Effects of exploitation on age, growth and mortality of the blackspot snapper, *Lutjanus fulviflamma*, at Mafia Island, Tanzania

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Abstract

Estimates of the growth parameters (*L*∞ and *K*), mortality coefficients (*Z*, *M* and *F*) and exploitation rate (*E*) for the blackspot snapper, *Lutjanus fulviflamma* (Forsskål) from the Mafia Island Marine Park (MIMP) and adjacent intensively fished areas in Tanzania were determined. Sectioned otoliths showed that *L. fulviflamma* in the MIMP attained a maximum age of 18 years, with a high proportion of fish between 6 and 10 years old. The maximum age was 8 years in the intensively fished areas, with a preponderance of 2- and 4-year-old fish. The size structures of the populations in the MIMP and that in the intensively fished areas were markedly different, with the MIMP fish averaging (±SE) 211.4 ± 0.38 mm TL, but 154.6 ± 0.32 mm TL in the intensively fished areas. The von Bertalanffy growth parameters were *L*∞ = 290.3 mm TL, *K* = 0.15 year⁻¹ and *t*₀ = 2.7 years. There was no significant difference in growth between the four populations (*L*∞: *F*-stat = 0.14, *P* = 1.000, and *K*: *F*-stat = 0.26, *P* = 0.992). Total mortality was 0.55 and 1.64 year⁻¹ in the MIMP and intensively fished areas, respectively, natural mortality 0.27 year⁻¹ and fishing mortality 0.18 and 1.37 year⁻¹ in the MIMP and intensively fished areas, respectively. The exploitation rate was 0.51 and 0.84 in the MIMP and intensively fished areas, respectively. The artisanal seine net fishery is directed mainly at younger fish in the intensively fished areas resulting in growth overfishing. The protracted life span, the slow growth and natural mortality rates imply that *L. fulviflamma* is vulnerable to overfishing and that the protection provided by the park, although limited, is vital for sustaining the fishery at Mafia Island.

Keywords: exploitation, growth, *Lutjanus fulviflamma*, marine protected area, mortality, Tanzania.

Introduction

The blackspot snapper, *Lutjanus fulviflamma* (Forsskål) (Lutjanidae), is an important commercial reeffish in Tanzania (Richmond 2002). Snappers (Lutjanidae) along with emperors (Lethrinidae), locally referred to as 'changau', they rank first in Mafia Island, contributing 41.6% to the total marine fish catches (1984–1992 Tanzania Annual Fisheries Statistics). The species, along with many other smaller inshore reef species, is caught primarily with handlines, bottom longlines, seine nets, portable traps, gillnets and spears. Seine nets rank first in Mafia Island catching an average of 112.5 kg fish boat⁻¹ day⁻¹ (1986–1991 Tanzania Annual Fisheries Statistics).

Mafia Island Marine Park (MIMP) (Fig. 1) in Tanzania was established in 1995. Although Chole Bay and Kitutia (Tutia) Reef were gazetted as marine...
Given the importance of snappers in the local, small-scale fisheries, the aim of this study was to examine the effects of exploitation on the population size and age structure, growth and mortality of *L. fulviflamma* occurring in the MIMP and in the adjacent, intensively fished areas of Mafia Island. One of the principal assumptions made was that the effects of fish movement between the park and the adjacent intensively fished areas did not mask the effects of regulated fishing on the population structure and abundance. This assumption is based on results of tagging studies, which showed that reef fishes generally have a high degree of site fidelity within a restricted home range (Munro & Williams 1985) and *L. fulviflamma* is regarded as a typical sedentary reef-associated species (Samoilys 1997; Samoilys & Carlos 2000).

**Materials and methods**

Fieldwork was conducted at four sampling sites around Mafia Island within the depth range of 2–10 m (Fig. 1). Two of the sampling sites, Chole Bay and Jujima Bay, are located within the MIMP and constitute areas of low fishing intensity (Table 1). The two intensively fished sampling sites outside of the park were Mfuruni and Tumbuju. In addition to the higher fishing intensity in these two areas there are reports of frequent (one incident a month) dynamite fishing (Horrill & Ngoile 1992).

