

**Abstract**—Goldband snapper (*Pristipomoides multidens*) collected from commercial trap and line fishermen off the Kimberley coast of northwestern Australia were aged by examination of sectioned otoliths (sagittae). A total of 3833 *P. multidens*, 80–701 mm fork length (98–805 mm total length), were examined from commercial catches from 1995 to 1999. The oldest fish was estimated to be age 30+ years. Validation of age estimates was achieved with marginal increment analysis. The opaque and translucent zones were each formed once per year and are considered valid annual growth increments (the translucent zone was formed once per year between January and May). A strong link between water temperature and translucent zone formation was evident in *P. multidens*. The von Bertalanffy growth function was used to describe growth from length-at-age data derived from sectioned otoliths. No significant differences in length-at-age were found between sexes and growth parameters were  $L_{\infty} = 598$  mm,  $K = 0.187/\text{yr}$ ,  $t_0 = -0.173$  ( $r^2=0.76$ ). Regression models of estimated age as a function of otolith and fish measurements indicated a significant relationship between estimated age and otolith weight ( $r^2=0.94$ ). Total instantaneous mortality ( $Z$ ) estimates generated from catch-at-age data of *P. multidens* from the northern demersal scalefish fishery (NDSF) were 0.65 for 1995–96, 0.87 for 1996–97, and 0.71 for 1997–98. Estimates of the annual instantaneous rate of natural mortality ( $M$ ) were 0.10–0.14. The NDSF population of *P. multidens* is considered to be exploited above optimum levels on the basis of these mortality estimates. The protracted longevity, moderately slow growth and low natural mortality rates of *P. multidens* predisposes this species as one vulnerable to overfishing, thus cautious management strategies will be required. Furthermore, capture of *P. multidens* from depths of 60 meters or greater results in a high mortality of fish because the physoclistous ruptures causing internal hemorrhaging and hence there is a low probability of survival of any fish returned to the sea. Thus traditional harvest strategies involving size limits will be inappropriate for these fish. Conversely, harvest strategies that include appropriately targeted spatial fishery closures may provide a useful additional means of preserving the spawning stock biomass of these fish and protect against recruitment overfishing.

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## Age validation, growth, mortality, and additional population parameters of the goldband snapper (*Pristipomoides multidens*) off the Kimberley coast of northwestern Australia

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The goldband snapper (*Pristipomoides multidens*, Day), known also as gold-banded jobfish, Day's jobfish and large-scaled jobfish, is widely distributed throughout the tropical Indo-Pacific Ocean region from Samoa in the Central Pacific to the Red Sea in the Western Indian Ocean and from southern Japan south to Australia (Allen, 1985). Along Western Australia, *P. multidens* is found as far south as Cape Pasley (34°S) and is landed in commercial quantities from the Ningaloo Reef area (23°30'S) northwards (Kailola et al., 1993; Newman, unpubl. data). They inhabit hard bottom areas and areas of vertical relief and large epibenthos from depths of 60 to at least 245 m and are concentrated in depths from 80 to 150 m (Allen, 1985; Newman and Williams, 1996).

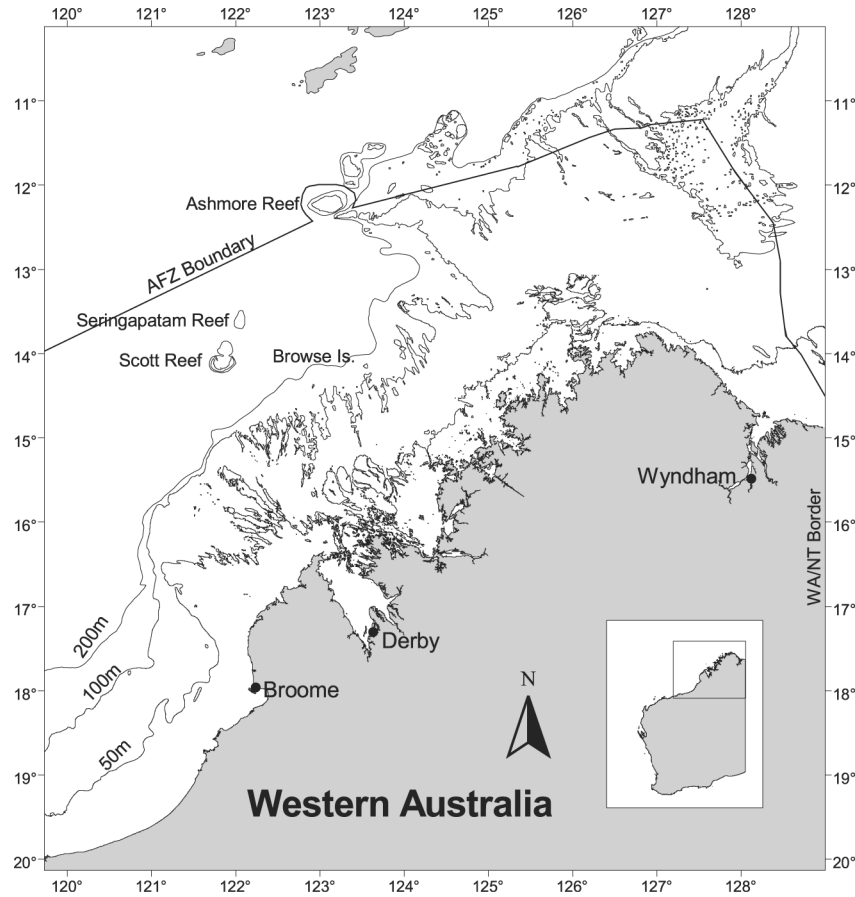
*Pristipomoides multidens* is a commercially important species throughout much of its range, forming an important part of the landed catch in both artisanal and developed fisheries (Dalzell and Preston, 1992; Newman, 2001). In Western Australia this highly valued resource is marketed whole, usually fresh on ice, and transported by road from regional ports to markets in most state capital cities. It is occasionally exported. In the Kimberley region, within the northern demersal scalefish fishery (NDSF), *P. multidens* has composed on average 37.7% of the landed catch from 1995 to 1999 (contributing on average 255 metric tons (t)/year). In terms of value to fishermen, it is second only to the red emperor snapper (*Lutjanus sebae*).

Information on the biology of *P. multidens* is limited. The juvenile habitats

of *P. multidens* have not been identified, although Newman (unpubl. data) obtained juveniles from uniform sedimentary habitat with no relief. In previous studies, several age determination techniques were used to determine the age of *P. multidens* but there were limited attempts at age validation (Edwards, 1985; Mohsin and Ambak, 1996; Richards<sup>1</sup>). The accurate determination of fish age is the key to estimating growth rates and mortality. Errors in determining fish age can result in ambiguous demographic parameters and provide misleading impressions of the production potential of fish stocks (Newman et al., 2000a). There is a lack of reliable information on the longevity, growth parameters, mortality rates, and population characteristics of *P. multidens*, despite its ecological and commercial importance.

