Maturation, reproductive seasonality, fecundity, and spawning frequency in *Lutjanus vittus* (Quoy and Gaimard) from the North West Shelf of Australia

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Abstract.—The reproductive biology of *Lutjanus vittus*, an important component of the trawl-fishery catch from the North West Shelf of Australia, was determined from random, stratified trawls made every 2 mo during August 1982–October 1983. The smallest mature female was 142 mmFL; half of the females at 154 mm (estimated 1+yr of age) were mature. The major spawning season was from September to April, although some spawning occurred in other months. A semilunar pattern of spawning activity was observed, with peaks in the proportion of spawning females ~3 d after the new moon and 6 d after the full moon. Individuals spawn about 22 times each lunar month. The diel changes in proportion of fish with ripe oocytes and early- and late-stage postovulatory follicles, together with data on maximum oocyte diameter, suggest that most individuals spawn between 11:00 and 15:00 h on peak spawning days. The relationship between batch fecundity (F) and fish fork length (L in mm) was exponential ($F=3.656\times10^{-6}\ L^{4.093}$) and with fish weight (W, g) was linear ($F=124.2\times W-3081$). Unlike gonad weight, batch fecundity did not decline as the spawning season progressed.

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Lutjanids are of great importance in fisheries throughout the tropics and subtropics, and *Lutjanus vittus* distributed throughout the Indo-West Pacific is a highly valued component of the multispecies trawl fishery of the North West Shelf of Australia (NW Shelf), comprising ~4% of the total catch of ~165,000 t between 1972 and 1980 (Jernakoff & Sainsbury 1990). Its early life history has been studied in Japan (Mori 1984); its biology, in New Caledonia (Loubens 1980a,b). Information on growth and mortality of this species on the NW Shelf has recently been published (Davis & West 1992). However, there is no published information on the reproductive biology of *L. vittus* that would pertain to the management of this fishery on the NW Shelf.

Some information on the reproductive biology of over 40 species of lutjanids is available (see review by Grimes 1987). Many studies have indicated that lutjanids are multiple spawners, based on the evidence of multimodal size-frequency distributions of oocytes, but techniques such as the hydrated oocyte and postovulatory follicle methods (Hunter & Goldberg 1980, Hunter & Macewicz 1980), for measuring spawning frequency in marine fishes, have not been applied to lutjanids (Everson et al. 1989). In this paper we present data on oocyte development, size-at-maturity of females, and batch fecundity in *L. vittus* from the NW Shelf. We also demonstrate both diel and semilunar spawning periodicity through an analysis of the temporal distribution of hydrated oocytes and early- and late-stage postovulatory follicles, and provide estimates of spawning frequency and annual fecundity.

Materials and methods

Specimens were obtained from the CSIRO North West Shelf program between August 1982 and October 1983 (Young & Sainsbury 1985). Details of the two-monthly random stratified trawl surveys of shelf waters within latitudes 116°E and 119°E are given in Davis & West (1992). A subsample of 20–40 *Lutjanus vittus*, which approximately represented the size-frequency composition of the total catch (Kimura 1977), was selected from each random trawl. Fork length was measured to the nearest 1 mm and total weight to the nearest 1 g. Fish were sexed and up to 200 ovaries per cruise were fixed in 10% formalin in seawater for histological and whole oocyte examination. Additional biological samples were collected from nonrandom trawls to investigate lunar and diel periodicity in spawn-

ing. Samples were also obtained at 4 h intervals during 6–9 October 1988 to further investigate diel periodicity of spawning.

In the laboratory, ovaries were blotted dry and then weighed to the nearest 0.1 g. Whole oocytes were obtained by cutting a complete cross-section 1–2 mm thick from the middle of the ovary, and teasing the oocytes apart with needles. Oocytes were examined in water under a stereomicroscope using transmitted light and brightfield illumination. We measured maximum oocyte diameter (MOD) as the diameter of the largest oocyte (to the nearest 20 μm) in the sample. Because oocytes were basically spherical, the orientation of oocytes with respect to the line of measurement was random.

The size-frequency distribution of oocytes within ovaries at different stages of maturity was determined. Sections 1–2 mm thick were cut from the middle of one ovary, the oocytes teased apart with needles, and further separated by immersion in an ultrasonic bath for ~5 min. Oocytes were pipetted into grooves on a perspex microscope slide and examined on a moving stage attachment on a stereomicroscope at 50×, using transmitted light. Orientation was random. As well as measuring each oocyte, we also noted its appearance so that the stage of development could be assessed.

We used whole-oocyte staging to assess ovarian maturity (Hilge 1977, Forberg 1983, West 1990). Our three-stage scheme (Table 1) differed from Hilge's (1977) in that we distinguished late-migratory nucleus oocytes (Fig. 1b) from yolked oocytes (Fig. 1a) by the presence of some translucence at the periphery of the vitelline area (West 1990). Ovaries with late-migratory nucleus oocytes or hydrated oocytes were considered ripe (Fig. 1c).

The relative gonadal index (RGI) was used to quantify the reproductive cycle (Erickson et al. 1985). This index is independent of body size and is based on the model, $W=\alpha_i S^{\beta i}$, where W is gonad weight (g), S is ovary-free body weight (kg), and α_i and β_i are parameters estimated for maturity stage i. As β_i did not differ significantly between the three maturity stages (ANCOVA, $F=1.304$, df 2,1046, $p=0.27$), a common β was used.

To study short-term spawning rhythms and to verify whole-oocyte staging, we histologically examined 477 ovaries from one cruise during the height of the spawning season (November–December 1982). Histological sections were 10 μm thick and stained with haematoxylin and eosin. The sequence of oocyte maturation is similar in most teleost species (Wallace & Selman 1981). We used the histological criteria of Yamamoto (1956) for assigning oocytes to developmental stages.

The presence of postovulatory follicles was noted in the histological material. These follicles are readily

Table 1

Whole-oocyte staging scheme in *Lutjanus vittus* based on appearance of the most advanced oocytes (modified from Hilge 1977) and corresponding histological stages (Yamamoto 1956) used to describe ovarian maturity.

