Growth and mortality of *Lutjanus vittus* (Quoy and Gaimard) from the North West Shelf of Australia

Tim L.O. Davis
Grant J. West
CSIRO Division of Fisheries, Marine Laboratories
GPO Box 1538, Hobart, Tasmania 7001, Australia

The tropical waters of the North West Shelf of Australia are highly productive (Tranter 1962) and support a diverse fish fauna (Sainsbury et al. 1985). A significant multispecies trawl fishery has developed in the region, its total catch peaking in 1973 at 37,000 t, although this had decreased to 2700 t in 1989 (Jernakoff and Sainsbury 1990). *Lutjanus vittus* is an important and highly valued fish in this trawl fishery, comprising about 4% of the total catch (Jernakoff and Sainsbury 1990).

Assessment of fish yields of the North West demersal trawl fishery is based mainly on a Beverton and Holt dynamic pool model (Sainsbury 1987), which requires estimates of mortality and growth parameters for each species. In this paper we investigate the age, growth, population structure, and mortality of *L. vittus* collected from random trawl surveys of the North West Shelf during 1982–83.

Materials and methods

Field collection

Material was obtained from the CSIRO North West Shelf program (Young and Sainsbury 1985), which surveyed the shelf waters within latitudes 116–119°E about every two months between August 1982 and October 1983 (Fig. 1). Fish were caught with a Frank and Bryce trawl (30.5 m foot rope and a 20 mm cod-end liner) towed at 3.5–4.5 knots for 30 minutes during the day. Demersal tows were made at computer-generated random positions in 13 strata defined by water depth (10–50 m, 50–120 m, and 120–210 m), sediment type (nominally shelly sand, sand, sandy silt, and silt), and two geographical zones in which different fishing regimes were planned in the future (Table 1). Sixty-two trawl positions were produced for each sampling survey, with effort being allocated according to the mean and variance of catches determined by preliminary surveys and the area of each stratum. On average, 58 trawls were completed each survey.

At each random station the total weight of *L. vittus* and the fork length by 10 mm classes of each *L. vittus* was recorded. A subsample of 20–40 fish, approximately representing the size/frequency composition of the total catch (Kimura 1977) was then selected from each station for further analysis. Fork length was measured to the nearest mm and total weight to the nearest g, and sex were recorded. Sagittal otoliths and urohyals were collected for age determination.

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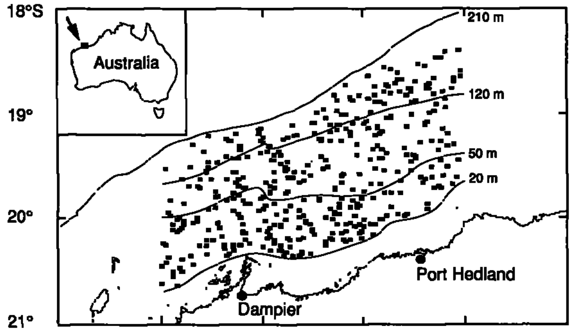

Figure 1
Distribution of 407 random stations sampled during seven cruises on the North West Shelf, September 1982–October 1983. The 20, 50, 120, and 200 m depth contours used to stratify sampling are shown.

Table 1
Stratified random trawl survey on the North West Shelf. The 13 strata sampled during each survey based on depth, geographical zones, and sediment type. Area (km^2) of each stratum and number of random trawls made in each stratum (in parenthesis) on each survey are shown.

	Sand	Shelly-sand	Silt	Sandy-silt
20–49 m				
116°E–117°30′E	3278(6)	3123(4)		
117°30′E–119°E	6309(6)	1732(4)		
50–119 m				
116°E–117°30′E	6123(7)	2381(4)		5505(5)
117°30′E–119°E	9679(7)	2381(4)		1423(5)
120–200 m				
116°E–117°30′E			4577(4)	
117°30′E–119°E		4886(4)	2412(2)	

