Biological characteristics and mortality of western butterfish (*Pentapodus vitta*), an abundant bycatch species of prawn trawling and recreational fishing in a large subtropical embayment

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Abstract—The western butterfish (*Pentapodus vitta*) is numerous in the bycatch of prawn trawling and recreational fishing in Shark Bay, Western Australia. We have thus determined crucial aspects of its biological characteristics and the potential impact of fishing on its abundance within this large subtropical marine embayment. Although both sexes attained a maximum age of 8 years, males grow more rapidly and to a larger size. Maturity is attained at the end of the first year of life and spawning occurs between October and January. The use of a Bayesian approach to combine independent estimates for total mortality, Z, and natural mortality, M, yielded slightly higher point estimates for Z than M. This result indicates that *P. vitta* is lightly impacted by fishing. It is relevant that, potentially, the individuals can spawn twice before recruitment into the fishery and that 73% of recreationally caught individuals are returned live to the water.

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The family Nemipteridae (threadfin breams) is found in tropical and subtropical waters of the Indo-west Pacific (Nelson, 1994). The western butterfish (*Pentapodus vitta*) (also known as "striped whiptail"[1]) is a small benthic nemipterid, which is endemic to Western Australia (Russell, 1990) and very numerous in Shark Bay on the west coast of this state (Heithaus, 2004). It is also very abundant in the bycatch of the prawn trawl and recreational fisheries in this large subtropical environment. However, as with the vast majority of bycatch species in embayments, no estimate has been made of the mortality of *P. vitta* due to fishing. Furthermore, although *P. vitta* is very abundant in certain environments, there are no data on the age composition, growth, and reproductive biology based on validated age data for a population of this species. Indeed, previous studies of the Nemipteridae have focused almost entirely on species of *Nemipteris* and *Scolopsis*, which are widely distributed throughout the Indo-Pacific, where they are an important component of commercial and artisinal fisheries (Sainsbury and Whitelaw, 1984; Young and Martin, 1985; Murty et al., 1992; Zacharia, 1998).

The present study elucidates key aspects of the biology of *P. vitta* and, in particular, length-weight relationships, size and age compositions, growth, size and age at maturity, duration of the spawning period, and mortality. Focus is also placed on ascertaining whether this species is hermaphroditic, as is the case with certain other nemipterids (Young and Martin, 1985). The question of whether the mortality of a species with the "characteristics" of *P. vitta* is particularly attributable to sub-

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[1] FishBase. http://www.fishbase.org/search.php [accessed June 2006].

stantial trawling and recreational fishing in an embayment has also been explored. For this purpose, we have used a model that reconciles the often imprecise and conflicting estimates of total and natural mortality that are obtained by using traditional approaches (Hall et al., 2004).

Materials and methods

Sampling regime

766 *P. vitta*, ranging from 90 to 198 mm in fork length (FL), were collected by trawling throughout Shark Bay in November and December 1997. Trawling was conducted at night by using twin 11-m prawn trawl nets with 50-mm mesh in the panels and 44-mm mesh in the codends, as are employed by commercial prawn trawl operators in Shark Bay. Each trawl lasted 20 minutes. The samples collected were used for estimating the mortality of western butterfish in Shark Bay. *Pentapodus vitta* (n=339), ranging from 31 to 215 mm in fork length, were also collected in many months from 1999 to 2004 by using trawls, hook-and-line fishing, and beach seines. These samples were used to obtain aging, growth, and reproductive data in the study.

Relationships of total length and weight to fork length

The fork length (FL) of each fish, and the total length (TL) of each fish whose caudal fin was not damaged, were measured to the nearest 1 mm. The relationship between TL and FL of each sex was then calculated by using the equation

$$TL = a + b \times FL,$$

to enable the TL of any fish with a damaged caudal fin to be estimated from its FL. The weight of each fish (W) was recorded to the nearest 1 g. The relationships between the fork length and weight of females and males were described by the equation

$$\log W = \log a + b \log FL.$$

Analysis of covariance (ANCOVA, α=0.05) was used to determine whether the relationships between TL and FL and between weight and FL of the males and females of *P. vitta* were significantly different (Zar, 1999).

