Retrospective stock assessment of the Emperor red snapper (*Lutjanus sebae*) on the Seychelles Bank between 1977 and 2006

E. M. Grandcourt, T. Hecht, A. J. Booth, and J. Robinson

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The stock status of the Emperor red snapper (*Lutjanus sebae*) on the Seychelles Bank was determined between 1977 and 2006 using models of yield-per-recruit (YPR) and spawner-biomass-per-recruit (SBR). Demographic parameters were derived from size frequency and size-at-age data from validated annuli in sagittal otoliths. The long lifespan (t_{max} = 28 years), slow growth rate (k = 0.14), empirically estimated low natural mortality rate (M = 0.12), and late age at sexual maturity (t_m = 9 years for males and females combined) predisposed the *L. sebae* resource to overfishing. Fish became vulnerable to the gear at a mean size (L_{c50} = 39.8 cm L_F) and age (3.1 years) before the attainment of sexual maturity at 62 cm L_F. Consequently, there was a large proportion of immature fish in landings (51.2% on average) and the full growth potential for the resource might not have been realized. For most years, the fishing mortality rates and SBR approximated the limit reference point $F_{30\%}$. The potential for recruitment-overfishing was identified for some years (1990 and 2004), and the dramatic increase in recent yields is further evidence that management of this fishery requires urgent attention. Previous length-based assessments probably overestimated sustainable harvest rates, which should be between 6.7% and 7.2% of the SBR.

Keywords: age, Emperor red snapper, growth, mortality, per-recruit assessment, reef fisheries.

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E. M. Grandcourt: Marine Environment Research Centre, Environment Agency – Abu Dhabi, PO Box 45553, Abu Dhabi, United Arab Emirates. T. Hecht and A. J. Booth: Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa. J. Robinson: Seychelles Fishing Authority, PO Box 449, Fishing Port, Victoria, Mahé, Seychelles. Correspondence to E. M. Grandcourt: tel: +971 2 6817171; fax: +971 2 6810008; e-mail: egrandcourt@ead.ae.

Introduction

The Emperor red snapper, *Lutjanus sebae*, known as "Bourzwa" in the Seychelles, is distributed throughout the Indo-West Pacific from the southern Red Sea and East Africa to New Caledonia, north to Japan and south to Australia. It occurs near coral or rocky reefs and also over adjacent sand flats and gravel patches between 5 and 180 m deep (Allen, 1985; Anderson, 1986). Juveniles are frequently commensal with sea urchins (Kuiter and Tonozuka, 2001), and are found in nearshore, turbid waters (Williams and Russ, 1992), mangrove areas (Allen, 1985), and around coastal and offshore reefs (Williams and Russ, 1992). Larger *L. sebae* are generally found deeper, although they are also known to move into shallower water during winter (McPherson *et al.*, 1988; Williams and Russ, 1992). Prey items include fish, crabs, other benthic crustaceans, and cephalopods. *Lutjanus sebae* is a large, long-lived species, attaining a maximum size of 116 cm fork length (McPherson and Squire, 1992) and maximum age of 34 years (Newman and Dunk, 2002). Despite an absence of data on its population structure, mixing, and identity, the population on the Seychelles Bank has been considered to be a unit stock for assessment purposes because of its remote location (e.g. Lablache and Carrara, 1988; Mees, 1992).

The snappers are among the most important commercial fish of tropical and subtropical seas (Randall, 1995). They are highly regarded as a food fish, often forming large components of catches throughout their range (Fischer and Bianchi, 1984). Their aggressive feeding behaviour also makes them particularly vulnerable to capture (Munro and Williams, 1985). Slow rates of growth, recruitment, and natural mortality, combined with the late attainment of sexual maturity predispose lutjanids to overfishing (Russ, 1991; Newman *et al.*, 2000; Newman, 2002; Newman and Dunk, 2002, 2003; Marriott *et al.*, 2007). Consequently, populations of *L. sebae* in the Indo-Pacific require management intervention because of their particularly low production potential (Newman and Dunk, 2002).

Lutjanus sebae is the most important commercially exploited demersal species in the Seychelles. It is caught mainly offshore on the Seychelles Bank by hook and line, although catches are also made with traditional heart-shaped bamboo traps set in coastal waters. The average annual landings of 282.9 t during the period 1987–2003 have approximated the sustainable estimate of annual yield of 380 t (Lablache and Carrara, 1988). However, there has recently been a dramatic increase in annual landings to an average of 692.8 t between 2004 and 2006, associated with increased targeting by the artisanal fishery.

The first stock assessments of *L. sebae* on the Seychelles Bank were made using the swept-area method applied to trawl survey data collected in the 1970s (Birkett, 1979; Tarbit, 1980; Marchal *et al.*, 1981; Kunzel *et al.*, 1983). However, these initial assessments were based on samples taken from smooth trawlable areas where fish densities are less than on more rugose substrata. Combined size frequency data from trawl surveys were used to derive a total population biomass estimate for *L. sebae* using length cohort analyses (Lablache and Carrara, 1988). Length-based techniques were used in the assessments of Mees (1992) and MRAG (1996), based on size frequency data sampled by the artisanal fishery. The principal constraint of length-based methods is the inability of modal analyses to discriminate older age classes, especially for long-lived, slow-growing species, resulting in unreliable estimates of mortality, growth rate, and longevity (Goeden, 1978; Langi, 1990; MRAG, 1996).

The estimation of key demographic parameters for tropical fish has been improved dramatically using the banding structures found in sagittal otoliths for age determination (see Choat and Robertson, 2002; Fowler, 1995, for reviews of age-based studies). The utility of annually deposited increments for deriving growth rates, longevity, and other population characteristics has been demonstrated for representative species of families important in the Seychelles demersal fishery, for example, the Lethrinidae, Lutjanidae, Scaridae, Serranidae, and Siganidae (Pilling *et al.*, 2000; Grandcourt, 2002, 2005; Marriott and Mapstone, 2006). Moreover, age-based stock assessment methods have been successfully applied to *L. sebae* in the Kimberly region of Western Australia (Newman and Dunk, 2002).

