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## Comparative biology of tropical *Lethrinus* species (Lethrinidae): challenges for multi-species management

L. M. CURREY\*†, A. J. WILLIAMS\*‡, B. D. MAPSTONE§, C. R. DAVIES§, G. CARLOS||, D. J. WELCH\*¶, C. A. SIMPFENDORFER\*, A. C. BALLAGH\*, A. L. PENNY\*, E. M. GRANDCOURT\*\*, A. MAPLESTON\*, A. S. WIEBKIN†† AND K. BEAN\*

\*Centre for Sustainable Tropical Fisheries and Aquaculture & School of Earth and Environmental Sciences, James Cook University, Douglas, Qld 4811, Australia, §CSIRO Marine and Atmospheric Research, G. P. O. Box 1538, Hobart, Tas 7001, Australia, ||Institute of Marine and Antarctic Studies, Private Bag 129, Hobart, Tas 7053, Australia, \*\*Biodiversity Management Sector, Marine, Environment Agency – Abu Dhabi, P. O. Box 45553, Abu Dhabi, United Arab Emirates and ††Department of Environment & Natural Resources South Australia, G. P. O. Box 1047, Adelaide, SA 5001, Australia

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Life-history characteristics of six tropical *Lethrinus* species sampled from the Great Barrier Reef World Heritage Area were compared. Two species groups were identified based on fork length ( $L_F$ ): large species with maximum  $L_F > 640$  mm (longface emperor *Lethrinus olivaceus*, yellowlip emperor *Lethrinus xanthurus* and spangled emperor *Lethrinus nebulosus*) and small species with maximum  $L_F < 480$  mm (Pacific yellowtail emperor *Lethrinus atkinsoni*, pink ear emperor *Lethrinus lentjan* and ornate emperor *Lethrinus ornatus*). Lifespan was not correlated with  $L_F$ . Early growth for all species was rapid and similar during the first few years of life, but coefficients of the von Bertalanffy growth function varied considerably among species. Growth also differed between sexes for *L. atkinsoni*. Reproductive characteristics varied among species, with peak periods of spawning occurring in November to December for *L. atkinsoni*, July to August for *L. nebulosus*, September to October for *L. olivaceus* and a protracted season for *L. lentjan*, although fewer samples were available for the last two species. Sex-specific  $L_F$  and age distributions and gonad histology of *L. lentjan* were suggestive of a functional protogynous reproductive pattern, as observed in other lethrinids. Gonad histology indicated non-functional protogynous hermaphroditism for *L. atkinsoni* and *L. nebulosus*. The diversity of life histories among these closely related species emphasizes the difficulty in devising single management strategies appropriate for multi-species fisheries and illustrates the importance of understanding species-specific life histories to infer responses to exploitation.

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†Author to whom correspondence should be addressed. Tel.: +617 47814158; email: leanne.currey@my.jcu.edu.au

‡Present address: Oceanic Fisheries Programme, Secretariat of the Pacific Community, BP D5, 98848 Noumea, New Caledonia

¶Present address: C2O Fisheries, Emerald Beach, NSW 2456, Australia

## INTRODUCTION

Coral reef ecosystems contain a wide diversity of fish species, some of which support fisheries from artisanal to commercial scales (Sadovy, 2005). Coral reef fisheries are now considered unsustainable in many areas (Newton *et al.*, 2007). This status will probably be exacerbated with future changes in climate (McClanahan *et al.*, 2008; Johnson & Welch, 2010) and increased exploitation pressure driven by growth in human populations and increasing commercial demand (Newton *et al.*, 2007; Wilson *et al.*, 2008). Knowledge of life histories of exploited species is fundamental to improving fisheries management.

Many coral reef fisheries are managed at the genus or family level despite recognition of the diversity of life histories among exploited species (Choat & Axe, 1996; Grandcourt, 2002; Gust, 2004; Heupel *et al.*, 2010). The diversity of species harvested together, difficulty in obtaining species-specific catch data and the uncertainties in identification make species-specific regulation difficult. The lack of life-history data about many exploited species makes inference of vulnerability to overexploitation and the need for, and effectiveness of, multi-species management strategies largely speculative. Fishes that are long-lived, have delayed maturity, large body size and low rates of natural mortality and recruitment decline in abundance more quickly and recover in abundance more slowly following exploitation, relative to populations with opposite life-history characteristics (Jennings *et al.*, 1998). The growing evidence of substantial difference in life history even within a genus makes it increasingly clear that management strategies should not be based on assumed uniformity of life-history characteristics. Knowledge of the range of life histories of harvested species is necessary to allow evaluation of the consequences of multi-species regulations for each of the species affected and, perhaps, consideration given to precautionary management strategies appropriate to the most vulnerable of the species under common regulation.

Fishes of the family Lethrinidae (emperors) are abundant in tropical and subtropical Indo-Pacific Ocean waters and occur in a range of marine environments, including reefs, seagrass beds, estuaries, and mangroves (Young & Martin, 1982; Kulmiye *et al.*, 2002). The family is one of the most important in coral reef fisheries throughout the Indo-Pacific Ocean (Carpenter & Niem, 2001) and comprises 39 species worldwide, with 29 species in the most common genus *Lethrinus* (Carpenter & Niem, 2001). Emperors, generally, are considered to be long-lived, with maximum ages commonly >20 years (Carpenter & Niem, 2001). Larger emperors, such as spangled emperor *Lethrinus nebulosus* (Forsskål 1775), can grow to 800 mm fork length ( $L_F$ ) (Randall, 1995), while smaller species, such as slender emperor *Lethrinus variegatus* Valenciennes 1830, normally do not exceed 200 mm  $L_F$  (Carpenter & Niem, 2001).

There is evidence of protogynous hermaphroditism for the majority of emperors, with sexual transition from mature females to males (Young & Martin, 1982; Sadovy de Mitcheson & Liu, 2008). Functional protogyny is confirmed for six species of *Lethrinus*, including Pacific yellowtail emperor *Lethrinus atkinsoni* Seale 1910 and pink ear emperor *Lethrinus lentjan* (Lacépède 1802), based on reliable evidence including: stages of sexual transition identified from histological series, intersexual gonads with simultaneous presence of mature testicular and ovarian tissue, observation of functional sex change and, to a lesser extent, size- or age-biased sex ratios (Sadovy de Mitcheson & Liu, 2008). Juvenile hermaphroditism has been reported for

some species and populations, where male emperors are derived from females prior to sexual maturity (Ebisawa, 1990, 1997, 1999; Grandcourt *et al.*, 2010). This is also referred to as non-functional protogynous hermaphroditism as individuals only ever function as one sex, despite the presence of ovarian and testicular tissues in immature gonads. These species are functionally gonochoristic (Sadovy de Mitcheson & Liu, 2008). Some studies provided evidence only on overlapping male and female size frequency and male gonad morphology of secondarily derived males for *L. nebulosus* (Ebisawa, 1990, 1999, 2006), but more recent research has provided histological evidence for non-functional protogynous hermaphroditism for *L. nebulosus* (Grandcourt *et al.*, 2010; Marriott *et al.*, 2010). It is important to understand the nature and diversity of the underlying reproductive biology of harvested species as this has a substantial bearing on the probable impact and response of populations to fishing and the effectiveness of alternative management measures (Huntsman & Schaaf, 1994; Grandcourt *et al.*, 2010).

The aims of this study were to compare and contrast the life-history characteristics of emperor species common to the Great Barrier Reef (GBR) which are subject to harvest by commercial and other fisheries there and elsewhere. The  $L_F$ , age, growth, mortality and reproductive characteristics are determined for *L. atkinsoni*, *L. nebulosus*, *L. lentjan* and longface emperor *Lethrinus olivaceus* Valenciennes 1830. More limited metrics are also estimated for the rarer ornate emperor *Lethrinus ornatus* Valenciennes 1830 and yellowlip emperor *Lethrinus xanthochilus* Klunzinger 1870. Biological characteristics are compared among species (and among regions for *L. atkinsoni*), and the implications of differences are considered in relation to the probable effects of exploitation on populations of these species and implications for multi-species management strategies.

## MATERIALS AND METHODS

### SAMPLE COLLECTION

A total of 3515 individuals from six emperor species were sampled from the GBR using two methods. First, 3460 individuals were collected from reefs in four regions of the GBR across 7° of latitude [Lizard Island, 14° S; Townsville, 18° S; Mackay, 20° S and Storm Cay, 21° S (Fig. 1)] between 1995 and 2005 inclusive as part of the Effects of Line Fishing (ELF) Experiment research fishing surveys (Mapstone *et al.*, 2004). All fishes were caught by contracted commercial fishers using standard gear comprising single Mustad 4279 8/0 hooks on 36.3 kg (80 lb) monofilament handlines and Western Australian pilchard *Sardinops sagax* (Jenyns 1842) as bait. Fishing effort was distributed evenly around each reef and across two depth strata (0–12 and 12–25 m) during daylight hours (Mapstone *et al.*, 2004). Four of the six reefs in each region had been no-take zones and closed to all forms of fishing for 10–12 years prior to 1995. The remaining two reefs in each region were open to fishing historically. One of the reefs closed to fishing in each region was opened to fishing (and pulse-fished) for 1 year in 1997 with a second closed reef in each region pulse-fished for 1 year in 1999. Increased fishing was encouraged in one of the two reefs open to fishing in each region during each of these 2 years, after which those reefs were closed to further fishing for a period of 5 years (Mapstone *et al.*, 2004). Sample sizes of the six emperor species considered by the surveys here were as follows: *L. atkinsoni* (2509), *L. nebulosus* (681), *L. lentjan* (144), *L. olivaceus* (73), *L. ornatus* (28) and *L. xanthochilus* (25).