This work represents the first comprehensive study of age, growth, and mortality of a population of *P. multidens* based on age estimates from sectioned otoliths and contributes to the management of these stocks. The objectives of this study were to validate aging and to provide age, growth, mortality and population characteristics of *P. multidens* from the Kimberley region of Western Australia that are based on age estimates from sectioned otoliths.

<sup>1</sup> Richards, A. H. 1987. Aspects of the biology of some deep water bottomfish in Papua New Guinea with special reference to *Pristipomoides multidens* (Day). Report 87-01, 31p. Fisheries Research and Surveys Branch, Department of Primary Industry, Port Moresby, Papua New Guinea.



**Figure 1**

Location of the northern demersal scalefish fishery (NDSF) off the Kimberley coast of northwestern Australia showing the 50-m, 100-m, and 200-m depth contours. The NDSF is bounded in the west by the 120°E latitude line, to the north by the boundary of the Australian fishing zone (AFZ), and to the east by the border with the Northern Territory. Fishing primarily occurs in depths of 80–140 m.

A further objective was to investigate the relationship between estimated age and the measurements of both otolith and fish dimensions to assess the applicability of these measurements in predicting the age of this species.

## Materials and methods

Commercial landings of *P. multidens* from the NDSF off the Kimberley coast of Western Australia were sampled from 1995 to 1999. Samples were acquired opportunistically from July 1995 to December 1996, whereas samples obtained from January 1997 to December 1999 were collected on a monthly basis among all vessels in the fleet. All specimens were captured with fish traps at depths of 60 to 200 m from 12°–20°S latitude (Fig. 1). Additional specimens were attained from research vessel cruises with fish traps.

All fish were measured to the nearest mm total length (TL), fork length (FL) and standard length (SL), weighed to the nearest g total weight (TW) and cleaned weight (CW),

and where possible, sex was determined by examination of the gonads. Cleaned weight is defined as the TW after removal of the gills and viscera. Length measurements were used to derive conversion equations with linear regression models [ $TL=a + b (FL)$ ,  $FL=a + b (TL)$ ,  $FL=a + b (SL)$  and  $SL=a + b (FL)$ ].

## Length-weight models

The relationships between FL and both TW and CW were described by the power function

$$W = aL^b,$$

where  $W$  = weight (TW or CW, g); and

$$L = FL \text{ (mm)}.$$

These relationships were fitted to log-transformed 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 weights-at-length (FL) relationships between sexes for *P. multidentis*. Length and weight data were transformed to natural logarithms to satisfy assumptions of normality and homogeneity. Multiple comparisons were performed with Tukey's honestly significant difference (HSD) test. Trends in mean length and weight of fish over time were assessed by using analysis of variance ( $\alpha=0.05$ ).

### Otolith preparation and analysis

Otolith removal, measurement, and preparation followed the procedures and protocols described in Newman et al. (1996), Newman et al. (2000b), and Newman and Dunk (2002). All age estimates were based on the analysis of thin transverse sections of otoliths. These thin sections were examined under a dissecting microscope at 10–30× magnification with reflected light on a black background.

The otoliths from eight juvenile *P. multidentis* (80–140 mm FL) were examined for daily bands with a different technique. One sagitta per fish was embedded in epoxy resin and a thick transverse section (>500  $\mu\text{m}$ ) was cut. The section was then ground and polished from each side to a level near the core (perpendicular to the long axis of the otolith) by hand with ebony paper (1000 grade) and lapping film (9 and 3  $\mu\text{m}$ ). A polished thin transverse section approximately 100  $\mu\text{m}$  thick was produced. The section was then examined with a compound microscope.

### Age validation

Marginal increment analysis, routinely used to validate fish age, relies on the assumption that if a translucent zone is laid down once a year, there should be a clear pattern of periodic growth on the edge of the otolith during the year. Marginal increment analysis is appropriate only if all fish in the population lay down the translucent zone at the same time. Thus, an annulus consists of a single opaque and a single translucent cycle within a 12-month period. The opaque zone is believed to form during periods of slow growth.

Marginal increment analysis usually implies measurement of marginal growth and hence many researchers have measured the width of the edge of the otolith section over an annual cycle. This measurement approach has an advantage in that it should be possible to plot growth of the edge over time to validate that only a single translucent mark is laid down each year. However, in *P. multidentis*, it can be difficult to determine a consistent location to measure on the otolith because of the inherent variability of their otoliths; hence this technique was not used in the present study.

Edge type analysis was adopted for the marginal increment analysis of *P. multidentis* and edge types were classified according to Pearson (1996) as either translucent, narrow opaque (opaque area less than half of the previous opaque zone), or wide opaque (opaque area greater than half of the previous opaque zone). Sectioned otoliths of fish of all ages were examined under a dissecting microscope with reflected light on a black background.

### Age determination

Because the peak spawning period of *P. multidentis* occurs in late March, all fish were assigned a birth date of 1 April to assure proper year-class identification. Ages were assigned from counts of annual growth increments consisting of alternating opaque and translucent rings from sectioned otoliths (opaque rings were counted). Annual growth increments 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 acusticus. Annual growth increments were counted without reference to fish length or date of capture. Each otolith section was examined on four separate occasions. When the counts differed, otolith sections were re-examined. In most cases that required resolution, the fourth and final count was used for analysis of age and growth because 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 annual growth increments) were considered indecipherable and were excluded from analysis of fish age.

Counts were compared and the precision of age estimates were calculated with the average percent error (APE) of Beamish and Fournier (1981). Greater precision is achieved as the APE is minimized. The relationship between fish length (FL) and age and otolith dimensions was assessed with linear regression techniques.

Timing of translucent zone formation in *P. multidentis* and mean sea surface temperatures (SST was assumed to reflect the temperature at depth) were compared by scaling values from the two data sets. The scaling process allowed direct comparison of each series and any time lags of one in relation to the other. Using the scaling score =  $1 - ((\text{maximum data value} - \text{data value}) \div \text{range})$ , where (in the month of November) mean SST for the month was 29°C, the maximum for the year (data set) was 29.7 and the range of the data values was 3.7, we calculated the scaled  $SST = 1 - ((29.7 - 29) \div 3.7) = 0.81$ ; in addition the scaled % frequency of otoliths with translucent edge types =  $1 - ((67 - 20) \div 67) = 0.30$ .

