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Regional patterns in reproductive biology of *Lethrinus miniatus* on the Great Barrier Reef

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Abstract. Uniformity in fish population biology is a common assumption in many fishery assessments and management arrangements. Although spatial patterns in population biology are often unknown, ignorance of significant variation within a fished stock has profound implications for fishery assessments and management. In the current paper, the reproductive biology of an exploited reef fish, *Lethrinus miniatus*, was examined for populations in the northern and southern regions of the Great Barrier Reef (GBR). Significant regional variation was observed in some reproductive parameters, but not others. In the northern region, the proportion of spawning females observed during the spawning season was significantly greater and the size at sex change significantly smaller than in the southern region. However, the spawning season, age at sex change and sex ratios did not differ significantly between the northern and southern regions. Size and age at maturity could not be estimated from either of these regions, but an estimate was obtained from the Capricorn–Bunker region at the southern tip of the GBR. The observed regional patterns in reproductive biology of *L. miniatus* populations have important implications for specific management arrangements such as size limits and seasonal closures, and for fisheries management in general.

Extra keywords: Lethrinidae, protogyny, reproduction, spawning omission.

Introduction

Spatial variation in reproductive biology is a relatively common feature of reef fish populations. Several authors have reported significant variation among locations in maturity schedules (Cowen 1990; Ebisawa 1999), spawning season (Ebisawa 1997, 1999), sex ratios (Buxton 1993; Adams *et al*. 2000), size or age at sex change (Cowen 1990; Buxton 1993; Ebisawa 1999; Adams *et al*. 2000; Platten *et al*. 2002) and fecundity (Ebisawa 1999). Significant spatial variation in maturity and sex change schedules may be facilitated by the relative plasticity in sex determination in hermaphroditic fish (Hovey and Allen 2000). Variations in the stage at which individuals mature or change sex may occur in response to either variations in local environmental conditions, such as water temperature (e.g. Conover and Heins 1987), or in response to changes in sex ratios of the population or local sub-population (Shapiro 1984).

Spatial variation in reproductive biology has important implications for fisheries management. For example, minimum legal sizes are often implemented in a fishery based on size at maturity information (Hill 1990). In a fishery with a single minimum size limit, variations in maturity schedules between locations within the fishery may result in recruitment overfishing of sub-populations that reach maturity at a larger size than that of the average for the whole population. Similarly, spawning closures implemented across a fishery at the one time will not protect all components of the stock if there are significant differences in the timing of the spawning season among geographic locations within the fishery. On the other hand, implementing spatially variable fishery regulations is logistically and legally more difficult than applying spatially uniform regulations.

The reproductive biology of lethrinids has received comparably less attention than that of other commercially important reef fish families, such as lutjanids (Grimes 1987) and serranids (Shapiro 1987), despite their importance to many coastal reef fisheries around the world (Carpenter 2001). The few available studies indicate that lethrinids are protogynous hermaphrodites, changing sex from females to males at some stage during their life (Young and Martin 1982; Ebisawa 1997, 1999; Bean *et al*. 2003; Sumpton and Brown 2004). It is generally considered that protogynous species are more vulnerable to increased fishing pressure than gonochoristic species, for which sexes are separate throughout life (Huntsman and Schaaf 1994) because fishing often impacts disproportionately on larger and older fish, which in protogynous populations are predominantly male (Bannerot *et al*. 1987). It has been hypothesised, therefore, that such impacts

could result in sperm limitation in harvested protogynous species (Coleman *et al*. 1996; Vincent and Sadovy 1998).

The redthroat emperor, *Lethrinus miniatus* (Forster, 1801), is an important species in the commercial and recreational line fisheries of the Great Barrier Reef (GBR) (Mapstone *et al*. 1996; Slade and Williams 2002), Norfolk Island (Church 1995) and New Caledonia (Carpenter 2001). In the multi-species Coral Reef Fin Fish Fishery (CRFFF) on the GBR, the annual commercial harvest of *L. miniatus* has increased steadily since the early 1970s to a peak of over 800 t in 2001 (Slade and Williams 2002), while recreational fishers harvest ∼400 t annually (Higgs 1999, 2001). The management arrangements for *L. miniatus* are uniform throughout the GBR. A minimum size limit of 380 mm total length (TL) and three nine-day spawning closures centred on the new moons in October, November and December apply to all fishers. A total allowable catch of 700 t was introduced in 2004 for commercial fishers only, while there is a possession limit of eight fish per person for recreational fishers.

Previous studies on the reproductive biology of *L. miniatus* on the GBR have provided preliminary estimates for some reproductive parameters from specific locations (Walker 1975; Bean *et al*. 2003; Sumpton and Brown 2004), but spatial pattern in reproductive biology of *L. miniatus* has not been examined previously. Williams *et al*. (2003), however, found substantial variation in age, growth and mortality of *L. miniatus* populations among regions of the GBR. These demographic patterns alone are likely to precipitate variations in reproductive potential of *L. miniatus* populations but they might also be accompanied by regional variations in reproductive parameters *per se* that could exacerbate or offset reproductive consequences of variable growth.

The objective of the current study was to increase the existing knowledge of lethrinid reproductive biology by estimating and comparing various reproductive parameters of *L. miniatus* between regions of the GBR. More specifically, the aims were to:

  (*i*)   estimate seasonality of spawning;
 (*ii*)   document sex ratios, size and age at maturity, and size and age at sex change;
(*iii*)   compare these parameters between the northern and southern regions of the GBR; and
(*iv*)   use the estimates of these reproductive parameters to develop hypotheses about the mating patterns and sexual strategies of *L. miniatus* relative to other studies of *L. miniatus* and other reef fish species.