Monthly fish samples (from May 1999 to April 2001) were obtained from seine nets operated from traditional (±8 m) sailing vessels (mashua). The sites frequently fished within and outside the park comprised ecologically similar sub-tidal patch reefs. Each fresh fish was blotted dry using cotton cloth prior to measurements. Total length (TL), fork length (FL) and standard length (SL) were measured to the nearest

<table>
<thead>
<tr>
<th></th>
<th>Jujima Bay</th>
<th>Chole Bay</th>
<th>Tumbuju</th>
<th>Mfuruni</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seine nets stretched mesh size (mm)</td>
<td>50–64</td>
<td>50–64</td>
<td>19–38</td>
<td>19–38</td>
</tr>
<tr>
<td>Number of fishing vessels</td>
<td>209</td>
<td>142</td>
<td>201</td>
<td>99</td>
</tr>
<tr>
<td>Number of fishermen</td>
<td>669</td>
<td>370</td>
<td>572</td>
<td>616</td>
</tr>
<tr>
<td>Effectively fished area by seine nets (km²)</td>
<td>184.28</td>
<td>72.18</td>
<td>89.70</td>
<td>71.44</td>
</tr>
<tr>
<td>Fishing effort (fishermen vessel⁻¹)</td>
<td>3.20</td>
<td>2.61</td>
<td>2.85</td>
<td>6.22</td>
</tr>
<tr>
<td>Fishing intensity index (fishermen km⁻²)</td>
<td>3.63</td>
<td>5.13</td>
<td>6.38</td>
<td>8.62</td>
</tr>
</tbody>
</table>

**Table 1.** Fishing activity for the study sites in shallow waters of Mafia Island. Data are based on Mafia District annual fisheries census conducted in March 1999.

millimetre. Mass (total and eviscerated) was measured to the nearest 0.1 g using a top loading balance and the sex of the fish was recorded. Both sagittal otoliths were removed, cleaned and dried, and stored in cross-referenced envelopes for age estimation. A laboratory thermometer was used to measure sea surface temperature (SST) daily, from which a monthly average was calculated. For comparison, linear-regression analysis was used to describe the relationships between TL, FL and SL. The length mass relationships were modelled using Mass \((g) = a \cdot TL^{b}\), where \(a\) and \(b\) are constants. Regression analysis was used to evaluate relationships between otolith and fish dimensions and mass from 2551 fish.

Otoliths were measured for total length (OTL) along the antero-posterior axis and width (OTD) (dorsoroventral) to the nearest 0.1 mm using vernier dial callipers, and weighed (OTW) to the nearest 0.0001 g using an analytical balance (Mettler AE 100). The paired left and right otoliths were tested for differences in otolith dimensions and mass using a paired \(t\)-test. There was no significant difference in OTL \((t = 1.323\), d.f. = 2489, \(P = 0.254\)), OTD \((t = 1.604\), d.f. = 2489, \(P = 0.058\)) and OTW \((t = 0.806\), d.f. = 2491, \(P = 0.421\)) between the left and right sagittae. Therefore, the otolith morphometrics referred to in the text are the average values of left and right sagittae for the individual fish.

To test whether burning would improve the readability of growth zones, a sample of 50 otoliths were burnt to a medium brown state over a low intensity ethanol flame. The burnt otoliths were then embedded, together with the unburnt otolith of the pair, in clear polyester casting resin and sectioned transversely through the nucleus using a double bladed diamond edged saw. The sections (0.5 mm) were mounted on clear glass slides with DPX mounting medium. An edged saw. The sections (0.5 mm) were mounted on clear glass slides with DPX mounting medium. An arbitrary scale of zone clarity was used to determine whether the remainder of the otoliths should be burnt, or not, for the estimation of age. Burning was not found to enhance readability. The remainder of the otoliths (left sagittae or the right one of the other was damaged) were then embedded in an unburnt state and sectioned as described above.