### Growth and mortality models

The von Bertalanffy growth function (VBGF) was fitted to estimates of length-at-age with nonlinear least squares estimation procedures. The VBGF is defined by the equation

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

where  $L_t$  = mean length of fish of age  $t$ ;  
 $L_\infty$  = asymptotic mean length;  
 $K$  = is a rate constant that determines the rate at which  $L_t$  approaches  $L_\infty$ ;  
 $t$  = age of the fish; and  
 $t_0$  = the hypothetical age at which the mean length is zero if it had always grown in a manner described by the VBGF.

**Table 1**

Length-weight relationships for *P. multidens* off the Kimberley coast of northwestern Australia. Estimates were obtained for the parameters  $a$  and  $b$  of the relationship  $W = aL^b$ , the sample size ( $n$ ), and the regression  $r^2$  value (lengths used are fork length [FL] in mm and the weight is total weight [TW] or cleaned weight [CW] in g).

Group	$a$	$b$	$n$	$r^2$
<i>P. multidens</i> (all fish—TW)	$2.483 \times 10^{-5}$	2.9501	3680	0.983
<i>P. multidens</i> (all fish—CW)	$2.356 \times 10^{-5}$	2.9425	3073	0.983
<i>P. multidens</i> (male—TW)	$2.156 \times 10^{-5}$	2.9737	1963	0.985
<i>P. multidens</i> (female—TW)	$2.825 \times 10^{-5}$	2.9281	1671	0.987

The von Bertalanffy growth curves for both sexes were compared with the likelihood ratio test of Cerrato (1990).

Estimates of the instantaneous rate of total mortality ( $Z$ ) were obtained from catch-at-age data 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 *P. multidens* 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 7) in year  $t$  and subtracting the natural logarithm of the catch per age class (e.g. age 8) in year  $t + 1$  for all fully recruited age classes. Mean total  $Z$  was then calculated across all fully recruited age classes. Instantaneous natural mortality rates ( $M$ ) were derived by using the general regression equation of Hoenig (1983) for fish, where  $\log_e Z = 1.46 - 1.01 \log_e t_{max}$  ( $t_{max}$ =the maximum age in years). The Hoenig equation has been shown to provide a reasonable approximation of  $M$  in tropical demersal fishes (Hart and Russ, 1996; Newman et al., 1996; 2000b).

The annual percentage removal was estimated by annual percentage =  $[F/Z (1 - e^{-Z})] \times 100\%$ . Exploitation rates ( $E$ ) were derived from the estimates of  $Z$  and  $F$  as defined by the equation  $E = F/Z$  ( $F$ =the instantaneous rate of fishing mortality derived from the relationship  $F=Z-M$ ). Reference points for target (optimal) and limit fishing mortality rates ( $F_{opt}$  and  $F_{limit}$ ) were calculated for *P. multidens* by using the estimate of natural mortality ( $M$ ), because  $F_{opt} = 0.5 M$  (Walters, in press) and  $F_{limit} = 2/3 M$  (Patterson, 1992).

## Results

A total of 3833 *P. multidens* (ranging in size from 80 to 701 mm FL [10.6–5770 g TW]) were examined for age analysis. Of the fish collected, 2063 were males ranging from 245 to 671 mm FL and from 296 to 5195 g TW, and 1751 were females ranging from 284 to 701 mm FL and from 450 to 5770 g TW. Length conversion equations were derived for total length:  $TL = (1.12 \times FL) + 21.84$  ( $n=2137$ ,  $r^2=0.995$ ); fork length:  $FL = (0.89 \times TL) - 16.61$  ( $n=2137$ ,  $r^2=0.995$ );  $FL = (1.12 \times SL) + 6.44$  ( $n=2148$ ,  $r^2=0.992$ ); and standard length:  $SL = (0.89 \times FL) - 2.14$  ( $n=2148$ ,  $r^2=0.992$ ).

## Length-weight models

Length-weight relationships were calculated separately for males, females, and for both sexes combined (Table 1). The relationship between TW and FL is presented in Figure 2. ANCOVA of TW-at-FL and CW-at-FL were both significantly different between sexes (TW:  $F=42.56$ ; df: 1, 3234;  $P<0.001$ ; CW:  $F=94.29$ ; df: 1, 2652;  $P<0.001$ ); males were larger than females. The length-frequency distribution for male and female *P. multidens* is shown in Figure 3.

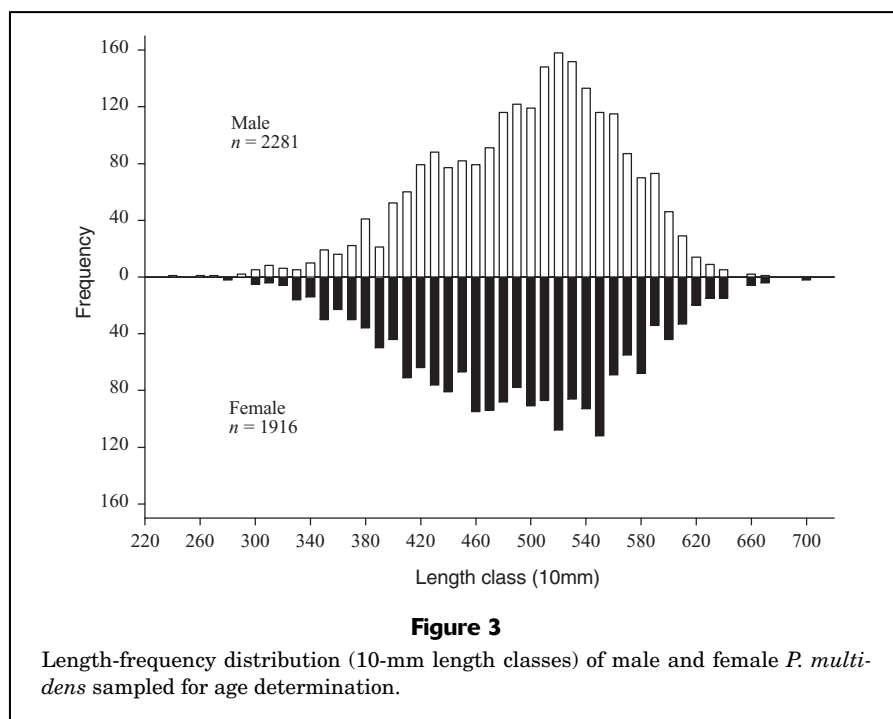
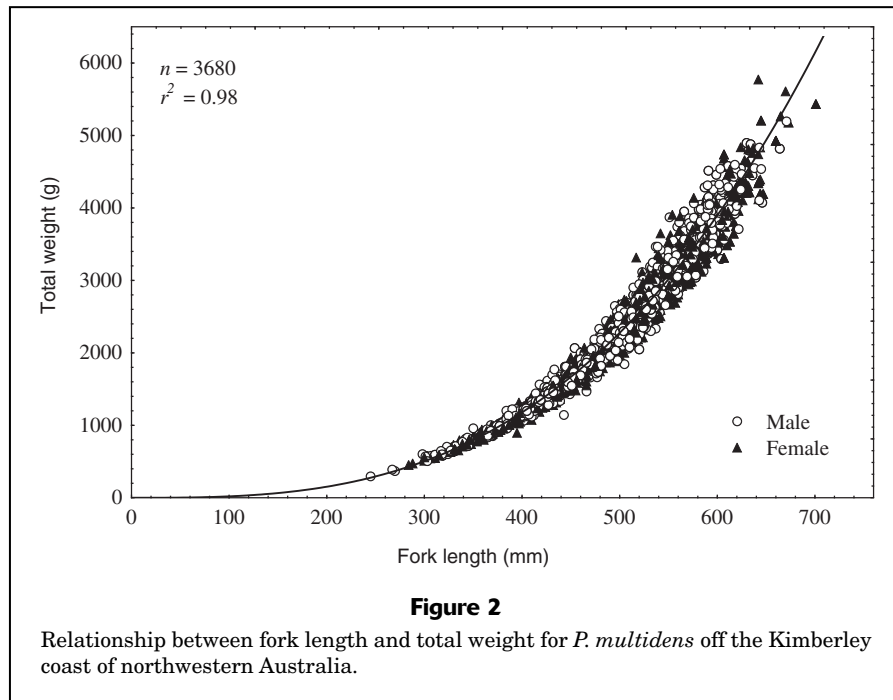
Temporal trends were evident in the mean length and weight of *P. multidens* over time. Mean FL was significantly different among years from 1995 to 1999 (ANOVA:  $F=31.29$ ; df: 1, 4193,  $P<0.001$ ), with (1995=1996=1997) > (1998=1999). Mean TW was also significantly different among years from 1995 to 1999 (ANOVA:  $F=89.33$ ; df: 1, 3295,  $P<0.001$ ), with 1995 > 1996 > 1997 > (1998=1999).