Materials and methods

Sample collection

In total, 1767 samples of *L. miniatus* in the form of frozen fish frames (head, skeleton and viscera) were collected from 14 commercial line fishing vessels operating from ∼18°S to
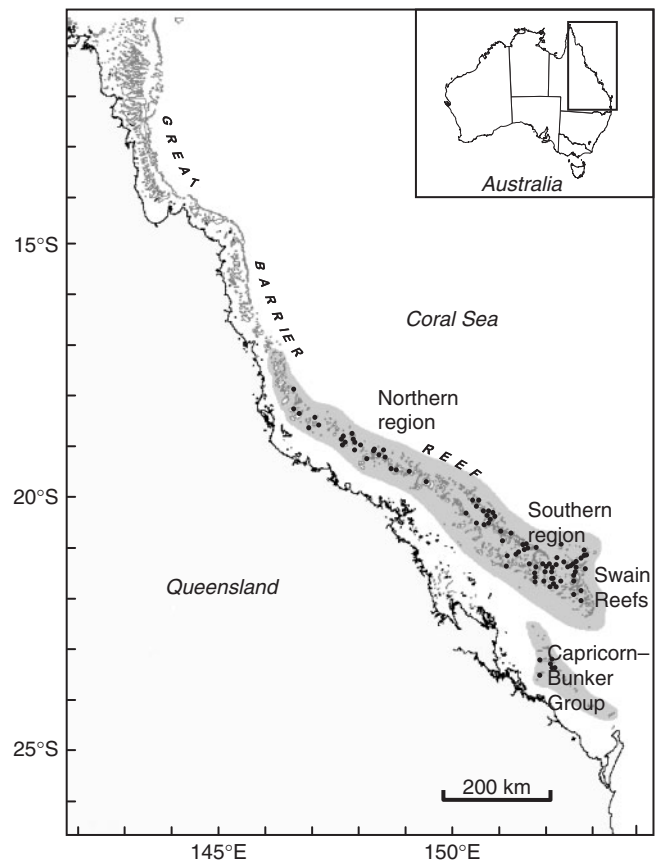

Fig. 1.   Distribution of *Lethrinus miniatus* on the Great Barrier Reef (shaded area) and the location of reefs sampled (●) within the northern and southern regions (from which *L. miniatus* were collected by commercial line-fishing vessels) and the Capricorn–Bunker region (from which a sample of small *L. miniatus* was collected during a research survey).

22.5°S within the GBR region (Fig. 1, Table 1). Samples were collected from December 1998 to December 2000 from a total of 91 reefs. Samples were not available from all months in each year due to the opportunistic nature of collecting samples from commercial fishers. Furthermore, length and sex information was not available from all samples as the gonads or skeleton were occasionally missing. Samples collected north and south of 20°S were divided into 'northern' and 'southern' regions respectively (Fig. 1). These regions were treated as discrete for several reasons. First, there was a clear separation (of ∼100 km) between the two nearest reefs sampled from north and south of 20°S. Second, 20°S marks a significant change in the structure and morphology of the reefs on the GBR, with the northern region dominated by crescentic reefs and the southern region dominated by lagoonal reefs (Hopley 1982; Kinsey and Hopley 1991). South of 20°S the reefs on the GBR are typically located further from the Queensland coastline and consequently further from terrestrial influences than reefs north of 20°S (Fig. 1). The reefs

Table 1. Monthly sample sizes of female and male *Lethrinus miniatus* collected from two regions located north and south of 20°S on the Great Barrier Reef between 1998 and 2000

Year	Month	Northern region		Southern region		Total
		Females	Males	Females	Males	
1998	December	33	38	0	0	71
1999	January	11	10	55	45	121
	February	0	0	22	16	38
	March	0	0	38	39	77
	April	0	0	48	27	75
	May	15	11	26	42	94
	June	0	0	27	15	42
	July	25	25	14	9	73
	August	8	1	24	16	49
	September	34	53	0	0	87
	October	15	10	20	19	64
	November	51	37	33	13	134
	December	54	29	4	12	99
2000	January	16	18	6	3	43
	February	0	0	24	6	30
	March	0	0	20	17	37
	April	7	12	20	7	46
	May	9	10	16	17	52
	June	0	0	0	0	0
	July	4	1	54	52	111
	August	24	15	27	23	89
	September	26	19	53	40	138
	October	17	22	23	19	81
	November	0	0	7	3	10
	December	25	28	6	4	63
Total		374	339	567	444	1724

south of 20°S are also spread over a larger distance across the continental shelf than reefs north of 20°S (Fig. 1). Third, this latitude is approximately the midpoint of the distribution of *L. miniatus* on the GBR. A total of 726 fish from 27 reefs were sampled from the northern region and 1041 fish were taken from 64 reefs in the southern region.

There was a minimum legal size limit for recreational and commercial harvest of *L. miniatus* of 350 mm TL (equivalent to 320 mm fork length, FL) during the collection of samples. Accordingly, individuals less than 320 mm FL were rare in the samples and no immature individuals were identified. To obtain estimates of size and age at maturity, it was necessary to collect smaller (<320 mm FL) individuals under research permit. However, the juvenile habitat for *L. miniatus* is unknown and individuals <150 mm FL have never been sighted (Williams *et al.* 2003). The Capricorn–Bunker region (Fig. 1), at the southern extremity of the GBR, was identified by commercial fishers as a location where small *L. miniatus* are relatively abundant. Accordingly, a researcher accompanied a commercial vessel to this region in September 2002 where an additional sample of 92 *L. miniatus* containing smaller (<300 mm FL) individuals was collected. The timing of this trip coincided with the peak spawning period in this region (Sumpton and Brown 2004) and therefore maximised

the contrast between mature and immature individuals. Samples were collected using hook and line (size 6 hooks) and were used only in the analysis of maturity schedules.