Given the problems associated with the use of size frequency data alone, age-based studies are required to improve investigations of stock status. This is imperative, particularly considering the potential implications of recent increases in catches of *L. sebae* from the Seychelles Bank. The objectives of this study were therefore to establish age-based estimates of longevity and the rates of growth and mortality, and to use yield-per-recruit (YPR) and spawner-biomass-per-recruit (SBR) models to assess the historical exploitation and stock status of *L. sebae* on the Seychelles Bank.

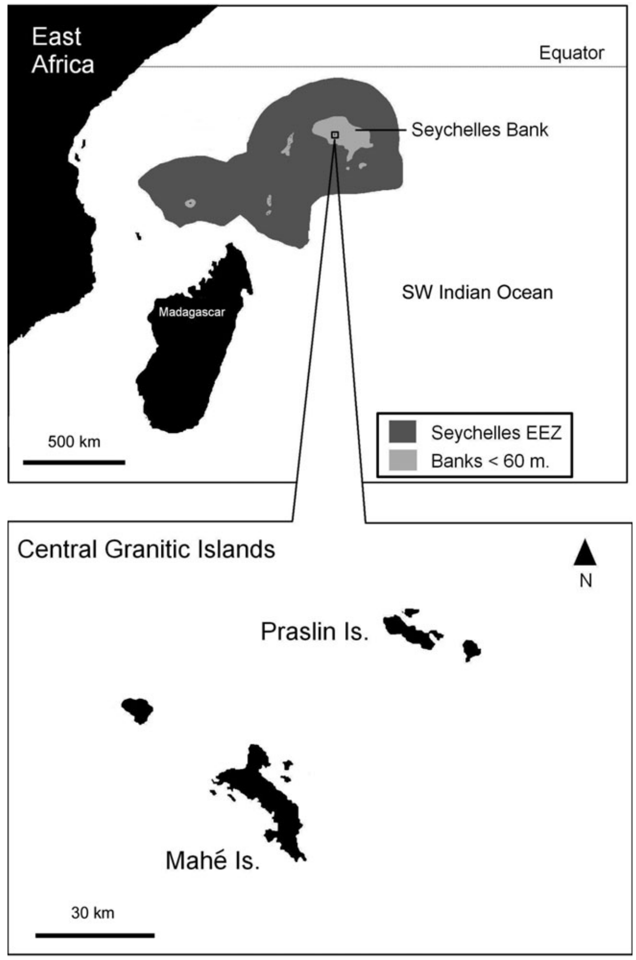

Figure 1. Location of the Seychelles Bank in the SW Indian Ocean, with details of the central granitic islands.

Material and methods

Study site and sampling protocol

Lutjanus sebae were collected from the Seychelles Bank, also known as the Mahé Plateau, which is located in the SW Indian Ocean at 4°S 56°E (Figure 1). The plateau has a surface area of 41 338 km^2 and is surrounded by an incomplete shallow rim of 10–20 m. Granite and coral outcrops form small banks and the maximum depth reaches 65 m (MRAG, 1996). Samples from the commercial fishery were collected from catch landings on Mahé, the largest of the central granitic islands.

Size frequency data were obtained from trawl surveys conducted in 1977 ($n = 224$), 1979 ($n = 1009$), and 1981 ($n = 1200$)—data are given in Lablache and Carrara (1988). Size frequency data were also collected for various years between 1989 and 2006 from commercial linefishing catches ($n = 45\,113$). Fish were selected at random from landings, and the fork length (L_F) was measured and recorded to the nearest centimetre.

Biological data were collected from fish obtained from commercial catches made during 2000. As the fish were gutted before sampling, sex could not be determined. Therefore, all demographic parameters related to both sexes combined. Samples were taken from 50 fish per month from a size range that included the smallest and largest fish in the landings. L_F and total length (L_T) measurements were recorded to the nearest millimetre, and wet weights to the nearest gramme. Sagittal otoliths were extracted, cleaned in water, dried, and stored in manila envelopes. One of each pair of sagittae was embedded in epoxy resin, and transverse sections of thickness ~200–300 μm were taken through the primordium, using a twin-blade saw. Otolith sections were mounted on glass slides with DPX mountant and examined under a low-power microscope (×10) with reflected light.

Age and growth

The age of each fish was estimated from the number of opaque bands observed in transverse sections of sagittae, because these had previously been determined to be deposited yearly in *L. sebae* otoliths from the Seychelles Bank (Hecht *et al.*, 2001). Growth was investigated by fitting the von Bertalanffy growth (VBGF) function (von Bertalanffy, 1938) to size-at-age data, using non-linear least-squares regression. The relationship between fork length and weight was obtained by fitting a power function to fork length and wet weight data, using least-squares regression.

Mortality and selectivity

Size-at-age data were used to construct an age–length key following the method of Ricker (1975). This was used to convert length frequency data for each year into age frequency distributions. The instantaneous rate of total mortality (Z) was subsequently estimated using the age-based catch curve method (Beverton and Holt, 1957).

Backward extrapolation of age-based catch curves was used to estimate the probability of capture for each year. The backward extrapolation of the best fit regression line to the intercept with the y-axis provided an estimate of the "expected" frequency of fish in age classes before they are fully recruited (assuming constant recruitment). The frequency in each age class as a proportion of that "expected" was used as an estimate of the probability of capture.

Selectivity curves were generated using the logistic function fitted to plots of the probability of capture against age and used to derive values of the mean age at first capture:

$$P = \frac{1}{1 + \exp\left[-r(t - t_{c50})\right]},$$

where P is the probability of capture, t_{c50} the mean age at first capture, and r is a constant, which increases in value with the steepness of the selection curve. The mean size at first capture (L_{c50}) was obtained by converting the mean age at first capture using the fitted VBGF function (von Bertalanffy, 1938). Least-squares linear regression analysis and one-way ANOVA were used to examine the time-trend in the mean size of fish in the landings and the mean size at first capture between 1989 and 2006. Juvenile retention (J) was calculated as the proportion of fish in landings that were below the mean size at first sexual maturity (62.0 cm L_F, according to Mees, 1992) for the *L. sebae* population on the Seychelles Bank.