The second method of sample collection was designed to capture small individuals that were rarely caught owing to the size selectivity of the gear used in the ELF surveys. Additional samples of juvenile *L. nebulosus* (29), *L. lentjan* (25) and *L. atkinsoni* (1) were collected in

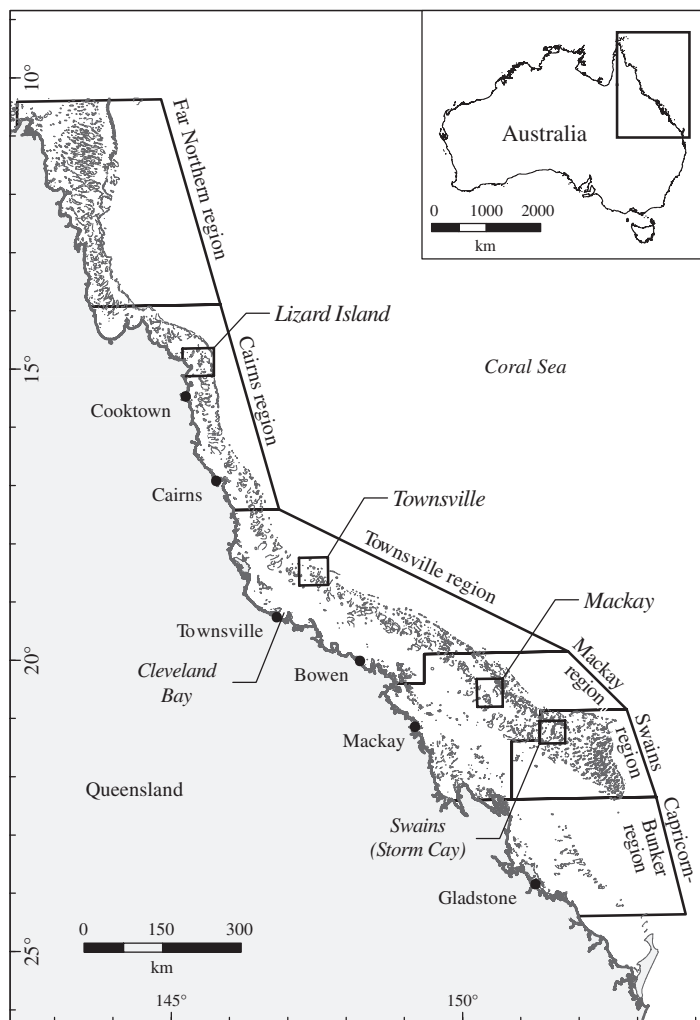


FIG. 1. Location of reefs sampled for *Lethrinus* within four regions of the Great Barrier Reef as part of the Effects of Line Fishing Experiment. Samples were collected from six reefs in each region within the areas indicated (□). Only samples from reefs for which no effects of prior or experimental fishing were evident were included for analyses to ensure that variable estimates were as near as possible to those for unfished populations. Juvenile samples were collected from Cleveland Bay, Townsville.

2008 by fishery-independent trawling and hook-and-line fishing in Cleveland Bay, Townsville (Fig. 1). Data from these samples were used to supplement data from the ELF surveys for estimation of mass-at- $L_F$  and growth only.

## PRELIMINARY ANALYSES

Estimates of life-history parameters may have been influenced by latitude (region), historical level of exploitation (open and closed reefs: zone) or experimental manipulations of fishing pressure during the ELF Experiment. The reefs sampled were subject to three treatment regimes: (1) reefs historically closed to fishing that remained closed throughout, (2) reefs historically closed to fishing that were opened for 1 year, pulse-fished and then reclosed and

(3) reefs historically open to fishing, pulsed with additional fishing for 1 year and then closed for 5 years. The objective of this study was to estimate the demographic parameters of relatively unexploited populations for the included species, predominantly from reefs that had been closed to fishing for many years. It was important to include only those other samples that could be inferred to be unaffected by historical fishing or the manipulations of the ELF Experiment while also retaining as many samples as possible to maximize sample sizes. Hence, data were included only from specimens that either (1) were from reefs that were closed to fishing before and throughout the ELF Experiment or (2) were found to have average  $L_F$ , mass and age that could be conservatively asserted to be not different ( $P > 0.05$ ) from samples collected at closed reefs. Preliminary statistical tests for (2) were possible with the available data for *L. atkinsoni*, *L. nebulosus*, *L. lentjan* and *L. olivaceus*, and resulted in exclusion of data only for *L. atkinsoni* from reefs historically open to fishing. All data, from all reefs, were included for all other species.

### SAMPLE PROCESSING

The  $L_F$  of all individuals was measured to the nearest mm and mass ( $M$ ) measured to the nearest 10 g in the field whilst fresh shortly after capture. Sagittal otoliths were removed from frozen heads following field trips, cleaned of any residual material and stored dry in paper envelopes. Otoliths were kept and read whole for *L. nebulosus* and *L. olivaceus*. Otoliths were sectioned for *L. atkinsoni* and *L. lentjan* because annual increments were difficult to distinguish in whole otoliths. These were embedded in clear casting polyester resin and cut transversely at 300–400  $\mu\text{m}$  through the core using twin diamond blades on a low speed saw. Sections were mounted on slides using the resin and covered with cover slips. Otolith sections from juveniles were polished using lapping paper prior to mounting on slides. No otoliths were sampled from *L. ornatus* and *L. xanthochilus* specimens.

Patterns of translucent and opaque increments in otoliths have been validated as being annual for a number of emperors, including *L. atkinsoni*, *L. nebulosus* and *L. lentjan* (Grandcourt, 2002; Marriott *et al.*, 2010) and ageing in this study was based on the assumption that increments had formed annually in the otoliths that were read from specimens considered likely to be at least 1 year of age. Sectioned and whole otoliths (placed in immersion oil) were viewed under reflected light and opaque increments were counted as detailed in Williams *et al.* (2003). Daily increments of sectioned otoliths from smaller, presumably, juvenile specimens were viewed using high power with transmitted light. The opaque increment closest to the margin of the otolith was only included in the count when the reader interpreted the increment as completely formed by reference to the otolith margin and the width of the penultimate increment. All otoliths were read by experienced readers, qualified against reference sets for each species, with a minimum of 24 h between repeated readings of the same otolith. There were a large number of otoliths from *L. nebulosus* and *L. atkinsoni*, so these otoliths were read once followed by a second reading of 25% of the sample to monitor for reading drift and precision. The precision of age estimates from the first and second reads was calculated using the index of average per cent error ( $I_{APE}$ ) (Beamish & Fournier, 1981) to set an acceptable level of precision ( $I_{APE} < 5.5\%$ ; Campana, 2001) for acceptance of final age estimates. Drift in readings (bias) was tested using age-bias plots (Campana *et al.*, 1995). The first or only count was accepted as the final age for *L. atkinsoni* and *L. nebulosus* if there was no significant drift or bias. Due to the small number of *L. lentjan* and *L. olivaceus* otoliths, each otolith was read three times and the age-bias plots and  $I_{APE}$  across all the three reads were examined. The final age was assigned as the agreed count between any two counts. Otoliths for which there was no agreement among three counts were excluded from analyses. Daily increments were counted three times for otoliths from juvenile specimens and the average count (as a proportion of the year) was assigned as the final age estimate.

Gonads of fishes from ELF samples were removed from fresh fishes in the field or from frozen fishes upon return to the laboratory. Gonads sampled up to 1999 were stored in FAACC (4% formaldehyde, 5% acetic acid and 1.3% calcium chloride) immediately after removal and in 10% phosphate-buffered formalin if sampled after 1999. Gonads were dried of excess fixative on absorbent paper after fixation and mass was measured to  $\pm 0.01$  g using a standard balance. Mass of gonads for which one lobe was damaged during processing was



estimated by doubling the mass of the intact lobe assuming that both lobes were of equal size (Bean *et al.*, 2003). Histological sections were taken and prepared following Adams (2003) and reproductive stage was classified as the most advanced non-atretic cell type present (West, 1990). The presence of brown bodies, atretic oocytes, vascularization and the relative thickness of the gonad wall were noted, all of which may indicate prior spawning (Sadovy & Shapiro, 1987). Ovaries and testes were classified into developmental stages adapted from Bean *et al.* (2003) (Table I). Females were classified into six stages: immature, resting, ripe, running ripe, spent and undetermined inactive (Adams, 2003). Males were classified into three stages: resting, ripe and spent.

## DEMOGRAPHIC ANALYSES

The  $L_F$  and age frequency distributions were constructed for each species using data from the ELF sampling only. A large sample size for *L. atkinsoni* enabled plotting of  $L_F$  and age frequency distributions for each region. The relationship between  $L_F$  and  $M$  was described using a power function of the form:  $M = aL_F^b$ , where  $a$  is the coefficient of the power function and  $b$  is the exponent. ANCOVAs were used to test for significant differences in transformed (linear)  $M$ -at- $L_F$  relationships among species, with  $L_F$  as the covariate of  $M$ .

The von Bertalanffy growth function (VBGF) was fitted by non-linear least-squares regression of  $L_F$  on age for each species, using data from both sampling methods. The form of the VBGF used to model length-at-age data was  $L_t = L_\infty(1 - e^{-K(t-t_0)})$ , where  $L_t$  is the  $L_F$  at age  $t$ ,  $L_\infty$  is the mean asymptotic  $L_F$ ,  $K$  is the growth coefficient or rate at which  $L_\infty$  is approached,  $t$  is the age of the fish and  $t_0$  is the age at which the fish has a theoretical  $L_F$  of zero. The VBGF was fitted with  $t_0$  constrained to zero ( $t_0 = 0$ ) for each species as the lack of smaller individuals produced biologically unrealistic estimates of growth in the sample and constraining  $t_0$  allowed biologically sensible comparisons among species for which a common age at  $L_F$  zero could be assumed (Kritzer *et al.*, 2001; Choat & Robertson, 2006). VBGFs were compared among species, and among regions (for *L. atkinsoni*), using likelihood ratio tests (Kimura, 1980) which are considered as the most reliable procedures for such comparisons (Cerrato, 1990). Multiple pair-wise tests were conducted and the critical significant  $P$ -value was adjusted accordingly using Bonferroni adjustment (Haddon, 2001). Sex-specific VBGFs were compared for *L. atkinsoni* and *L. nebulosus* as an exploratory measure to determine any difference between sexes, as these species have been identified as non-functional protogynes (functional gonochores) (Grandcourt *et al.*, 2010; Marriott *et al.*, 2010). A common range of age classes was used in all statistical comparisons to assure validity of the tests (Haddon, 2001).