Sample processing

The FL of all samples was measured from thawed frames to the nearest millimetre, and sagittal otoliths were removed and cleaned of any residual material. Estimates of age were obtained from sectioned otoliths using the procedures outlined by Williams *et al.* (2005). The algorithm developed by Williams *et al.* (2005) was used to assign age in months (rounded to the nearest whole year) to each individual, as samples were collected across all months of the year whilst otolith increments are deposited at a similar time each year. Gonads were removed and preserved in a solution of 40% formaldehyde (9%), acetic acid (4%) calcium chloride (1%) for later histological examination. After fixation, each pair of ovaries or testes was dried of excess fixative, and gonad mass (M_G) was measured to the nearest 0.01 g. Where only one gonad lobe was available, due to damage during processing, M_G was estimated by multiplying the mass of the single complete lobe by two. It was assumed that this provided a reasonably accurate measure of M_G, as the two gonad lobes are generally equal in size for *L. miniatus* (Bean *et al.* 2003).

Histology and reproductive staging

Histological sections were taken from all gonads following the procedures outlined by Bean *et al.* (2003). Ovaries were staged based on the most advanced non-atretic cell type present (West 1990). Additional features used in histological staging included the presence of brown bodies, atretic oocytes, vascularisation, and the relative thickness of the gonad wall, all of which may indicate prior spawning (Sadovy and Shapiro 1987). Ovaries and testes were classified into developmental stages adapted from Bean *et al.* (2003). Females were classified into five stages: Immature, Resting, Ripening, Ripe and Hydrated. Males were classified into four stages: Spent, Post-spawn resting, Pre-spawn resting and Ripe. Female stages Ripe and Hydrated were treated as a single Ripe stage for analyses because of the relatively low number of hydrated females. Similarly, male stages Post-spawn resting and Pre-spawn resting also were treated as a single Resting stage in analyses, as both are resting stages.

Reproductive biology

Wet mass (M_T, g) of samples collected from commercial fishers was not available directly, as fishers provided only filleted fish frames. Consequently, M_T was estimated using the relationship between FL and M_T estimated by Williams (2003) where:

$$M_T = 8.04 \times 10^{-6} \times FL^{3.13}$$

A gonado-somatic index (I_G) was calculated for each sample using:

$$I_G = \frac{M_G}{M_T} \times 100$$

Mean monthly I_G values for mature fish were plotted separately for males and females from each region to determine the peak spawning period for *L. miniatus*. The proportion of samples in each mature female and male reproductive stage in each month were also plotted for each region to examine the ovarian and testicular development patterns throughout the year, and the degree of spawning activity occurring in each month in each region.

The size at sex change was estimated by regression for each region using the logistic equation,

$$P_s = (1 + e^{-\ln 19(s - s_{50}^k)/(s_{95}^k - s_{50}^k)})^{-1}$$

where P_s is the proportion of males in each 10 mm length class s, s_{50}^k is the length at which 50% of the population are males in region k, and s_{95}^k is the length at which 95% of the population are males in region k.

The logistic function provided a poor fit to the pattern of age at sex change. Accordingly, a second order polynomial function was used to describe the pattern of age at sex change for each region, as it provided the best fit to the data. The

form of the polynomial function was,

$$P_x = a^k x^2 + b^k x + c^k$$

where P_x is the proportion of males in each age class x, and a^k, b^k and c^k are coefficients of the polynomial function in each region k. Likelihood ratio tests (Haddon 2001) were used to test for differences in the size and age at sex change between the northern and southern regions.

The sex assigned from histology was used to calculate the sex ratios for each region, which were compared between regions using a chi-square contingency test and compared with an expected ratio of 1 : 1 by a χ^2 goodness of fit test.

The sample collected from the Capricorn–Bunker region that included smaller *L. miniatus* was used to estimate the size and age at maturity using the logistic equation,

$$P_m = (1 + e^{-\ln 19(m - m_{50})/(m_{95} - m_{50})})^{-1}$$

where P_m is the proportion of mature fish in age or 10 mm length class m, m_{50} is the age or length at 50% maturity, and m_{95} is the age or length at 95% maturity.

Results

Spawning season

Mean monthly I_G values for mature females were highest in July to October in the northern region and July to September in the southern region (Fig. 2). The mean monthly I_G values
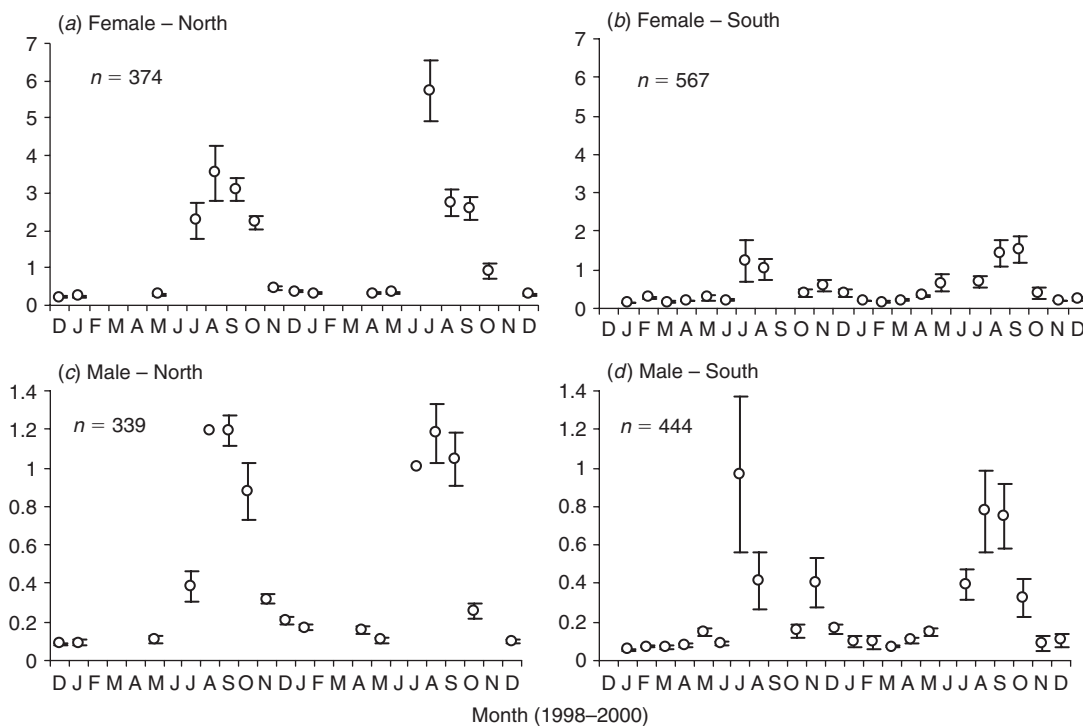