## Age validation

Otoliths displayed alternating opaque and translucent zones. A consistent annual trend was evident; the translucent zone was laid down from January to May and the opaque zone formed from June to December. The trend in thin opaque zone formation in June and July was replicated in both 1997 and 1998. Figure 4 clearly demonstrates that the opaque and translucent zones are laid down once a year and represent valid annual growth increments. Because the marginal increment analysis involved random sampling across all age classes in the sampled population, the validation of annual growth increments can be expected to hold across all age classes. In addition, the formation of the translucent zone in the sagittal otoliths of *P. multidens* and the annual cycle of sea surface temperatures in the Kimberley region of northwestern Australia were found to be closely related (Fig. 5).

## Otolith structure, analysis, and functionality

The sagittae of *P. multidens* are somewhat laterally compressed, elliptical structures. The distal surface is concave and the rostrum and postrostrum are somewhat pointed. The sagittae are characterized by variable growth reticulations along the dorsal edge from the postrostrum to

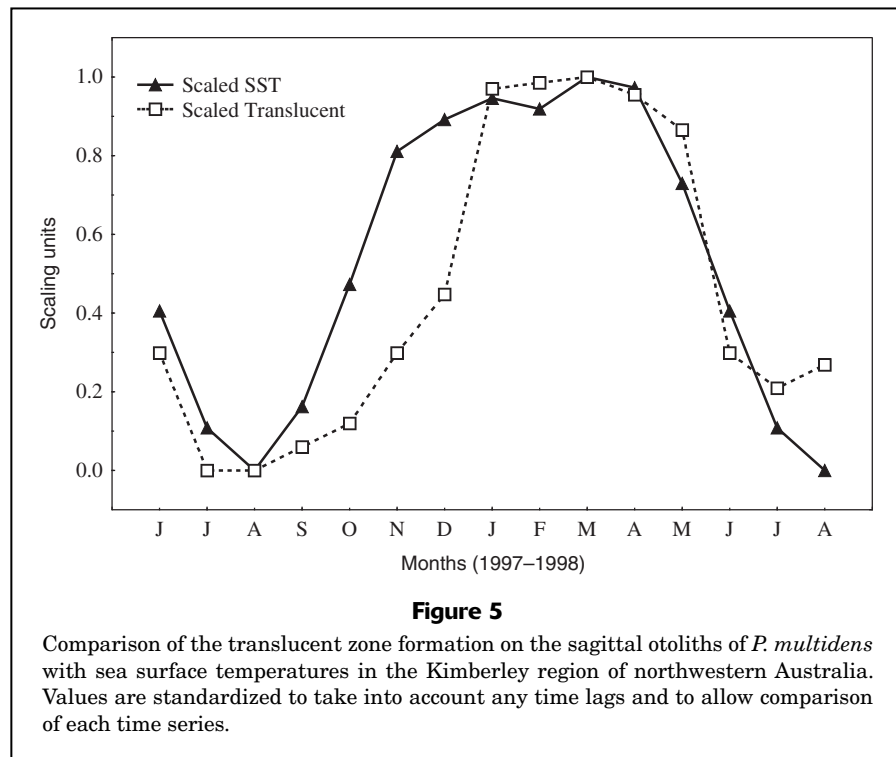
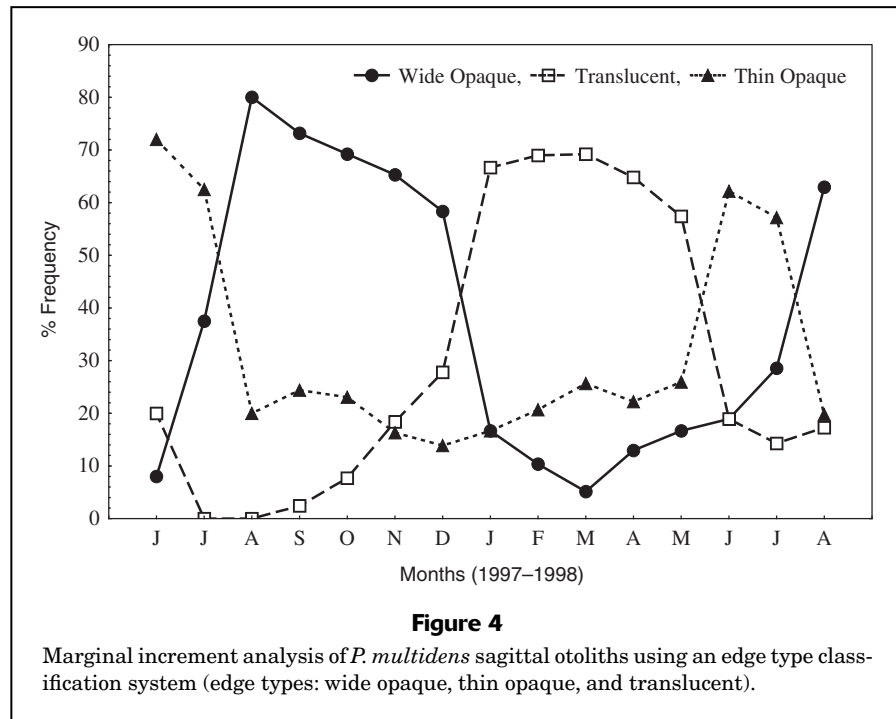


the antirostrum and along the ventral edge from the postrostrum to the rostrum. A curved sulcus crosses the proximal surface longitudinally, and the depth of the sulcal groove increases with fish age.

