuously increase in weight with increasing age. The continuous growth of *L. sebae* otoliths with increasing age is noticeably independent of somatic growth. The regression model explains 85–88% (depending on the sex of the fish) of the variance for *L. sebae*. The dependence of otolith growth in weight on temporal scales directly signifies that otolith weight may be confidently used as a proxy for determining fish age. The robust nature of the otolith weight–age relationship further indicates that monitoring of the age composition of catches in the NDSF may in future be obtained from random samples of otolith weights in the population. The derivation of age estimates from otolith weight–age relationships is relatively inexpensive and may enable large sample sizes to be collected. However, it is recommended that the otolith weight–age relationship be re-examined at regular intervals (e.g. every three years) in order to assess whether the established relationship persists through time. These proxy age estimates can then be combined with commercial catch data to construct age-structured population models to assess the effect of exploitation on *L. sebae* in the NDSF. It should be noted that otolith weight–age relationships are likely to vary among regions, hence there is a need to establish these relationships within each area of study and the application of established relationships from other regions should be undertaken with caution.

*Lutjanus sebae* are long lived and slow growing. The rate of growth of both sexes is relatively consistent through the first 5–7 years of life, with asymptotic length reached on average after 10 years. The large sample size of *L. sebae* collected from the NDSF is considered representative of the population and therefore estimates of the VBGF are likely to be robust. Asymptotic length is achieved late, after approximately 50% of their life span. There is a marked change in growth rate between sexes at approximately 7–8 years of age associated with gonad maturation. The age-at-maturity for both sexes of *L. sebae* has

been estimated to be approximately 8 years (Newman, unpublished data).

There was a significant difference between female and male growth curves with males attaining a larger size, with the asymptotic length of male fish on average 30% higher than that of female fish. Some of the growth differences evident between sexes may result from behavioural differences associated with their mode of reproduction and the effects of egg production and spawning on growth potential. In summary, *L. sebae* exhibit marked differential growth between sexes with marked separation in length-at-age evident from age 7 onwards. This pattern of size differentiation between sexes within the *Lutjanus* genus is consistent with recent studies in the Indo-Pacific region all indicating that males reach a larger size-at-age than females (Davis & West, 1992; McPherson & Squire, 1992; Newman *et al.*, 1996, 2000b).

The observed length-at-age in the NDSF is lower than that reported by Newman *et al.* (2000a) from the central Great Barrier Reef. Factors which may contribute to the observed differences include regional differences in growth or biases associated with gear selectivity. However, as the GBR population sampled by Newman *et al.* (2000a) was considered to represent a relatively unfished population and contained many large fish, the observed length at age in the NDSF may represent a change from the early 1980s to the present as a consequence of size selective fishing over time. That is, if larger fish were more vulnerable to capture, then the faster growing fish within an age class were be selectively removed from the population and the result would be a reduced mean length-at-age for older age classes. Hence,  $L_{\infty}$  would be underestimated.

The Hoenig (1983) equation has provided similar estimates of  $M$  to those derived from age-based catch curves for unfished populations (Newman *et al.*, 1996, 2000b; Hart & Russ, 1996). This is due to the inverse relationship between longevity and natural mortality (species with high mortality rates cannot survive long enough to reach old age and conversely, long lived fish must have low rates of  $M$  in order to survive long enough to reach old age). The range of  $M$  estimates for *L. sebae* used in this study is similar to that observed for other long-lived lutjanid species in the Indo-Pacific region (e.g. Newman *et al.*, 1996, 2000a). Therefore, we consider the estimate of  $M$  used in this study to be reasonable.

*Lutjanus sebae* were fully recruited into the commercial fishery in the NDSF by age 8. The estimates of  $Z$  obtained from 1997/98 to 1998/99 in the NDSF were in the range 0.24 to 0.37, with estimates of  $F$  ranging

from 0.12 to 0.27. The difference in the mortality estimates derived from catch-at-age data requires further investigation. The current estimates of  $F$  in the NDSF vary above the target  $F_{opt}$  and some are in excess of the limit  $F_{limit}$ . Therefore, there may be a need to constrain fishing mortality of *L. sebae* in the NDSF. This study will form the basis of a detailed age-structured stock assessment for this species.

#### *Fishery management implications*

The long life span, relatively slow growth, low rates of natural mortality, large size and age at maturity (Newman, unpublished data) in association with the low estimate of  $F_{opt}$  indicates that stocks of *L. sebae* cannot sustain high harvest rates. In addition, the ability of fishers in the NDSF to harvest *L. sebae* at small sizes and several age classes below the size-at-maturity of 8 years (Newman, unpublished data) makes them especially vulnerable to over-exploitation. The level of exploitation of this species in the NDSF needs to be carefully monitored. Furthermore, the degree of survivorship of fish below the minimum legal size needs to be investigated and considered in future assessments.

Monitoring of the age structure of the *L. sebae* population in the NDSF is likely to be a much more sensitive indicator of the effects of exploitation than monitoring of catch and effort data in isolation. This is due to the likelihood of the catch rate data being affected by hyperstability, that is, high, stable CPUE may persist long after declines in overall population abundance have occurred. As *L. sebae* occur in aggregations over hard bottom areas that can be easily located on an on-going basis by fishers using global navigation systems and high intensity depth sounders, the number of these aggregation areas is likely to decrease with fishing pressure but catch rates once an aggregation area is found are likely to remain somewhat stable.

Given the low production potential of *L. sebae*, harvest strategies of low frequency or low intensity are suggested for the sustainable exploitation of these fish stocks in the Indo-Pacific region. The *L. sebae* resource in the NDSF is currently being managed with an innovative total allowable effort/individually transferable effort unit system, however the highly mobile, efficient and wide ranging capacity of the NDSF fleet may require more complex management arrangements to maintain future breeding stock levels. Furthermore, as a consequence of the apparent low survival rate for released (tagged) fish in the fishing depths of the NDSF fleet, the traditional use of legal minimum sizes to increase survival to spawning sizes is

not a practical option. Inclusion of targeted spatial or temporal closures within the effort management framework is however likely to be a useful mechanism to maintain spawning stock biomass and protect against recruitment overfishing.

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