The instantaneous rate of total mortality ( $Z$ ) was estimated for each species from age-based catch curves (Ricker, 1975) using only data from ELF samples and following the approach used by Newman *et al.* (2000) and Williams *et al.* (2003). Additional estimates of total mortality ( $Z$ ) were obtained for each species by fitting the linear equation:  $\ln Z = 1.44 - 0.982 \ln t_{\max}$ , where  $t_{\max}$  is the maximum age observed (Hoenig, 1983). This method was also used to derive regional estimates of  $Z$  for *L. atkinsoni* as data were insufficient for catch curves in all regions.

## REPRODUCTIVE BIOLOGY

An estimate of spawning season for each species was inferred from examination of ELF samples. These surveys were primarily done over 4–5 months during the austral spring and summer of each year to coincide with the spawning period of common coral trout *Plectropomus leopardus* (Lacépède 1802) (Mapstone *et al.*, 2004) and so samples were not available for all months throughout the year. The gonado-somatic index ( $I_G = M_G/M \times 100$ , where  $M_G$  = gonad mass) was calculated for each sample to provide a relative measure of reproductive activity (Sadovy, 1996). The  $M$  for specimens that had not been weighed at the time of capture was estimated using the species-specific  $L_F$  and  $M$  relationship derived from weighed individuals (*L. atkinsoni*:  $n = 94$ ; *L. nebulosus*:  $n = 151$ ; *L. lentjan*:  $n = 17$ ; *L. olivaceus*:  $n = 15$ ). It was assumed that estimates of  $M$  represent a reasonable relative index for  $I_G$  because only the monthly patterns in  $I_G$ , rather than the absolute values of  $I_G$ , were

TABLE I. Histological description of *Lethrinus* spp. reproductive development

Developmental stage	Histological description
Immature female	Ovary small, dominated by pre-vitellogenic oocytes and strands of stromal tissue within the lamellae filamentous or absent. No evidence of prior spawning; no brown bodies, oocyte atresia or intra-lamellar muscle bundles
Resting female	Ovary oval in transverse section, dominated by pre-vitellogenic oocytes. Evidence of prior spawning indicated by the presence of brown bodies, atretic oocytes and intra-lamellar muscle bundles
Ripe female	Ovaries in active vitellogenesis, yolk globule and occasionally migratory nucleolus stages present. Thin gonad wall, oocyte atresia and brown bodies rare and strands of stromal tissue within the lamellae were thin
Running ripe female	Ovary in active vitellogenesis, containing hydrated oocytes, yolk globule and migratory nucleus stage oocytes also present. Post-ovulatory follicles, indicative of recent spawning, occasionally present. Brown bodies and oocyte atresia rare and strands of stromal tissue within the lamellae thin and filamentous
Spent female	Ovary generally disorganized and undergoing atresia, with muscle bundles and extensive vascularization. Many contain brown bodies. Pre-vitellogenic oocytes, the most advanced healthy oocyte present
Undetermined inactive female	Ovary contains some gonial and pre-vitellogenic oocytes but unable to determine if fish has spawned previously (mature) and is in a resting state or is an immature female
Resting male	Testes triangular in transverse section with ventral ovarian lumen present. Dominated by testicular tissue which may contain crypts of gonial and spermatocytes. Any spermatozoa present is commonly found in spermatocysts alongside inter-lamellar mesenteries. Evidence of prior spawning as a male indicated by well-developed, but collapsed and empty, major sperm sinuses
Ripe male	Testis dominated by spermatozoa, both within spermatocysts and filling all sperm sinuses. Early stages of sperm development are rare and occur along the peripheral margins of the gonad lamellae
Spent male	Testis is loose, disrupted and highly vascularized, containing few spermatocysts (ruptured) of any sperm stage. Sperm sinuses are empty or collapsed

required to determine the spawning season. The proportion of samples in each mature female and male reproductive development stage in each month were also plotted for each species to provide alternative indicators of spawning activity in each month.

The  $L_F$  and age at sex change was estimated by regression for each species (ELF samples) using the logistic equation:  $P_s = [1 + e^{-\ln 19(s-s_{50})(s_{95}-s_{50})}]^{-1}$ , where  $P_s$  is the proportion of males (relative to mature females) in each 20 mm  $L_F$  class or at age  $s$ , and  $s_{50}$  and  $s_{95}$  are the  $L_F$  or age at which 50% and 95% of the population are males.

Sex ratio (mature females:mature males) was estimated for each species and compared to 1:1 using  $\chi^2$  goodness of fit tests with Yates correction for continuity (d.f. = 1).

## RESULTS

### DEMOGRAPHIC ANALYSES

The six fishes examined were divided into two groups based on size characteristics (Fig. 2). *Lethrinus nebulosus*, *L. olivaceus* and *L. xanthochilus* had large maximum  $L_F$  (640, 734 and 644 mm) and large modal  $L_F$  (each 460 mm). *Lethrinus atkinsoni*, *L. lentjan* and *L. ornatus* had small maximum  $L_F$  (480, 388 and 363 mm) and small modal  $L_F$  (260–300 mm).

Age estimates were relatively precise for *L. atkinsoni* ( $I_{APE} = 2.68\%$ ) and *L. nebulosus* ( $I_{APE} = 3.16\%$ ), but less precise for *L. lentjan* ( $I_{APE} = 5.98\%$ ) and *L. olivaceus* ( $I_{APE} = 9.96\%$ ). Age-bias plots for all species illustrated no consistent pattern of drift between otolith increment readings, with overlap in 95% C.I. for all ages (Fig. 3).

Age frequency distributions varied considerably for each of the four species for which data were available. The modal age of the samples, indicating full recruitment to the common gear configuration used in the GBR line fisheries, was 3 years for *L. olivaceus*, 4 years for *L. nebulosus*, 8 years for *L. lentjan* and 16 years for *L. atkinsoni* (Fig. 4) corresponding to c. 20, 17, 42 and 44% of estimated maximum age. The catch of the larger species (*L. nebulosus* and *L. olivaceus*) was predominate in younger age classes (<6 years), with right-skewed frequency distributions and maximum ages of 24 and 15 years. The smaller *L. atkinsoni* and *L. lentjan* had older modal ages, a greater proportion of samples at older ages, and maximum ages of 36 and 19 years, respectively (Fig. 4). Maximum size was not correlated with maximum age ( $r^2 = 0.15$ ,  $P > 0.05$ ).

A large sample size enabled investigation of regional  $L_F$  frequency and age distributions for *L. atkinsoni*. Modal size was smallest in the most northern region, Lizard Island (300 mm), while all other regions shared a slightly larger modal size (320 mm) (Fig. 5). The largest *L. atkinsoni* individuals (>420 mm) were sampled from the most southern region, Storm Cay. A similar range of ages was observed in all regions, although a small number of older individuals (>30 years) were sampled in Storm Cay (Fig. 5). The modal age was greatest in Storm Cay (21 years), followed by Lizard Island (18 years), Mackay (15 years) and Townsville (10 years) (Fig. 5).

The slope of the  $M$  and  $L_F$  relationship indicated that species become more heavy-bodied with increasing  $L_F$  and the relationship between  $M$  and  $L_F$  was approximately isometric ( $b = c. 3$ ) for *L. atkinsoni*. Growth was positively allometric for *L. olivaceus* which became slightly more rotund with age when compared to *L. nebulosus* and *L. lentjan*, which had negatively allometric growth (Table II).

The  $L_F$ -at-age data and model fits of the VBGF differed among species (Table II). Likelihood ratio tests revealed that patterns of growth differed significantly among species ( $\chi^2 = 242.15$ , d.f. = 9,  $P < 0.001$ ) and the growth pattern was significantly different between each species pair except between *L. atkinsoni* and *L. lentjan* (Table III). There was no significant difference in growth among regions of the GBR