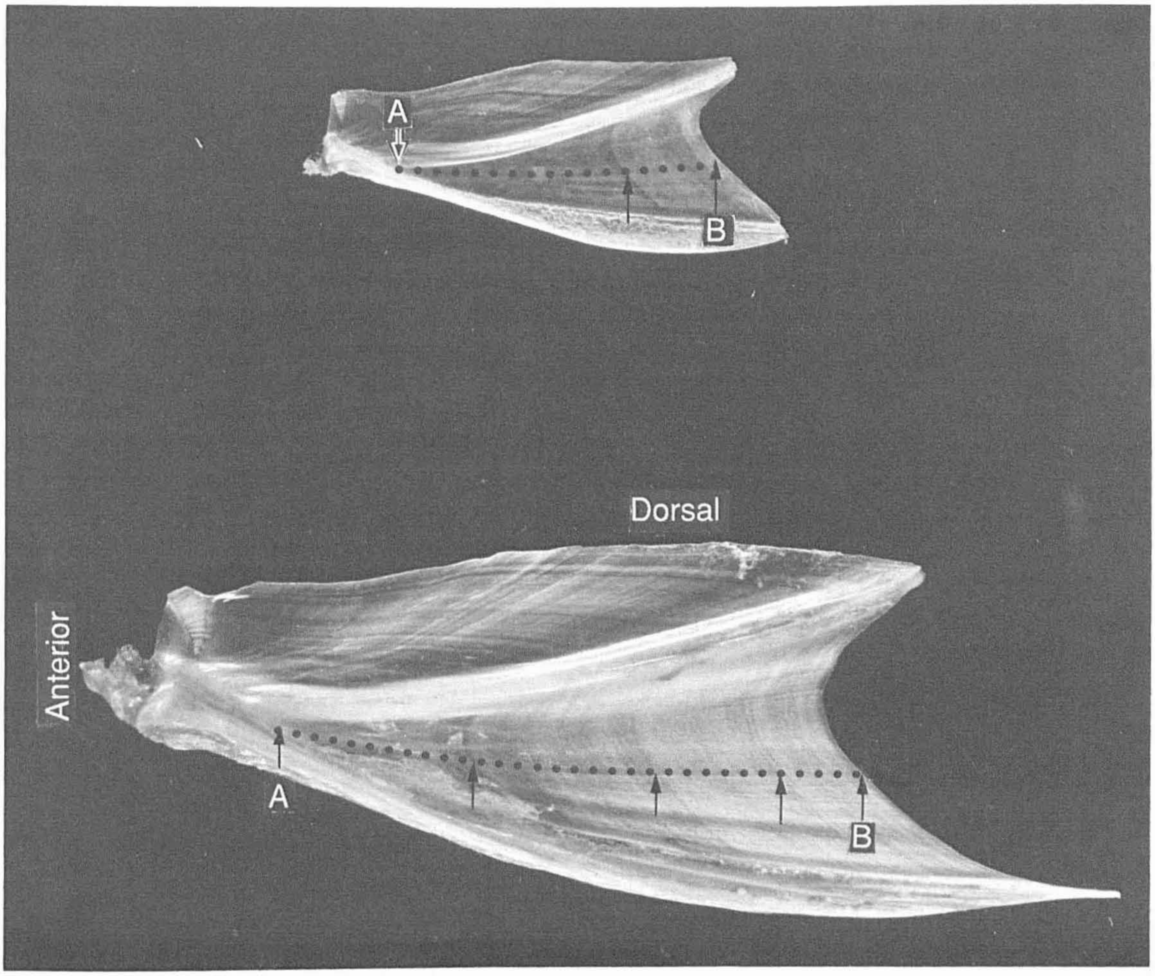

Figure 2
Urohyal bone of *Lutjanus vittus* with one check (129 mm FL) and three checks (242 mm FL). A–B taken as line of measurement.

Age determination

A preliminary examination of the sagittal otoliths, urohyals, scales, and vertebrae from 60 *L. vittus* indicated that checks were more clearly defined in otoliths and urohyals than in other hard parts. Due to their thickness and opacity, otoliths in older fish required sectioning because inner checks were obscured. As urohyals required little preparation before reading, they were chosen as the primary ageing structure; their only disadvantage being that checks in older fish were represented by a cluster of bands, so that determining the point at which the check was formed was somewhat subjective. Otoliths were referred to only when interpretation of urohyals was difficult. Urohyals were frozen and the flesh later removed by dipping in boiling water for 5 minutes, scrubbing, rinsing, and air drying before long-term storage.

Urohyals were examined dry on a black surface under incident light using a dissecting microscope. Checks under this lighting appeared as dark (hyaline) bands (Fig. 2). The distance from the origin to each check and the outer margin of the urohyal was measured along the axis indicated in Figure 2. The periodicity of check formation was determined from analysis of the temporal pattern of marginal increment development (distance from the outermost check to the outer margin of the urohyal) calculated as the index of completion (C) using the formula of Tanaka et al. (1981):

$$C = W_n / W_{n-1}, \qquad (1)$$

where W_n = marginal increment, and W_{n-1} = previous complete increment. Analysis of variance was used to test for significant differences in this index with time of year after arcsine square-root transformation.

Growth analysis

Two forms of length-at-age data were available: lengths were back-calculated to the last annulus (Whitney and Carlander 1956, Carlander 1981) to provide length-at-age data unconfounded by differences in the time of year of sampling. Absolute age-at-observed-length was also assigned, using an artificial January 1 birthdate.

The von Bertalanffy growth curve parameters were fitted to both sets of length-at-age data by direct nonlinear least-squares estimation. The null hypothesis that there was no difference between males and females in the three growth-curve parameters was tested using the extra sum-of-squares principle (Draper and Smith 1981, Ratkowsky 1983). The mean lengths at the last annulus of fish aged 1–6 years were also compared between sexes using analysis of variance.