The precision of otolith readings of *P. multidens* was relatively high (APE of 10.4%). Given the variability encountered among otoliths, this APE reflects a moderately

high level of precision among otolith readings and indicates that the aging protocol adopted is replicable.

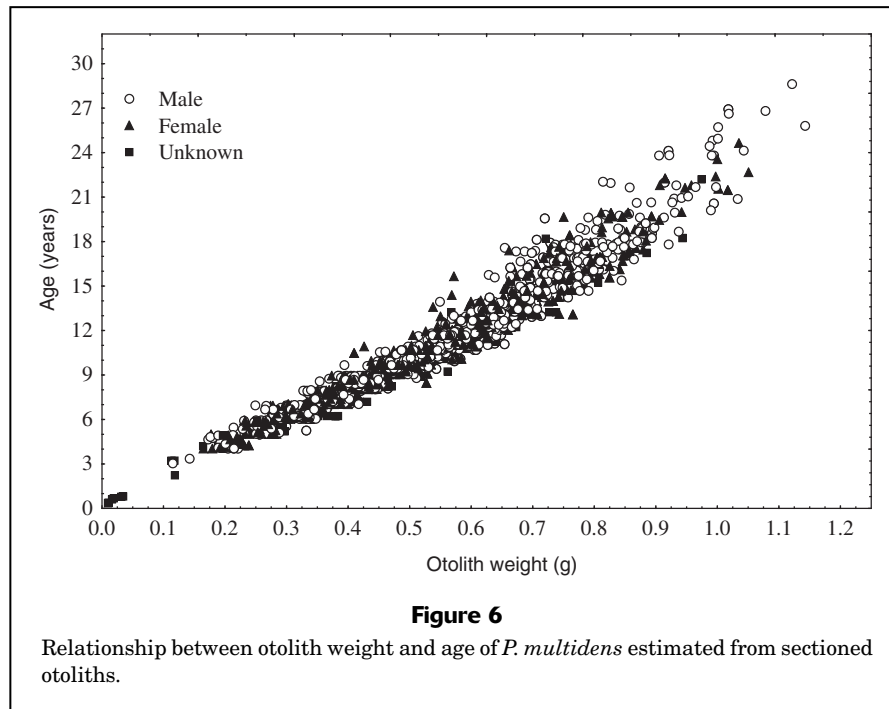
Otolith length and breadth were useful predictors of fish length in *P. multidens*, accounting for more than 77% of the variability (Table 2). In contrast, otolith weight and, in particular, height were poor predictors of fish length (Table 2). Otolith weight was the best predictor of fish age for *P. multi-*



*dens*, accounting for 94.4% of the variability in age (Table 2, Fig. 6). Otolith height was also a useful predictor of fish age, accounting for 88% of the variability in age. In contrast, otolith length and breadth were poor predictors of age for *P. multidens* (Table 2).

### Growth and mortality models

The von Bertalanffy growth curve was fitted to FL-at-age for all *P. multidens* (Fig. 7), and separately for each sex (Table 3). Growth in FL of *P. multidens* is relatively fast to

**Table 2**

Comparisons among otolith dimensions and length and age of *P. multidentis*. The predictive equations are of the simple linear regression form  $y = a + bx$  (OW=otolith weight; OL=otolith length; OB= otolith breadth; OH=otolith height). For regression analyses, fish length (FL) and age were used as the dependent variables (all regressions were significant at  $P < 0.001$ ). The standard error (SE) of the estimate is a measure of the dispersion of the observed values about the regression line.

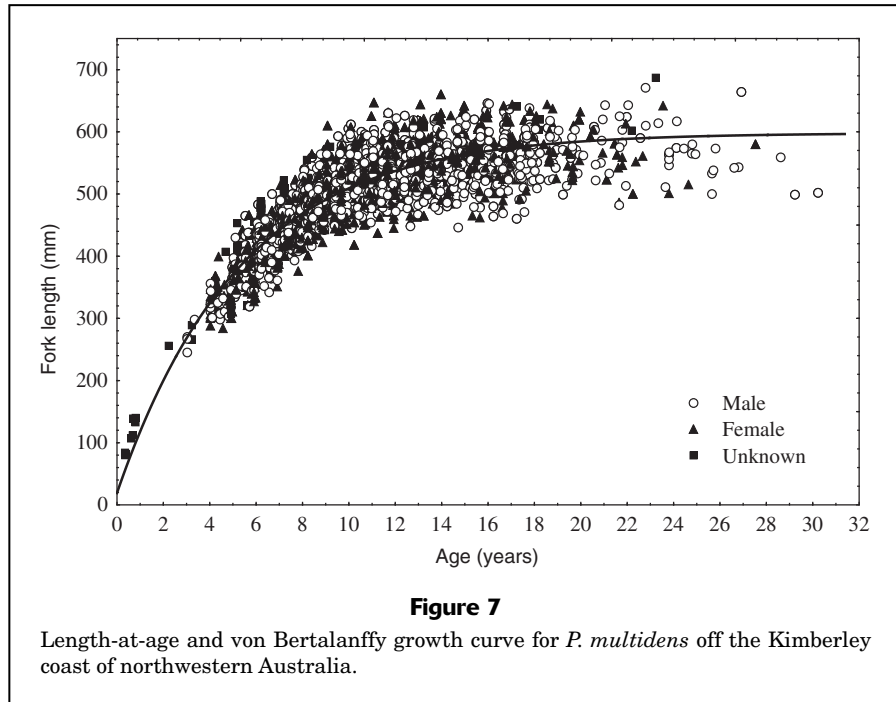
Dependent variable	Independent variable	Sample size	Equation	$r^2$	SE of estimate
FL	OW	2590	$FL = (315.37 \times OW) + 339.46$	0.68	37.57
FL	OL	2493	$FL = (33.47 \times OL) - 111.43$	0.77	32.08
FL	OB	3745	$FL = (50.43 \times OB) - 124.36$	0.83	28.48
FL	OH	3988	$FL = (118.39 \times OH) + 175.14$	0.53	48.36
Age	OW	2408	$Age = (21.86 \times OW) - 0.68$	0.94	0.94
Age	OL	2305	$Age = (1.77 \times OL) - 21.68$	0.58	2.63
Age	OB	3469	$Age = (2.40 \times OB) - 19.14$	0.60	2.49
Age	OH	3652	$Age = (8.52 \times OH) - 12.81$	0.88	1.36

age 9 but is much reduced in age cohorts beyond 9 years of age. Parameters of the VBGF are listed in Table 3. FL-at-age of *P. multidentis* was not significantly different between sexes (log-likelihood=0.9836, test statistic=1.001,  $P > 0.05$ ; no significant differences were found among parameters of the VBGF; see also Fig. 7). Generalized VBGFs of *P. multidentis* from previous studies were compared to that derived from our study (Fig. 8).