Whole-oocyte stage	Histological stage
1 Unyolked	
Transparent with visible nucleus, becoming granular and translucent with increasing size.	**Perinucleolus stage** Cytoplasm purple, outer cell membrane not differentiated at 400×.
Granular, translucent with brownish tinge, becoming darker with increasing size, but not opaque.	**Yolk-vesicle stage** Pale vacuoles (yolk vesicles) and a thin but distinct pink-staining zona radiata both present.
2 Yolked	
Completely opaque except for perivitelline border.	**Yolk-granule stage** Yolk granules appear as pink spheres. Fat vesicles coalesce to form larger vesicles around the central nucleus at the end of this stage.
	Early-migratory nucleus stage Nucleus moves out from center of the cell, being replaced by one or two fat vesicles.
3 Ripe	
Distinguished from Yolked stage when parts of the yolk become translucent.	**Late-migratory nucleus stage** Nucleus moves to the periphery of the cell and some of the yolk granules coalesce.
Oocyte is translucent except for the oil droplet.	**Hydrated-oocyte stage** Yolk granules coalesce to form a uniform pink-staining mass.

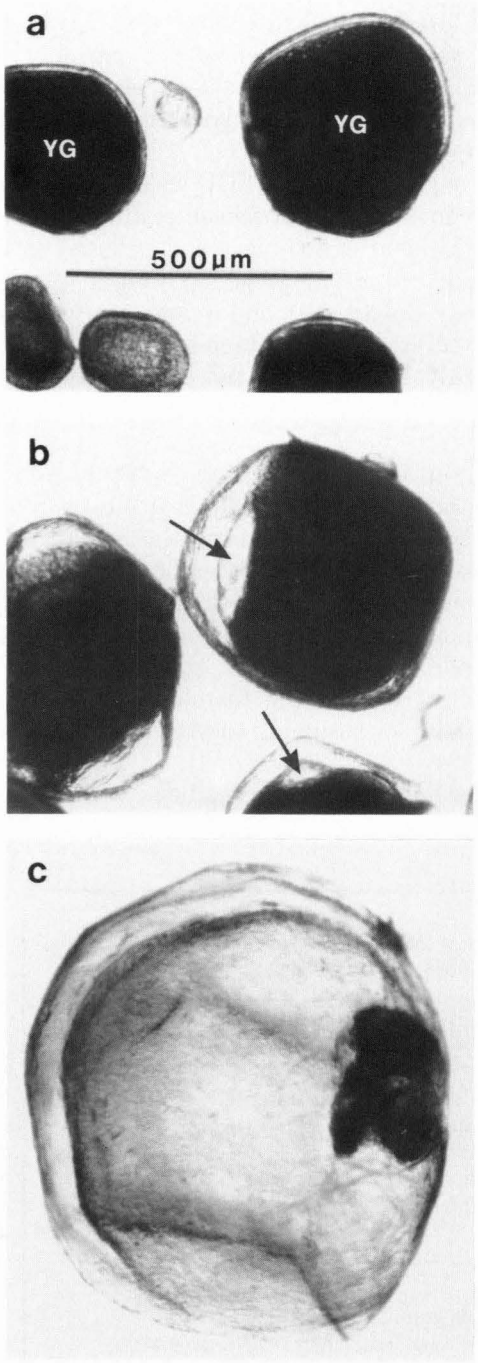

Figure 1
Photomicrographs of whole oocytes of *Lutjanus vittus* representing **(a)** yolk granule (YG) stage, in which the oocyte is completely opaque except for the translucent perivitelline border; **(b)** late-migratory nucleus stage, in which parts of the peripheral yolk have coalesced and become translucent (arrowed); and **(c)** ripe-oocyte stage, in which whole oocyte is translucent, except for the oil droplet. Scale bars 500µm.

identifiable within 12 h after spawning because the folds of the follicle layer are still discrete (Hunter & Goldberg 1980), but they become progressively more compact until they appear as a solid mass of cells. We recorded an early stage where the lumen was open and the wall of the follicle clearly visible (Fig. 2a) and a late stage where the follicle had collapsed and the follicle layer could not be traced around its periphery (Fig. 2b).

Batch fecundity was determined using the gravimetric method (Hunter et al. 1985) to count numbers of hydrated but unovulated oocytes in weighed subsamples of formalin-fixed ovaries. Each subsample consisted of a wedge of tissue extending from the periphery to the lumen of the ovary. In order to estimate the energetic costs of spawning, the dry weight of hydrated oocytes was determined in nine fish. About 100 oocytes were removed from each formalin-fixed ovary. Oocytes

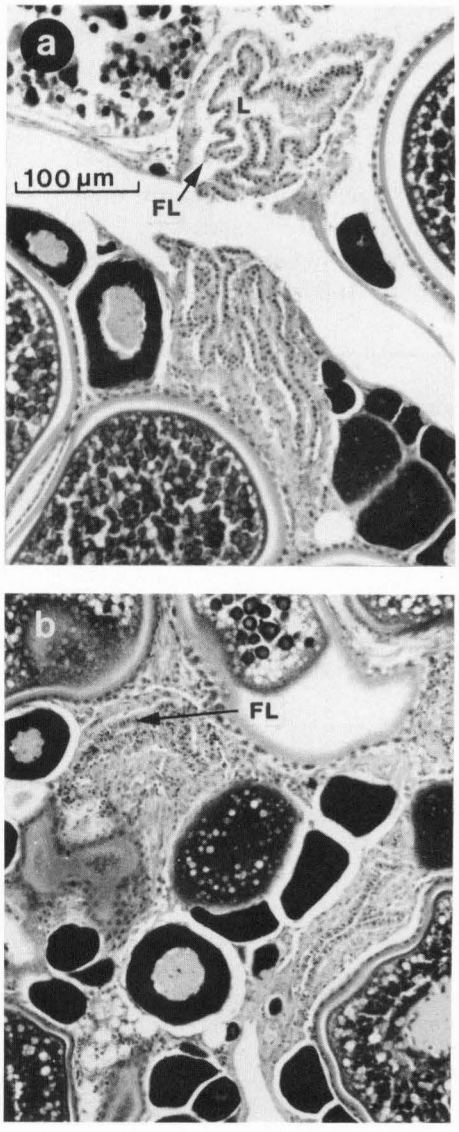

Figure 2
Photomicrographs of transverse section of *Lutjanus vittus* ovary stained with haematoxylin and eosin, showing **(a)** early-stage postovulatory follicles, in which the lumen (L) is open and the folds of the follicle layer (FL) are discrete, and **(b)** late-stage postovulatory follicles, in which the follicle has collapsed and the follicle layer is no longer discrete. FL = follicle layer; L = lumen. Scale bars 100 µm.

were washed in freshwater, counted, dried for at least 24 h at 60°C, and weighed to the nearest 0.1 mg.