Validation of the aging method and age determination

The sagittal otoliths of each *P. vitta* were removed, cleaned, and stored in labelled paper envelopes. Because a preliminary examination demonstrated that the growth zones were often easier to discern in sectioned than in whole otoliths, all fish were aged by using sectioned otoliths. Transverse sections of each otolith, 0.3–0.5 mm thick, were cut through the primordium by using a low-speed jewellery saw and then ground using 9-μm lapping film. These sections were then mounted on glass slides and viewed with transmitted light under a dissecting microscope.

Validation that a single growth zone is formed each year in otoliths of *P. vitta* was undertaken by using marginal increment analysis. The distance between the outer edge of the outermost opaque zone and the periphery of the otolith section (the marginal increment) was measured on the sectioned otoliths of each fish caught between June 1999 and May 2000. The marginal increment was then expressed either as a proportion of the distance between the primordium and the outer edge of the opaque zone, when only one opaque zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present. All measurements were made with the Leica Image Manager 1000 (Leica Microsystems AG, Wetzlar, Germany).

Ages were assigned to each *P. vitta* on the basis of the number of opaque zones (annuli) in sectioned otoliths and by taking into account the dates of capture and the birth date of the fish. The birth date was designated as 1 December because this date corresponded approximately to the mid-point of the period when, on the basis of gonadosomatic indices and the trends shown by gonadal and oocyte development, *P. vitta* spawn (see “Discussion” section). The opaque zones were counted in the region between the primordium and the proximal surface along the ventral and dorsal margins of the sulcus acousticus, where the opaque bands were usually well defined and thus easily identified. The opaque zones in each otolith were counted without knowledge of the length or date of capture of the fish from which that otolith had come.

The precision of the counts from 175 *P. vitta* otolith sections made by the senior author (JCM) on two separate occasions and between JCM’s second count and a count made by another experienced reader, was assessed by using the index average percent error (IAPE) of Beamish and Fournier (1981). The IAPE values were low (i.e., 0.7%) for the two counts made by the senior author (JCM)) and for JCM’s second count and that of the independent reader (i.e., 3.9%), demonstrating a high level of precision for the otolith readings. Because the senior author was more experienced in reading the otoliths of *P. vitta,* his second round of counts (and these were almost invariably the same as in the first round of counts) was used for determining the ages of individual fish.

Growth

Fish caught by all methods in all months (except those obtained during extensive trawling in November and December 1997)—fish that collectively covered the full size range of *P. vitta*, were used to provide data for constructing growth curves. The large samples collected by trawling in November and December 1997 were excluded because they would have introduced an excessive bias towards the larger fish at younger ages (see Ricker

[1975] for importance of limiting bias by using data from multiple sampling methods). Von Bertalanffy growth equations were fitted to the fork lengths of the female and male fish at their estimated ages at capture by using nonlinear regression in the Statistical Package for the Social Sciences software (SPSS 12.0.2 for Windows, SPSS Inc., Chicago, IL). The lengths at age of small fish whose sex could not be determined were allocated randomly to both the male and female data sets used for calculating the growth curves. The von Bertalanffy growth equation is

$$L_t = L_\infty(1 - \exp^{-k(\mathrm{t}-t_0)}).$$

where L_t = the estimated length at age t;
L_∞ = the asymptotic length;
k = the rate at which L_t approaches L_∞; and
t_0 = the hypothetical age at zero length.

A likelihood-ratio test was used to compare the growth curves of the females and males of *P. vitta* (Cerrato, 1990). The hypothesis that a common growth curve could be fitted for the two sexes was rejected at the a= 0.05 level of significance if the test statistic, calculated as twice the difference between the log-likelihoods obtained by fitting a common growth curve for both sexes and by fitting separate growth curves for each sex, exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters (i.e., 3) in the two approaches.