The instantaneous rate of natural mortality (M) was estimated using the empirical equation derived by Hoenig (1983). As the maximum observed age of 28 years was considered to have underestimated longevity, the maximum age of 34 years recorded by Newman and Dunk (2002) for *L. sebae* in the Kimberly region of Western Australia was used instead. The instantaneous rate of fishing mortality (F) was calculated for each year by subtracting the natural mortality rate (M) from the total mortality rate (Z) derived from age-based catch curves. The calculation was also made using the upper and lower 95% confidence intervals for Z, to derive a range of estimates of fishing mortality rate. Least-squares linear regression and one-way ANOVA were used to evaluate the time-trend in the instantaneous fishing mortality rate between 1977 and 2006. The annual harvest rate (H) or the percentage removal by the fishery was estimated from $H = (F/Z(1 - e^{-Z})) \times 100$.

Per-recruit analyses and fishery assessment

The Beverton and Holt (1957) YPR model, modified by Govender *et al.* (2005), was used to estimate YPR and SBR for each year. A per-recruit approach was used because there were no suitable catch-rate data available for more complicated age-structured stock assessment models (see Quinn and Deriso, 1999, for an overview of alternative approaches).

The modifications to the model include a time-step of 1 month, allowing for monthly variations in the fishing mortality rate (F). As fishing effort for *L. sebae* is primarily concentrated during the calm inter-monsoon periods, monthly catches for each year were used to apportion F. YPR (in g) was calculated as follows:

$$\text{YPR} = \sum_{t=0}^{t_{\max}} \tilde{N}_t W_{t+1/2} \frac{F_t S_t}{F_t S_t + M}\left(1 - \exp(-F_t S_t - M)\right),$$

where $t_{\max}$ is the maximum observed age in the fishery and is considered a plus-group, F_t the instantaneous fishing mortality rate that varies monthly, M the monthly instantaneous natural mortality rate, and N_t the number of fish surviving to age t, calculated from the recursive equation:

$$\tilde{N}_t \begin{cases} R & \text{if } t = 0 \\ \tilde{N}_{t-1}\exp(-F_{t-1}S_{t-1} - M) & \text{if } 0 < t < t_{\max} \\ \dfrac{\tilde{N}_{t_{\max}-1}\exp(-F_{t_{\max}-1}S_{t_{\max}-1} - M)}{1 - \exp(-F_{t_{\max}}S_{t_{\max}} - M)} & \text{if } t - t_{\max} \end{cases},$$

where R is the number of recruits and is set to 1. S_t is the selectivity at age t. It is assumed that selection is knife-edged and therefore set to 0 if $t < t_c$ and 1 if $t \geq t_c$, where t_c is the mean age at first capture. W_t is the mean weight at age t, such that

$$W_t = a[L_\infty(1 - \exp(-k(t - t_0)))]^b,$$

where a and b are parameters of the length–weight relationship, and L_∞, k, and t_0 are derived from the VBGF function.

SBR (in g), expressed as a proportion of the unexploited level, was calculated as

$$\text{SBR} = \sum_{t=0}^{t_{\max}} N_t W_t G_t,$$

where G_t is the fraction of mature fish at age t and was assumed to be knife-edged, i.e. set to 0 if $t < t_m$ and 1 if $t \geq t_m$, where t_m is the mean age at first sexual maturity of 9.03 years, obtained by converting the mean size at first sexual maturity (L_{m50}) of 62.0 cm L_F obtained by Mees (1992) for *L. sebae* on the Seychelles Bank, using the inverse of the VBGF function. The trend in SBR between 1977 and 2006 was established using least-squares linear regression and one-way ANOVA.

The effects of increasing the selectivity characteristics of the handline fishery were evaluated using the YPR and SBR models. The YPR and SBR at the current mean age at first capture and the mean age at first sexual maturity ($t_{c50} = t_m$) were estimated. The differences in YPR and SBR were used to evaluate the impacts on the fishery at the existing fishing mortality rate.

Target and limit biological reference points were defined as the instantaneous rates of fishing mortality associated with values of SBR of 40% ($F_{40\%}$) and 30% ($F_{30\%}$) of unexploited levels. These were selected based on the meta-analyses of Mace (1994), given the absence of a stock–recruitment relationship for *L. sebae*, and estimated from the SBR model. Estimates of annual landings of *L. sebae* were obtained from a stratified catch and effort data recording system (Seychelles Artisanal Fisheries Databases, 1990–2006) and used to define the exploitation pattern between 1989 and 2006.

Results

Age and growth

Alternating translucent and opaque bands were observed in the sectioned otoliths when viewed with reflected light under low-power magnification (Figure 2). The distance between bands became smaller from the nucleus out towards the outer margin. In all, 514 fish were aged, the size range being 23.0–86.4 cm L_F. Age estimates ranged between 1 and 28 years. Growth, in

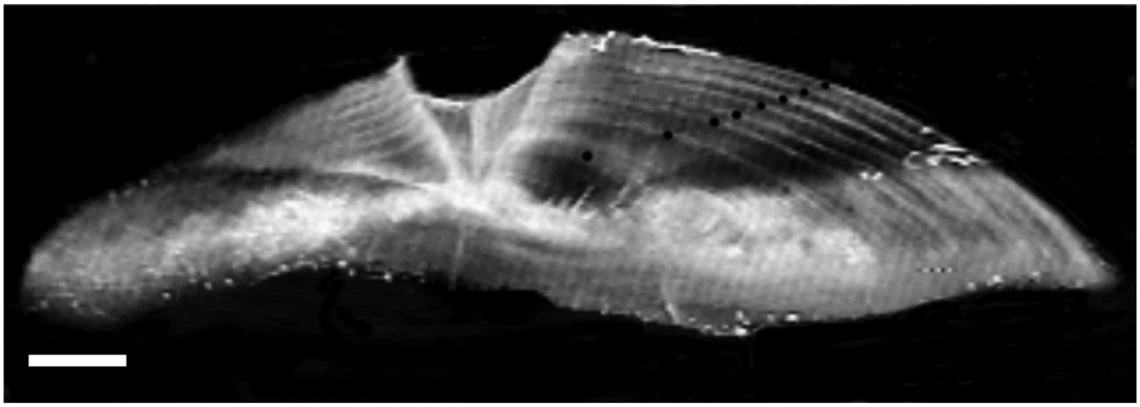

Figure 2. Photomicrograph of a transverse section through the sagittal otolith of *L. sebae* (44.9 cm L_F), viewed with reflected light. Dots show the position of annuli and the axis along which readings were made (scale bar = 1 mm).