The maximum observed age of *P. multidentis* in the Kimberley region was 30 years. Given that the *P. multidentis* resource in the Kimberley region has been exploited for over 20 years, it is possible that in an unfished population the longevity of *P. multidentis* may be closer to 40 years.

These two estimates of maximum age in *P. multidentis* were applied to the Hoenig (1983) equation in order to derive an estimate of  $M$ . Consequently,  $M$  was considered to be in the range of 0.104–0.139, representing an annual survivorship of 87–90% for an unfished population. This range of  $M$  estimates for *P. multidentis* is similar to that observed for other long-lived lutjanid species in the Indo-Pacific region (Newman et al., 1996, Newman et al., 2000a; Newman and Dunk, 2002).

The longevity of female and male *P. multidentis* was somewhat similar at 27 and 30 years, respectively. The age structures of *P. multidentis* in the commercial catch differed among years. The 1995 sample had a peak in year



class 5 and relatively strong age classes 6, 8, and 10, but abundance per age class declined rapidly to age 20, after which few fish were found to be older (Fig. 9). The 1996 and 1997 samples were somewhat similar. In 1996 relatively strong year classes were present from age 5 through to age 11, and abundance per age class declined rapidly to age 26 (Fig. 9). One year later, the 1997 sample had relatively strong year classes present from age 6 through to age 12 (Fig. 9), providing further evidence of the annual formation of growth increments.

The 1998 sample had relatively strong 6, 7, and 8 age classes, and abundance per age class declined rapidly to age 24 (Fig. 9). The 1999 sample was similar to the 1998 sample with relatively strong 6, 7, and 8 age classes, and abundance per age class declined rapidly to age 20 (Fig. 9). Age classes 9 through 12 were somewhat eroded in the 1998 and 1999 samples in comparison to the 1996 and 1997 samples. In all years, abundance per age class declined rapidly to age 20, and fish older than 20 years were not well represented in the catch over the five years of catch sampling. In most years there was a strong mode of age-6 individuals present and this mode may reflect the age at full recruitment to the sampling gear (fish traps).

*Pristipomoides multidens* less than age 6 were in general not fully recruited to the sampled population and were therefore excluded from the mortality estimates derived from catch-at-age data. The year-specific total annual rate of mortality,  $Z$ , of *P. multidens* in the NDSF, was 0.65 for 1995–96 (fish aged 6–21 years), 0.87 for 1996–97 (fish aged 6–21 years), and 0.71 for 1997–98 (fish aged 6–21 years), representing an annual percentage removal of approximately 38%, 49%, and 41%, respectively, for each

**Table 3**

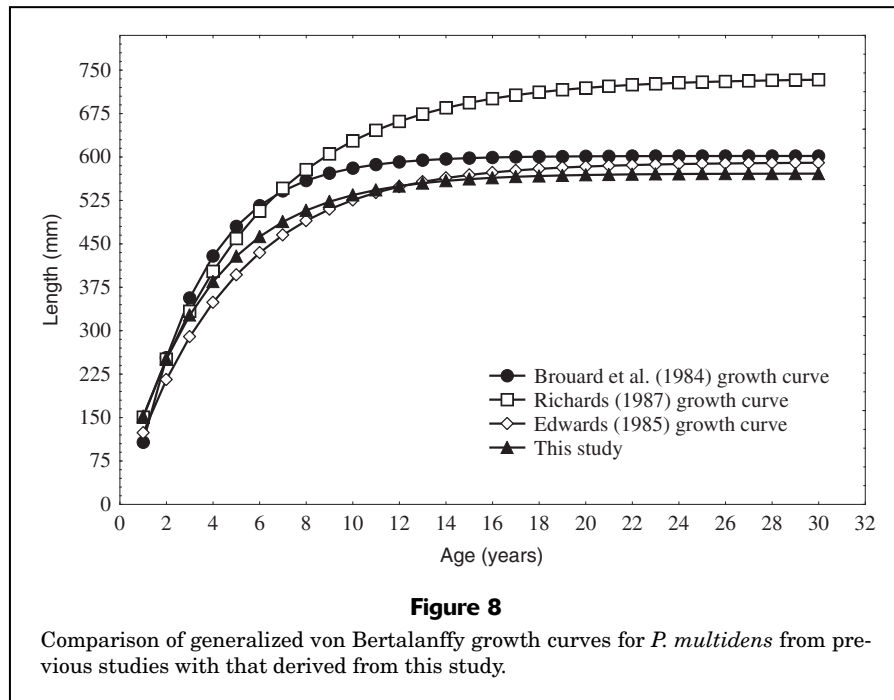
Growth parameters derived from the von Bertalanffy growth function and population characteristics of *P. multidens* off the Kimberley coast of northwestern Australia ( $n$ =sample size, FL is in mm, and age ( $t$ ) is in years).

Parameters	Male	Female	Total
$n$	1879	1600	3479
$L_{\infty}$	594.49	603.23	598.08
$K$	0.1868	0.1867	0.1873
$t_0$	-0.3601	0.0018	-0.1730
$r^2$	0.7394	0.7875	0.7630
$n$	2281	1916	4573
$FL_{mean}$	501.5	493.5	495.1
$FL_{min}$	245	284	80
$FL_{max}$	671	701	701
$n$	1872	1597	3833
$t_{mean}$	10.24	9.54	9.73
$t_{min}$	3	4	0.35
$t_{max}$	30	27	30

year (Table 4). In addition, exploitation rates were 0.79, 0.84, and 0.80, respectively.

The optimum fishing mortality rate,  $F_{opt}$  for *P. multidens* was estimated to be 0.052–0.069, and the limit reference point,  $F_{limip}$  was estimated to be 0.069–0.092 (see Table 4). These results indicate that only approximately 6% of the



**Table 4**

Summary of total mortality ( $Z$ ) estimates for *P. multidentis* derived from catch-at-age data based on ages determined from sectioned otoliths. Estimates of fishing mortality ( $F$ ) are derived by subtraction because  $Z = F + M$  and are compared to estimates of optimum fishing mortality rates.