Reproductive biology

The gonads of each fish that could be sexed macroscopically were removed and weighed to the nearest 0.01 g and, in the case of ovaries, staged macroscopically by using the scheme of Laevastu (1965) and the histological characteristics of the ovaries. For histology, ovaries of a random subsample of female *P. vitta* from each month of the year were preserved in Bouin's fixative for 48 hours, after which they were dehydrated in an ascending series of alcohol concentrations, embedded in paraffin wax, cut into 6-μm thick sections, and stained with either Ehrlich's haematoxylin and eosin or Mallory's trichrome (Humanson, 1972). On each histological slide, the maximum and minimum diameters of 30 randomly selected oocytes, which had been sectioned through their nuclei, were recorded to the nearest 5 μm. The mean of these two measurements for each oocyte was considered to represent the diameter of that oocyte (see Foucher and Beamish, 1980).

The gonadosomatic indices (GSIs) of females and males ≥1 year of age were determined from the equation

$$W1/W2 \times 100,$$

where $W1$ = weight of gonad; and
$W2$ = weight of whole fish minus the weight of gonad.

Mortality

Age-frequency distributions for female and male *P. vitta* caught during extensive trawling in November and December 1997 were used to estimate the instantaneous rate of total mortality (Z) for both females and males. Age classes on the descending limb of the age-frequency distribution for each sex (i.e., immediately after the peak in this distribution), were considered fully recruited to the fishery (Ricker, 1975). The catch curve for each sex was analysed by using the assumptions that Z and the levels of annual recruitment are constant and that the age composition of fully recruited fish represents a random sample from a multinominal distribution with uniform selectivity from the age of full recruitment (Hall et al., 2004). The value of Z was estimated by maximizing the log-likelihood by using the SOLVER routine in Microsoft™ Excel (vers. 2002, Microsoft Inc., Redmond, WA). The data for *P. vitta* were randomly resampled with replacement and analyzed to create 1000 sets of bootstrap estimates. The point estimate for Z was taken as the median of the 1000 bootstrap estimates. The 95% confidence limits were calculated as the 2.5 and 97.5 percentiles of the corresponding estimated values. The likelihood-ratio test used to compare growth curves was also used to compare the catch curves for the two sexes.

Estimates of natural mortality, M, for female and male *P. vitta* were calculated from the relationship between natural mortality, growth, and water temperature (Pauly, 1980). This relationship was refitted to Pauly's data for 175 fish stocks by using SPSS 12.0.2 for Windows (SPSS Inc., Chicago, IL). The values of k (per year) and L_∞ (cm TL), estimated from the asymptotic FL in the growth curves derived for *P. vitta*, and the water temperature, T, were then inserted into SPSS to obtain point estimates and associated 95% confidence limits for M, thereby taking into account the uncertainty of the parameter estimates and the variation of the data around the regression line. The mean annual bottom water temperature in Shark Bay is 23.1°C (data provided by Department of Fisheries Western Australia).

The values for mortality, derived for each sex by using the above approaches, were combined with the estimates of total mortality obtained from the maximum recorded ages of the two sexes with Hoenig's (1983) regression model for fish and those obtained with a simulation approach (Hall et al., 2004). This method reconciles the inconsistencies among the individual estimates of mortality and, through combining the different values, improves the precision of the resulting estimates of natural and total mortality. To provide a more precise estimate, the simulation routine was modified slightly from that described by Hall et al. (2004) to use the number of males or females within the sample that were older than a specified age rather than the age associated with the oldest of those fish.

Results

Relationships of total length and weight to fork length

The relationships between the FL and TL of females and males, which covered essentially the full size range of *P. vitta*, did not differ significantly ($P>0.05$) and therefore the length data for the two sexes were pooled. The linear relationship between FL and TL for both sexes of *P. vitta* combined is described by the equation

$$TL = -2.35 + 1.12\ FL \qquad (n=344,\ r^2=0.99).$$

Moreover, because the relationship between weight and fork length of western butterfish did not differ significantly between males and females ($P>0.05$), these data for the two sexes were pooled. The relationship between weight and fork length for both sexes combined was described by the equation

$$\log W = \log 1.22x\ 10^{-5} + 3.06 \log FL \quad (n=1026,\ r^2=0.99).$$

Validation of aging method

The mean monthly marginal increments on sectioned otoliths of western butterfish with one, two, three, and four–seven opaque zones reached their maxima in October, after which they declined markedly to their minima in either November or December and then rose progressively over the ensuing months (Fig. 1). The pronounced decline and then progressive rise, exhibited by the mean monthly marginal increments on the otoliths of western butterfish, irrespective of the number of opaque zones, demonstrates that a single opaque zone is formed in the otoliths of *P. vitta* each year and that the number of such zones can thus be used to age this species accurately.