Population structure and mortality

Sex-specific length-frequency distributions and sex-specific age-length keys were obtained from the subsamples from each random station, pooled for each sampling period. It was assumed that neither the sex ratio nor the sex-specific growth rate varied in some systematic way between the different strata. The log-likelihood ratio χ^2 was used to test for departures from a 1:1 sex ratio.

For each sampling period in 1983, the length frequency of the total population was determined using the following equation (K.J. Sainsbury, CSIRO Div. Fish., pers. commun. 1991):

$$F_i = \sum_{j=1}^{j=13} f_{ij} A_j / n_j, \qquad (2)$$

where F_i is the relative frequency of size-class i in the population, f_{ij} is the frequency of size-class i in stratum j, A_j is the area of stratum j, and n_j is the number of trawls in stratum j. These length frequencies were then broken down by sex, using sex-specific length-frequency distribution determined for each sampling period in 1983. The sex-specific age structure at each sampling period was then calculated using the sex-specific age-length keys determined for each sampling period (Ricker 1975, Kimura 1977). A catch curve for each sex was then constructed (Gulland 1969) and total instantaneous mortality estimated by least-squares linear regression of the descending right-hand of the catch curve. Equality of mortality rates between the sexes was determined by analysis of covariance.

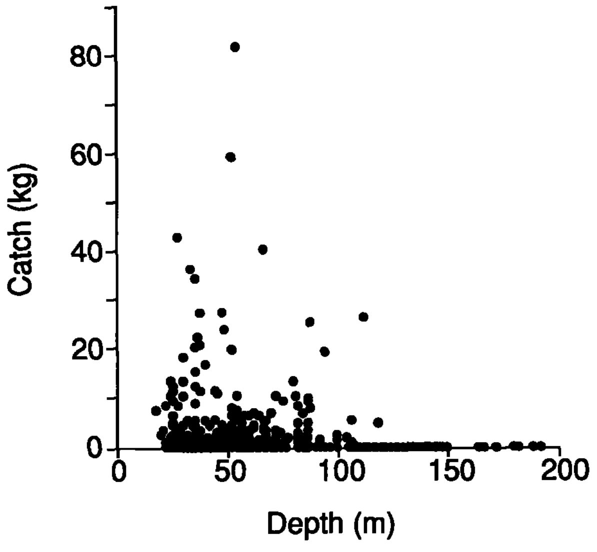

Figure 3
Catch per trawl of *Lutjanus vittus* by water depth on the North West Shelf of Australia, 1982–83.

Results

Depth distribution

Lutjanus vittus were caught in depths from 20 m (the shallowest depth sampled) to 120 m, with the largest catches being at 30–70 m (Fig. 3). There was a positive correlation between individual fish lengths and depth (r 0.337, t 24.7, df 4754, $P<0.001$). While almost the full size-range was encountered at most depths, there was a marked absence of fish <200 mm at depths >90 m (Fig. 4).

Length/weight relationship

In the regression of log weight/log length, the test for homogeneity of slopes between sexes was found to be not significant (ANCOVA, F 0.318, df 1, 2604, P 0.57) and, assuming a common slope, there was no significant difference in the intercepts for the two sexes (ANCOVA, F 1.76, df 1, 2605, P 0.19). Both sexes and juveniles whose sex could not be determined were then combined and a general relation between length (L in mm) and weight (W in g) for *L. vittus* was determined:

$$W = 9.99 \times 10^{-6} L^{3.086}$$

$$(F\ 367248,\ \text{df}\ 1,\ 2797,\ P<0.001).$$

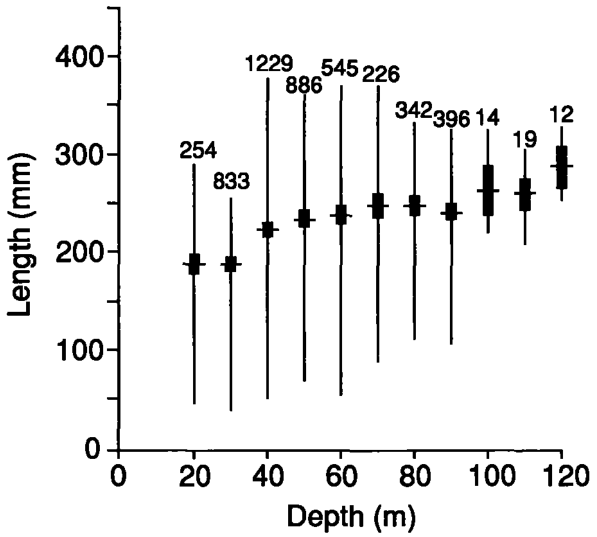

Figure 4
Mean length, 95% confidence limits (vertical bars), length range, and sample size of *Lutjanus vittus* by 10 m depth intervals.