Year	$Z$	$F$	$F_{opt}$	$F_{limit}$
1995–96	0.649	0.510–0.545	0.052–0.069	0.069–0.092
1996–97	0.869	0.730–0.765	0.052–0.069	0.069–0.092
1997–98	0.710	0.571–0.606	0.052–0.069	0.069–0.092

available stock of *P. multidentis* can be harvested on an annual basis in a sustainable manner and that annual harvest rates should not exceed 10% of the average stock size.

## Discussion

Sagittal otoliths were determined to be valid structures for age determination in *P. multidentis*. The edge-type classification system of three edge types used in this study is capable of indicating whether the opaque zone has just been formed or whether a new translucent zone is ready to form. The use of marginal increment analysis (MIA) of individuals of all ages exhibits a clear trend and demonstrates conclusively that annual growth increments are formed once per year. Annual growth increments were most conspicuous in the ventral lobe of the sagittal otoliths. However, we observed that experience is a critical factor in increasing the agreement and hence precision

of successive counts of annual growth increments in *P. multidentis*.

The spring–summer peak in opaque zone formation observed in our study is in accordance with the peak in opaque zone formation identified by Fowler (1995) and Beckman and Wilson (1995) for tropical fishes. The translucent zone (the period of fast growth in the otoliths) is formed in the summer months (January to May) and the opaque zone (the slow growth period) is formed in the winter-spring months (June to December). Translucent zones are relatively thin. Declining sea-surface temperature (which was assumed to reflect water temperature change at depth) was associated with the onset of opaque zone formation in the otoliths of *P. multidentis*. Furthermore, reproduction is unlikely to play a significant role in the timing of translucent zone formation in *P. multidentis* because spawning occurs primarily in the March–April period. These results indicate that water temperature, doubtless in association with other factors, provides a stimulus that influences the endolymph fluid

chemistry of these fish, culminating in the formation of annual growth increments.

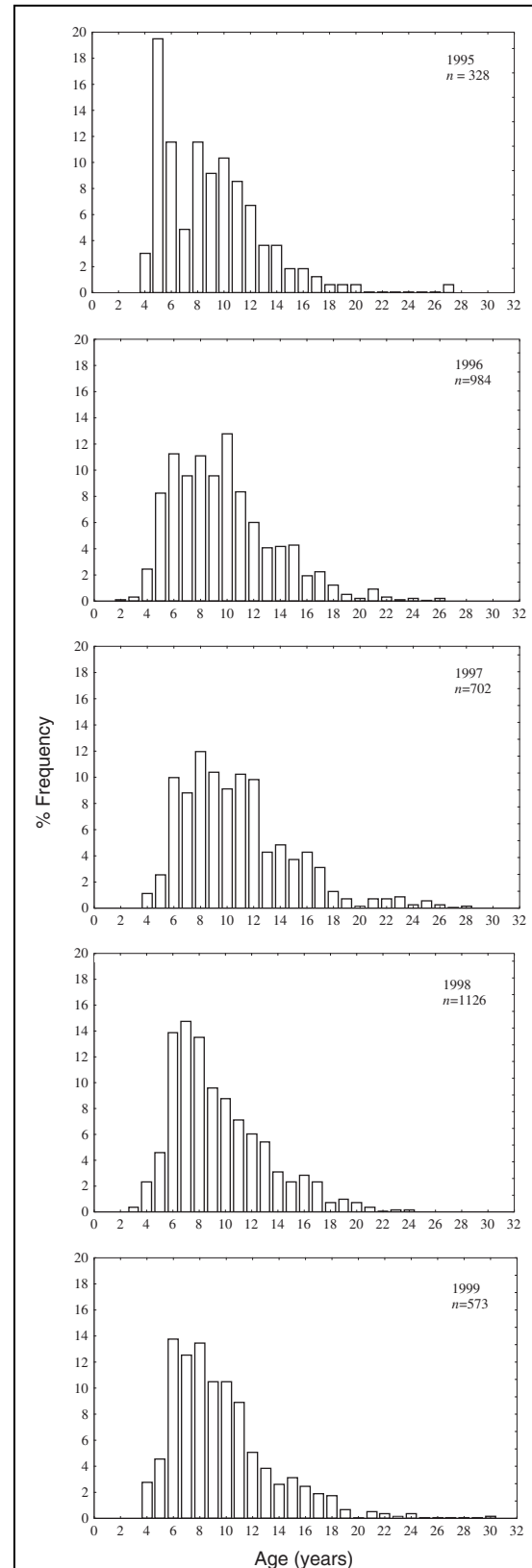
Female and male fish older than 20 years of age were uncommon in the landed catch. Fish of both sexes between 5 and 12 years of age were common in the landed catch. The maximum age of *P. multidens* observed in our study was much greater than that recorded previously. Richards<sup>1</sup> reported a maximum age of 14 years in Papua New Guinea from counts of daily rings on otoliths, whereas Brouard et al. (1984) recorded a maximum age of only 8 years in Vanuatu with a similar method. Edwards (1985) analyzed vertebrae and scales of this species in the Timor Sea and reported a maximum age of 14 years. In contrast, Mohsin and Ambak (1996) estimated a maximum age of only 5 years from the east coast of peninsular Malaysia with length-frequency analysis. Variation in the longevity estimates of earlier works is related to the aging methods used and their biases. For example, growth increments in vertebrae are often difficult to detect despite the presence of numerous discontinuities in bone growth (Marriott and Cappo, 2000). Alternatively earlier longevity estimates may have been drawn from sample populations biased by gear selectivity or from populations with varying degrees of exploitation.

Otolith weight was a good predictor of age in *P. multidens*, accounting for 94% of the variability in age. The strong linear relationship between otolith weight and fish age from a very large sample size implies that otolith weight may be used as a proxy for age. The coefficient of determination of the regression model is affected by the degree of colinearity of the independent variables. The high  $r^2$  value observed in our study provides the basis for a first-order age approximation. Thus, the potential exists for an age–otolith-weight key to be derived for *P. multidens*, as for an age-length key, whereby the age composition of the landed catch in future years may be obtained by weighing large numbers of otoliths. However, the accuracy and precision of adopting this monitoring strategy remains to be tested.

The fit of the regression model for the otolith weight–age relationship was much more precise than the fit of the fork-length–age relationship as described by the von Bertalanffy growth model. Considerable variation in length was observed within most age groups for both sexes. The large variation in length at a given age makes it difficult to accurately determine the age of *P. multidens* from length data alone. For example, fish ranging in length from 450 to 550 mm FL may vary in age from 5 to 30 years. This variability may explain the very low estimate of maximum age obtained by Mohsin and Ambak (1996), which was derived with length-frequency analysis.