The sections were best viewed under reflected light over a black background using a binocular dissecting microscope at magnification \(\times 10\). Under these conditions the translucent zone appears dark and the opaque zone, inhibiting the passage of light, appears bright. Validation of the zones as annuli was determined using marginal zone analysis by plotting the monthly per cent of opaque and translucent margins against time. Without any reference to the size of the fish, the first author (A.T.K.) read the otoliths twice, approximately 3 weeks apart followed by the second author (T.H.), who read the otoliths once. If the age estimates of the three readings differed by one or two rings the mid-reading was accepted and when the age estimates differed by three or more years the otolith was rejected. The notation used for ageing was as follows; 0-year old = end of year in which fish was spawned, 1-year old = end of first year of life, etc.

Length-at-age data for males and females, and sexes combined, were fitted to the Schnute and the three-parameter Von Bertalanffy growth models, using both absolute and relative error structures (Schnute 1981). The models were fitted using a downhill simplex search, a non-linear minimisation routine to obtain parameter estimates of the selected growth model. For each model and error structure, a non-parametric one-sample runs test was applied to test for randomness, and a Bartlett’s test was used to test for homoscedasticity of the residuals. The appropriate growth model was chosen on the basis of random and homoscedastic residuals. Variance estimates were calculated using conditioned parametric bootstrap re-sampling (Efron 1982). Upper and lower confidence intervals of the predicted length-at-age were constructed from the bootstrap data using the percentile method described by Buckland (1984). A likelihood ratio test (Cerrato 1990) was used to compare the growth model parameters obtained for the fish from various sites inside and outside of the MIMP.

Instantaneous total annual mortality \((Z)\) estimates were obtained from linearized catch curves (Sparre & Venema 1992). The slope of a straight line fitted to points greater than the age of full recruitment to the fishery provided an estimate of \(Z\). Natural mortality \((M)\) was obtained from Pauly’s (1980) equation,

\[
\log_{e} M = -0.0066 - 0.279 \log_{e} L_{\infty} + 0.6543 \log_{e} K + 0.4634 \log_{e} T
\]

where \(T\) is 27.6 °C and \(L_{\infty}\) and \(K\) are the von Bertalanffy growth parameters. Fishing mortality \((F)\) and exploitation ratio \((E)\) were obtained by substitution into the equations:

\[
F = Z - M
\]

and

\[
E = F / Z
\]

respectively Gulland 1983).

Fishing intensity index was estimated from the annual fisheries statistic surveys for Mafia District conducted in March 1999. Data on the effectively fished area at each site was estimated on the basis of
sea surface area from the British Admiralty Chart No. 1032 (channels between Kilwa Point and North of Mafia Channel). Based on the type of fishing gear, boats and methods, the fishing grounds were assumed to extend from the shoreline to the 10-m isobath. The measurements for each sampling area were re-digitised five times using a digital planimeter and the average area was used to calculate the fishing intensity index (fishermen km$^{-2}$).

**Results**

A total of 12 564 specimens of *L. fulviflamma*, ranging from 88 to 297 mm TL and from 11.4 to 433 g TW, were collected from the four sites between May 1999 and April 2001. Mean sizes of the fish caught in the four sampling sites differed significantly ($F = 1844.3$, d.f. = 7, $P < 0.001$). Females attained a significantly larger size than males in all four sites (Table 2). In the intensively fished areas, Mfuruni and Tumbuju, the population was dominated by fish in the size range between 146 and 196 mm TL, while those within the MIMP, Chole Bay and Jujima Bay were dominated by fish that ranged from 206 to 246 mm TL (Fig. 2).

Otoliths increased in size with fish size. The relationship between fish total length and otolith length and width, and between eviscerated fish mass and otolith mass, were isometric and linear, and the relationship between fish total length and otolith mass was an exponential function (Table 3).