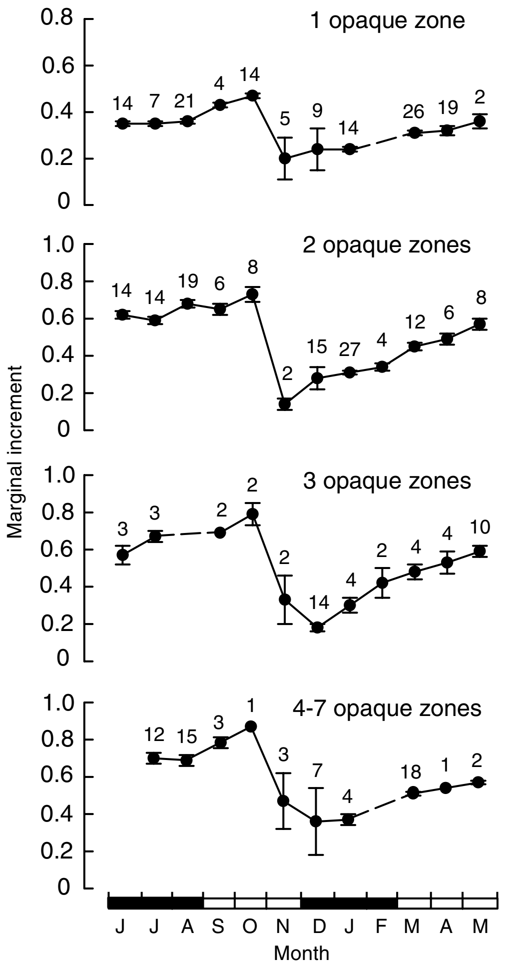

Figure 1

Mean monthly marginal increments (±1 standard error) for sagittal otoliths of the western butterfish (*Pentapodus vitta*), derived from samples collected between 1999 and 2004. Sample size is given for each month. The closed rectangles represent the summer and winter months and the open rectangles the autumn and spring months.

Growth

The von Bertalanffy growth curve provided a good fit to the fork lengths at age of the females and males of *P. vitta* (Fig. 2). This good fit is reflected in the high coefficients of determination (r^2) of 0.942 for females and 0.924 for males and by the values for t_0 being close to zero (Table 1). The von Bertalanffy growth curves of the females and males of *P. vitta* in Shark Bay differed significantly ($P<0.05$), and the difference in L_∞ between females and males contributed more to the difference than that of either k or t_0.

Females were more prevalent than males in length classes below 160 mm, whereas the opposite was true above this length (Fig. 3A). However, age-frequency distributions showed that females were more prevalent in all age classes (Fig. 3B). The overall sex ratio was 1.4 females:1 male.

Reproductive biology

Because virtually all *P. vitta* became mature at the end of their first year of life, the GSIs for all fish ≥1 year of age were calculated. The mean monthly GSIs for female western butterfish remained low (<0.9) in winter (June to August) and early spring (September), but then increased sharply from September to reach a maximum of 4.0 in late spring (November), before declining markedly during mid-summer (January) (Fig. 4). Although the pronounced seasonal trend displayed by the mean monthly GSIs for males was very similar to that for females, the maximum mean monthly GSI of males was approximately one tenth of that for females.