Size-at-maturity ($L_{0.50}$) was defined as the smallest length at which half of the fish had yolked or ripe-stage ovaries. Weighted least-squares nonlinear regression was used to select the model (Gompertz curve) that best described the relationship between proportion of mature fish and fish length. The simplest model was chosen in which higher parameter models did not significantly improve the fit using the *F*-ratio statistic (Schnute 1981).

RGI's were log-transformed to stabilize variances, and a 2×2 factorial ANOVA was used to test for differences in RGI's between samples collected in August and October and between consecutive years. Differences in RGI over the four periods sampled during the main spawning season (September 1982–April 1983) were tested using ANOVA, and the period effect was partitioned into a linear component and deviations from a linear component to test for trends.

The log-likelihood ratio χ^2 was used to test for independence in contingency-table data (frequency of fish with and without postovulatory follicles by time of day, month, etc.). Cells with expected frequencies <5 were excluded from statistical tests. Repeated-measures ANOVA was used to test for differences in the numbers of eggs/mg tissue taken from the inner and outer walls, and from anterior, middle, and posterior parts of the ovary of five fish. The relationship between log fecundity and log length at different times of the spawning season was examined using ANCOVA.

Results

Maturation of ovaries

Size-frequency and stage of whole oocytes in ovaries representing the developmental sequence of maturation (Fig. 3) indicated that the size of oocytes is correlated with their stage of development but there is considerable overlap between stages. The pattern of oocyte development is asynchronous. Apart from the inference that *L. vittus* is a multiple spawner, the number of spawnings cannot be inferred from modes in the size-frequency distribution (Hunter & Goldberg 1980).

Size-at-maturity

Ovaries were considered mature if their most advanced oocytes were yolked or ripe, as judged by the appearance of the whole oocyte. To avoid including mature fish that had regressed to an unyolked stage towards the end of the spawning season, only data taken between September and February were used. The smallest ripe female observed was 142 mm long (Fig. 4). All fish >220 mm were mature (Fig. 5). The Gompertz curve was fit to the proportion of mature females by 10 mm length groupings:

$$Y(t) = y_\infty e^{-e^{-g(t-t_0)}}, \quad (1)$$

where $Y(t)$ = proportion mature at length t, and y_∞, g, and t_0 are parameters. This provided the best fit with the least number of parameters. The length at which 50% of females were mature ($L_{0.50}$) was calculated to be 154 mm. $L_{0.50}$ is reached at age-1 (Davis & West 1992), and all females at age-3 and older were mature (Fig. 5).

Spawning season

Only data on fish >200 mm were used to describe seasonal changes. The main spawning season appears to be September–April (Fig. 6). The presence of fish with hydrating oocytes throughout the year indicates the spawning season is protracted, although only four fish with hydrated oocytes were collected in June and August 1983. Some mature fish had only unyolked oocytes in their ovaries during April–August (Fig. 6).

The mean relative gonadal index (RGI) peaked in September–October and then declined gradually, reaching its lowest value in June (Fig. 6). There was a marked and significant increase in mean RGI during August–October (2×2 factorial ANOVA, month effect, F=309, df 1,339, p<0.001), with the same increase in both years (interaction effect not significant: F=2.4, p>0.1), and there was a weak but significant difference between years (F=4.3, p<0.05). There were significant differences in RGI between the four periods sampled during the main spawning season, September 1982–April 1983 (ANOVA, F=50.5, df 3,706, p<0.001), predominantly due to a linear component (F=130.1, df 1,706, p<0.001) caused by a decline in RGI over this period (slope –0.236, SE 0.021). On the other hand, there was no significant difference in proportion of ripe fish throughout this period (likelihood ratio x^2 = 6.3, df 3, p=0.10), nor any indication of a decline in the proportion. This suggests that spawning activity remained at about the same level during the main spawning period but that gonads of individual fish were depleted by successive spawnings.

Lunar periodicity in spawning activity

Ovaries of mature fish (n=374) sampled in November–December 1982 were examined histologically for evidence of spawning activity. Data were grouped into 1 d periods according to moon age. Two measures of spawning were used: proportion of fish with postovulatory