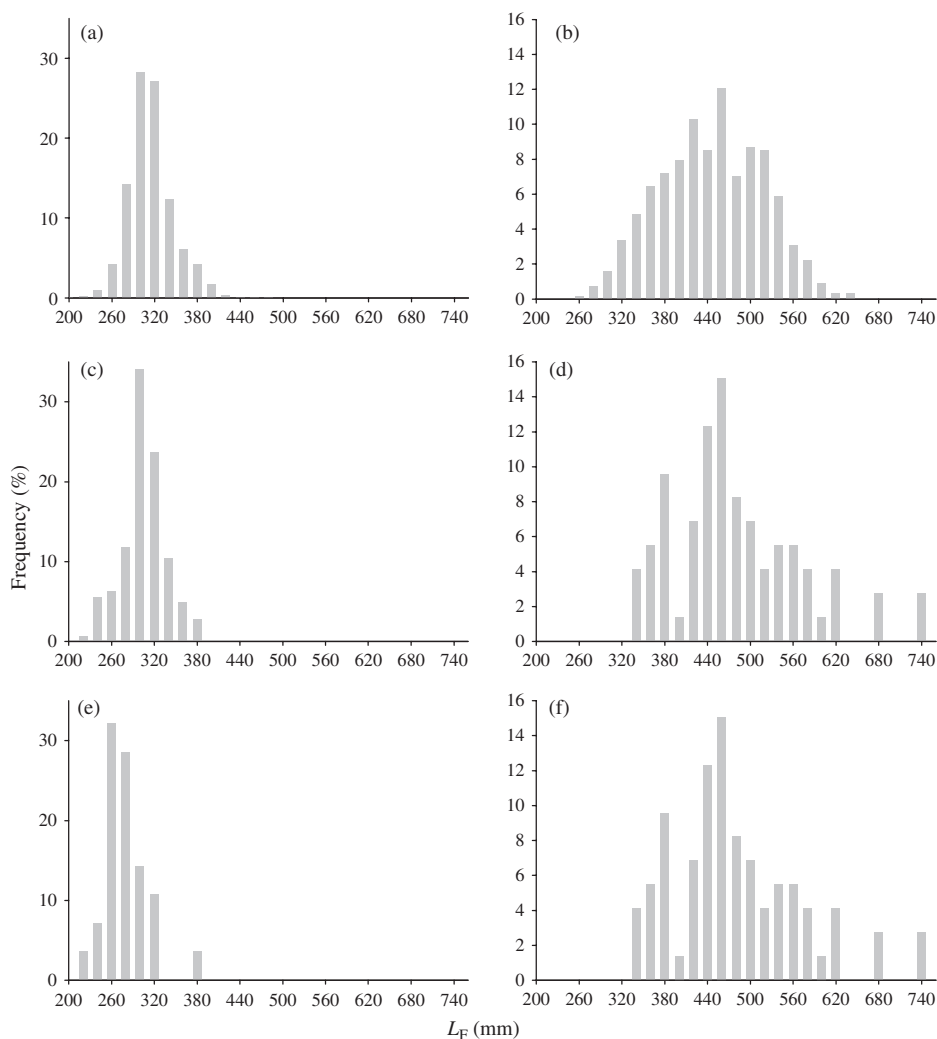


FIG. 2. Fork length ( $L_F$ ) per cent frequency distributions for (a) *Lethrinus atkinsoni* ( $n = 1710$ ), (b) *Lethrinus nebulosus* ( $n = 681$ ), (c) *Lethrinus lentjan* ( $n = 144$ ), (d) *Lethrinus olivaceus* ( $n = 73$ ), (e) *Lethrinus ornatus* ( $n = 25$ ) and (f) *Lethrinus xanthurus* ( $n = 28$ ) on the Great Barrier Reef (note difference in y-axes).

for *L. atkinsoni* ( $\chi^2 = 0.57$ , d.f. = 9,  $P > 0.05$ ). Species with greater sample sizes displayed higher variability in  $L_F$ -at-age (Fig. 6). The presence of small young individuals provided better estimates of early growth in species for which these were available in adequate numbers (*L. nebulosus* and *L. lentjan*). Thus, growth estimates were constrained to  $t_0 = 0$  as a sensible estimate for the parameter and for consistency in comparisons as juveniles were not available for all species (Table II). *Lethrinus nebulosus* and *L. lentjan* displayed the highest values of  $K$ , and reached an  $L_\infty$  by  $<10$  and  $<5$  years of age, with slow growth thereafter. Similarly, *L. atkinsoni* had a relatively flat growth curve, with rapid growth in the first 5–10 years

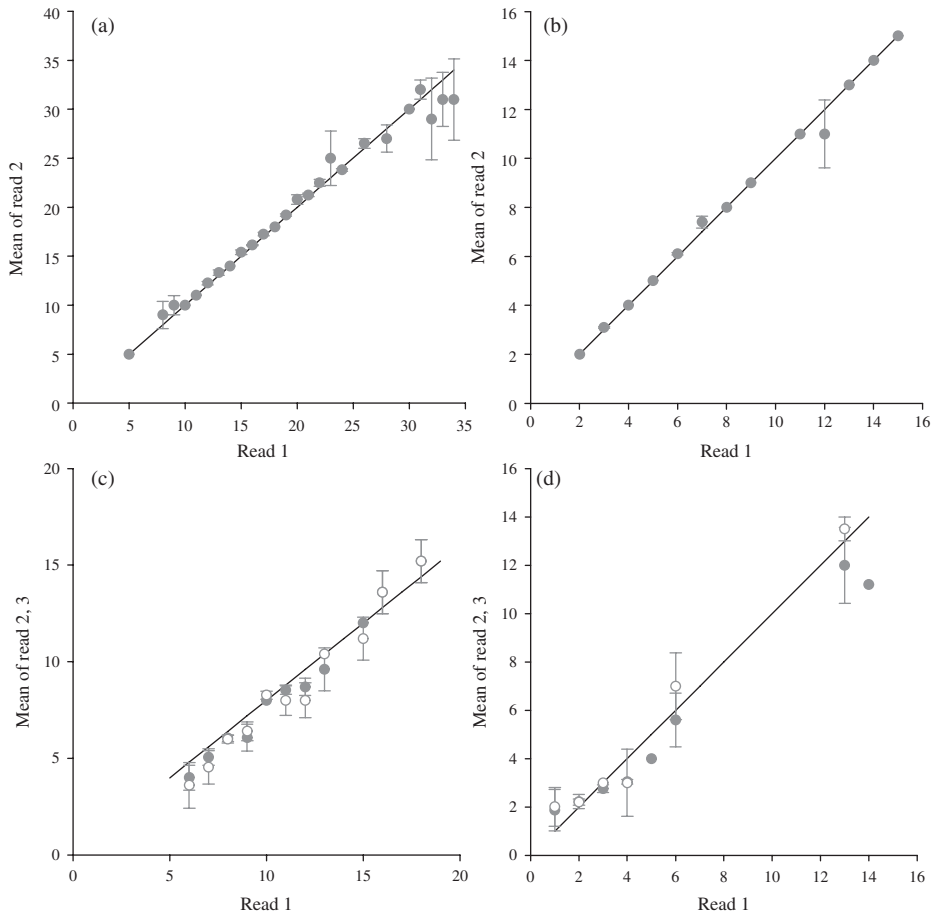


FIG. 3. Age-bias plots (with 95% C.I.) for (a) *Lethrinus atkinsoni*, (b) *Lethrinus nebulosus*, (c) *Lethrinus lentjan* and (d) *Lethrinus olivaceus*.

of life and slower subsequent growth. *Lethrinus olivaceus* was longer for any given age <15 years and reached a larger average  $L_{\infty}$  than all other species. The paucity of larger, older samples for *L. olivaceus* (>5 years) and *L. nebulosus* (>15 years), however, influenced the estimate of growth for these species. Percent lifespan at which 50%  $L_{\infty}$  was reached was similar among species with 50%  $L_{\infty}$  reached at young ages (1–2 years) relative to maximum ages for all species (Table II).

Growth patterns by sex for *L. atkinsoni* and *L. nebulosus* were also investigated as previous studies have identified these species as non-functional protogynous hermaphrodites. Sex-specific growth plots of  $L_F$ -at-age for females and males overlapped in all species (Fig. 6). Pair-wise comparisons for *L. atkinsoni* and *L. nebulosus* indicated that VBGF growth estimates differed between sexes for *L. atkinsoni* ( $\chi^2 = 28.02$ , d.f. = 3,  $P < 0.001$ ), with males growing faster to asymptote (higher  $K$ ), reaching a smaller  $L_{\infty}$ , lower percent lifespan at 50%  $L_{\infty}$  and 50%  $L_{\infty}$  reached at a younger age relative to the females (Table II). The paucity of individuals of age <5 years for which sex was identified, however, may have influenced

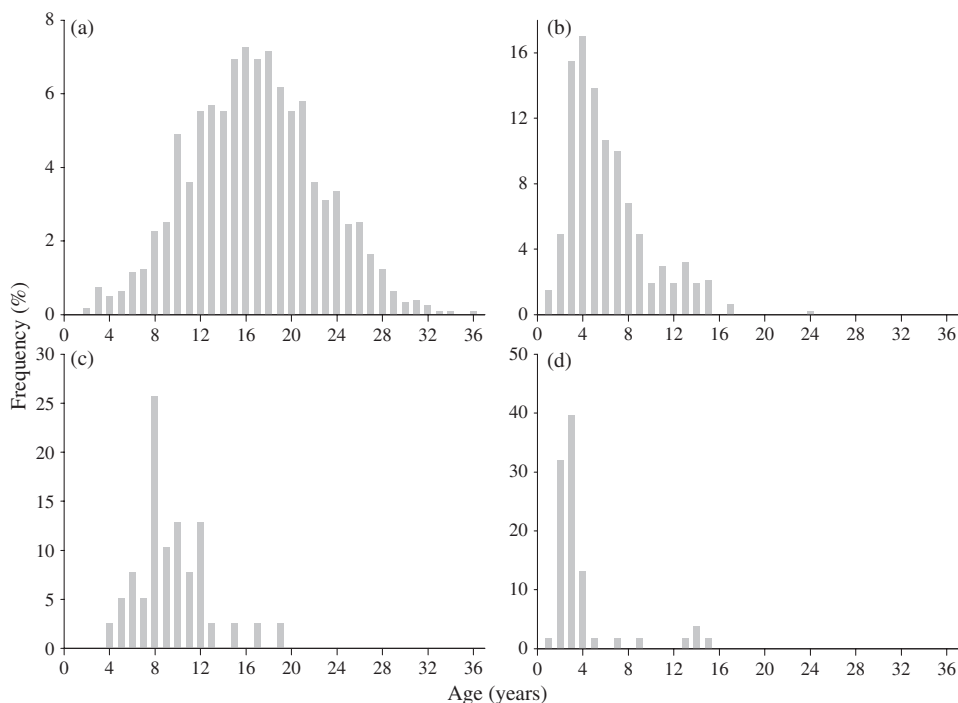


FIG. 4. Age per cent frequency distributions for (a) *Lethrinus atkinsoni* ( $n = 1227$ ), (b) *Lethrinus nebulosus* ( $n = 470$ ), (c) *Lethrinus lentjan* ( $n = 39$ ) and (d) *Lethrinus olivaceus* ( $n = 53$ ) on the Great Barrier Reef (note difference in y-axes).

the sex-specific growth estimates. VBGF estimates were not significantly different between sexes for *L. nebulosus* ( $\chi^2 = 2.13$ , d.f. = 3,  $P > 0.05$ ).