The monthly per cent frequency of occurrence of translucent and opaque otolith margins of mature and immature fish in relation to temperature are shown in Fig. 3. In mature fish, the opaque zone was deposited in the warmer months from November to May and the translucent zone during the cooler months from June to September. The analysis suggests that the period of

<table>
<thead>
<tr>
<th>Study sites</th>
<th>Jujima Bay</th>
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<th>Tumbuju</th>
<th>Mfuruni</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F, 217.1 ± 0.8 M, 209.1 ± 0.7</td>
<td>F, 214.6 ± 0.8 M, 204.8 ± 0.7</td>
<td>F, 159.0 ± 0.7 M, 153.0 ± 0.6</td>
<td>F, 157.8 ± 0.6 M, 153.5 ± 0.6</td>
</tr>
<tr>
<td>Jujima Bay (M)</td>
<td>*</td>
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<td>**</td>
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<tr>
<td>Chole Bay (F)</td>
<td>*</td>
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<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Chole Bay (M)</td>
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<td>**</td>
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<tr>
<td>Tumbuju (F)</td>
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<td>**</td>
<td>**</td>
<td>NS</td>
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<tr>
<td>Tumbuju (M)</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>NS</td>
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<tr>
<td>Mfuruni (F)</td>
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<td>**</td>
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<tr>
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<td>**</td>
<td>**</td>
<td>**</td>
<td>NS</td>
</tr>
</tbody>
</table>

*P < 0.01, **P < 0.001,
F, female; M, male; NS, not significant, ±SE.
fast growth for mature fish is from June to September, while juvenile fish grow faster during the period November to May. From these results it can be concluded that one opaque and one translucent zone, irrespective of the maturity status of the individual fish, represent an annulus.

Of the 2650 otoliths examined, 13.1% were rejected as unreadable. Alternate opaque and translucent rings were easily visible in most otoliths (Fig. 4). Otoliths of fish ranging between 4 and 12 years old were easily interpreted, although those of younger fish were sometimes difficult to read because of unclear differentiation in growth zones. The otoliths of older fish (>12 years) showed signs of stacking of growth zones, a condition described as a common otolith growth pattern in particularly long-lived species (Buxton & Clarke 1991, 1992).

Eighteen age classes (1–18 years) were defined for the fish in the MIMP, while only nine age classes (0–
8 years) were defined for the intensively fished areas. Fish in the MIMP included a high proportion of individuals between 6 and 10 years old, whereas in the intensively fished areas 2–4 years old fish predominated. A likelihood ratio test (Cerrato 1990) to compare von Bertalanffy growth parameters (after exclusion of zero and 1-year-old individuals) showed no significant differences in the growth rate between females and males \( L. \) fulviflamma, except in Chole Bay where females grew faster than males (Table 4). Furthermore, there were no significant differences in growth rate between all four populations of \( L. \) fulviflamma (Table 5). The von Bertalanffy growth function that best described the growth of \( L. \) fulviflamma on Mafia Island (Fig. 5) was

\[ L_t = 290.3(1 - \exp^{-0.15(t+2.7)}) \]

An analysis of covariance revealed significant differences between the slopes of instantaneous total mortality (\( Z \)) from the four sites, and between female and male (\( F = 7.1, \text{ d.f.} = 7, P < 0.001 \)) (Table 6, Fig. 6). Fish from the intensively fished areas showed significantly higher total mortality than in the MIMP (Table 7). No significant differences in \( Z \) were observed between females and males at all sites (Table 7). Natural mortality (\( M \)) of \( L. \) fulviflamma was estimated at 0.27 year\(^{-1}\). Fishing mortality (\( F \)) for female and male \( L. \) fulviflamma ranged between 1.02 and 1.44 year\(^{-1}\) in the intensively fished areas and between 0.15 and 0.38 year\(^{-1}\) in the MIMP areas (Table 6), which was also mirrored by the exploitation ratios. In the MIMP, \( E \) ranged between 0.36 and 0.58, but was between 0.79 and 0.84 in the intensively fished areas.

**Discussion**

Previous studies on age and growth of lutjanids indicated that species in this family are generally slow growing and long-lived, with Brody growth coefficients of 0.1–0.25 year\(^{-1}\) and a maximum age of 25 years.