All female western butterfish that were ≥1 year old and caught between February and August (apart from a few in July) possessed ovaries at stage I or II (i.e., they were virgin or immature; Fig. 5). Females with

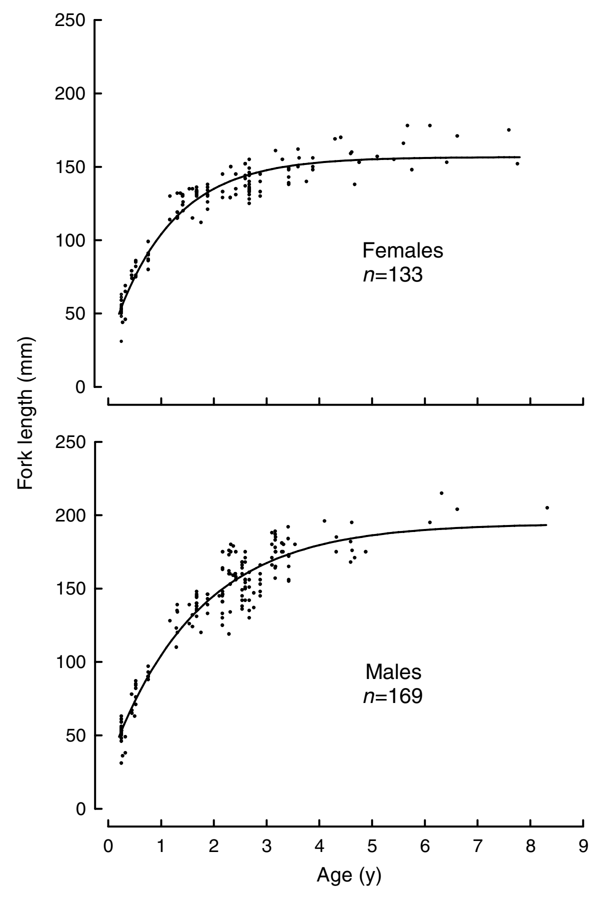

Figure 2

Von Bertalanffy growth curves fitted to fork lengths at age for individual females and males of western butterfish (*Pentapodus vitta*).

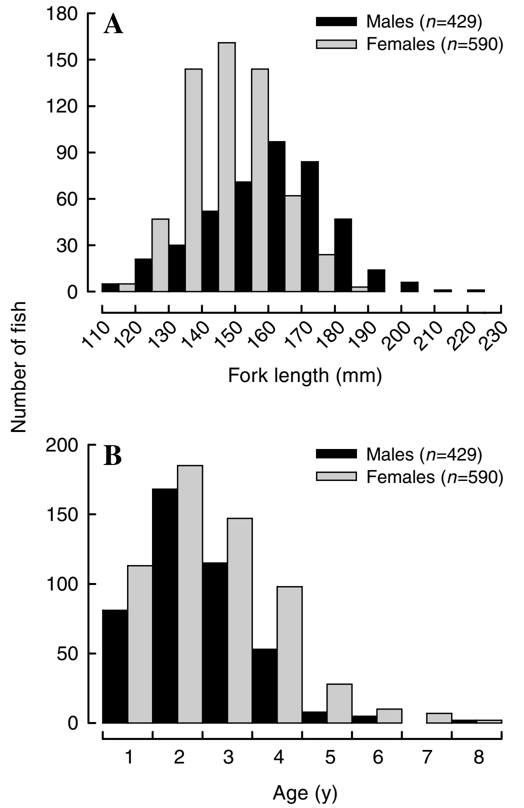

Figure 3

(**A**) Length-frequency and (**B**) age-frequency distributions for males and females of western butterfish (*Pentapodus vitta*).

Table 1

Von Bertalanffy growth parameters and their upper and lower 95% confidence limits for females and males of the western butterfish (*Pentapodus vitta*) in Shark Bay. r^2= coefficient of determination; n=number of fish in sample.

Sex	Confidence intervals	k (/year)	L_∞ (mm FL)	t_0 (years)	r^2	n
Females	Estimate	0.886	156.6	−0.233	0.942	133
	Upper	0.928	159.2	−0.058		
	Lower	0.844	154.0	−0.408		
Males	Estimate	0.602	194.4	−0.282	0.924	169
	Upper	0.624	197.9	−0.189		
	Lower	0.580	190.9	−0.375		

stage-III (developing) and stage-IV (maturing) ovaries were first found in July and were also present in September. Fish with stage-V (prespawning) and stage-VI (spawning) ovaries collectively dominated the samples obtained in October to December and were still the most prevalent group in January. The samples in January also contained one fish with stage-VIII (recovering spent) and some with stage-II ovaries but none with ovaries at stages III or IV (Fig. 5). The above trends provide strong evidence that any female with ovaries