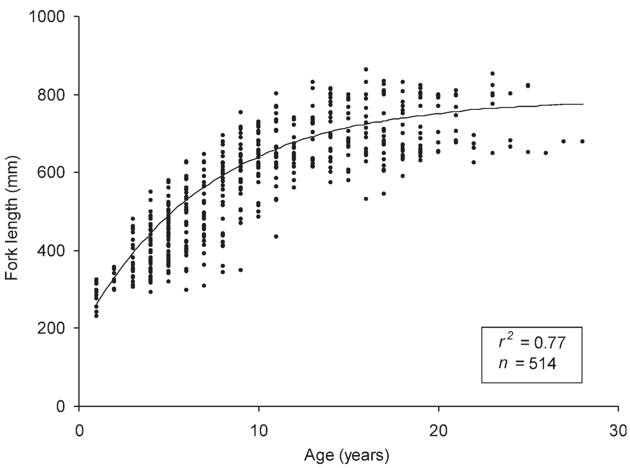

Figure 3. VBGF function, $L_t = 78.7(1 - e^{-0.14(t-1.9)})$, fitted to size-at-age data for *L. sebae*.

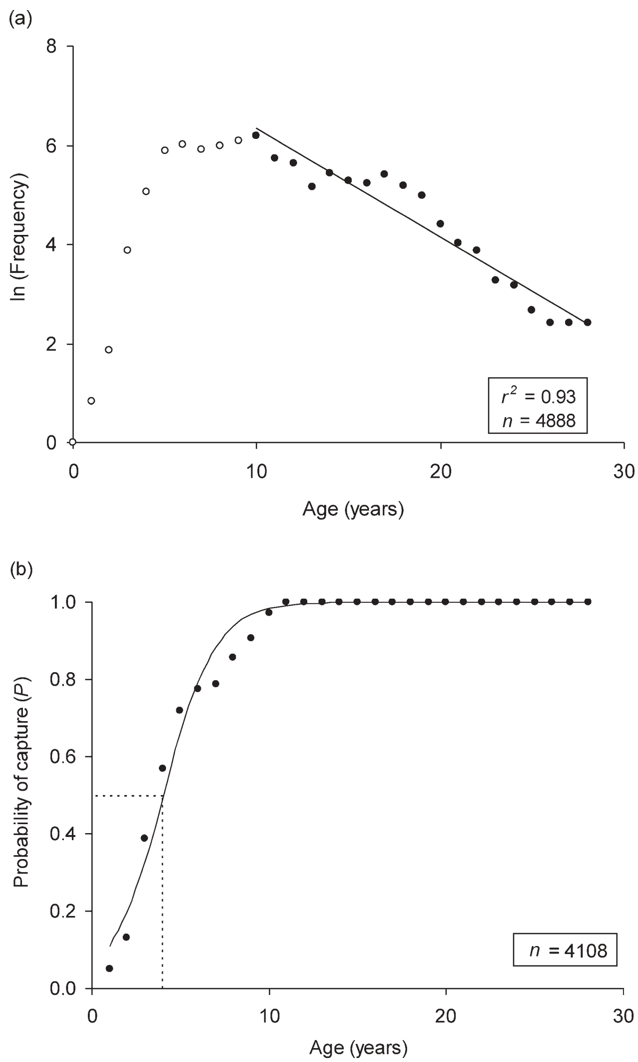

Figure 4. (a) Age-based catch curve and (b) selectivity curve for *L. sebae* in 2005. Only dots in the descending limb were included in the estimation of the instantaneous rate of total mortality (Z). The mean age at first capture (t_{c50}) is indicated by the dotted line.

general, was slow, most of the increase in size with age occurring up to age 10, and there was a high degree of individual variability in size-at-age (Figure 3). Parameters of the VBGF function were $k = 0.14$, $L_\infty = 78.7$ cm (L_F), and $t_0 = -1.9$ years ($n = 514$, $r^2 = 0.77$). The length–weight relationship ($W = 0.019\ L_F^{3.01}$) provided a good fit to length and weight data ($r^2 = 0.97$).

Mortality and selectivity

The instantaneous total mortality rate (Z) estimated from the age-based catch curves (Figure 4a for 2005) ranged from 0.18 year^{-1} in 1977 to 0.23 year^{-1} in 2004 (Table 1). The age (t_{c50}) at which 50% of fish were recruited to the handline fishery ranged from 2.5 years in 1994 to 4.0 years in 2006 (Figure 4b for 2005), with a corresponding size (L_{c50}) of 36.3 and 44.8 cm L_F, respectively. The mean age (3.1 years) and size (39.8 cm L_F) at which *L. sebae* was vulnerable to the gear (average for all years of handline fishery data) were considerably lower than the age (9.0 years) and size (62.0 cm L_F) at which sexual maturity is anticipated. Consequently, juvenile retention was high, with 51.2% of the

Table 1. Sample sizes (n), total mortality rate (Z), fishing mortality rate (F), target fishing mortality rate ($F_{40\%}$), limit fishing mortality rate ($F_{30\%}$), harvest rate (H), and selectivity parameters (L_{c50}, t_{c50}) for *L. sebae* on the Seychelles Bank from 1977 to 2006.