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**Table 4.** Likelihood ratio test comparing von Bertalanffy growth parameters (VBGF) between female and male \( Lutjanus \) fulviflamma collected from shallow waters at Mafia Island (F, female and M, male)

<table>
<thead>
<tr>
<th>Study sites</th>
<th>( L_0 ) (mm)</th>
<th>Parameter</th>
<th>( F )-stat</th>
<th>( P )-value</th>
<th>( K ) (year(^{-1}))</th>
<th>( F )-stat</th>
<th>( P )-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jujima Bay</td>
<td>300.4</td>
<td>304.5 mm</td>
<td>0.31</td>
<td>0.815</td>
<td>0.12 year(^{-1})</td>
<td>0.000</td>
<td>0.14 year(^{-1})</td>
</tr>
<tr>
<td>Chole Bay</td>
<td>293.5</td>
<td>284.9 mm</td>
<td>0.17</td>
<td>0.15</td>
<td>0.14 year(^{-1})</td>
<td>0.18 year(^{-1})</td>
<td></td>
</tr>
<tr>
<td>Tumbuju</td>
<td>277.2</td>
<td>281.1 mm</td>
<td>0.20</td>
<td>0.055</td>
<td>0.14 year(^{-1})</td>
<td>0.19 year(^{-1})</td>
<td></td>
</tr>
<tr>
<td>Mfuruni</td>
<td>312.0</td>
<td>328.0 mm</td>
<td>1.00</td>
<td>0.10</td>
<td>0.17 year(^{-1})</td>
<td>0.19 year(^{-1})</td>
<td></td>
</tr>
</tbody>
</table>

**Table 5.** Likelihood ratio test for comparing von Bertalanffy growth parameters (VBGF) between four populations of \( Lutjanus \) fulviflamma collected from shallow waters at Mafia Island

<table>
<thead>
<tr>
<th>Study sites</th>
<th>( L_0 ) (mm)</th>
<th>Parameter</th>
<th>( F )-stat</th>
<th>( P )-value</th>
<th>( K ) (year(^{-1}))</th>
<th>( F )-stat</th>
<th>( P )-value</th>
</tr>
</thead>
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<td>0.19 year(^{-1})</td>
<td></td>
</tr>
<tr>
<td>Mfuruni</td>
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<td>328.0 mm</td>
<td>1.00</td>
<td>0.10</td>
<td>0.17 year(^{-1})</td>
<td>0.19 year(^{-1})</td>
<td></td>
</tr>
</tbody>
</table>

**Table 6.** Instantaneous total (\( Z \)) and fishing (\( F \)) mortalities (year\(^{-1}\)), and the exploitation rate (\( E \)) of \( Lutjanus \) fulviflamma collected from shallow waters of Mafia Island. Natural mortality (\( M=0.27 \text{ year}^{-1} \))

<table>
<thead>
<tr>
<th>Study sites</th>
<th>Mortality &amp; exploitation rate</th>
<th>Sex</th>
<th>Chole Bay</th>
<th>Jujima Bay</th>
<th>Mfuruni</th>
<th>Tumbuju</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( Z )</td>
<td>Female</td>
<td>0.42</td>
<td>0.49</td>
<td>1.37</td>
<td>1.71</td>
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<tr>
<td></td>
<td></td>
<td>Male</td>
<td>0.56</td>
<td>0.65</td>
<td>1.63</td>
<td>1.29</td>
</tr>
<tr>
<td></td>
<td>( F )</td>
<td>Female</td>
<td>0.15</td>
<td>0.22</td>
<td>1.10</td>
<td>1.44</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Male</td>
<td>0.29</td>
<td>0.38</td>
<td>1.36</td>
<td>1.02</td>
</tr>
<tr>
<td></td>
<td>( E )</td>
<td>Female</td>
<td>0.36</td>
<td>0.45</td>
<td>0.80</td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Male</td>
<td>0.52</td>
<td>0.58</td>
<td>0.83</td>
<td>0.79</td>
</tr>
</tbody>
</table>
The only previous study on growth of L. fulviflamma was that of Loubens (1980) in New Caledonia, where the species attains a maximum age of about 20 years. Brothers (1982) concluded that the protracted breeding season, weakly expressed seasonal growth variations and almost uniform water temperature in areas where lutjanids occur are the major reasons why age and growth studies have generally not been undertaken on these fishes. However, of late it has been shown that annuli on hard parts may occur more frequently in tropical reef species than was previously thought (Sainbury & Whitelaw 1984; Longhurst & Pauly 1987; Manooch 1987). This study confirms that otoliths can be used to age lutjanids in the tropics.