Annulus formation

Evidence that checks are formed annually was obtained by examining the index of completion at about 2-month intervals throughout one season. The index of completion is a measure of the amount of bone growth since the last check was formed, expressed as a proportion of the previous growth increment. The indices of completion for fish aged 1–6 years were combined after each age-group was observed to follow the same seasonal changes in the index (Fig. 5). There were significant ($P<0.001$) differences in this index with time of year for urohyals having one, two, three, four, five and six checks (ANOVA, *F* 31.4, df 4, 172; *F* 80.1, df 6, 246; *F* 100.7, df 6, 263; *F* 40.0, df 6, 141; *F* 15.5, df 6, 69; *F* 88.8, df 5, 233, respectively). While there was considerable variation in this index at any one sampling period, there was a steady increase in the mean index from October to August, followed by a marked drop between August and October. It appears that checks are laid down some time between August and October.

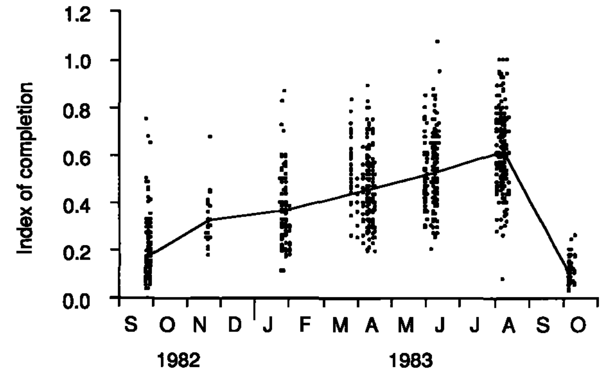

Figure 5
Seasonal change in the index of completion (amount of bone growth since the last check was formed) in *Lutjanus vittus* urohyals with 1–6 checks. Individual indices are plotted against day of sampling, and the line links the mean index for each sampling period.

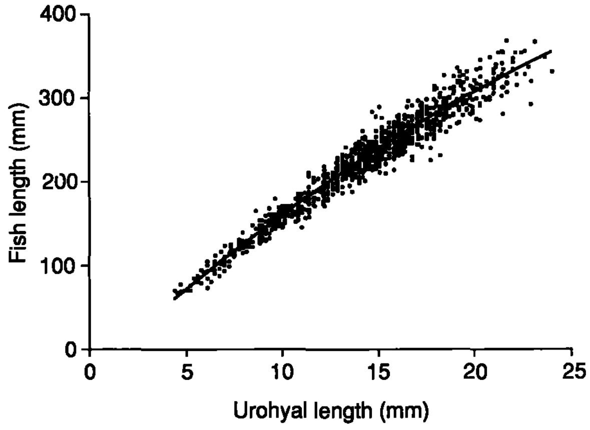

Figure 6
Curvilinear relationship between urohyal length and fish length in *Lutjanus vittus*.

Back-calculation

Lengths were back-calculated to the last annulus, using a proportional method based on the regression of fish length on urohyal length—the body proportional hypothesis (BPH) of Francis (1990). A quadratic equation best described the relationship between body length (L in mm) and urohyal length (U in mm) (Fig. 6):

$$L = -25.48 + 20.485U - 0.193U^2 \quad (r^2\ 0.95,\ \mathrm{df}\ 1102).$$

The mean absolute difference between using BPH and SPH (regression of fish length on urohyal length) was 1.6 mm; BPH back-calculated smaller lengths in fish <150 mm and larger lengths in fish >200 mm.

Growth

Von Bertalanffy growth curves were fitted to length-at-age data for each sex separately. Fish whose sex

Table 2

Mean lengths back-calculated to the last annulus, 95% confidence limits, and sample number (n) at each age (years) for male and female *Lutjanus vittus*.

Age (yr)	Mean length (mm)	95% CL	n
Males			
1	90	87–93	92
2	164	160–167	104
3	214	210–217	122
4	261	256–266	66
5	295	288–302	52
6	313	304–322	22
7	338	330–347	14
Females			
1	89	87–92	92
2	167	163–170	148
3	216	214–219	159
4	251	247–253	115
5	276	271–282	45
6	291	284–298	17

could not be identified (104 juveniles) presented a problem, because excluding them created a bias since fish that could be sexed in age-class 1 (40 males and 40 females) were larger animals. There were significant differences ($P<0.001$) in back-calculated and observed lengths between age-class 1 males, females, and juveniles (one-way ANOVA, F 50.7, df 2, 181; F 89.0, df 2, 181, respectively). Multiple comparison by the Tukey test indicated that age-class 1 fish that could be sexed were significantly larger than juveniles by about 17 mm for back-calculated lengths and 33 mm for observed lengths. To eliminate this bias, juveniles were ranked by size. The smallest was randomly assigned a sex, and then each juvenile in order was assigned to alternate sexes. The mean lengths back-calculated to the last annulus at each age for male and female (including assigned sexes in age-class 1) are presented in Table 2 and Figure 7.