Year	n	Z	F (95% CI)	$F_{40\%}$	$F_{30\%}$	H (%)	L_{c50} (cm L_F)	t_{c50} (years)
1977	224	0.18	0.06 (0.02–0.10)	0.10	0.14	5.3	54.8	6.5
1979	1 009	0.20	0.07 (0.01–0.14)	0.09	0.13	6.7	51.5	5.6
1981	1 200	0.20	0.07 (0.01–0.15)	0.08	0.11	6.7	43.7	3.8
1989	883	0.22	0.10 (0.07–0.13)	0.08	0.11	8.8	44.3	3.9
1990	4 689	0.22	0.10 (0.07–0.13)	0.07	0.10	8.9	24.1	2.9
1991	8 575	0.21	0.09 (0.06–0.13)	0.07	0.09	8.3	28.4	2.7
1993	3 320	0.21	0.08 (0.05–0.12)	0.07	0.10	7.7	37.9	2.8
1994	4 259	0.20	0.08 (0.05–0.12)	0.07	0.09	7.4	36.3	2.5
1995	6 458	0.21	0.09 (0.06–0.12)	0.07	0.09	8.1	37.5	2.7
1996	4 763	0.21	0.09 (0.06–0.13)	0.07	0.10	8.3	40.0	3.1
1997	3 008	0.21	0.09 (0.06–0.12)	0.07	0.09	8.2	37.4	2.7
2000	2 807	0.20	0.08 (0.04–0.11)	0.08	0.10	6.9	41.8	3.5
2003	228	0.22	0.10 (0.02–0.17)	0.07	0.10	8.9	40.5	3.2
2004	1 140	0.23	0.10 (0.07–0.13)	0.07	0.10	9.3	39.5	3.0
2005	4 888	0.22	0.10 (0.07–0.13)	0.08	0.10	8.7	41.3	3.4
2006	4 108	0.21	0.09 (0.07–0.13)	0.08	0.11	7.9	44.8	4.0
Mean	3 222	0.21	0.09 (0.05–0.13)	0.08	0.10	7.9	40.2	3.5

Table 2. Juvenile retention (J), SBR, and YPR for *L. sebae* on the Seychelles Bank from 1977 to 2006.

Year	J (%)	SBR (%) (95% CI)	YPR (g)
1977	–	58.1 (41.3–74.9)	5 646
1979	–	47.6 (28.0–67.3)	5 144
1981	–	41.6 (19.3–63.8)	4 233
1989	56.0	32.3 (23.1–41.5)	4 147
1990	66.6	28.4 (20.0–36.9)	3 524
1991	54.2	30.1 (20.7–39.5)	3 465
1993	50.2	33.3 (23.3–43.4)	3 567
1994	42.9	33.4 (22.8–44.0)	3 393
1995	48.5	31.3 (21.8–40.8)	3 501
1996	46.7	31.9 (22.1–41.8)	3 800
1997	51.5	30.8 (21.7–39.9)	3 457
2000	38.4	38.9 (26.1–51.8)	4 005
2003	51.2	29.9 (14.1–45.8)	3 763
2004	65.7	28.0 (19.8–36.1)	3 606
2005	53.7	30.7 (22.2–39.3)	3 787
2006	40.6	36.5 (33.4–39.5)	4 281
Mean	51.2	35.2 (23.7–46.7)	3 957

catch landed by the handline fishery between 1989 and 2006 being most likely immature (Table 2).

There was an increasing trend in the mean size at first capture (L_{c50}) between 1989 and 2006, although year was not a significant factor (ANOVA: $p = 0.09$, 12 d.f.), and there was no significant change in the mean size of fish in landings over the same period (ANOVA: $p = 0.90$, 12 d.f.). The mean size of fish in trawl samples (67.0 cm L_F) was greater than the mean size caught in the handline fishery (59.2 cm L_F).

The instantaneous rate of natural mortality (M) derived from the Hoenig (1983) equation was 0.12 year^{-1}. Instantaneous fishing mortality rates (F) ranged from 0.06 (1977) to 0.1 year^{-1} (2003–2005), with harvest rates ranging from 5.3% (1997) to 9.3% (2004; Table 1). Annual rates of fishing mortality derived from trawl samples for 1977, 1979, and 1981 were lower than those obtained from the handline fishery subsequently (Figure 5a).

Per-recruit analyses and fishery assessment

The optimum fishing mortality rate corresponding to an SBR of 40% of unexploited levels ($F_{40\%}$) ranged from 0.07 to 0.1 year^{-1}. The limit fishing mortality rate ($F_{30\%}$) corresponding to an SBR of 30% of unexploited levels ranged from 0.10 to 0.14 year^{-1}. F exceeded $F_{40\%}$ in 12 of 16 years, and exceeded $F_{30\%}$ in 1991 and 2004. The harvest rates (mean for all years) associated with the target and limit biological reference points of 6.6% and 8.8%, respectively, indicate that *L. sebae* has a low production potential.

YPR ranged from 3393 g (1994) to 5646 g (1977) with SBR ranging from 28.0% (2004) to 58.1% (1997) of the unexploited levels (Table 2). The ANOVA indicated a significant difference between years ($p < 0.05$, 14 d.f.). During most years, the fishing mortality rates and consequently the relative SBR approximated the limit reference point, indicating that overall, the resource has been exploited close to threshold levels (Figures 6 and 7). Exceptions are the years for which estimates were based on trawl samples, plus 2000 and 2006, where above-average relative SBR values were also recorded. Although during 1990 and 2004, the point estimates of relative SBR were less than the limit reference points, indicating that there may have been recruitment-overfishing (Figure 5b), this was not definitive, because the limit reference point was still within the 95% confidence intervals of these estimates. The ANOVA indicated significant variability ($p < 0.05$, 14 d.f.) in SBR between 1977 and 2006.

YPR and SBR were estimated to increase by 51.8% and 56.2%, respectively, at the existing fishing mortality rate if the selectivity characteristics of the handline fishery were modified so that the mean age at first capture was assumed equal to the mean age at first sexual maturity ($t_{c50} = t_m$; Figure 6).