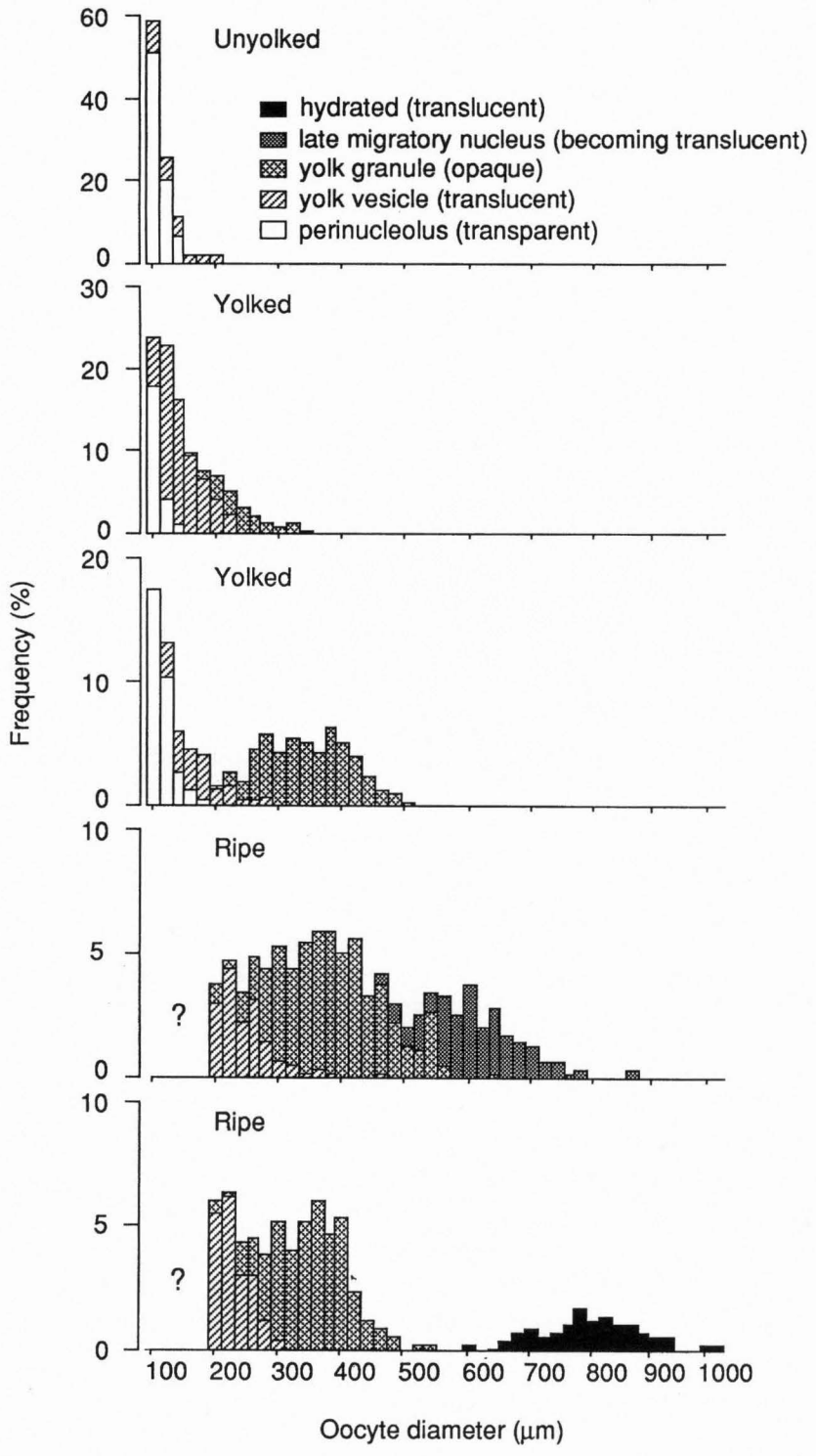

Figure 3

Oocyte size-frequency distribution and oocyte stage, by 20 μm intervals, in *Lutjanus vittus* ovaries representing the developmental sequence of maturation (see Table 1 for details). An ovary classified as Ripe indicates that it contained late-migratory nucleus-stage oocytes or ripe oocytes. Only oocytes >200 μm diameter were measured in Ripe stage-5 ovaries, whereas in other ovaries all oocytes >100 μm were measured.

follicles, and proportion of fish with late-migratory nucleus or hydrated-oocyte stages. The former showed a clear cyclical pattern with two peaks of spawning activity during the month of sampling (Fig. 7). Various sinusoidal curves were fit to the proportion of mature fish with postovulatory follicles sampled each day. The following model, which has a period of 29 d and allows one or two peaks of possibly unequal heights per period, was chosen:

$$y = A+B \sin(x) + C \cos(x) + D \sin(2x) + E \cos(2x), \quad (2)$$

where $t=t/29 \times 2\pi$, and t = moon age (d). A regression weighted by the number (n) in each sample was fit to arcsine (angular) root-transformed data. Proportions of 1 were replaced by $n-1/4$ divided by n. The fitted model accounted for 85.9% of variance in the data. The smaller peak occurred 3 d after the new moon, and the larger peak 6 d after the full moon.

No simple pattern of spawning was apparent from the proportion of fish with late migratory nucleus or hydrated oocyte stages captured each day, presumably because such a pattern was confounded by the effects of time of day (see next section). As postovulatory follicles probably persist for a day, and maybe longer in other species (Hunter & Goldberg 1980, Hunter et al. 1986), their detection does not depend on the time of day of sampling.

Diel periodicity in spawning activity

The November–December 1982 samples were also examined for evidence of diel periodicity in spawning. Only mature fish

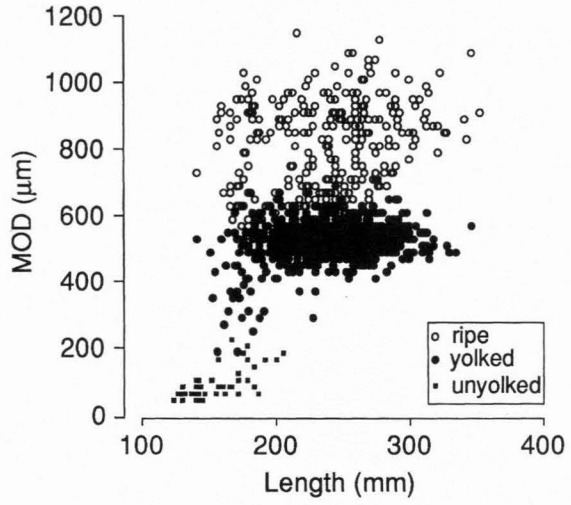

Figure 4

Diameter of the largest oocyte (MOD) of *Lutjanus vittus* by fish length. Ovaries classified as Yolked and Ripe indicate that fish are mature. Data were collected at height of the spawning season (October–February).

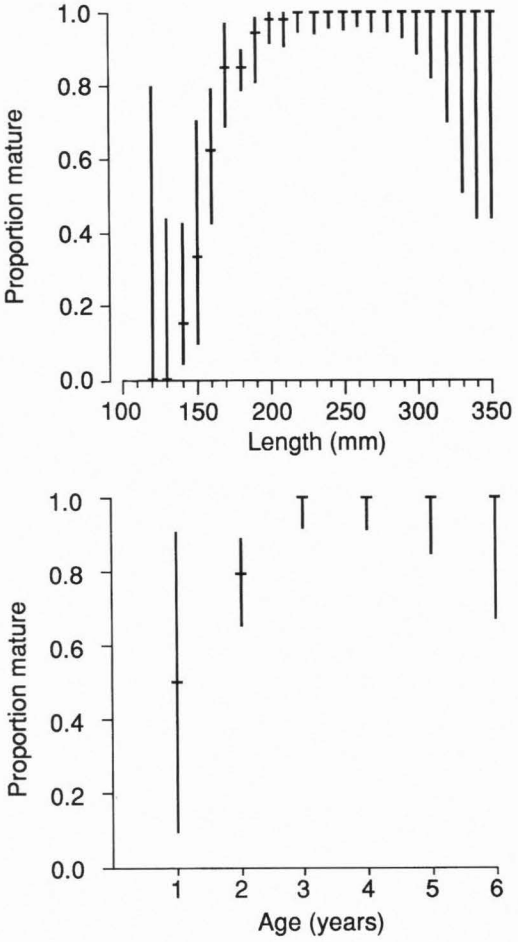

Figure 5

Proportion of total female *Lutjanus vittus* that are mature by 10 mm length-classes and by age-class during the height of the spawning season. Shown are 95% binomial confidence limits. Age data from Davis & West (1992).

caught during days of major spawning activity (lunar days 2–10 and 18–29) were considered. Two measures that proved useful in detecting changes in spawning activity on temporal scales of less than a day were the proportion of mature fish with ripe-stage ovaries based on whole-oocyte staging, and maximum oocyte diameter (MOD).