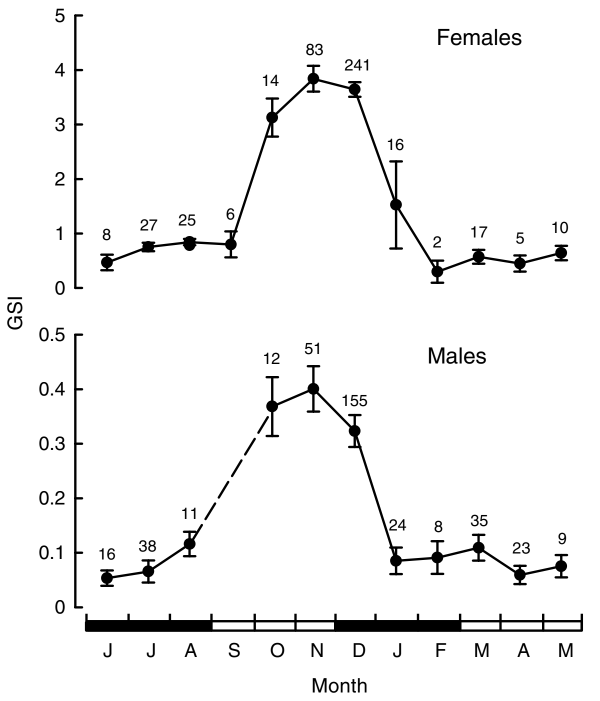

Figure 4

Mean monthly gonadosomatic indices (GSI) (±1 standard error) for females and males of western butterfish (*Pentapodus vitta*) that were ≥1 year old. Monthly sample sizes are given above each mean.

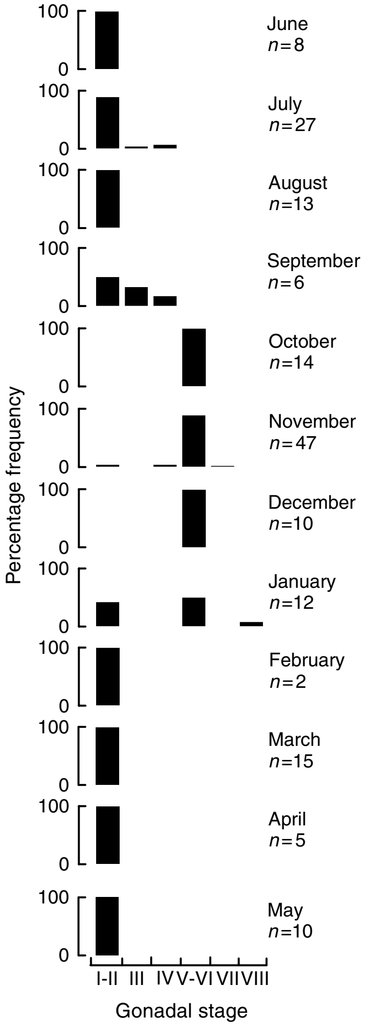

Figure 5

Histograms showing percent frequency of occurrence of each of the various gonadal stages in female western butterfish (*Pentapodus vitta*) in each month of the year.

that had developed to at least stage III by September would have progressed through to maturity during the ensuing months of the spawning period if it had not been removed from the population.

In each month, the distribution of oocyte diameters in the mature ovaries of *P. vitta* produced a well-defined mode between ~20 and 80 *μ*m, which represented chromatin nucleolar- and perinucleolar-stage oocytes. Cortical alveolar oocytes were present in some ovaries in July and September, when oocyte diameters had reached a maximum of 200 and 150 µm, respectively. These larger oocytes and also yolk granule oocytes were abundant between October and December and reached a maximum diameter of 380 *μ*m. The contribution of cortical alveolar and yolk granule oocytes declined in January. Hydrated oocytes were found in several ovaries in October, December, and January and postovulatory follicles were present in some ovaries during November.