There was a distinct seasonal pattern in fishing activity, with most fishing mortality (65%) during the calm inter-monsoon months, which coincide with peaks in spawning activity

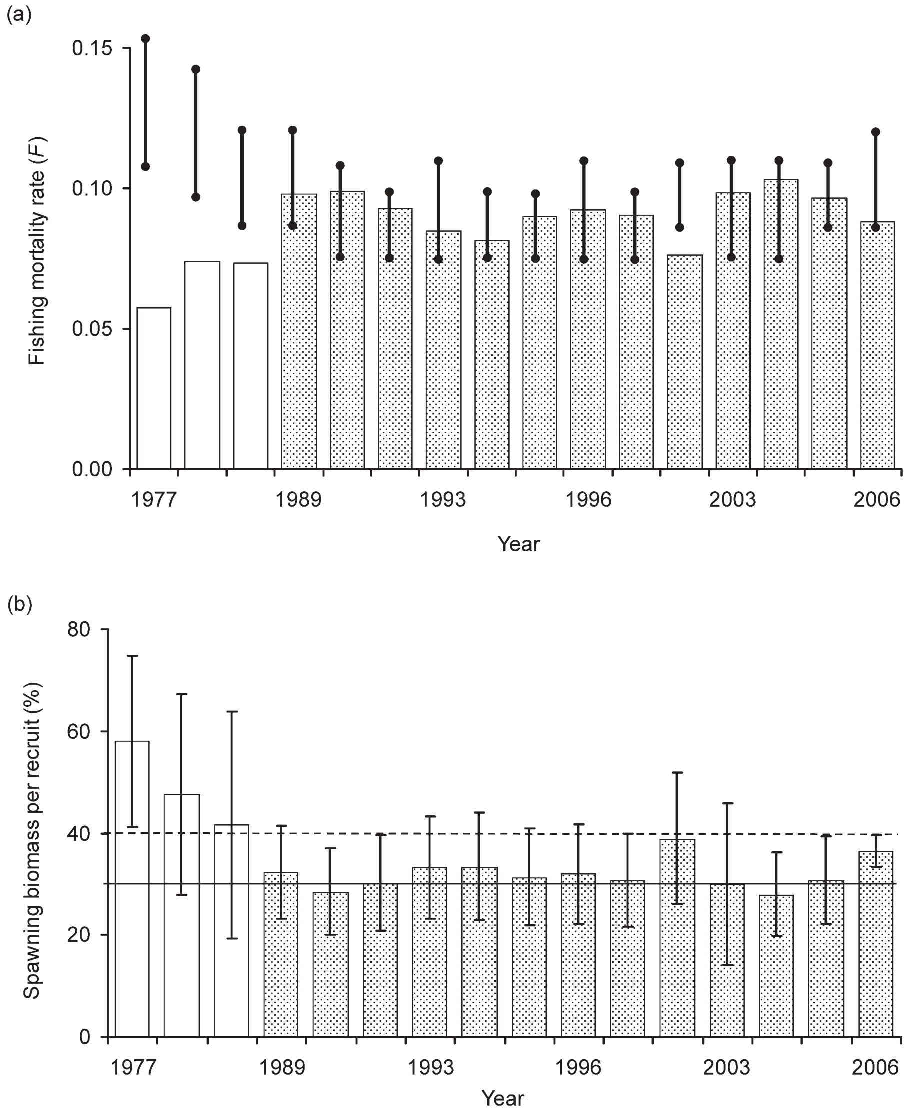

Figure 5. (a) The instantaneous fishing mortality rate for *L. sebae* on the Seychelles Bank between 1977 and 2006. Unshaded bars represent years for which estimates were based on trawl samples. Upper and lower limits of the vertical lines show the rate of fishing mortality associated with SBRs of 30% ($F_{30\%}$) and 40% ($F_{40\%}$) of unexploited levels, respectively. (b) The SBR for *L. sebae* on the Seychelles Bank between 1977 and 2006 ($\pm$95% CI), showing the optimum, SBR_{opt} (dashed line), and the limit, SBR_{limit} (solid line), values. Unshaded bars represent years for which estimates were based on trawl samples.

(Figure 7). Landings of *L. sebae* ranged from 101.8 t (1988) to 823.5 t (2005), with a mean of 344.4 t for all years for which complete catch data were available. Trends in annual catches showed that there was a dramatic increase in landings in recent years, from 349.4 t in 2003 to 823.5 t in 2005. However, this trend was not reflected by the relative change in estimated fishing mortality rates for the same years (Figure 8).

Discussion

There were marked differences in the size and age structure of trawl samples, which were composed of larger, older fish than catches made by the handline fishery. This resulted in higher estimates of SBR and lower estimates of fishing mortality up to 1981 than in subsequent years. The handline fishery operates over rough grounds where fish density is greater, whereas the trawl samples came from smooth trawlable areas. In addition to habitat type, the differences observed could be due to the selectivity characteristics of the gear. Alternatively, the disparity in size composition could reflect changes in the stock structure over time, associated with the development of the fishery.

A principal constraint of the analyses is the assumption that the stock–recruitment relationship follows that based on the meta-analyses of temperate groundfish stocks (Mace, 1994). A more detailed understanding of recruitment would have helped to elucidate the variability in stock sizes and yields over the study period. Other sources of error include the use of a single age–length key from size-at-age data collected during 2000, and the associated assumption that there is no interannual variability in growth. This would be particularly important where the growth rate changes as a fishery develops in association with density-dependent factors. In addition to a time-series of age–length keys, a finer spatial resolution in length frequency

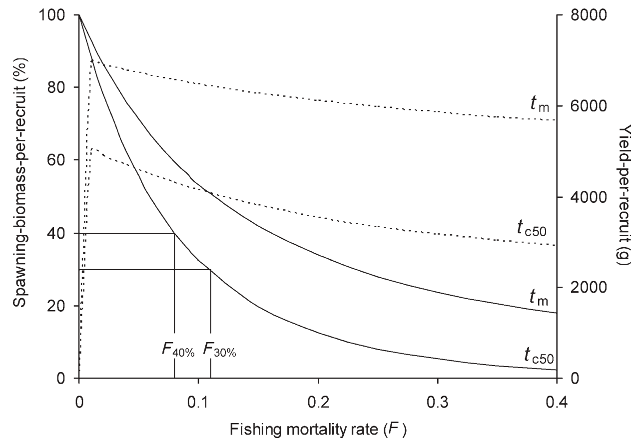

Figure 6. Curves of YPR (dashed lines) and SBR (solid lines) for *L. sebae* on the Seychelles Bank, showing the SBR associated with the target (F_{opt}) and limit (F_{limit}) biological reference points. The relationships show the impacts, on yields and the SBR, of increasing the current mean age at first capture (t_{c50}) to the mean age at first sexual maturity (t_m).