Back-calculated length-at-age data minimize the effects of seasonal growth but do not completely eliminate it, because the time of check formation ranges over several months (Fig. 5). Assigning an absolute age using an arbitrary birthdate will only compensate for growth differences between fishes caught at different times of the year when there is little seasonal variation in growth rate. However, assigning absolute ages does enable age-class 0 data to be used in determining growth curves (Fig. 8). While back-calculated lengths cannot use age-class 0 data, they do enable a more realistic time-scale parameter (t_0) to be estimated.

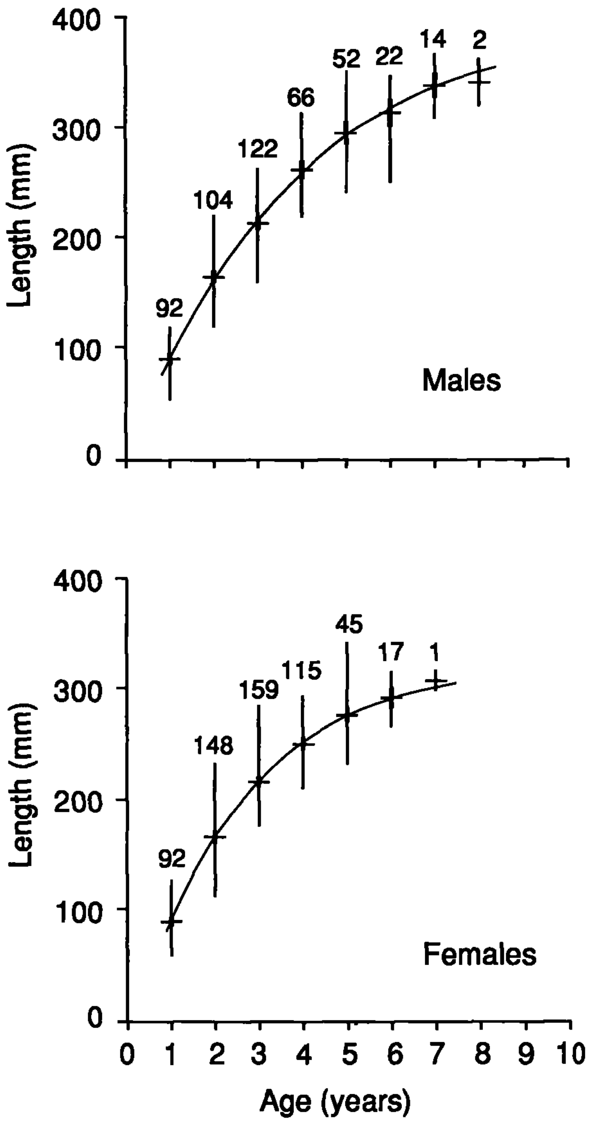

Figure 7

Growth of male and female *Lutjanus vittus*. Mean back-calculated lengths to the last annulus, 95% confidence limits (vertical bars), range, and sample size have been plotted. Von Bertalanffy growth curves were fitted to individual observations.

The least-squares estimates of the von Bertalanffy growth curve parameters are quite different between the sexes for both forms of length-at-age data (Table 3). Independent of any assumed growth curve, there were significant differences in mean back-calculated lengths between sexes for age-classes 4–6 years (ANOVA, F 42.1, df 1, 311, $P<0.001$) but age-classes 1–3 were not significantly different (F 0.32, df 1, 605, P 0.569). Only fish whose sex was determined

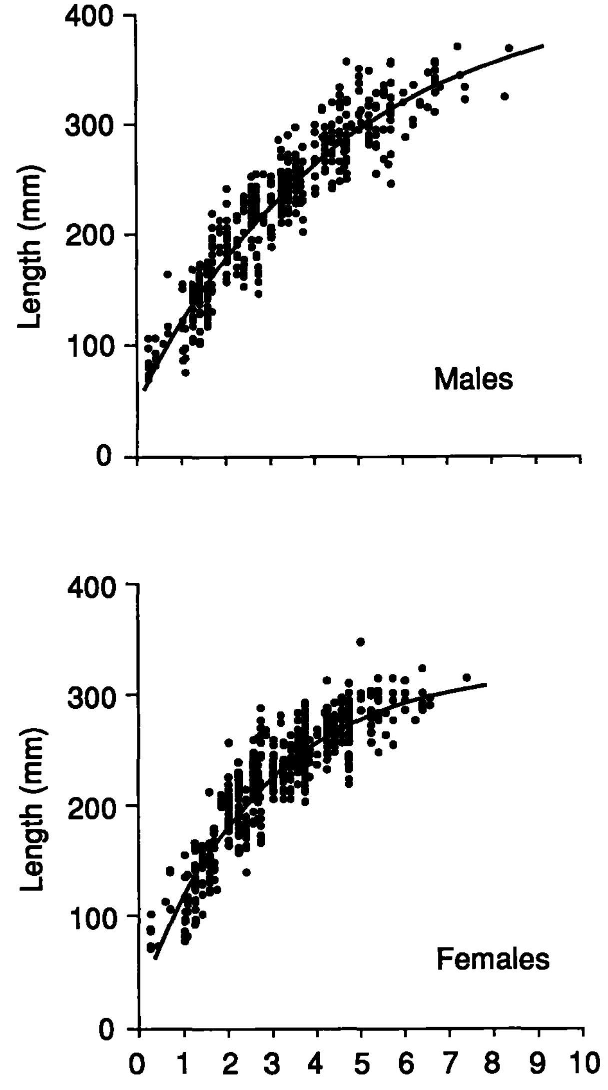

Figure 8
Growth of male and female *Lutjanus vittus* assigned an absolute age assuming a 1 January birthdate.