Mortality

The age-frequency distributions for both female and male western butterfish caught during extensive trawling in November and December of 1997 had a modal peak at 2 years of age (Fig. 3B). Because the age at full recruitment was thus considered to be 3 years, catch curve analysis was undertaken with data for the 3+ and older age classes. The resulting point estimate for the instantaneous rate of total mortality, Z, was significantly greater ($P<0.05$) for males (1.15/year) than for females (0.91/year) (Table 2). Likewise, the simulation method of Hall et al. (2004), based on the number of individuals above 5 years of age (2 males and 13 females for sample sizes of 130 and 253, respectively), yielded a greater point estimate of Z for males (1.34/year) than females (0.89/year). The point estimate for Z, derived by inserting the maximum ages for female and male butterfish (8 years for both males and females), into the refitted Hoenig (1983) equation for fish, was 0.55/year for the two sexes (Table 2). The point estimates for the instantaneous rate of natural mortality, M, derived by inserting the parameter values for western butterfish into the refitted Pauly (1980) equation, were higher for females (1.78/year) than males (1.28/year).

The combined point estimate for Z derived using the method of Hall et al. (2004) was greater for males (1.14/year) than females (0.89/year; Fig. 6). This method yielded a slightly higher point estimate of M for males (0.80/year) than females (0.71/year) (Fig. 6).

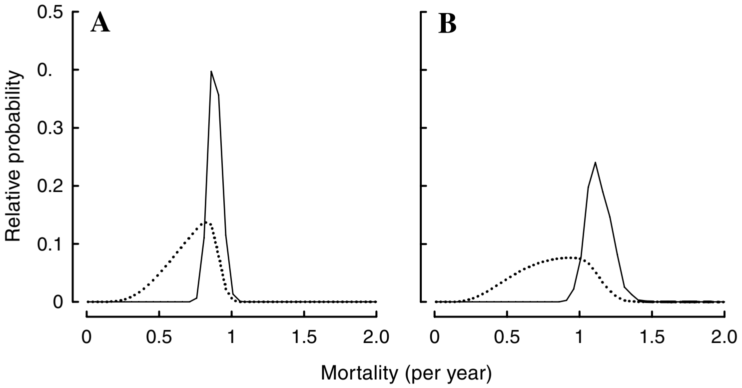

Figure 6

Combined posterior probability distributions for Z (solid line) and M (dotted line) for (**A**) females and (**B**) male western butterfish (*Pentapodus vitta*).

Discussion

Validation of aging method, age composition, and growth

The validation that the opaque zones of *P. vitta* are formed annually, together with the very high repeatability of their counts in sectioned otoliths, demonstrate that the number of these opaque zones (annuli) in sectioned otoliths can be reliably used for aging this nemipterid. Stephenson and Hall (2003) demonstrated that the annuli in sectioned otoliths of another nemipterid, *Nemipterus furcosus*, in Western Australia are also formed annually.

The vast majority of the *P. vitta* caught in Shark Bay were less than seven years old and the oldest individual was just over eight years old. The pattern of growth for females and males differed. Thus, the males of each age were, on average, larger than females after the first year of life and had a greater L_∞. However, most of the growth of both sexes occurs during the first three years of life.

Spawning period

The highly elevated mean monthly GSIs of females and males between October and December and the restriction of females with mature ovaries to the period between

Table 2

Point estimates and their 95% confidence intervals for total mortality, Z, and natural mortality, M, for the western butterfish (*Pentapodus vitta*), calculated by using life history models, estimation of longevity based on simulation, catch curve analysis and Bayesian analysis. Methods used for main interpretations of mortality are in bold.