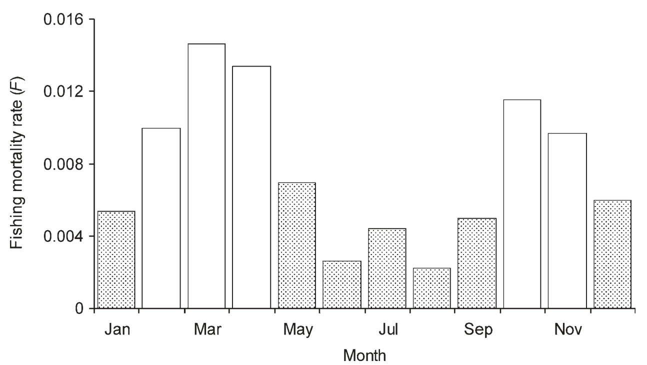

Figure 7. Monthly fishing mortality rates (mean values for all years) for *L. sebae* on the Seychelles Bank, illustrating the seasonal nature of the fishery and the coincidence of maximum effort with peaks in spawning activity (unshaded bars).

and size-at-age data will be required in future to elucidate local differences in demographic parameters and the impacts of fishing.

A total population biomass of 2360 t with a sustainable annual yield of 380 t was estimated for *L. sebae* on the Seychelles Bank, using length cohort analyses (Lablache and Carrara, 1988). As annual catches had approximated or been within this limit until recent years, it was thought that the fishery for *L. sebae* was sustainable. Retrospectively, the sustainable yields estimated by Lablache and Carrara (1988) should not have exceeded 208 t or 8.8% of the adult stock biomass. Our study demonstrates that the production potential for *L. sebae* has probably been overestimated in the past, and highlights the importance of incorporating age-based demographic parameters into stock assessments for relatively long-lived, slow-growing, tropical species.

Trends in annual catches showed that there was a dramatic increase in landings, from 349.4 t in 2003 to 823.5 t in 2005. This trend was not reflected by the relative change in fishing mortality rates for the same years. Because of the selectivity characteristics of the handline fishery, yields comprised a large proportion (up to 65.7% in 2004) of fish under the mean size at which sexual maturity is achieved (assuming individuals mature at 62 cm). The reduction in abundance of these cohorts is not immediately evident, and changes in the rate of fishing mortality may only be detected after a time-lag associated with the growth of juvenile fish through to the fully recruited age classes. Therefore, future analyses may indicate that the extent of both growth- and recruitment-overfishing was in fact much more severe than that reported here for recent years.

The difference in selectivity parameters between years could have been caused by the use of different hook sizes and/or differences in areas and depth strata fished. Changes in the size composition of the population as a consequence of recruitment pulses, for example, could also have caused selectivity parameters to differ. Still, both yield and adult stock size could be increased if the selectivity characteristics of the handline fishery were to be modified so that the mean age at first capture was equal to the mean age at first sexual maturity ($t_{c50} = t_m$). This demonstrates that the full growth potential for the resource might not be realized, but there are no practical means of achieving this. Constraining recent increases in catches of *L. sebae* is necessary and consistent with resource conservation. In the absence of quota systems and effort controls, management options are limited, market restrictions (such as a ban on exports) being one of the few alternatives.

There was a distinct seasonal pattern in the fishery with most fishing mortality (65%) during the calm inter-monsoon months. The spawning activity of *L. sebae* on the Seychelles Bank peaks during the same periods, February–April and September/October (Lablache and Carrara, 1988). A particular management concern, therefore, is the potential disruption of reproductive activity associated with the increase in effort during spawning seasons.

Lutjanus sebae has been the subject of many demographic and stock assessment investigations which have estimated VBGF parameters for use in yield equations and mortality models (Table 3). The divergent parameter estimates have been attributed to alternative methods of age estimation used, such as scales (Druzhinin and Filatova, 1980) and vertebrae (Yeh *et al.*, 1986; Liu and Yeh, 1991), and often, the lack of age validation (Newman and Dunk, 2002). As a result of the inability of modal analyses to discriminate older age classes, in general, higher estimates of the growth coefficient (k) and lower asymptotic length (L_∞) are obtained by methods that rely on length frequency distributions. The implications for resource assessment are profound, because this positive bias translates into overestimates of true production potential, and may lead to inappropriate management advice (Langi, 1990). As the VBGF parameters obtained here ($k = 0.14$, $L_\infty = 78.7$ cm L_F) are derived from validated annuli (Hecht *et al.*, 2001) and compare with results from other studies that have used validated methods of age estimation (Newman *et al.*, 2000; Newman and Dunk, 2002), our estimates are considered to have improved the understanding of growth characteristics for *L. sebae* on the Seychelles Bank.