The estimates of  $Z$  from catch curves ranged from 0.21 to 0.25 year<sup>-1</sup> (Fig. 7 and Table IV), but did not differ significantly among species ( $F_{2,93} = 2.13$ ,  $P > 0.05$ ). Low sample sizes for *L. lentjan* resulted in a high level of uncertainty in estimates of  $Z$ . The low frequencies of *L. olivaceus* at older age classes combined with the criteria used for inclusion of data in catch curves would have resulted in estimates based on only two data points and so it was not possible to estimate  $Z$  from catch curves for this species. Estimates of  $Z$  from the Hoenig (1983) method and from catch curves were similar for *L. lentjan*, but Hoenig (1983) estimates were lower than those from catch curves for all other species (Table IV). Region-specific estimates of  $Z$  for *L. atkinsoni* from the Hoenig (1983) method varied slightly, with mortality lowest for Storm Cay. Mortality was greater and similar among Lizard Island, Mackay and Townsville regions (Table IV).

## REPRODUCTIVE BIOLOGY

Trends in mean  $I_G$  and developmental stages of ovarian tissue, for the months from which gonad samples were collected, indicated differences in the timing of reproduction among the four species examined. Mean values of  $I_G$  were highest, corresponding to a peak spawning period, for *L. atkinsoni* females in November

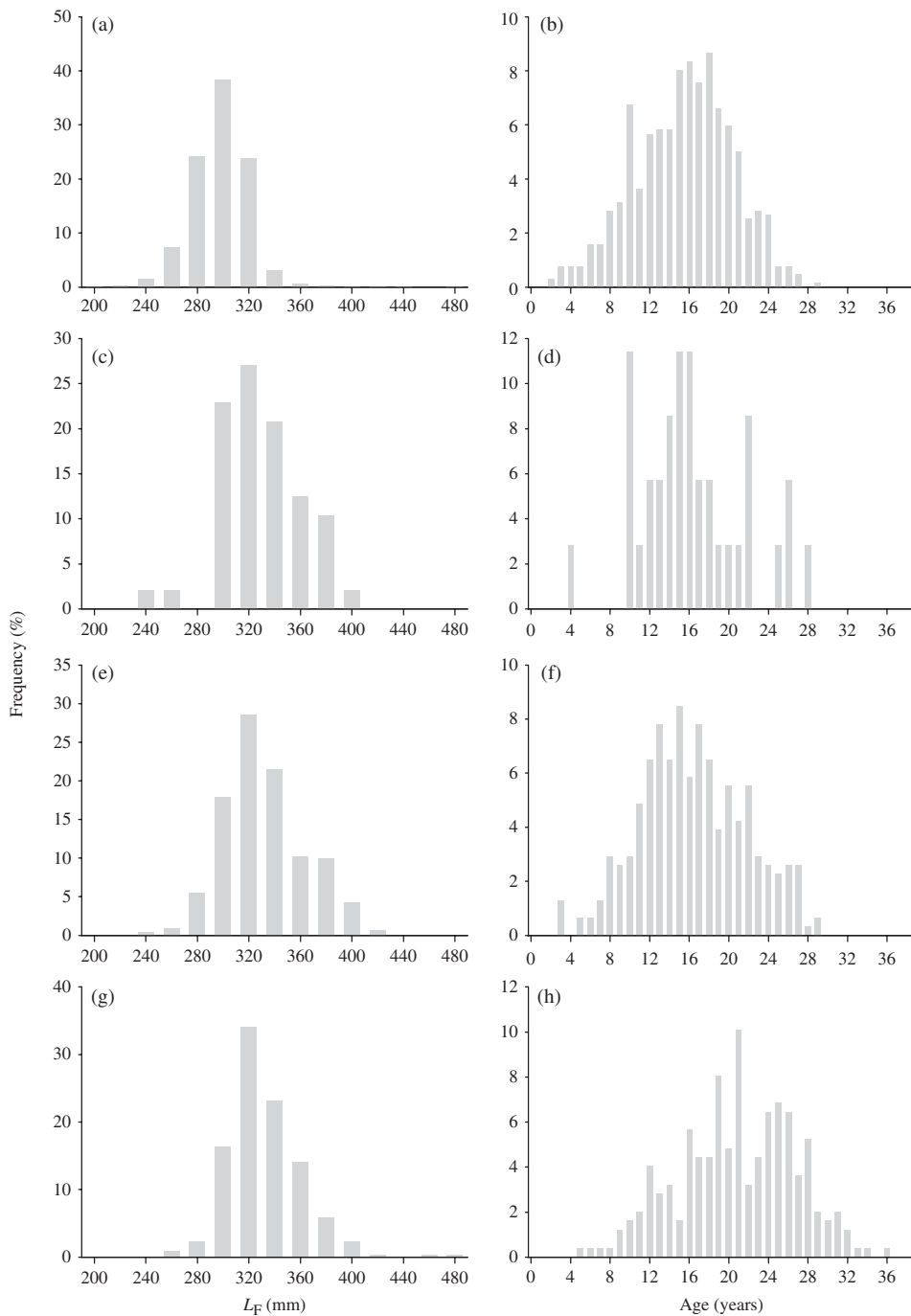


FIG. 5. (a, c, e, g) Fork length ( $L_F$ ) and (b, d, f, h) age frequency distributions for *Lethrinus atkinsoni* among four regions: (a, b) Lizard Island, (c, d) Townsville, (e, f) Mackay and (g, h) Storm Cay on the Great Barrier Reef. Sample sizes ( $n$ ) are: 879 (a); 635 (b); 48 (c); 35 (d); 441 (e); 307 (f); 341 (g); 248 (h).

TABLE II. Growth parameter estimates for the fork length ( $L_F$ ) and mass ( $M$ ) relationship, von Bertalanffy growth function (VBGF) coefficients ( $L_\infty$  = asymptotic  $L_F$ ;  $K$  = the von Bertalanffy growth coefficient;  $t_0$  = the age at theoretical  $L_F = 0$ ), age at 50%  $L_\infty$  and % lifespan at 50% mean  $L_\infty$  for four *Lethrinus* species from the Great Barrier Reef.  $a$  and  $b$  are coefficients of the relationship between  $L_F$  and  $M$  ( $M = aL_F^b$ ). Effects of Line Fishing data were used for all analyses, but juvenile samples were used only in estimates of  $L_F$  and  $M$  relationships and growth. All VBGF estimates were constrained by  $t_0 = 0$ . Sex-specific VBGF estimates are provided for *Lethrinus atkinsoni*

Species	$a$ ( $\times 10^{-8}$ )	$b$ ( $\pm 95\%$ C.I.)	$L_\infty$ (mm)	$K$ ( $\text{year}^{-1}$ )	$t_0$ (year)	Age (years) at 50% $L_\infty$	% Lifespan at 50% $L_\infty$
<i>L. atkinsoni</i>	1.60	3.03 (2.94–3.12)	322	0.32	0	2	5.56
<i>L. atkinsoni</i> (females)			332	0.25	0	2	6.25
<i>L. atkinsoni</i> (males)			311	0.42	0	1	3.23
<i>Lethrinus nebulosus</i>	3.95	2.86 (2.80–2.91)	477	0.62	0	1	4.17
<i>Lethrinus lentjan</i>	7.20	2.75 (2.60–2.89)	305	0.75	0	1	5.26
<i>Lethrinus olivaceus</i>	0.38	3.20 (3.09–3.32)	660	0.47	0	1	7.69

to December and July to August for *L. nebulosus* females (Fig. 8). High spawning activity (mean  $I_G$ ) was suggested in September to October for both *L. olivaceus* and *L. lentjan* but data were missing for some months and so these patterns need to be viewed with caution.

The temporal pattern in spawning activity based on mature ovarian stages (ovaries in active vitellogenesis) followed a pattern similar to the  $I_G$  values for all species (Fig. 8), as ripe females were observed in periods of high mean  $I_G$  values. It is the presence of hydrated (running ripe) females, however, that is the definitive indicator of peak periods of spawning activity (Table I). Few females in this developmental stage were observed for any species. Presence of *L. atkinsoni* females with hydrated oocytes coincided with high mean  $I_G$  in November to December and September to

TABLE III. Results of likelihood ratio tests comparing von Bertalanffy growth function (constrained estimates,  $t_0 = 0$ ) (see Table II) between *Lethrinus* species for age classes 1–15 years

Species	d.f.	$\chi^2$	$P$
All species	9	242.15	<0.001
<i>Lethrinus nebulosus</i> v. <i>Lethrinus olivaceus</i>	3	154.03	<0.001
<i>Lethrinus nebulosus</i> v. <i>Lethrinus atkinsoni</i>	3	1408.73	<0.001
<i>Lethrinus nebulosus</i> v. <i>Lethrinus lentjan</i>	3	283.25	<0.001
<i>Lethrinus olivaceus</i> v. <i>Lethrinus atkinsoni</i>	3	954.80	<0.001
<i>Lethrinus olivaceus</i> v. <i>Lethrinus lentjan</i>	3	231.86	<0.001
<i>Lethrinus atkinsoni</i> v. <i>Lethrinus lentjan</i>	3	2.45	>0.05