A clear diel cycle of spawning was evident (Fig. 8). Proportions of ripe-stage fish in samples taken at different times throughout the day were significantly different (likelihood ratio x^2=69, df 7, p<0.001). Proportions of ripe fish were highest between 08:00 and 14:00 h, and no ripe fish were present by 16:00 h. The mixture of ripe and unripe ovaries between 11:00 and 15:00 h could indicate that spawning for that day had already begun and that some of the fish were spent or that only a portion of fish spawned each day. The temporal distribution of MOD showed a similar pattern. Fish about to spawn that day were clearly separable from other fish by MOD at 11:00 h. The MOD's of all but one fish sampled after 15:00 h were the same as nonspawning fish, suggesting that most spawning occurred between 11:00 and 15:00 h on these days, which more or less coincided with rising daytime tides.

Postovulatory follicle data from the same subset of fish also showed a diel pattern (Fig. 9, page 232). The proportion of fish with early- or late-stage postovulatory follicles differed significantly with time of sampling (early-stage likelihood ratio x^2=130, df 7, p<0.001; late-stage likelihood ratio x^2=131, df 7, p<0.001). Fish with early-stage postovulatory follicles were first detected at 12:00 h. By 17:00 h the proportion of fish with early-stage postovulatory follicles had reached its highest level (91%). Thereafter the proportion declined, until by 04:00 h none were present in fish sampled. Late-stage postovulatory follicles followed a similar temporal pattern, with a peak that lagged the early stage by 12–14h. The very few late-stage postovulatory follicles in samples at 17:00 h may have resulted from spawning early that day or late spawn-

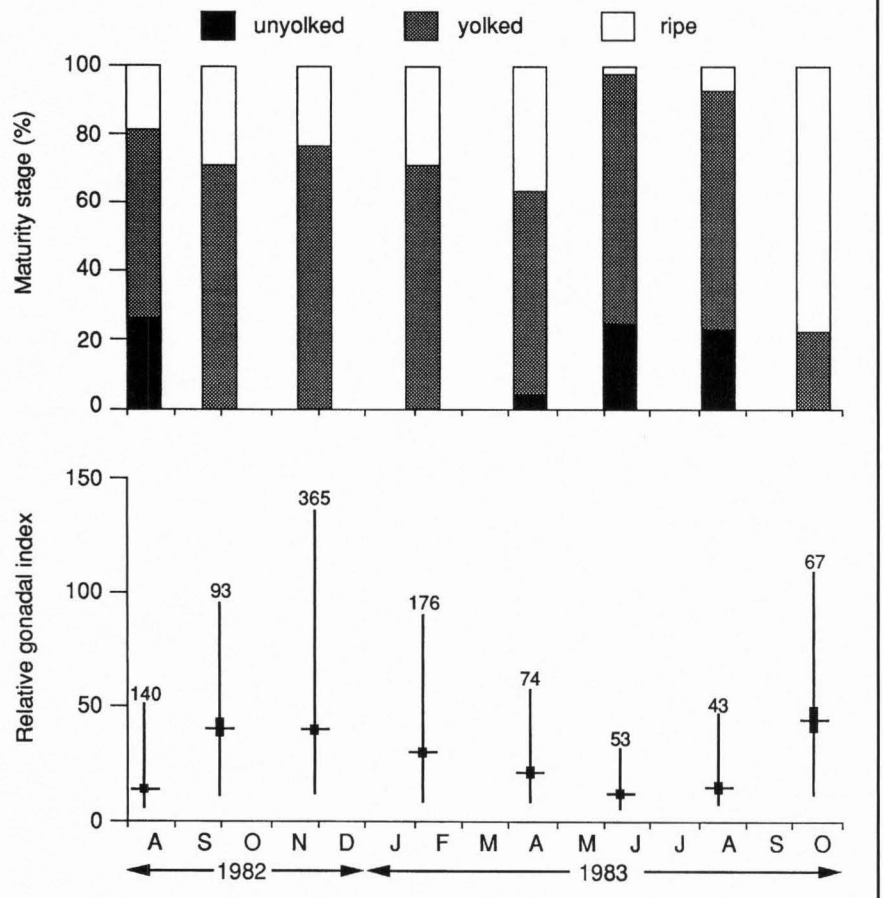

Figure 6

Mean relative gonadal index, 95% confidence limits and range, and proportion of female *Lutjanus vittus* at each maturity stage determined by whole-oocyte staging plotted against the mean date of each sampling period. Number in each sample is shown.

ing on the previous afternoon. In either case, the late stage appears to persist for about 24 h. Only 13% of fish examined from this subset did not have postovulatory follicles, and most of these (74%) were from fish sampled between 09:00 and 15:00 h. This would be consistent with the hypotheses that follicles persist for 24 h or less and that most fish spawn daily during the major periods of spawning activity.

The diel pattern of spawning indicated by data collected in November–December 1982 was supported by further sampling every 4 h over 6–9 October 1988. The proportions of ripe fish in samples taken at different times throughout the day were significantly different (likelihood ratio x^2=110, df 6, p<0.001). Ripe fish were found between 12:00 and 16:00 h (Fig. 10). The temporal distribution of MOD followed the same pattern observed in November–December 1982.

Spawning frequency

As postovulatory follicles in *L. vittus* persist for ~24 h, they provide a good indication of spawning over the previous 24 h and can be used to determine spawning frequency. Parameter A from Eq. 2 provides an estimate of the proportion of females spawning each day averaged over the 29 d lunar cycle. On average, females spawn 21.7 times each lunar cycle (95%CL=19.3–23.9). If we assume that this spawning intensity occurs during October–April, then females spawn at least 150 times each year.