Method of analysis	Z or M (/year)	Point estimate	Lower 95% CI	Upper 95% CI
Males				
Catch curve analysis	Z	1.15	0.96	1.33
Simulation (number of fish >5 years old)	Z	1.34	0.90	1.95
Refitted Hoenig (1983) fish equation	Z	0.55	0.19	1.52
Combined Z (Bayesian method)	**Z**	**1.14**	**1.01**	**1.35**
Refitted Pauly (1980)	M	1.28	0.42	3.91
Combined M (Bayesian method)	**M**	**0.80**	**0.37**	**1.23**
Females				
Catch curve analysis	Z	0.91	0.78	0.99
Simulation (number of fish >5 years old)	Z	0.89	0.69	1.11
Refitted Hoenig (1983) fish equation	Z	0.55	0.19	1.52
Combined Z (Bayesian method)	**Z**	**0.89**	**0.82**	**1.01**
Refitted Pauly (1980)	M	1.78	0.56	5.35
Combined M (Bayesian method)	**M**	**0.71**	**0.39**	**0.97**

October and January implies that *P. vitta* spawns during these latter four months. This conclusion is consistent with hydrated oocytes or postovulatory follicles or a combination of both being found only in fish caught between October and January. Furthermore, the precipitous decline in the mean monthly GSIs between December and February and the presence of only stage-II ovaries in February strongly indicates that spawning does not extend into this month. Because spawning activity peaked between October and January, the western butterfish was given a birth date of 1 December when an age was assigned to each fish. Because mature ovaries of *P. vitta* often contained a relatively wide size range of vitellogenic oocytes and, in many cases, also either hydrated oocytes or postovulatory follicles, this species is considered a multiple spawner *sensu* deVlaming (1983), namely individual females release eggs on more than one occasion in a spawning season.

Is there evidence that *Pentapodus vitta* is hermaphroditic?

Our data demonstrate that, in the population of *P. vitta* in Shark Bay, the females are relatively more abundant than males in length classes below 160 mm, whereas the reverse is true of length classes above that length (Fig. 3A). In contrast, the prevalence of females was always greater than that of males in each age class. The trend towards an increasing prevalence of males vs. females with increasing body length can thus be attributed to the males growing faster. The fact that there was not a progressive shift towards an increase in one sex with increasing age and none of the gonads of the 178 fish examined contained both ovarian and testicular tissue provides overwhelming circumstantial evidence that *P. vitta* is gonochoristic. Like *P. vitta*, other nemipterid species also exhibit a size-related skew in their sex ratios that can be explained by differences in growth rates between the two sexes (e.g., Young and Martin, 1985; Lau and Sadovy, 2001; Raje, 2002; Granada et al., 2004). The trend among gonochoristic nemipterids, for their males to grow larger than their females, presumably reflects a selective advantage of being large during courtship or mating (Granada et al., 2004). In contrast to these gonochoristic species, some nemipterids are protogynous hermaphrodites, e.g., *Scolopsis monogramma, S. taeniopterus* and *S. bilineatus* (Young and Martin, 1985).

Mortality

The point estimates for natural mortality, M, derived for males and females of *P. vitta* with Pauly's (1980) equation, were inconsistent with the point estimates derived for total mortality, Z. This conclusion is drawn from the fact that the point estimates for M were greater than those for Z from both Hoenig's (1983) equation for fish and catch curve analysis, thereby paralleling the situation with several other species (see Hall et al., 2004), and also those derived from the simulation and Bayesian methods of Hall et al. (2004). The use of the method of Hall et al. (2004) reconciled the inconsistencies between M and Z for *P. vitta* and provided more precise estimates, particularly for M. Because the point estimates for Z were only slightly greater than those for M, the population of *P. vitta* in Shark Bay does not appear to have been subjected to heavy fishing pressure. In this context, it is relevant that, because the vast majority of *P. vitta* attain maturity by the end of their first year of life, most individuals will have had the opportunity to spawn at least twice before they become fully recruited into the trawl fishery. Furthermore, recreational anglers return about 73% about of the western butterfish they catch in Shark Bay live to the water (Sumner et al.[2]).

Pentapodus vitta lives for up to eight years, but grows very rapidly early in life and attains maturity by the end of the first year of life. The males of *P. vitta* grow more rapidly and reach a larger size than their females. The western butterfish is a gonochoristic species that, in Shark Bay, spawns between mid-spring and mid-summer. Although commercial and recreational fishermen obtain large numbers of *P. vitta* as bycatch in Shark Bay, this fishing does not appear to have a marked impact on the numbers of this very abundant species in this large subtropical embayment.

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