Fig. 2. Mean monthly gonado-somatic index (I_G) values for mature females (*a,b*) and all males (*c,d*) of *Lethrinus miniatus* within two regions located north and south of 20°S on the Great Barrier Reef. Error bars are standard errors. Note the difference in *y*-axis scales for males and females.

for males were highest in July to October in both regions (Fig. 2). Missing data in June 1999 in the northern region and June 2000 in both regions precluded the specific verification of whether spawning commenced in July or June in either region. Based on I_G, however, it appears that the spawning season for *L. miniatus* is similar in both regions of the GBR and spans at least 3 to 4 months during the austral winter and early spring. Average I_G values for both females and males were substantially higher in the northern region than in the southern region during the spawning season (Fig. 2).

The monthly trend in the frequency of mature ovarian stages (ovaries in active vitellogenesis) suggested a similar temporal pattern in spawning activity to the monthly I_G values for both regions (Fig. 3). In the northern region, there was some evidence of spawning in the months of May and November in 1999, and January and April in 2000, but the majority of spawning activity occurred between July and October (Fig. 3). In the southern region, a relatively large proportion of ripe females was present in the months of May in 1999 and 2000, and in November 1999 (Fig. 3), although

the majority of ripe individuals occurred between July and September (Fig. 3). There were 11 hydrated females sampled from the northern region and two sampled from the southern region. These hydrated females were present in August and September in both regions (Fig. 3).

The proportion of ripe females during the peak spawning months was significantly greater in the northern region than in the southern region ($t_{6, 0.05}$, $P < 0.001$). Between 59% and 100% of females were ripe during the peak spawning months in the northern region whereas no more than 43% of females were ripe in any month in the southern region (Fig. 3). This large difference between regions was not an expected result. The relationship between size and reproductive stage was examined to determine if the low number of ripe females in the southern region was related to the size of ripe females. The proportion of ripe ovaries during the spawning season was relatively consistent among size classes in the northern region and exceeded 70% of all ovaries in all but one size class (Fig. 4). In contrast, the proportion of ripe ovaries during the spawning season in the southern region
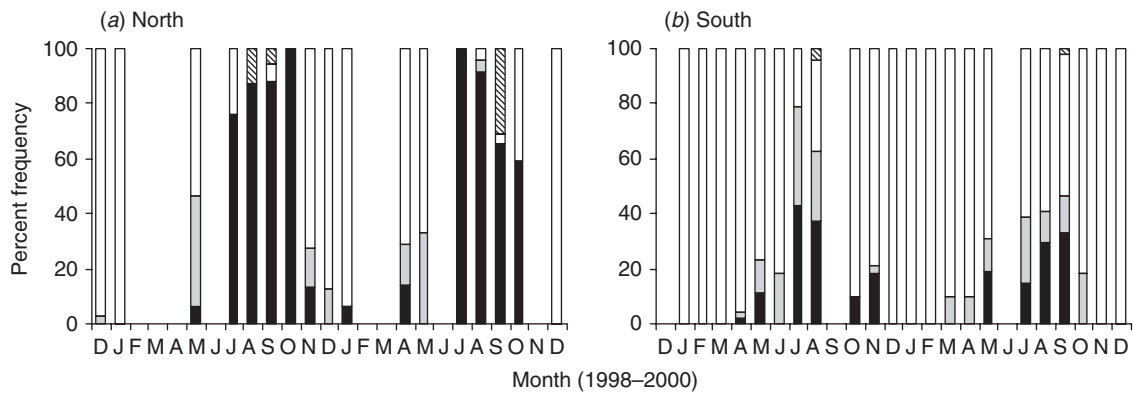

Fig. 3. Monthly frequencies of mature ovarian stages (□ resting, ▨ ripening, ■ ripe, ▩ hydrated) of *Lethrinus miniatus* within two regions located (*a*) north (*n* = 374) and (*b*) south (*n* = 567) of 20°S on the Great Barrier Reef.
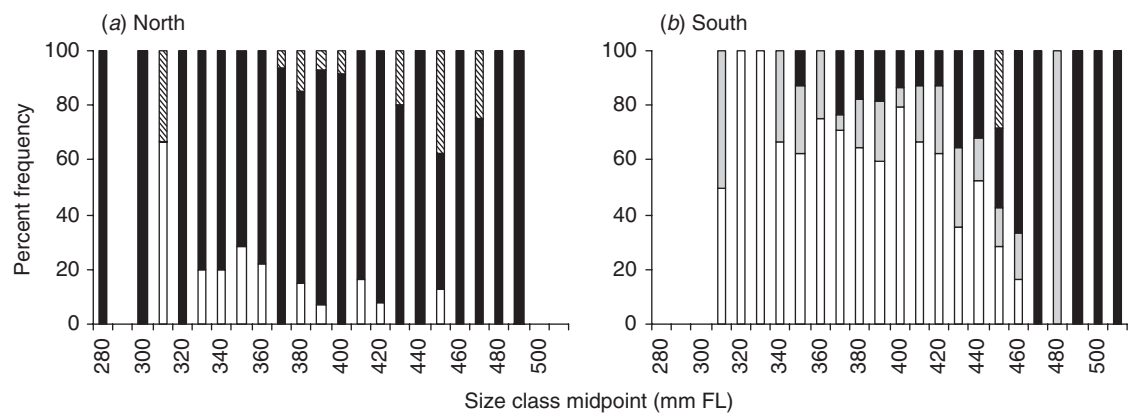