Batch fecundity

In order to determine the most appropriate sites in the ovary from which to take subsamples to determine batch fecundity, the number of eggs/mg tissue was determined for six regions of the ovary of five fish. Wedges of ovary were taken from both inner and outer walls at anterior, middle, and posterior parts of each right-hand ovary. There were no significant differences in numbers of eggs between inside and outside (ANOVA, F=0.016, df 1,4, p=0.91) or anterior, middle, or center (ANOVA, F=1.45, df 2,8, p=0.29) nor any interaction between the effects (ANOVA, F=0.54, df 2,8, p=0.60). A paired t-test indicated that egg counts from a wedge of tissue taken from the middle-outside position did not differ significantly between left and right ovaries (t=−0.008, df 4, p=0.99). Subsequently, batch fecundity was estimated from the mean of three subsamples taken from the anterior, middle, and posterior of either the left or right ovary of 29 fish. The coefficient of variation for estimates from three subsamples was 0.02–0.21, with a mean of 0.11.

The relation between fish length (L, mm) and batch fecundity (F) was best described by the equation

$$F = 3.656 \times 10^{-6} L^{4.093} \quad (F=26.1, \text{ df } 1,27, p<0.001), \qquad \text{(Fig. 11)}$$

and the relation between fish total weight (W, g) and batch fecundity by the equation

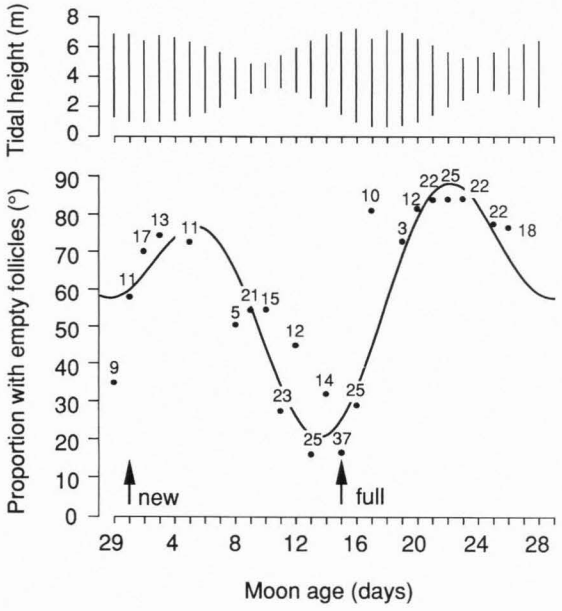

Figure 7

Proportion of mature female *Lutjanus vittus* with early- or late-stage postovulatory follicles plotted against time of sampling (expressed as moon age). A sinusoidal curve with a period of 29 d and two peaks of unequal height were fit to arcsine (angular) root-transformed data. Lunar tide cycle, indicated by maximum and minimum heights of daily tides, has also been plotted, and the number in each sample is shown.

$F = 124.2 \times W - 3081$ (F=17.7, df 1,27, p<0.001).

Batch fecundity varied markedly between fish of the same size. As the data were obtained from four different periods during the spawning season, we tested to see whether the different spawning periods could explain some of the variability in batch fecundity. There is some suggestion that batch fecundity might be higher in November and decline over the spawning season, following the seasonal pattern of RGI (Fig. 11). However, in the regression of log fecundity/log length, the test for homogeneity of slopes between sampling periods 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 four periods (ANCOVA, F=1.76, df 1,2605, p=0.19).

Oven-dried weights of hydrated oocytes were determined on 9 fish. Egg weight did not vary with fish length (F=0.28, df 1,8, p=0.61) or with maximum oocyte diameter (F=0.88, df 1,8, p=0.37). The mean dry weight of individual hydrated oocytes was 0.012 mg (SE 0.0005).

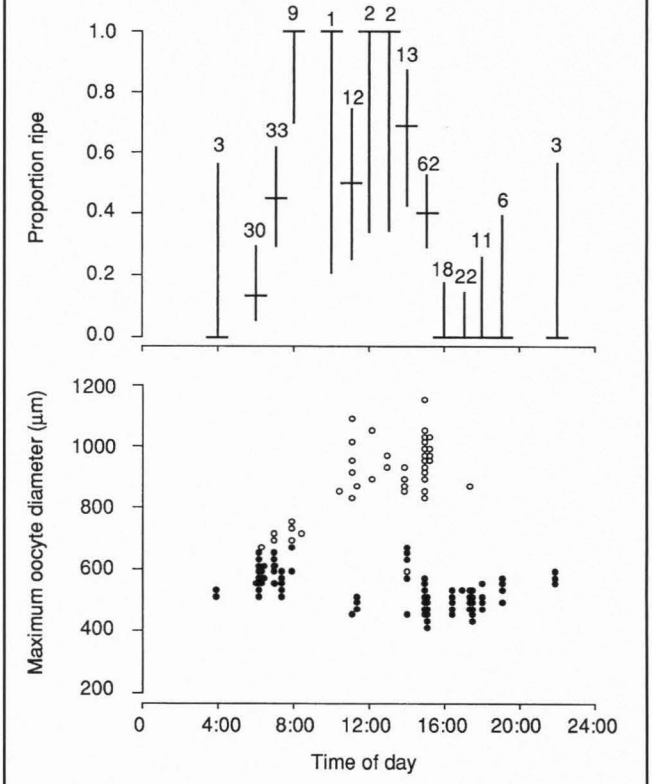

Figure 8

Proportion of mature female *Lutjanus vittus* with ripe-stage ovaries, and maximum oocyte diameter (MOD) in individuals caught at different times of the day. Samples taken during periods of major spawning activity (lunar days 2–10 and 18–29) during November–December 1982. Oocytes have been assigned to ovarian maturity stages: Ripe (○) and Yolked (●). Shown are 95% binomial confidence limits for proportions and number in each sample.

Discussion

The smallest ripe female observed in this study was 142 mm long, which is close to the length-at-first-maturity of female *L. vittus* from New Caledonia (Loubens 1980a). In a review of size-at-first-maturity, Grimes (1987) found consistent differences between insular and continental species of lutjanids and between shallow and deepwater groups in the ratio of length-at-first-maturity to maximum length. Female *L. vittus* clearly fall into the continental shallow group that mature early at ~44% of their maximum length.