Growth was most rapid through age 9 for both sexes. From age 9 onwards somatic growth slows with increasing age. The estimation of growth parameters is dependent upon adequate sampling across the length range of any species. The fish sampled in our study ranged in length from 80 to 701 mm FL, covering most of the length range of *P. multidens*. Therefore, it is unlikely that the growth parameters of *P. multidens* are biased because of inadequate sampling across the length range.

Despite methodological differences in age estimation, the estimates of  $K$  derived from the studies of Richards<sup>1</sup>



**Figure 9**

Age-frequency distributions of *P. multidens* in the northern demersal scalefish fishery from 1995 to 1999.

( $K=0.188$ ), Ralston (1987;  $K=0.188$ ), and Edwards (1985;  $K=0.219$ ) were somewhat similar to that observed in this study ( $K=0.187$ ). However, the asymptotic lengths reported by Richards<sup>1</sup> and Ralston (1987) were larger than our estimates, which were again similar to those of Edwards, 1985). In contrast, the estimates of  $K$  derived by Brouard et al. (1984), Brouard and Grandperrin (1985), and Mohsin and Ambak (1996), which ranged from 0.28 to 0.50, provided overestimates of the growth potential of *P. multidens* as observed in our study. Clearly, methodological differences in age estimation have the potential to unduly influence growth parameter estimation and may provide misleading impressions of the production potential of these fishes.

The similarity of growth in length-at-age between sexes indicates that there is little trade off in energetic investment into reproductive activity after sexual maturity at the expense of somatic growth as there is for some *Lutjanus* species (Newman et al., 1996, 2000b). Information on energy partitioning in the *Pristipomoides* is not known. However, females with a large body size would be reproductively “fitter” if they could accommodate a large mass of hydrated eggs prior to spawning, especially in a multiple male, multiple female spawning system.

The long life span of *P. multidens* and other lutjanid species (Loubens, 1980; Newman et al., 1996, 2000a; Newman and Dunk, 2002; Rocha-Olivares, 1998) may be an evolutionary adaptation that supports iteroparity. Many demersal reef fish are highly fecund, but egg and larval survivorship is low; therefore, spawning over numerous years may be necessary to maintain stable populations. In addition, numerous years of reproductive output may also be required to contend with environmental variability (e.g. the incidence of cyclones, El Niño–La Niña cycling), which may substantially influence recruitment success. Extended periods of high exploitation results in decreases in the spawning stock biomass and constriction of the age structure of fish populations, and thus diminishes the number of effective spawnings. Any reduction in the number of effective spawnings may result in a decrease in ecological fitness and hence limit the adaptive capacity of the species to combat environmental or anthropogenic induced stress.

Variation in life expectancy due to fishing pressure has the potential to bias estimates of  $M$  used in our study. To account for any  $M$ -associated difference, a range of  $M$  estimates have been considered in our study. *Pristipomoides multidens* were fully recruited to the commercial fishery in the NDSF by age 6. Catch-at-age data showed relatively consistent estimates of  $Z$  among years from 1995–96 through to 1997–98 and a relatively broad age structure in the landed catch.

### Fishery management implications

Throughout much of its range *P. multidens* composes a significant proportion of the demersal catch of tropical multispecies fisheries. Within these multispecies fisheries *P. multidens* is taken as part of the directed target catch or as a part of the retained catch. In fish trawl-based fisheries, *P. multidens* can be harvested at all stages of their

life history from juvenile to adult, making them especially vulnerable to overexploitation. In contrast, fisheries that use trap and line methods of capture (using bait to attract fish) only have the capacity to harvest fish in the subadult-to-adult phase of their life history. Hence, the method of capture and harvest strategy adopted has the capacity to influence the sustainable exploitation of the *P. multidens* resource.

Of particular relevance to fishery managers is the capacity that fish trawl-based fisheries have in being capable of continuing to function and to be economically viable (driven by the more productive, lower value species) while populations of higher valued species such as *P. multidens* become depleted. Thus, careful monitoring of the *P. multidens* resource will be required, particularly in trawl-based fisheries. Fishery managers need to be responsive to the intrinsic vulnerability of *P. multidens* to overharvesting as a corollary of its life history characteristics. Furthermore, fish such as *P. multidens*, which have low rates of natural mortality, low growth potential, extended longevity, mature relatively late in life and are either dead or moribund as a consequence of internal hemorrhaging when the physoclistous is ruptured during capture, are likely to be particularly sensitive to exploitation pressure. The apparent low survival rate for released fish in the fishing depths of the NDSF fleet indicates that the traditional use of legal minimum sizes to increase survival to spawning sizes and hence increase overall yields is not a practical option.

Populations of *P. multidens* have a low productive capacity and hence are vulnerable to overfishing as a consequence of slow growth, extended longevity, late maturity, and low rates of natural mortality. The demersal fish resources of the NDSF, of which *P. multidens* is a significant part, is currently being managed with an innovative total allowable effort system that allocates individually transferable effort units equitably to each licensee. 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. The incorporation of appropriately targeted spatial or temporal (or both spatial and temporal) closures within the existing effort management framework is likely to provide an additional useful and robust mechanism to maintain spawning stock biomass and protect against recruitment overfishing. In the wider Indo-Pacific region, fishery managers should consider harvest strategies of low frequency or low intensity in conjunction with targeted spatial or temporal closures to protect the spawning stock biomass of these fishes.

Harvest strategies such as setting fishing mortality at or near natural mortality ( $F=M$ ) were often prescribed prior to the 1990s (Gulland, 1970). Recently, the adoption of harvest strategies such as setting  $F = F_{0.1}$  were thought to be quite conservative, but usually resulted in  $F = M$  harvest strategies (Walters, in press). Following the meta-analysis of Myers et al. (1999), who examined stock-recruitment curve slopes expressed as maximum reproductive rates per spawner at low spawner biomass, Walters (in press) has reported that optimal fishing mortality rates are substantially lower than natural mortality rates for most species and stocks. 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. Consequently, exploitation rates for long-lived reef fishes need to be very conservative.

The declines evident in the length and weight of fish in the landed catch over the duration of our study support the finding of the high levels of  $F$ . These data support the estimates of the annual percentage removals that indicate that the NDSF population of *P. multidens* is currently exploited above optimum levels. The age structure of the *P. multidens* stock within the NDSF currently consists of close to 30 age classes (ages 2 to 30 years). Therefore, depletion of the spawning stock biomass of these fishes will result in long population recovery times and the economic loss associated with recovering and rebuilding these fisheries may persist longer. A minimum of 30 years would be required for the fished population to recover in terms of both virgin spawner biomass and age structure. The results of our study provide the basis for a more detailed age-structured stock assessment for this species.

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