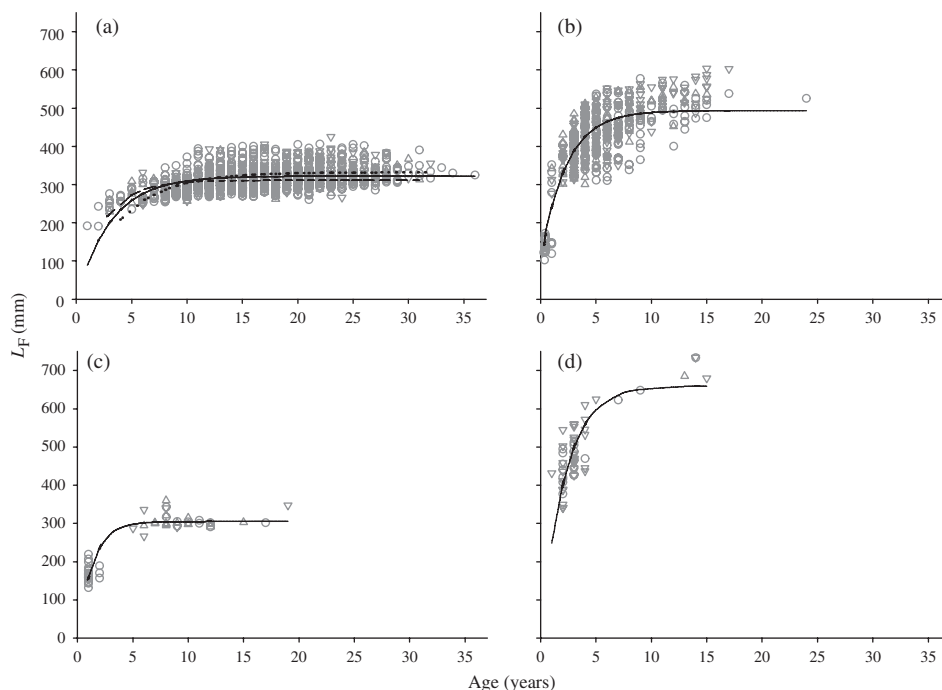


FIG. 6. Fork length ( $L_F$ )-at-age data and fitted von Bertalanffy growth function curves for four *Lethrinus* species: (a) *Lethrinus atkinsoni* ( $n = 1222$ ), (b) *Lethrinus nebulosus* ( $n = 482$ ), (c) *Lethrinus lentjan* ( $n = 55$ ) and (d) *Lethrinus olivaceus* ( $n = 53$ ) from the Great Barrier Reef Effects of Line Fishing (unknown sex,  $\circ$ ; females,  $\blacktriangle$ ; males,  $\triangle$ ) and Cleveland Bay juvenile samples ( $\bullet$ ). Separate growth curves are shown for male (---), female (.....) and all (—) individuals for *L. atkinsoni*.

October. Hydrated oocytes were also identified during the potential peak spawning months of September to October for *L. lentjan* but one running ripe female was also identified in March to April. These running ripe females, combined with ripe females observed in all months sampled, suggest a protracted spawning season.

No intersexual gonads were observed in this study, but some male testes contained remnant female oocytes and all male testes contained a lumen indicating male development from a female ovary. The proportion of females and males at  $L_F$  or age was variable (Fig. 9) in each species.

The only species for which a functional protogynous ontogeny was indicated by the fit of a logistic function was for sex and  $L_F$  data for *L. lentjan* [Fig. 9(e)]. This species showed an increase in proportion of males with increasing  $L_F$ , with 50 and 95% of the male population at 270.03 and 317.75 mm (Fig. 9). There were insufficient age data to fit any model to the proportion of males-at-age for *L. lentjan* [Fig. 9(f)].

The other three species did not display evidence for functional protogynous sex change with  $L_F$  or age. A greater proportion of males at smaller  $L_F$  were observed for *L. atkinsoni* and no pattern was indicated with age [Fig. 9(a), (b)]. The proportion of males with  $L_F$  and age appeared to be similar for *L. nebulosus* [Fig. 9(c), (d)]. There were insufficient samples of *L. olivaceus* to determine any relationship in  $L_F$  or age at sex change (only two males).



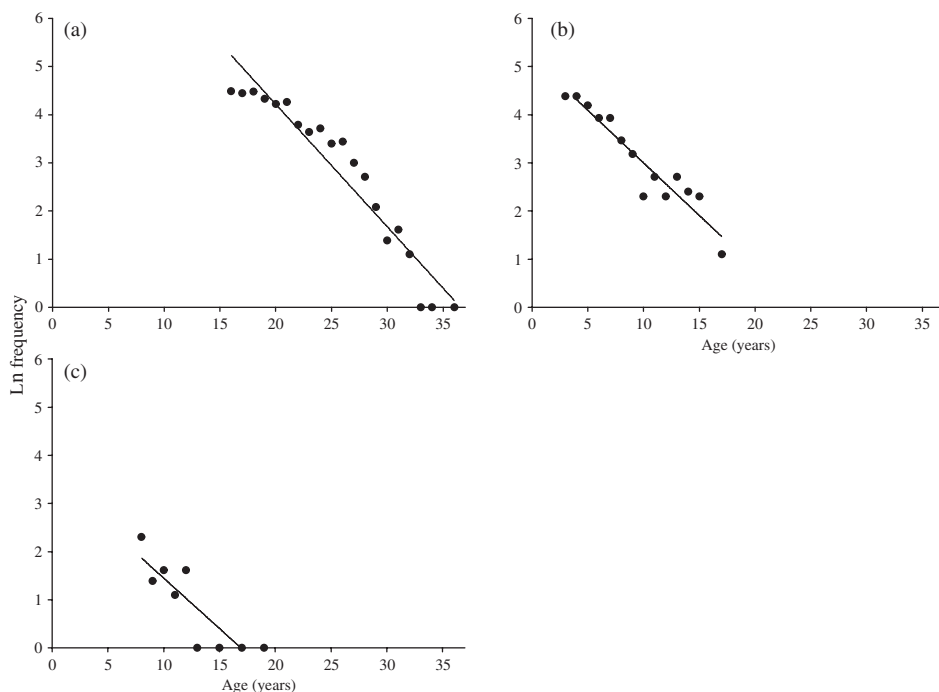


FIG. 7. Catch curves for three *Lethrinus* species: (a) *Lethrinus atkinsoni*, (b) *Lethrinus nebulosus* and (c) *Lethrinus lentjan* from the Great Barrier Reef. The curves were fitted by: (a)  $y = -0.255x + 9.311$  ( $r^2 = 0.916$ ), (b)  $y = -0.219x + 5.183$  ( $r^2 = 0.907$ ) and (c)  $y = -0.209x + 3.541$  ( $r^2 = 0.743$ ). The slopes of the regressions are an estimate of the rate of total mortality ( $Z$ ) for each species.

The observed sex ratio was statistically different to 1:1 for three of the four species. *Lethrinus atkinsoni* ( $\chi^2 = 16.42$ , d.f. = 1,  $P < 0.001$ ) and *L. olivaceus* ( $\chi^2 = 31.44$ , d.f. = 1,  $P < 0.001$ ) were both female-biased (22.50:1 and 1.44:1, respectively) and *L. lentjan* ( $\chi^2 = 5.57$ , d.f. = 1,  $P < 0.05$ ) was male-biased (0.57:1). The sex ratio for *L. nebulosus* was not significantly different from 1:1 ( $\chi^2 = 0.48$ , d.f. = 1,  $P > 0.05$ ).

## DISCUSSION

Some clear similarities and substantial differences in aspects of life histories were evident among four exploited *Lethrinus* species in the GBR. Estimated rates of total mortality and growth in the first few years of life were remarkably similar among species, but species varied in lifespan, maximum size and spawning season. Such variation in life histories among a suite of species captured within a single fishery is likely to precipitate different responses to fishing pressure. These results have important implications for the development of management strategies for multi-species fisheries and suggest that accounting for species-specific variation in life history should be a consideration in setting multi-species harvest regulations.

The size and age distributions of the species were in part a function of the size selectivity of the sampling gear used. Young, small individuals were not adequately

TABLE IV. Maximum age ( $A_{\max}$ ), age range and estimates of mean  $\pm$  s.e. total mortality ( $Z$ ) from catch curves and from the Hoenig (1983) method for four *Lethrinus* species from the Great Barrier Reef. Effects of Line Fishing data were used for mortality estimates, while juvenile samples were only used in age range. Region-specific estimates are provided for *L. atkinsoni*

Species	$A_{\max}$ (range) (years)	Catch curve $Z \pm$ s.e. (year <sup>-1</sup> )	Hoenig $Z$ (year <sup>-1</sup> )
<i>Lethrinus atkinsoni</i>	36 (1–36)	0.26 $\pm$ 0.01	0.12
<i>L. atkinsoni</i> (Lizard Island)	29 (2–29)	–	0.15
<i>L. atkinsoni</i> (Townsville)	28 (4–28)	–	0.16
<i>L. atkinsoni</i> (Mackay)	29 (3–29)	–	0.15
<i>L. atkinsoni</i> (Storm Cay)	36 (5–36)	–	0.13
<i>Lethrinus nebulosus</i>	24 (0.3–24)	0.22 $\pm$ 0.02	0.17
<i>Lethrinus lentjan</i>	19 (1–19)	0.21 $\pm$ 0.02	0.22
<i>Lethrinus olivaceus</i>	15 (1–15)	–	0.28

sampled and no fishes of  $<217$  mm  $L_F$  were obtained because they were less vulnerable to the gear used in this study. Other factors such as species-specific behaviour, habitat preferences of species, limitations of the ELF surveys to depths shallower than 30 m (Marriott *et al.*, 2007) and sampling only during daylight hours (Newman & Williams, 1995) also may have influenced species-specific availability to the sampling protocol used. Pooling samples across years and regions would also probably have increased variation in the demographic metrics if regional variation in size or age existed (Ruttenberg *et al.*, 2005; Williams *et al.*, 2007a), which could be investigated only for *L. atkinsoni*. Regional comparisons for *L. atkinsoni* (this study) identified variation in modal size and age, mortality estimates, but no significant differences in growth with region were observed. Nevertheless, this study provides valuable baseline information for this genus, and the sampling strategy and gear used reflects those used by the commercial and recreational line fisheries on the GBR, which are managed by uniform strategies over all the regions sampled. Thus, the demographic characteristics of the sample were likely to reflect the properties of relatively unfished populations that would be affected by harvest on the GBR.