Fig. 4. Proportion of mature ovarian stages (□ resting, ▨ ripening, ■ ripe, ▩ hydrated) for *Lethrinus miniatus* collected during the peak spawning months (Jul–Oct) in 10 mm size classes within two regions located (*a*) north (*n* = 153) and (*b*) south (*n* = 214) of 20°S on the Great Barrier Reef.
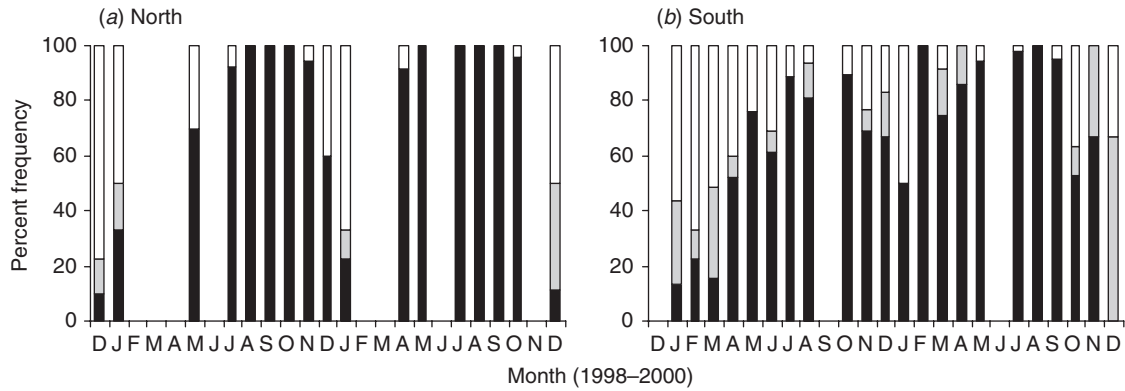
Fig. 5.   Monthly frequencies of testicular stages (□ resting, □ spent and ■ ripe) of *Lethrinus miniatus* within two regions located (*a*) north (*n* = 312) and (*b*) south (*n* = 392) of 20°S on the Great Barrier Reef.
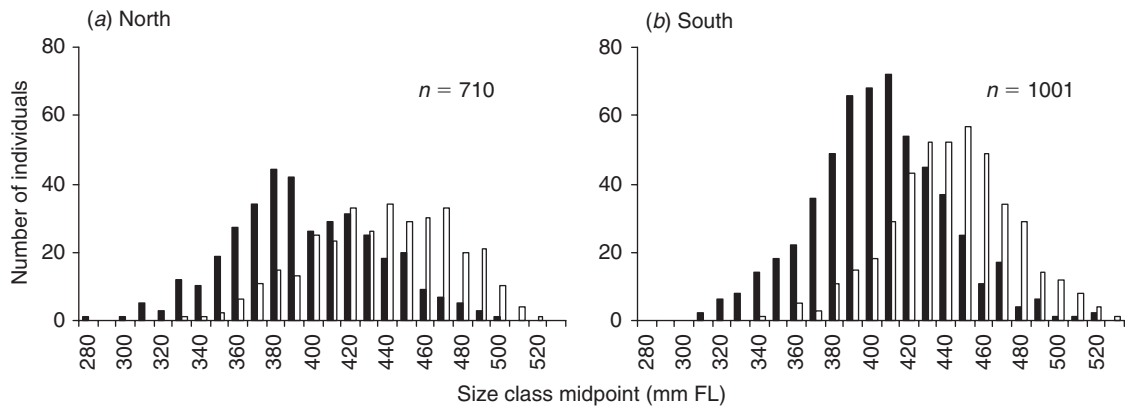

Fig. 6.   Size frequency distributions for females (■) and males (□) of *Lethrinus miniatus* from two regions located (*a*) north and (*b*) south of 20°S on the Great Barrier Reef.

generally increased with size, and ripe ovaries did not exceed 50% of all ovaries until the 450 mm FL size class (Fig. 4). Ripe females were observed at a much smaller size in the northern region (280 mm FL) compared with the southern region (350 mm FL).

Males appeared to be capable of spawning over an extended period of time either side of the spawning season (as defined by the presence of active females) in both regions, as indicated by the monthly trend in the frequency of testicular stages (Fig. 5). Greater than 50% of males had sperm present in all months except December and January in the northern region and December through March in the southern region (Fig. 5).

Size and age at sex change

There was a large overlap in the size distributions of males and females in both regions, although females dominated the smaller size classes and males dominated the larger size classes (Fig. 6). Likelihood ratio tests indicated the pattern in the size at sex change differed significantly between the northern and southern regions ($\chi^2 = 7.80$, d.f. = 2, $P = 0.02$),

which was attributed to a difference in the size at which 50% of the population had changed sex from female to male (size at 50% sex change) ($\chi^2 = 7.35$, d.f. = 1, $P = 0.007$). The size at 50% sex change was 13 mm greater in the southern region compared with the northern region (Fig. 7, Table 2). Furthermore, the size at which males first appeared in the population was slightly smaller in the northern region (325–334 mm FL size class) compared with the southern region (335–344 mm FL size class) (Fig. 7). There was also a greater proportion of females in some larger size classes in the southern region compared with the northern region (Fig. 7).