Otolith mass was almost linearly related with fish age and eviscerated mass, but by an exponential function with fish length. Similar changes in otolith dimensions with age and fish length were described for other fish species (Boehlert 1985; Anderson, Morison & Ray 1992; Jones & Wells 1998). This suggests that the otoliths of L. fulviflamma continue to increase in mass even if the fish has reached its maximum length. One opaque and one translucent ring were laid down on blackspot snapper otoliths per annum. Available evidence suggests that a seasonal temperature difference of 2–3 °C was sufficient to cause ring formation in Lutjanus kasmira (Forsskål) (Morales-Nin & Ralston 1990). The seasonal SST difference of 3.7 °C in Mafia Island would theoretically also be adequate to cause the deposition of growth zones on the otoliths of L. fulviflamma. Seasonal growth cycles in tropical fish might also be related to physiological changes induced by food abundance, feeding regimes and reproductive cycles (Pajuelo & Lorenzo 2001). Irrespective, whatever the cause, the otoliths provided
a reliable method for the estimation of the age of this species.

The analysis of otolith zone formation in *L. fulviflamma* showed a dichotomous pattern. In sexually mature fish the opaque ring (fast growth zone) was deposited during the cooler months (June to September), but in immature fish opaque zone deposition occurred during the warmer months (November to May). These differences in the periodicity of zone formation, as suggested by Pajuelo & Lorenzo (2001), appear to be related to reproduction and food abundance. In Tanzanian coastal waters, food is more abundant in the warmer months than in the cooler months (Bryceson 1982), and Nzioka (1979) and Kaunda-Arara & Ntiba (1997) found that *L. fulviflamma* has a protracted breeding season lasting from

Table 7. Tukey test for comparing total mortality of female and male *Lutjanus fulviflamma* collected from shallow waters of Mafia Island

<table>
<thead>
<tr>
<th>Study sites</th>
<th>Jujima Bay (M)</th>
<th>Jujima Bay (F)</th>
<th>Chole Bay (M)</th>
<th>Chole Bay (F)</th>
<th>Tumbuju (M)</th>
<th>Tumbuju (F)</th>
<th>Mfuruni (M)</th>
<th>Mfuruni (F)</th>
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<td>***</td>
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<td>***</td>
<td>NS</td>
<td>NS</td>
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<tr>
<td>Chole Bay (F)</td>
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<td>NS</td>
<td>***</td>
<td>NS</td>
<td>***</td>
<td>***</td>
<td>***</td>
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<tr>
<td>Chole Bay (M)</td>
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<td>Tumbuju (F)</td>
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<td>Tumbuju (M)</td>
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<td>Mfuruni (F)</td>
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<td>Mfuruni (M)</td>
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* P < 0.05, ** P < 0.01, *** P < 0.001.
F, female; M, male; NS, not significant.
September to March in East African coastal waters. Therefore, in sexually mature fish, most of the available surplus energy was presumably channelled into gonadal recrudescence rather than somatic growth during the warmer months. During cooler months, when reproductive energy requirements are low, somatic growth was accelerated, resulting in the deposition of opaque zone on the otoliths. In sexually immature fish the opaque zone was deposited during the warmer months when food is abundant. The results suggest that it is important to analyse growth patterns of tropical reef-fishes in relation to the size at sexual maturity.