The spawning season on the NW Shelf is protracted: While *L. vittus* spawned throughout the year, the major spawning period appeared to be September–April. Loubens (1980a) determined from GSI and visual staging that *L. vittus* spawn during October–February in New Caledonia (Loubens 1980a). *Lutjanus*

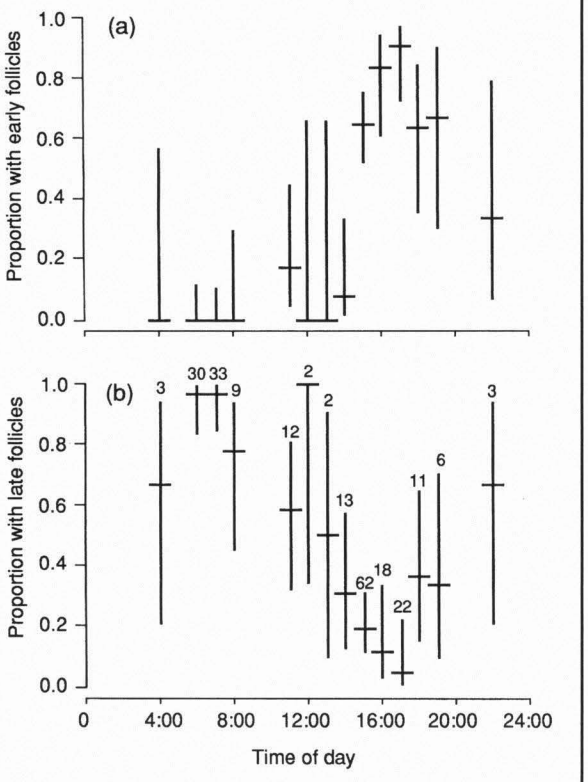

Figure 9

Proportion of mature female *Lutjanus vittus* with **(a)** early and **(b)** late-stage postovulatory follicles plotted against time of sampling. Samples taken during periods of spawning (lunar days 2–10 and 18–29) during November–December 1982. Shown are 95% binomial confidence limits for proportions and number in each sample.

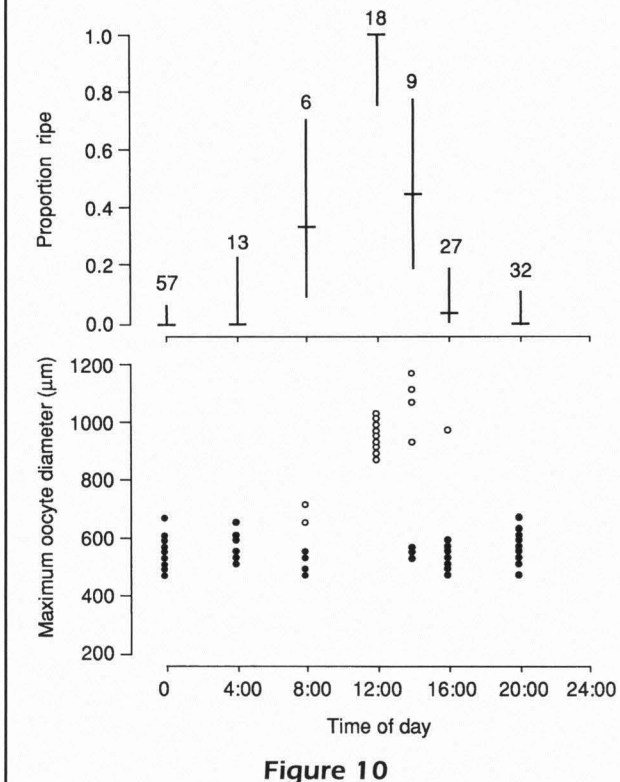

Figure 10

Proportion of mature female *Lutjanus vittus* with ripe ovaries, and maximum oocyte diameter (MOD) of individuals caught at different times of the day. Samples taken during 6–10 October 1988. Oocytes have been assigned to ovarian maturity stages: Ripe (○) and Yolked (●). Shown are 95% binomial confidence limits for proportions and number in each sample.

vittus tends to comply with Grimes' (1987) generalization that continental species, regardless of latitude, have a restricted spawning season.

The pattern of restricted spawning in *L. vittus* may be linked with the production cycle on the NW Shelf, as has been suggested for other continental species of lutjanids (Grimes 1987). The nutrient source is slope-water washing up onto the NW Shelf in summer when the Leeuwin Current is no longer flowing (Holloway et al. 1985, Tranter & Leech 1987). Enrichment is greatest between December and April. In winter the south-east trade winds blow, there is little stratification of the water column, and the plankton are dispersed (Tranter & Leech 1987). These winds abate by late August or early September, enabling the water column to become highly stratified and the plankton more concentrated (Tranter & Leech 1987). This would result in improved feeding conditions for larvae and coincides with the start of major spawning activity.

During the major spawning period, individual *L. vittus* spawn a number of times. Serial spawning has been inferred in a number of lutjanids: *L. purpureus* (De Moraes 1970), *L. kasmira* (Rangarajan 1971), *L. griseus* (Campos & Bashirullah 1975), *L. synagris* (Erhardt 1977), *Pristipomoides multidens* and *P. typus* (Min et al. 1977), *Rhomboplites aurorubens* (Grimes Huntsman 1980), *P. filamentosus* (Ralston 1981), *Etelis carbunculus* (Everson 1984), *E. coruscans* and *Aprion virescens* (Everson et al. 1989). While serial spawning appears to be commonplace in lutjanids, the number of batches of eggs spawned each season has not been determined conclusively for any species (Grimes 1987). Our data suggest that *L. vittus* spawn about 22 times/mo during late November and early December. If this spawning intensity were maintained throughout the whole spawning period (October–April), then most individuals would spawn about 150 times/yr. Even if spawning intensity were half this rate for the remainder of the season, then *L. vittus* would spawn about 90 times/yr.