The pattern of age at sex change differed from the pattern of size at sex change in both regions (Fig. 7). The proportion of males in each age class increased from less than 10% at 3 years to over 70% at 9 years for both regions. Although the proportion of males fluctuated greatly in the following age classes, there was a general trend for the proportion of males to decrease after 9 years of age (Fig. 7), which was not expected for a protogynous species or for a gonochore. Likelihood ratio tests indicated that the pattern of age at sex change was not significantly different between the northern
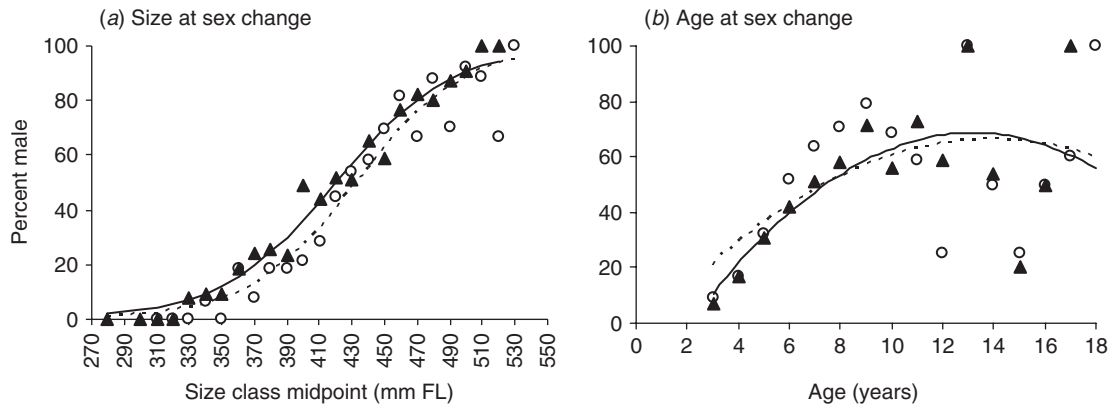
Fig. 7. Percentage of male *Lethrinus miniatus* and estimated sex change schedules from two regions located north (▲, solid lines, $n = 713$) and south (○, dashed lines, $n = 1007$) of 20°S on the Great Barrier Reef. A logistic function was used to describe (*a*) the size at sex change, and a second order polynomial function used to describe (*b*) the age at sex change. Parameters of the sex change functions are provided in Table 2.

Table 2. Parameters of age and size-specific sex change for *Lethrinus miniatus* from two regions located north and south of 20°S on the Great Barrier Reef

Location	Size-specific sex change			Age-specific sex change				
	s_{50} (mm FL)	s_{95} (mm FL)	R^2	a	b	c	R^2	age_{50} (years)
Northern region	420	525	0.98	-5.6×10^{-3}	0.15	-0.28	0.47	7.4
Southern region	433	530	0.94	-3.8×10^{-3}	0.10	-0.07	0.28	7.4

s_{50} and s_{95} are the length (FL) at which 50% and 95%, respectively, of the population are males; a, b, and c are coefficients of the second-order polynomial function used to describe the pattern of age at sex change in each region; age_{50} is the earliest age at which 50% of individuals were male.

and southern regions ($\chi^2 = 1.59$, d.f. = 2, $P = 0.66$). A single estimate of the age at 50% sex change was not possible for either region, as the fitted polynomial functions suggested that after the initial increase in the proportion of males to over 50%, the proportion of males then decreased below 50% in older age classes. The earliest age at which 50% of individuals changed sex, however, was 7.4 years for both the northern and southern regions (Table 2).

Sex ratio

The female : male sex ratio was 1.10 : 1 in the northern region and 1.28 : 1 in the southern region. A chi-square contingency test indicated that the sex ratios were not significantly different between regions ($\chi^2 = 2.22$, d.f. = 1, $P = 0.14$). Consequently, data were pooled across regions to compare the overall sex ratio to a 1 : 1 sex ratio. A Chi-square goodness of fit test suggested that the sex ratio for the data pooled across regions (1.20 : 1) was significantly different from 1 : 1 ($\chi^2 = 14.48$, d.f. = 1, $P = 0.0001$).

Size and age at maturity

Samples collected from reefs in the Capricorn–Bunker region ranged in size from 179 mm to 460 mm FL and from one to

seven years of age (Fig. 8). The smallest and youngest mature female in the sample was 250 mm FL and two years of age, while the largest and oldest immature female was 313 mm FL and three years old (Fig. 8). The size and age at which 50% of the sample was mature, estimated from the logistic function, was 280 mm FL and 2.1 years of age (Fig. 8), and 95% of individuals would be expected to be mature at 333 mm FL and 4.0 years of age.

Discussion

Significant variation in reproductive biology of *L. miniatus* between the northern and southern regions of the GBR was observed in some reproductive parameters, but not others. The size at sex change and the proportion of spawning females observed during the spawning season varied significantly between the northern and southern regions. The spawning season, age at sex change and sex ratios, however, did not differ significantly between the northern and southern regions. These regional patterns in reproductive biology provide some insight into the sexual strategies of *L. miniatus* and have important implications for management of the species on the GBR and fisheries management in general.
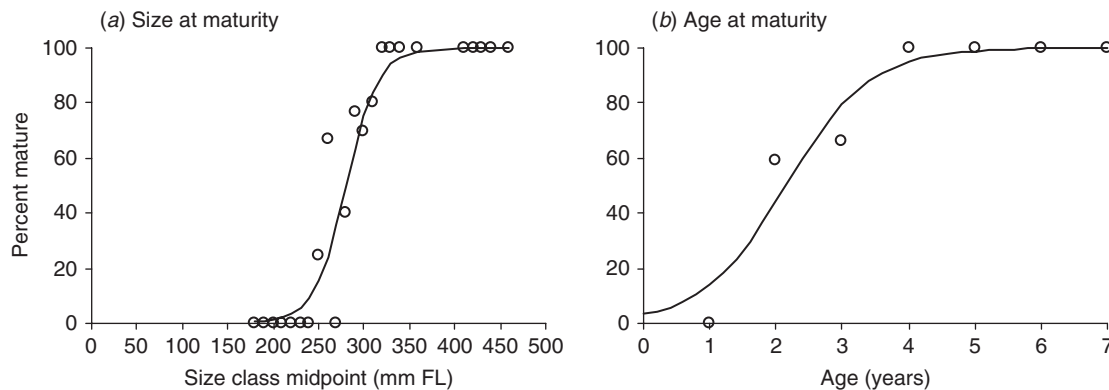
Fig. 8. Percentage of mature female *Lethrinus miniatus* and estimated logistic maturation schedules for the Capricorn–Bunker region of the Great Barrier Reef related to (*a*) size (*n* = 88) and (*b*) age (*n* = 88).