Maximum age for lethrinids varies among species and locations, and lifespan does not appear to be linked with size. The species with the highest maximum ages (*L. atkinsoni* and *L. nebulosus*) displayed very different  $L_{\infty}$ , supporting the assertion of a lack of relationship between age and length across the genus. The longest lived species in this study was the smaller *L. atkinsoni*, with estimated maximum age of 36 years. This is the oldest individual recorded for the *Lethrinus* genus. The previous maximum age for this species was estimated at 24 years in Okinawa (Ebisawa & Ozawa, 2009) and New Caledonia (Loubens, 1980a). Other longer lived emperors include *L. nebulosus* (30 years, Marriott *et al.*, 2011; 29 years, Al-Mamry *et al.*, 2007; 28 years, Andrews *et al.*, 2011; 24 years, this study), sky emperor *Lethrinus mahsena* (Forsskål 1775) (27 years; Grandcourt, 2002) and trumpet emperor *Lethrinus miniatus* (Forster 1801) (24 years, Ebisawa, 2006; Ebisawa & Ozawa, 2009). The maximum age estimate for *L. lentjan* in this study is the same as that reported by Grandcourt (2002). A similar maximum age estimate for *L. nebulosus* of 21 years

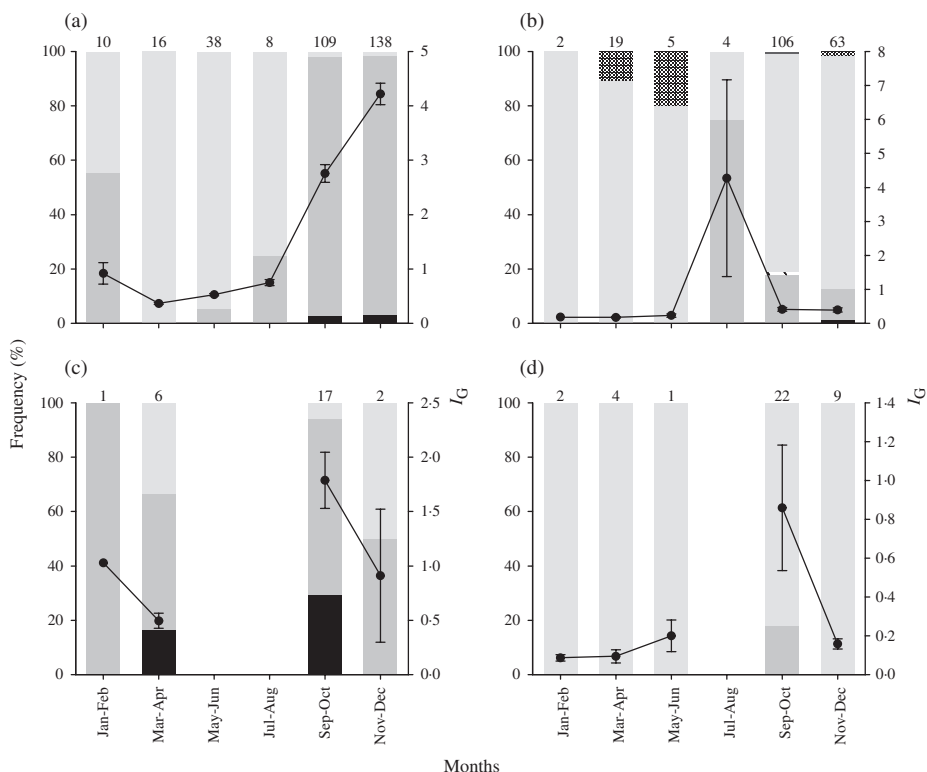


FIG. 8. Monthly percent frequencies of ovarian stages [immature (▨), undetermined inactive (■), resting (□), spent (▤), ripe (▦) and running ripe (▧)] and mean  $\pm$  s.e. monthly gonado-somatic index ( $I_G$ ) values ( $\bullet$ ) for female (a) *Lethrinus atkinsoni*, (b) *Lethrinus nebulosus*, (c) *Lethrinus lentjan* and (d) *Lethrinus olivaceus* from the Great Barrier Reef. Numbers above bars show sample sizes.

was observed by Edwards *et al.* (1985) in the Gulf of Aden, although individuals of 28–30 years have been reported elsewhere (Al-Mamry *et al.*, 2007; Andrews *et al.*, 2011; Marriott *et al.*, 2011). Grandcourt *et al.* (2006) reported a much younger age of 14 years for the *L. nebulosus* in the Arabian Gulf, highlighting the considerable variation in growth and lifespan that can occur within the same species from different locations. Region-specific effects of fishing cannot be ruled out as a factor contributing to differences in lifespan among regions, however, and this difference between the Arabian Gulf and the GBR may be related to the impact of a long history of fishing in the Arabian Gulf (Grandcourt *et al.*, 2006; Ebisawa & Ozawa, 2009). Samples were collected only from exploited populations by Grandcourt *et al.* (2006), compared to areas both open and closed to fishing in this study, where no evidence of differences between fished and unfished populations was apparent. Marriott *et al.* (2011) reported older *L. nebulosus* from samples also collected from fished populations (30 years, Western Australia), but it is thought that fishing history in that region would not be as extensive as in the Arabian Gulf. The maximum age estimate for *L. olivaceus* provided in this study appears to be the first reported.

Growth varied among the fishes, although it was clear that all four species increased in size at a relatively high rate and reached around 50% of  $L_\infty$  during the first year

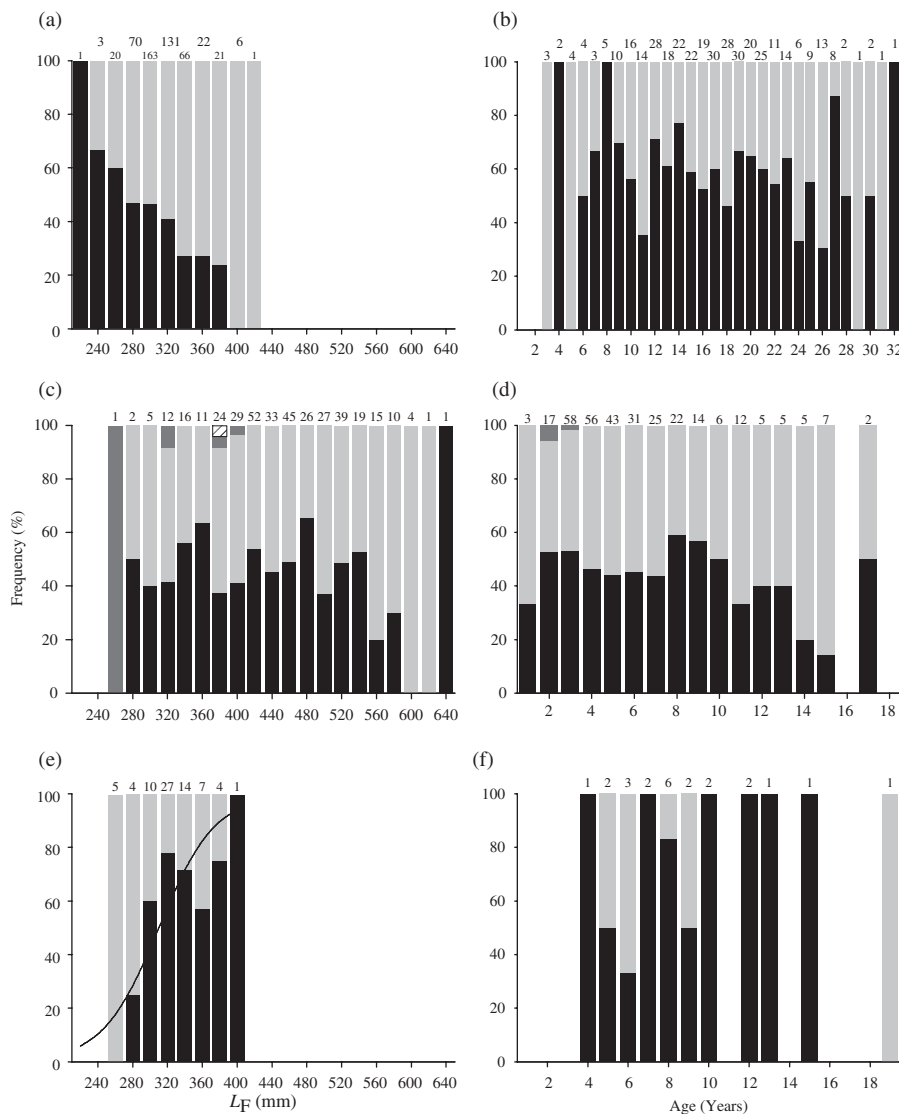


FIG. 9. Proportion (%) of mature male (■), mature female (■), immature female (■) and undetermined inactive females (□) in each (a, c, e) fork length ( $L_F$ ) or (b, d, f) age class for three *Lethrinus* species: (a, b) *Lethrinus atkinsoni*, (c, d) *Lethrinus nebulosus* and (e, f) *Lethrinus lentjan* from the Great Barrier Reef (GBR). (e) Predicted proportion of mature males (relative to mature females) was estimated using logistic function (—) fitted to *L. lentjan* from the GBR. Numbers above bars are sample sizes.

or two of life. Additional juvenile samples of *L. nebulosus* and *L. lentjan* provided better estimates of growth for these species with little difference between VBGF curves when  $t_0$  was unconstrained or constrained. In comparison, the constrained VBGFs appeared to provide greater clarity for early growth for *L. atkinsoni* and *L. olivaceus*. This suggests that, although constraining  $t_0$  can result in biased parameter estimates due to the strong correlation among VBGF parameters, constrained VBGFs

may provide more biologically meaningful results when data for early life stages are unavailable. Growth curves of the smaller *L. atkinsoni* and *L. lentjan* and the larger *L. nebulosus* indicated that these species reached an  $L_{\infty}$  at a relatively young age compared with their estimated lifespan. This 'square' growth pattern, in which juveniles grow rapidly to maturity and then greatly slow down somatic growth (Choat & Robertson, 2006), has been observed in other lethrinids (Ebisawa & Ozawa, 2009) and other groups of coral reef fishes, including the lutjanids (Newman & Williams, 1996) and acanthurids (Choat & Robertson, 2006; Claisse *et al.*, 2009). The paucity of larger, older individuals for *L. olivaceus* and *L. atkinsoni*, however, meant that the few individuals in this age and size class did not fit well to the constrained VBGF. These species may grow continually throughout life (*L. olivaceus*) or slow their growth (beyond 10 years for *L. nebulosus*), rather than reach an asymptotic size. Regional variation in growth patterns has been demonstrated for some lethrinids (Williams *et al.*, 2003, 2007b; Marriott *et al.*, 2011), but no significant differences were detected here among regions for *L. atkinsoni* on the GBR.