Greatest spawning activity in *L. vittus* was shortly after the full and new moons. A lunar rhythm in spawn-

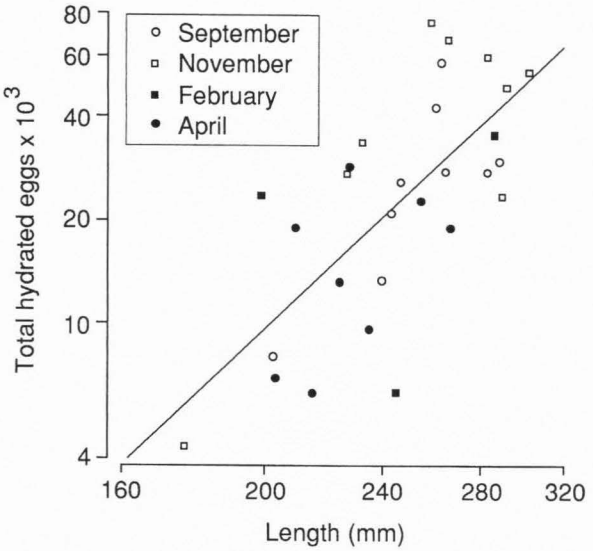

Figure 11
Relation between batch fecundity and fish length of *Lutjanus vittus* at four different spawning periods (scales are logged).

ing has been reported in many teleosts and some lutjanids, with most spawning activity close to the time of the full moon; e.g., *L. vaigiensis* (Randall & Brock 1960), *L. griseus* (Starck 1970), *L. synagris* (Reshetnikov & Claro 1976), *L. kasmira*, *L. rufolineatus*, and *P. multidens* (Mizenko 1984; although aquarium populations of *L. kasmira* spawned at the new and full moon [Suzuki & Hioki 1979]).

Many hypotheses have been proposed to explain why lunar reproductive cycles have developed in fishes (see reviews by Johannes 1978, Thresher 1984, Gladstone & Westoby 1988, Robertson et al. 1990). We cannot adequately explain why *L. vittus* has a well-developed lunar reproductive pattern. Spawning is probably linked to the lunar tidal cycle rather than moonlight per se, as it occurred chiefly after new and full moons and during daylight. The North West Shelf is a region of strong semidiurnal tides which flow predominantly cross-shelf at the shelf break and alongshelf near the coast (Holloway 1983). Spawning during spring tides would therefore disperse the eggs of *L. vittus* alongshelf rather than cross-shelf. There would be a clear advantage for larvae if they were advected to the midshelf or further offshore because these areas have greater productivity (Young et al. 1986). There is, however, no evidence for dispersal offshore; both larvae and adults of *Lutjanus* spp. are primarily found on the inner shelf (Leis 1987).

Frequency of spawning was determined from the proportion of females with postovulatory follicles. Our findings indicate that postovulatory follicles persist for <1 d, whereas studies on other species have found that they persist for <15 h (Takita et al. 1983), <2 d (Hunter & Goldberg 1980, Hunter et al. 1986, Clarke 1987), or slightly longer (Alheit et al. 1984). Our data on postovulatory follicles suggest that females on average spawn about 22 times each lunar month. The proportion of females spawning each day peaks about 3 d after the new moon and 6 d after the full moon.

It seems unusual that *L. vittus* spawns during early afternoon. Thresher (1984) reviewed 22 pelagic egg-producing families, including lutjanids, and found that most spawned around dusk, as did Colin & Clavijo (1988) who examined 26 species associated with coral reefs. Lutjanids produce pelagic eggs (Suzuki & Hioki 1979) and all other reports indicate that they spawn at or after dusk (Wicklund 1969, Starck 1970, Suzuki & Hioki 1979). Possibly spawning is linked to the state of the tide, rather than the time of day per se. In both 1982 and 1988, spawning activity coincided with rising tides; it may have been coincidental that these were during daylight hours.

Batch fecundity increased exponentially with fish length and linearly with fish weight. The variability in batch fecundities did not appear to be due to errors in using the gravimetric method. The mean coefficient of variation of estimates was 0.11, and it never exceeded 0.21. Care was taken to exclude ovaries that had partially spawned (identified by the presence of early-stage postovulatory follicles), and only those ovaries that had a clearly identified mode of partly-hydrated oocytes were used for estimates. Also, batch fecundities did not appear to differ between sampling periods. One might have expected a decline in fecundity as ovary weight declined over the season. Another possible reason for the variability in batch fecundity might have been that samples were taken at different phases of the lunar cycle. However, our data are inadequate to test this hypothesis.

Comparison of the fecundity of *L. vittus* with that of other lutjanids is not particularly useful, due to inconsistencies in methods of estimation and uncertainty as to whether true batch fecundities have been estimated (see review by Grimes 1987). It is, however, useful to consider the energetic costs of spawning by *L. vittus* considering its high annual fecundity. A 300 mm long female *L. vittus* would shed about 7.6 million eggs annually if it spawned 150 times/yr, or 4.5 million eggs if it spawned 90 times/yr. Assuming a calorific content for dried eggs of 25 kJ/g (the mean for a range of gadoids; Hislop & Bell 1987), then the annual energy expended on spawning (not including reproductive behavior) would be ~1300 kJ for 90 spawnings, and 2200 kJ for 150 spawnings. Estimation of reproductive effort or efficiency (egg energy/dietary energy × 100)

requires information on daily ration, which is not available for *L. vittus* and apparently has not been determined for any other lutjanid. *Nemipterous furcosis*, a co-occurring species on the N.W. Shelf, has a daily ration in the wild of 2.3% for 23–29 cm fish (K.J. Sainsbury, CSIRO Div. Fish., pers. commun. 1992). *Epinephalus guttatus* of similar size to *L. vittus* have a daily ration of 4% when fed surplus food once each day in the laboratory (Menzel 1960). Assuming a somewhat generous daily ration of 4% for *L. vittus* and a mean prey energy content of 4.2 kJ /g wet weight (Crisp 1971) would result in an approximate annual reproductive efficiency of 4.8% for 90 spawnings and 8% for 150 spawnings. This is similar to an annual reproductive effort in *Engraulis mordax* of 8–11% (Hunter & Leong 1981), a much smaller, shorter-lived species. The reproductive efficiency of the goby *Pomatoschistus microps* is considered to be among the highest ever calculated (Rogers 1988), although its efficiency was calculated using energy consumed over the 16 wk period of spawning and not the whole year. The reproductive efficiency of *P. microps*, calculated using annual energy intake, would be ~8.7–13.5%. The reproductive efficiency of *L. vittus* is comparatively high considering that this effort is sustained over many years.

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