Spawning season

A peak spawning period for *L. miniatus* was identified between July and October using monthly trends in both I_G and frequency of ovarian stages. The months of peak spawning were similar in both the northern and southern regions, although the monthly trend in the frequency of mature ovarian stages suggested some spawning may have occurred outside this period in the southern region. The peak spawning period is consistent with previous observations from the northern (Walker 1975) and southern (Sumpton and Brown 2004) extremities of the species' distribution on the GBR, suggesting a common spawning period throughout the species' range on the GBR. The similarity in spawning season between regions and the consistency in observations between the current study and previous studies contradict the suggestion by Sumpton and Brown (2004) that *L. miniatus* populations spawn earlier at lower latitudes on the GBR.

Spawning omission

Although the spawning season for *L. miniatus* is similar throughout the GBR, the proportion of ripe females collected during the spawning season was significantly lower in the southern region than in the northern region. Similarly, the data from Sumpton and Brown (2004) showed that the proportion of ripe females rarely exceeded 25% of all females during the spawning season in the southern region of the GBR, although the authors did not comment on this feature. Notably, this observation is inconsistent with results for most other coral reef fish populations, including other lethrinids, in which more than 50% of females have been found to be ripe for at least one month of the spawning season (Sadovy 1996). Results from the current study indicate that the low proportion of ripe females in the southern region is due to a relatively large proportion of smaller females (<450 mm FL) persisting in the resting stage during the spawning season. In a recent review of spawning omission in fishes, Rideout *et al.* (2005) classified this type of spawning omission as 'Resting', where

all oocytes remain in the pre-vitellogenic stage throughout the year and the individual is incapable of spawning in the current year. The reason why most smaller females do not spawn during some years, before reaching a certain size, is unclear, but for other species, spawning omission has been linked to low food availability (Pollock 1984; Bell *et al.* 1992; Burton 1994; Rideout *et al.* 2000), reduced water temperature (Pawson *et al.* 2000; Pörtner *et al.* 2001) and geographic position at the edge of the species' distribution (Fennessy and Sadovy 2002). For *L. miniatus*, spawning has been observed at cooler water temperatures and at much higher latitudes than the southern region sampled in the current study (Church 1995), suggesting latitude and temperature may not be limiting factors for reproductive activity in the southern region of the GBR. It is unclear whether food limitation contributes to spawning omission in the southern region, as there are no data available on the distribution and abundance of prey species of *L. miniatus* on the GBR, or elsewhere, or on their variation over time.

Mating pattern and sexual strategy

Populations of *L. miniatus* were found to be significantly female-biased in both regions, but the bias was small. Studies that have incorporated a broader size range of samples found that populations of *L. miniatus* on the GBR typically have a much larger female bias (Bean *et al.* 2003; Sumpton and Brown 2004) than the results here indicate. This difference is most likely due to the sample collection from commercial fishers in the current study being restricted by a minimum size limit, and thus small individuals (<320 mm FL) were underrepresented in the sample.

A female-biased population is typical for protogynous reef fish (Sadovy and Shapiro 1987) and suggests a polygynous mating pattern for *L. miniatus*, whereby a single male pair-spawns consecutively with several females. Such a mating system is further supported by the difference in size between testes (around 1% bodyweight) and ovaries (up to 5% bodyweight) during the spawning season. The unrealised potential

for an increase in the size of testes suggests a mating system for *L. miniatus* with little or no sperm competition (Sadovy *et al*. 1994; Sadovy 1996) and is consistent with other pair-spawning reef fish (Sadovy 1996). Unfortunately there have been no direct observations of wild spawning events to confirm this type of mating system for *L. miniatus*, or for any other lethrinid, although Suzuki and Hioki (1978) observed pair-spawning for *Gymnocranius griseus*, a coastal lethrinid of the Indo-Pacific, in a controlled aquarium environment.

Sumpton and Brown (2004) and Young and Martin (1982) have suggested protogyny is the predominant sexual strategy for *L. miniatus*. The presence of transitional individuals is considered a necessary condition from which to infer protogyny in fish populations (Sadovy and Shapiro 1987). No transitional gonads were observed histologically in the current study, although transitional individuals have been found to comprise only between 0.05% (Sumpton and Brown 2004) and 0.6% (Bean *et al*. 2003) of *L. miniatus* populations on the GBR, and are often found in very low frequencies in other reef fish populations (Sadovy and Shapiro 1987; Munday *et al*. 1998; Adams *et al*. 2000). The absence of transitional individuals from monthly samples in the current study suggests that either sex transition in *L. miniatus* is very rapid, or that protogyny is not the only, nor perhaps even the dominant, sexual strategy in the species. Bean *et al*. (2003) argued in favour of rapid sexual transition based on the complete absence of any female tissue in *L. miniatus* testes. It is also possible that only a proportion of females change sex (Warner 1982; Sadovy and Shapiro 1987), resulting in a reduced probability of sampling transitional individuals. The presence of a small number of females in some of the largest size classes, particularly in the southern region, and the tendency for the proportion of males to decrease after eight years of age is evidence in support of a proportion of female *L. miniatus* not changing sex. For the proportion of males to decrease in older age classes, however, there would also need to be diminished survival of males, or net emigration of older males from the population, or both.

Sex change in *L. miniatus* is more strongly correlated with size than age, given the poor relationship between age and the proportion of males in the population. The size at sex change in *L. miniatus* is also very flexible, as indicated by the large overlap in the size distributions of males and females observed for populations in both regions of the GBR. Such a large overlap is indicative of a social control of sex change, whereby females are able to change sex to male to maintain some threshold sex ratio (Shapiro 1981; Ross *et al*. 1983; Sadovy and Shapiro 1987; Cowen 1990; Vincent and Sadovy 1998) rather than changing sex at a predetermined size or age. However, the controlling mechanism for sex change remains unclear for the majority of protogynous fish (Sadovy 1996), including *L. miniatus*.