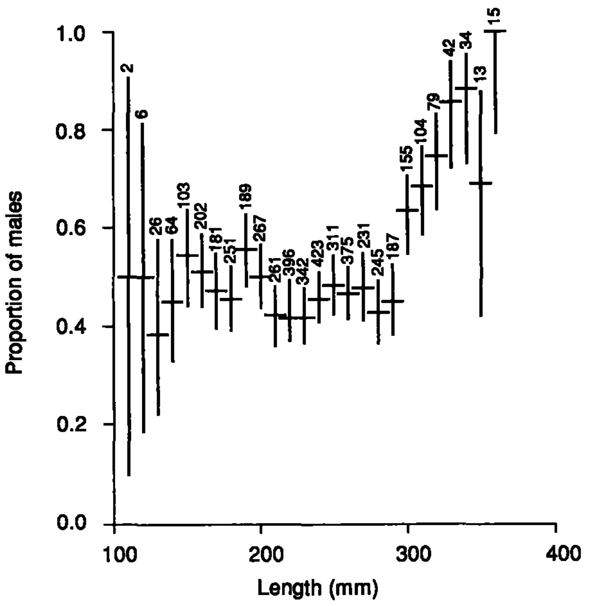

Figure 9
Proportion of males by 10mm length-class. Means, 95% binomial confidence limits (vertical lines), and sample size are plotted.

were used in this analysis. Both males and females grow at the same rate for the first three years, after which females grow at a markedly slower rate than males.

Sex ratio

There was a marked departure from a 1:1 sex ratio (Fig. 9; likelihood ratio χ^2 152.1, df 29, $P<0.001$) which can be attributed to different growth rates between the sexes. Below 300mm, sex ratios did not differ from 1:1 (likelihood ratio χ^2 23.3, df 18, P 0.18) but in all larger size groups there was a predominance of males.

Table 3
Estimated parameters (± SE) of the von Bertalanffy growth curve for *Lutjanus vittus*.

	Growth curve parameters				*F* test of parameter estimates		
	df	L_∞ (mm)	K	t_0 (yr)	*F*	df	*P*
Back-calculated length-at-age							
Males	473	403(10.4)	0.26(0.01)	0.02(0.05)	21.7	3, 1045	<0.001
Females	578	323(6.6)	0.39(0.02)	0.17(0.04)			
Length at absolute age							
Males	486	422(15.9)	0.22(0.02)	−0.56(0.09)	19.9	3, 1066	<0.001
Females	586	325(7.7)	0.37(0.03)	−0.23(0.08)			

Length-frequency distributions

Length-frequency distributions of the population were determined separately for males and females (Fig. 10). Each length-class was separated into age-classes based on the urohyal data. There was a jump in age-class between samples taken in August and October because a new check was formed in the intervening period. While