Among lutjanids, larger female size has been observed in various Atlantic, Caribbean, and Hawaiian species (Grimes, 1987). Conversely, the general trend for the genus in the Indo-Pacific is for males to grow to a larger mean size-at-age than females (McPherson and Squire, 1992; Newman *et al.*, 1996, 2000; Newman, 2002; Kritzer, 2004). Sex-specific growth differences for *L. sebae* follow this pattern, with males significantly larger than females on both the east (McPherson *et al.*, 1985) and west coasts of Australia (Newman and Dunk, 2002). The larger size of males has also been noted by Tarbit (1980) for *L. sebae* on the Seychelles Bank. As the sex of fish in our study was not

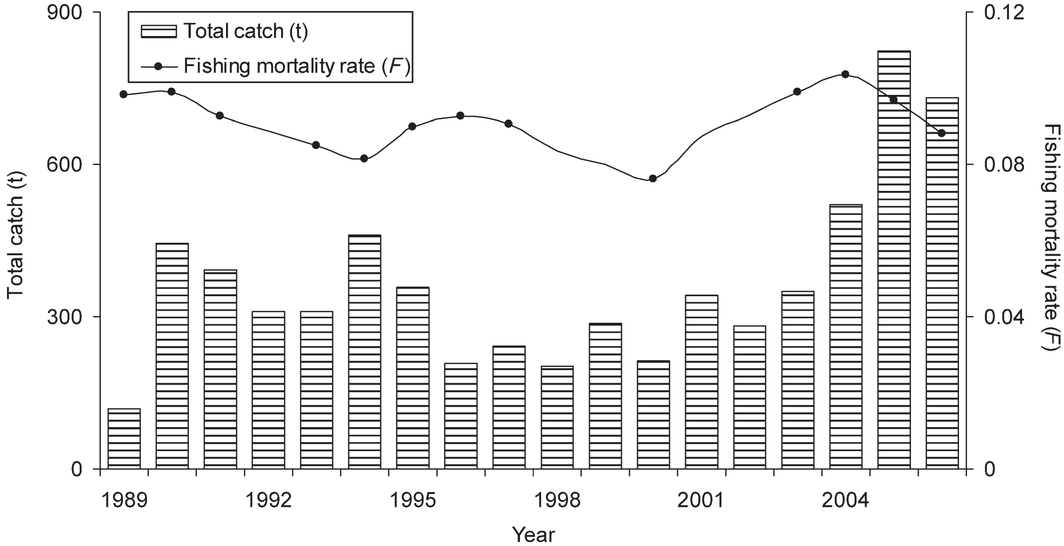

Figure 8. Historical trends in catches and the instantaneous rate of fishing mortality for *L. sebae* on the Seychelles Bank.

Table 3. VBGF parameters (k and L_∞) for *L. sebae* by location and data source.

k	L_∞	Location	Data source	Reference
0.15 (m)	62.8	Western Australia	Otolith annuli	Newman and Dunk (2002)
0.27 (f)	48.3			
0.14	79.2	Great Barrier Reef, Australia	Otolith annuli	Newman *et al.* (2000)
0.14 (m)	91.0	Great Barrier Reef, Australia	Otolith annuli	McPherson *et al.* (1988)
0.21 (f)	72.0			
0.15 (m)	102.5	Great Barrier Reef, Australia	Otolith annuli	McPherson and Squire (1992)
0.18 (f)	88.7			
0.16	85.1	Gulf of Aden	Annuli in scales	Druzhinin and Filatova (1980)
0.16	84.1	Arafura Sea, Australia	Annuli in vertebrae	Liu and Yeh (1991)
0.13	81.7	Arafura Sea, Australia	Annuli in vertebrae	Yeh *et al.* (1986)
0.14	78.7	Seychelles Bank	Otolith annuli	This study
0.18	99.1	Seychelles Bank	Length frequency data	MRAG (1996)
0.19	97.4			
0.16*	92.9*	Seychelles Bank	Length frequency data	Mees (1992)
0.31	95.1			
0.38 (m)	90.0			
0.27 (f)	84.0			
0.23	96.0	Seychelles Bank	Length frequency data	Lablache and Carrara (1988)
0.25	100.0			
0.22	98.0	Seychelles Bank	Length frequency data	de Moussac (1988)

*Note that these estimates were obtained from 2- to 5-year-old cohorts only.
Sex-specific growth parameters are indicated by m (male) and f (female).

determined, further investigation of sex-specific growth characteristics are needed, particularly given the importance of incorporating differences into per-recruit models.

Although the maximum age of *L. sebae* was estimated to be 34 years in the Kimberly region of Western Australia, perhaps longevity may be more than 40 years, given that the population had been fished for two decades (Newman and Dunk, 2002). Consequently, the maximum age of 28 years recorded here is considered to be an underestimate of longevity, notably given that *L. sebae* has a long history of exploitation on the Seychelles Bank. It is also of note that annuli in thin otolith sections of a closely related species (*Lutjanus bohar*) from the same location suggest a maximum age of 55 years (Marriott and Mapstone, 2006).

Previous estimates of natural mortality rate for *L. sebae* on the Seychelles Bank range from 0.36 (Mees, 1992) to 0.48 year^{-1} (Lablache and Carrara, 1988). These were obtained using the Pauly (1980) empirical relationship, which has been shown to overestimate natural mortality for long-lived, slow-growing, species (Ralston, 1987; Russ *et al.*, 1998). Although our estimate of 0.12 year^{-1} is more in line with those of Yeh *et al.* (1986; $M = 0.13$ year^{-1}) and

Newman and Dunk (2002; $M = 0.104-0.122$ year^{-1}), authors who also used the Hoenig (1983) equation, it could have been overestimated if longevity is more than 40 years (Newman and Dunk, 2002).

As the size at sexual maturation was based on macroscopic examination of the gonads (Mees, 1992), detailed histological study would improve the estimate, because this has provided a more accurate and reliable result (West, 1990). Still, there was a high juvenile retention rate (51.2% on average) because fish were vulnerable to the gear at a mean size ($L_{c50} = 39.8$ cm L_F) that is considerably smaller than the mean size at which first sexual maturity is anticipated (62.0 cm L_F). This has been mentioned as an important management issue in previous assessments, specifically because of the associated potential for recruitment-overfishing (Mees, 1992). However, mitigation through gear restrictions such as hook size regulations are unlikely to succeed owing to enforcement constraints, and may be inappropriate given the multispecies nature of the fishery. Minimum size limits are also unsuitable, because a high level of barotraumas-related mortality would be expected for released fish given that most of the catch comes from depths of 55–70 m (Mees, 1992). Area closures may offer a solution, in particular if juvenile and adult habitats differ, although further research would be required to determine spatial and depth distributions by sexual identity and development stage.

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