The estimated maximum age of 18 years for the blackspot snapper in this study was 2 years lower than the maximum recorded value of 20 years in New Caledonia (Loubens 1980). The $K$ values of *L. fulviflamma* in this study (0.13–0.19 year$^{-1}$) were within the reported range (0.1–0.25 year$^{-1}$) for most snappers (Manooch 1987). The maximum known length of *L. fulviflamma* in the Western Indian Ocean is 350 mm TL (Fischer & Bianchi 1984). This is considerably larger than the observed and predicted maximum lengths in this study, which may be a reflection of a general decline in size resulting from the sustained and steady increase in fishing effort around Mafia Island.

The effects of exploitation on life history parameters have been described for several temperate species (Buxton 1993). However, conclusive discussions on tropical inshore reef fisheries have often been hampered by the lack of information on the response to exploitation (Jennings & Lock 1996). As with temperate species, the most probable immediate responses to high fishing mortality would be a narrowing and shifts in the mode of population size and age distributions (Ricker 1975; Miranda, Wingo, Muncy & Bates 1987), and density dependent changes such as changes in the size and age at sexual maturity (Buxton 1993; Lizaso, Goni, Renones, Charton, Galzin, Bayle, Jerez, Ruzafa & Ramos 2000); changes which ultimately lead to growth and recruitment overfishing (Russ 1991; Russ & Alcala 1996).

The most important result of this study was the difference in the age and size structure of the fish in the MIMP and in the intensively fished areas. In the MIMP, where seine nets of <50 mm stretched mesh are prohibited, the majority of the fish were between 206 and 246 mm TL (6–10 years old). The use of the larger meshed seine nets here might explain the paucity of fish<201 mm TL. In the areas outside the park the bulk of the fish ranged between 146 and 196 mm TL (2–4 years old). However, the smaller meshed seine nets (19–38 mm stretched mesh) used in these areas would not exclude the capture of larger fish. The absence of larger fish (>246 mm TL) in the highly exploited areas is therefore most likely a consequence of the higher fishing intensity and the selective removal of larger fish by the fishery.

Wantiez, Thollot & Kulbicki (1997) produced similar evidence when comparing the average size of *L. fulviflamma* around five New Caledonia islands. They showed that after 5 years of protection the maximum size had increased from 21–24 cm TL to over 27 cm TL. Similarly, Munro (1983) showed substantial shifts towards a reduced size structure of ten major coral reef fish groups with increasing fishing intensity.

The estimates of $Z$ and $E$ for *L. fulviflamma* were higher in the heavily fished areas of Mfuruni and Tumbuju, than for Chole Bay and Jujima Bay in the park. It is suggested that these are consequences of the higher fishing intensity at Mfuruni and Tumbuju (Table 7). A low estimate of natural mortality is considered to be characteristic of stocks that cannot support heavy fishing pressure (Gulland 1983). Those with higher $M$ generally can withstand a higher fishing mortality because the fishery removes the fish that would otherwise have died from natural causes (Gulland 1983). The low $M$ estimate for *L. fulviflamma* on Mafia Island is therefore an added measure of concern for the long-term sustainability of the fishery at the current rate of $F$.

Gulland (1983) suggested that, as a rule of thumb, a fish stock is optimally exploited at a level of $F$, such that $E = 0.5$, where $F_{\text{opt}} = M$. The calculated exploitation ratios of 0.36 and 0.58 at Chole and Jujima Bays suggest that the fish in the MIMP are optimally exploited, while the fish at Mfuruni and Tumbuju, with $E = 0.79$ and 0.84, are overexploited. Moreover, given the longevity of *L. fulviflamma*, the species is particularly vulnerable to growth overfishing, already reflected by the paucity of the larger age classes in the heavily fished areas outside the MIMP in comparison with those at Chole Bay and Jujima Bay. These findings contribute towards the general body of knowledge that marine protected areas are probably one of the few, if not the only, effective options, for the management of long-lived tropical reef fish species. The effects of the different levels of fishing intensity inside and outside the MIMP are reflected by the population size and age structure data as well as the estimates of total mortality, and suggest that the MIMP plays a vital role for sustaining the fishery for blackspot snapper on Mafia Island.
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References