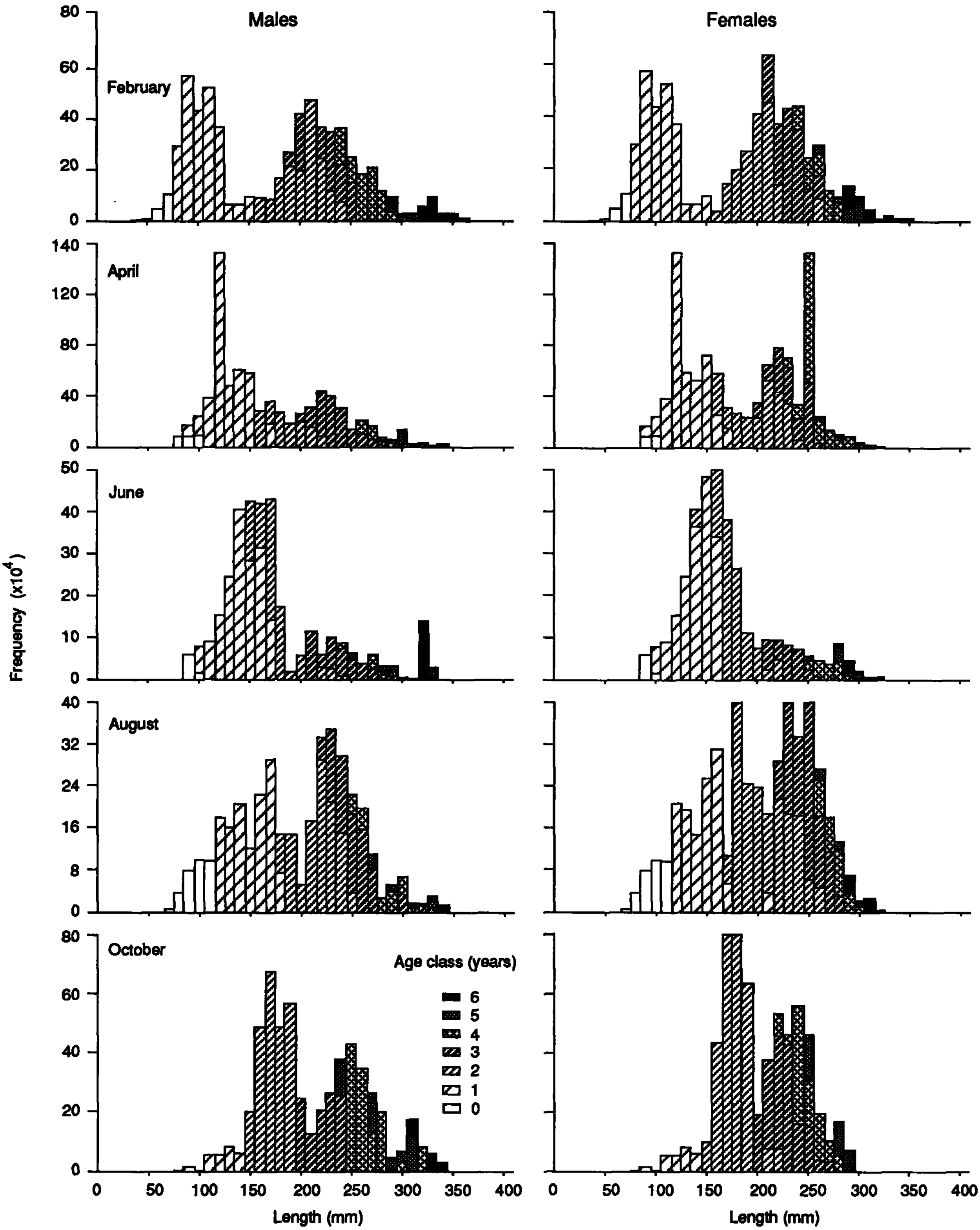

Figure 10

Total population length-frequency distribution of male and female *Lutjanus vittus* at each sampling period in 1983. Hatching within each distribution indicates the age-class structure determined from urohyal ageing. All age-groups increment by 1 year, August–September, due to check formation.

separation of sexes would have reduced variance in the length-frequency distribution of the older age-classes due to growth differences between sexes, there was still considerable size overlap of age-classes and difficulty in identifying modes after age 2 (Fig. 10). There was a clear progression in the length of age-classes 1 and 2 through the year, although age-class-2 fish of both sexes were somewhat larger than expected in February based on the progression in length of this age-class in subsequent months.

Mortality

The relative abundance of each age-class by sex was determined for the five periods sampled in 1983 (Fig. 11). A line was fitted by least squares to the descending limb of the catch curve. Fish not considered to be fully recruited to the sampling gear (circled points) were excluded. There was no significant difference in the slopes of the lines for males and females (ANCOVA, *F* 0.85, df 1, 47, *P* 0.36) and no significant sex effect (ANCOVA, *F* 1.23, df 1, 47, *P* 0.27) so a catch curve was fitted to the combined data. The instantaneous rate of annual mortality (Z) for males and females was estimated to be 0.98 (SE 0.076).

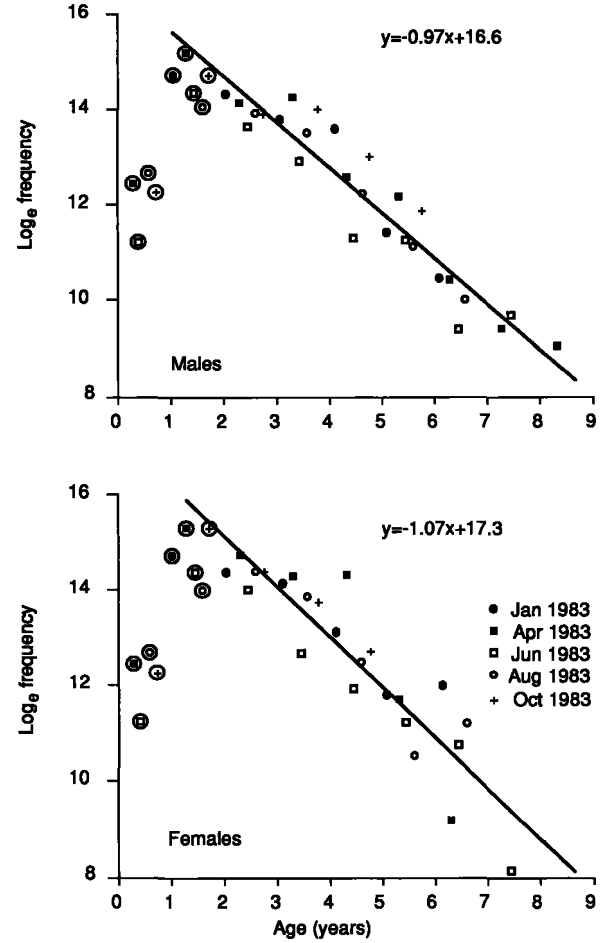

Figure 11

$\mathrm{Log_e}$ frequency against absolute age for male and female *Lutjanus vittus*. Data for fish <2 years old (circled) were excluded from the regressions, as they were incompletely recruited age-classes.