The size at 50% sex change for *L. miniatus* was significantly larger in the southern region compared with the

northern region of the GBR, although the difference, on average, was only 13 mm in length. If sex change in *L. miniatus* is under social control, an increase in fishing pressure may reduce the size at sex change as females change sex at a smaller size to compensate for the removal of larger males (e.g. Buxton 1993; Platten *et al*. 2002). It is unlikely, however, that the smaller size at sex change in the northern region is a result of fishing pressure alone, as historic (Mapstone *et al*. 1996) and recent (Slade and Williams 2002) fishing effort has been greater in the southern region of the GBR, where the size at 50% sex change was larger. Regional variation in growth appears a likely explanation for the difference in the size at sex change, given that the average maximum size of *L. miniatus* is larger in the southern region than in the northern region of the GBR (Williams 2003; Williams *et al*. 2003). A larger size at 50% sex change may be a mechanism to maintain a constant sex ratio for a population reaching a larger maximum size (Charnov and Skúladóttir 2000; Allsop and West 2003), assuming sex change is under social control. This hypothesis is supported by the fact that sex ratios did not differ significantly between the northern and southern regions.

Size and age at maturity

Estimates of size and age at 50% maturity obtained in the current study from the Capricorn–Bunker region are substantially smaller and younger than estimates obtained from the same region by Sumpton and Brown (2004). The estimate of Sumpton and Brown (2004) is most likely an overestimate, however, as they classified all mature resting females as immature, as they were unable to distinguish between immature and mature resting females. Although maturity could not be estimated from the northern or southern regions, the large proportion of ripe females in nearly all size classes in the northern region suggests that maturity in that region probably occurs at a similar size to the Capricorn–Bunker region.

Implications for fisheries management

A spawning closure for commercial and recreational fishers in the CRFFF was implemented in 2004 for three nine-day periods around the new moons in October, November and December. The closures are intended to protect the spawning activity of reef fish, particularly spawning aggregations of the main target species, common coral trout *Plectropomus leopardus*. *Lethrinus miniatus*, however, will gain little, if any, protection of spawning activity from the closures, as they do not coincide with the peak spawning period for *L. miniatus* (July–October). Furthermore, the efficacy of the spawning closures depends on more than aligning the closures with peak spawning periods. For spawning closures to be most effective (i.e. more effective than closures at other times), there must be evidence of intentional targeting of spawning aggregations or an increase in catchability of a species during the spawning season. There is little documented evidence consistent

with either of these scenarios for *L. miniatus* or any other species in the CRFFF on the GBR (Mapstone *et al.* 2001).

The current minimum size limit for *L. miniatus* on the GBR is 380 mm TL (~350 mm FL) for all fishers, which is intended to allow 50% or more of fish to reach maturity and spawn before becoming vulnerable to the fishery. Based on the maturity estimate from the Capricorn–Bunker region, the current minimum size limit appears to be meeting the stated objective, as 100% of females were found to be mature at 350 mm FL. However, this estimate of maturity was obtained from a single region of the GBR. It will be important to determine whether maturity varies among regions of the GBR to establish whether the current minimum size limit is appropriate for all regions of the GBR.

The use of a minimum size limit is complicated by the finding that 50% of females in the southern region of the GBR do not spawn in all seasons until they reach ~450 mm FL. From a management perspective, the females that do not spawn in a given season are effectively 'immature' for the years they do not contribute to egg production. Therefore, although the current minimum size limit may be allowing 100% of females to reach maturity before becoming vulnerable to the fishery, it is likely that many of these females, at least in the southern region of the GBR, do not spawn before being harvested. Furthermore, the larger females are likely to be very important to the spawning stock, as their relative contribution to egg production is disproportionately greater than would be expected if the majority of mature females in all size classes were spawning every year. Consequently, there is the potential for fishing to greatly reduce the reproductive output of *L. miniatus* in the southern region by more than might be suggested by the relationship between maturity schedules and the minimum legal size limit, assuming that fishing diminishes the abundance of larger females in the population. Clearly, it will be important to determine the causal factor(s) for spawning omission in order to predict the potential effects of fishing on the reproductive potential of *L. miniatus* in the medium- to long-term.

The use of a minimum size limit for *L. miniatus* is further complicated by the protogynous sexual strategy of *L. miniatus*. The majority of the male population of *L. miniatus* are vulnerable to harvest (>350 mm FL), and therefore *L. miniatus* may be particularly vulnerable to sperm limitation arising from overfishing of males. An increase in the current minimum size limit, or the introduction of a maximum size limit, are two mechanisms that may offer some protection from harvest to a proportion of the male population. The effectiveness of size limits, however, relies on a high survival rate of released fish. Survival rates of released *L. miniatus* on the GBR are likely to be high, as the majority of line fishing occurs in less than 25 m (Mapstone *et al.* 2001), where barotrauma is less likely to occur.

Results from the current study highlight the importance of gaining an understanding of the spatial patterns in reproductive biology of exploited fish populations. Failure to take account of spatial variation in reproductive biology in fisheries assessments and subsequent management arrangements may lead to over- or under-exploitation of stocks. For example, where spatial variation in reproductive biology of a stock precipitates spatial variation in productivity, applying uniform management arrangements may result in less productive components of the stock being overfished while potential yields may not be realised from more productive components of the stock. At face value, such spatial structure provides strong evidence in support of spatially explicit management strategies that accommodate observed spatial patterns in population biology. However, spatially explicit management strategies will be difficult to implement, particularly for coral reef fisheries, due to the high costs involved with the need for continued spatial assessments of the stock and the difficulties associated with enforcing the boundaries for spatially explicit management controls. An alternative, perhaps more conservative, approach would be to adopt a management strategy that explicitly incorporates the spatial structure into the stock assessment but applies a single management strategy across the stock as a whole that is least likely to result in the collapse of any component of the stock.

Acknowledgments

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