Estimates of  $Z$  were similar among the species considered. *Lethrinus atkinsoni* had the highest mortality rate estimated from catch curves, despite being the longest lived of the four species. One potential explanation for this is that mortality rates vary throughout life for this species, with changes occurring when they move between juvenile and adult habitats (*e.g.* seagrass to reef). There are no previous estimates of mortality available for *L. atkinsoni* with which to compare these results, but total mortality estimates differed mostly between methods for this species, with a much lower estimate from the Hoenig (1983) algorithm compared to the other three species. Estimates of  $Z$  from Hoenig's (1983) method were similar to other reported rates of  $Z$  for *L. nebulosus* (0.44 year<sup>-1</sup>, Edwards *et al.*, 1985; 0.20 year<sup>-1</sup>, Grandcourt *et al.*, 2006) and *L. lentjan* (0.14 year<sup>-1</sup>, Grandcourt, 2002). The indication of slightly greater mortality of *L. atkinsoni* in the Storm Cay Region than elsewhere differed in spatial pattern from previous findings for *L. miniatus*, for which highest estimates were observed in the Mackay region (Williams *et al.*, 2007b). Lower mortality estimates have been observed for *L. nebulosus* in the southern Gascoyne region (compared to the northern region) of Western Australia, a reverse latitudinal variation than observed for *L. atkinsoni* (Marriott *et al.*, 2011).

The duration of spawning season and the months during which spawning occurs vary among lethrinids. Spawning activity occurs over a period of months, particularly during spring and summer seasons, for the majority of fishes for which information is available. Ebisawa (1999) reported spawning of *L. atkinsoni* in waters of Okinawa and Yaeyema peaked in spring, which corresponds to the results presented here. Previous work has suggested that *L. lentjan* spawn almost year-round with two main peaks in  $I_G$  identified (Mobiha, 1991). Data from this study support Mobiha (1991) and *L. lentjan* may also have a protracted spawning season or spawn more than once each year in GBR waters. More samples are required to test this hypothesis. Spawning of *L. nebulosus* has been reported in all seasons, with autumn-winter peaks in the Arabian Sea (McIlwain *et al.*, 2006) and GBR (this study) and spring-summer peaks in spawning off north-western Australia (Kuo & Lee, 1990), in Okinawan waters (Ebisawa, 1990) and in the Arabian Gulf (Grandcourt *et al.*, 2006). Greatest spawning activity could occur in months of missing data for both *L. olivaceus* and *L. lentjan* and further systematic sampling is required during all months for each species to test the preliminary findings reported here.

Previous studies indicate that protogyny is the most common reproductive pathway for lethrinids (Young & Martin, 1982; Bean *et al.*, 2003). Revised criteria defining functional protogyny by Sadovy de Mitcheson & Liu (2008) characterize protogyny by evidence of: stages of sexual transition *via* detailed histological series, intersexual gonads, simultaneous presence of mature testicular and ovarian tissue, observations of functional sex change and, to a lesser extent, size- or age-biased sex ratios. Detailed information on the reproductive development of many lethrinids is scarce, however, and variation exists among species and among regions (Ebisawa, 1990).

Observation of intersexual gonads in lethrinids is difficult as sexual transition can be rapid. Transitional individuals have been observed for *L. miniatus* (Bean *et al.*, 2003; Sumpton & Brown, 2004), *L. nebulosus* (Ebisawa, 1990; Marriott *et al.*, 2010), *L. atkinsoni* (Ebisawa, 1999), spotcheek emperor *Lethrinus rubrioperculatus* Sato 1978 (Ebisawa, 1997), *L. lentjan*, *L. variegatus* and longspine emperor *Lethrinus genivittatus* Valenciennes 1830 (Young & Martin, 1982), although no transitional individuals were observed for any species in this study. Testes for each species in this study possessed a lumen formed from a female ovarian lumen, indicating that males were most likely derived from females through sexual transition (Ebisawa, 1990), but it was not possible to determine unequivocally whether sex change was prior to or following maturation as females.

Lethrinids change sex over a range of sizes and ages (Young & Martin, 1982; Sumpton & Brown, 2004; Sadovy de Mitcheson & Liu, 2008; Marriott *et al.*, 2010) and some studies suggest that only a proportion of fishes may change into males (*e.g.* *L. miniatus*; Sumpton & Brown, 2004; Williams *et al.*, 2006). The only species in this study that conformed to the sex-specific size and age distributions expected for functional protogynous species was *L. lentjan*, with males tending to be older and larger and females generally smaller and younger. The presence of an old female *L. lentjan* (19 years) may be evidence that a proportion of females do not change sex. Studies from the Seychelles (Grandcourt, 2002) and Red Sea (Wassef, 1991) support the inference of protogynous hermaphroditism for *L. lentjan*.

Functional protogynous hermaphroditism was not apparent for *L. atkinsoni* and *L. nebulosus*. Instead, non-functional juvenile protogynous hermaphroditism was suggested, with the pathway of sex change from immature females to primary males, as all male gonads that were observed featured a remnant female lumen, but mature males and females were observed over a wide range of sizes and ages and the males reached a smaller average  $L_{\infty}$  than females. This strategy has been inferred for a number of reef fishes (Fennessy & Sadovy, 2002; Adams, 2003; Ebisawa, 2006; Sadovy de Mitcheson & Liu, 2008), including *L. atkinsoni*, *L. nebulosus* and *L. lentjan* (Loubens, 1980b; Ebisawa, 1990, 1999; Grandcourt *et al.*, 2010; Marriott *et al.*, 2010). Such sex differentiation in the juvenile stage produces a population that appears to have separate sexes (functional gonochorism) even though males have developed from immature females. Identification of primary males is difficult, as testicular morphology does not differ according to developmental pathway for some species (Fennessy & Sadovy, 2002; Sadovy de Mitcheson & Liu, 2008) and all males sampled were mature, so it was not possible to verify whether the small males in this study developed from immature females. Other characteristics including differences in sex-specific growth often are observed for non-functional protogynous species, *e.g.* *L. atkinsoni* and *L. nebulosus* (Ebisawa & Ozawa, 2009; Marriott *et al.*, 2011). Sex-specific growth was investigated for these



species. Significantly, different growth curves were identified for *L. atkinsoni*, but not for *L. nebulosus*.

It is difficult to predict the response of a species to increased fishing pressure, when understanding of biological variables is limited (Huntsman & Schaaf, 1994; McClanahan & Hicks, 2011). Similarly, assessment of the utility of uniform management strategies for multiple species affected by a fishery is difficult when knowledge of the biology of the harvested species is poor. Differences in life-history characteristics (e.g. growth rate, lifespan, reproductive strategy and fecundity) can result in markedly different effects of exploitation on multiple species under the same fishery management regime (Schindler *et al.*, 2002). Fishing, generally, is expected to affect long-lived species, such as *L. atkinsoni*, more severely than shorter lived species with higher rates of turnover, especially where large sizes are reached early in life and fishes are vulnerable to capture over much of their lives. The results from this study suggest, however, that some long-lived species may be less vulnerable to exploitation than expected. For example, *L. atkinsoni* was relatively small, not fully recruited to the GBR line fishery until *c.* 16 years of age and individuals of both sexes were reproductively mature from age 3 years. Hence, for the selectivity of the gear used in this study, *L. atkinsoni* individuals would have some protection from harvest for the first 45% of life and around one-third of their reproductive life. The other species considered here also apparently matured well before recruiting to the fishery and were not fully selected for the first 20–40% of life, despite having rapid early growth. This information provides the basis for assessment of the utility of generic management such as gear regulation and general or species-specific minimum sizes of harvest.

Variation in sexual ontogeny within or among species also complicates assessments of multi-species management effectiveness. Huntsman & Schaaf (1994) suggest that reproductive capacity is diminished at even moderate fishing effort with some protogynous stocks potentially more severely affected than gonochoristic species. Predicting the effect of fishing on functional protogynous populations is complicated, as size-selective targeting may reduce the abundance of larger males, while female biomass is also diminished by the sex change of individuals to males with age (Alonzo *et al.*, 2008). Thus, alternative reproductive strategies such as non-functional protogyny may provide some natural buffer against adverse effects of exploitation on reproduction.

Species-specific harvest strategies for all species affected by a fishery often are not feasible. The application of a regulation across multiple species (e.g. for lethrinids) or families may assist enforcement and reduce fisher ambiguity of species identification. Comparisons of biological characteristics of multiple species harvested together allow for consideration of whether common management strategies are appropriate to all or most affected species, and allow informed decisions about whether regulations should be adjusted to be precautionary for most, if not all, of the species under uniform management. Species-specific information, preferably monitoring, is important to demonstrate performance against targets or reference points that avoid unsustainable exploitation of species with life-history characteristics less robust to fishing pressure (Myers & Worm, 2005). The lethrinid species considered here are components of multi-species fishery catches worldwide (Carpenter & Niem, 2001; Kulmiye *et al.*, 2002; Ebisawa & Ozawa, 2009; Grandcourt *et al.*, 2010) and the demographic information reported provides a foundation for assessing the utility

of multi-species fisheries management strategies that might be applied in diverse situations.

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