Discussion

Lutjanus vittus was caught at depths of 20 m (the shallowest depth sampled) to 120 m, with larger fish tending to inhabit deeper waters. This tendency has also been observed in other shallow-water lutjanids such as *L. aya* (Moseley 1966), *L. griseus* (Starck 1971), and *L. bohar* (Wright et al. 1986).

Most ageing studies on lutjanids have relied on otoliths as the principal structure (see review by Manooch 1987).However, a few authors (i.e., Reshetnikov and Claro 1976, Pozo and Espinosa 1982, Claro 1983, Palazón and González 1986) have used urohyals. Reshetnikov and Claro (1976) had difficulty determining the boundaries of the annual increment after the second or third annulus in urohyals because the annuli were made up of multiple bands. It was our experience that, despite this problem, increments were still easier to measure on urohyals than on whole otoliths, and preparation was far less time-consuming.

Our preliminary investigation indicated that the same number of checks were formed on a variety of hard structures, including urohyals. Data on marginal increments in urohyals showed a seasonal pattern with one check being formed each year, consistent with most other studies on lutjanids in tropical waters. However, studies on two lutjanid species from Cuban shelf waters have suggested that checks are formed twice a year (Espinosa and Pozo 1982, Pozo and Espinosa 1982).

The growth of male and female *L. vittus* was significantly different after 3 years of age, with females growing markedly slower than males. There are few documented cases of growth rates differing between sexes in lutjanids. However, female *L. vittus* in New Caledonia were found to grow at a slower rate, and slight growth differences were found in *L. amabilis* in New Caledonia (Loubens 1980) and *L. synagris* in Trinidad (Manickchand-Dass 1987). All mature females observed were 3 years of age or older (unpubl. data), and it seems likely that females grow more slowly than males at this stage because they expend proportionally more energy on gamete production than do males. Stunting in females from a sexually precocious population of *Lates calcarifer* was also attributed to channeling energy into gonadal growth at the expense of somatic growth at a relatively early age (Davis 1984).

Length-frequency distributions did not show the modal structure one would expect knowing the age structure of the population. The length-frequencies showed three modes, whereas direct ageing suggested there should be at least six. Length-based methods of ageing work best with fish that spawn over a short period of time, have short life spans, and are fast growing; characteristics not typical of lutjanids (Manooch 1987).

A preponderance of females at larger sizes has been reported in studies of other lutjanids, e.g., *L. synagris* (Rodriguez Pino 1962, Erhardt 1977), *Etelis carbunculus* (Everson 1984), *E. coruscans, Aprion viriscens* (Everson et al. 1989), and *Rhomboplites aurorubens* (Grimes and Huntsman 1980). The latter authors attributed the preponderance to differential mortality and longevity. *L. vittus* goes against this trend: males predominate the larger size-classes, as is the case for *Lutjanus amabilis* (Loubens 1980) and *Lutjanus buccanella* (Thompson and Munro 1983). The preponderance of males at larger sizes appears to be due largely to a reduction in growth rates of mature females.

No significant differences were found in the instantaneous rate of annual mortality (Z) between male and female *L. vittus*. One of the assumptions of estimating mortality using the catch curve method of Gulland (1969) is that the mortality rate is constant for all years used in the estimation. This may not be the case for female *L. vittus* after 6 years of age. However, the data points in the oldest age-groups are based on smaller sample sizes, so the mortality curve at this stage should be interpreted with caution. Using the relationship between natural mortality (M) and the growth coefficient (K) for snappers and groupers determined by Ralston (1987) from published data provides us with estimates for M of 0.59 for males and 0.92 for females. The value for males seems reasonable, but that for females is unlikely if total mortality is about 0.98. Clearly, regression methods to produce estimates of M such as those used by Pauly (1980) and Ralston (1987) should be applied with caution.

Acknowledgments

This paper is dedicated to the memory of Mr. Otto Augustine, a technician with the CSIRO Division of Fisheries. He was responsible for the ageing of many fish species in the Division's programs from the late sixties up until his death in 1990. He determined the age and marginal increment data used in this paper. We wish to thank W. Thomas for laboratory assistance and all people who assisted in the fieldwork on the Northwest Shelf Program. We are grateful to K.J. Sainsbury for providing length-frequency and catch data from his research program, and K. Haskard for statistical advice. S. Blaber and J.S. Gunn reviewed the manuscript.

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