

Comparative biology of key inter-reefal lethrinid species on the Great Barrier Reef

Project Milestone Report

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Acronyms Used In This Report

CRFFF	Coral Reef Fin Fish Fishery
ELF	Effects of Line Fishing (Experiment)
FL	Fork length
GBR	Great Barrier Reef
GSI	Gonadosomatic Index
IAPE	Index of Average Percent Error
TACC	Total allowable commercial catch
TL	Total length
VBGF	von Bertalanffy growth function
W	Whole wet weight

Introduction

Life-history characteristics among families of coral reef fish are diverse (Gust *et al.*, 2002; Sale, 1991), ranging from long-lived fishes of the family Serranidae with low rates of natural mortality (Ferreira and Russ, 1992) to short-lived, fast-growing species of Gerridae with a high rate of natural mortality (Grandcourt *et al.*, 2006b). Furthermore, variability in biological characteristics exists among species within the same family, including epinepheline and plectropomid serranids on the GBR and in the Torres Strait (Pears *et al.*, 2006; Williams *et al.*, 2008). The species within these subfamilies display different demographic characteristics, with smaller epinephelines (e.g. *Cephalopholis cyanostigma*, 260 mm maximum size (Mosse *et al.*, 2002) growing to over forty years of age, and species with somewhat shorter lifespans reaching lengths of greater than one metre (Pears *et al.*, 2006). This variation in the life history characteristics of coral reef fish means that the resilience to anthropogenic influences may also be variable, making some species more resilient than others. The implication of this is that management strategies should not assume uniform life history characteristics even within the same family and underlies the need for research at the species level.

The family Lethrinidae (emperors) are abundant in tropical and subtropical Indo-Pacific waters and occur in a range of marine environments, including reefs, seagrass beds, estuaries and mangroves (Hamilton, 2005; Kulmiye *et al.*, 2002; Young and Martin, 1982). Thirty-nine species are recognised within the family (Carpenter and Niem, 2001) and the few scientific studies conducted have demonstrated that a variety of life histories exist among species and locations. Lethrinids are generally long-lived, with maximum ages commonly reaching greater than twenty years of age (Carpenter and Niem, 2001). Larger emperors such as *Lethrinus nebulosus* (spangled emperor) can reach 800 mm in length (Randall, 1995), while smaller species such as *Lethrinus variegatus* (slender emperor) do not normally exceed 200 mm (Carpenter and Niem, 2001).

Reproductive development for a number of lethrinid species has been identified as protogynous hermaphroditism, with sexual transition from females to males (Bean *et al.*, 2003; Grandcourt *et al.*, 2006a; Young and Martin, 1982). This is normally identified by the presence of female characteristics in adult male gonad tissue and the predominance of females in younger and smaller classes and males in the larger and older classes (Sadovy and Shapiro, 1987; Young and Martin, 1982). However, other studies report different reproductive pathways for some lethrinids such as juvenile hermaphroditism, whereby sex change occurs prior to reaching sexual maturity (Ebisawa, 1990; Ebisawa, 1997; Ebisawa, 1999). Clearly there is a need to clarify the reproductive strategies within the Lethrinidae family to enable a better understanding of the resilience of lethrinids to exploitation (Simpfendorfer *et al.*, 2007).

Research on lethrinids has much of the family's range, including Japanese waters (Ebisawa, 1990, 1997, 1999), Arabian Sea (Grandcourt *et al.*, 2006a; Kulmiye *et al.*, 2002; McIlwain *et al.*, 2006) and Southwest Pacific (Loubens, 1980a, 1980b; Williams *et al.*, 2006; Williams *et al.*, 2007a, 2007b). Most of the research on lethrinids in Australian waters has been focused on *Lethrinus miniatus* (red throat emperor), a target species in the Great Barrier Reef (GBR) Coral Reef Fin Fish Fishery (CRFFF). Information for this species has been reported on growth, mortality, and reproductive development (Bean *et al.*, 2003; Sumpton and Brown, 2004; Williams *et al.*, 2006; Williams *et al.*, 2003; Williams *et al.*, 2007a; Williams *et al.*, 2007b). In addition to *L. miniatus*, at least a further 22 species of lethrinids are known from the waters of the GBR (Carpenter and Niem, 2001). These species have received less attention in Australian waters and detailed biological information is lacking for most despite the commercial importance to countries from the Western Pacific Ocean to the Indian Ocean

(Carpenter and Niem, 2001; Ebisawa, 1997, 1999; Grandcourt *et al.*, 2005; Kulmiye *et al.*, 2002).

The harvest of lethrinids on the GBR is managed by the Queensland Department of Primary Industries and Fisheries by a number of input and output controls including species-specific minimum legal size limits and recreational possession limits, and a Total Allowable Commercial Catch (TACC). *L. miniatus* is often a target species for commercial and recreational fishers and is managed under a species-specific TACC. All other lethrinids are managed under a single 'Other Species' TACC, which also includes species of lutjanids, serranids, labrids and scarids, and are either bycatch (caught in the fishery and released) or byproduct (caught by the fishery and retained at times). In addition to those that occur in reef habitats, one common species *Lethrinus laticaudis*, occur primarily in inshore waters and are not managed as part of the CRFFF.

The aims of this study were to describe the biology of four lethrinid species that occur on the Great Barrier Reef: *Lethrinus nebulosus* (spangled emperor), *L. atkinsoni* (yellow-tailed emperor), *L. olivaceus* (long-nosed emperor) and *L. lentjan* (pink-eared emperor). Biological characteristics investigated included size, age, growth, mortality and reproduction. The biological characteristics were compared between species and the implications of differences considered in relation to the resilience of populations to fishing.

Methodology

Sample collection

A total of 2,285 lethrinids (Table 1) were sampled from reefs in four regions of the Great Barrier Reef (Lizard Island, Townsville, Mackay and Storm Cay) over eleven years from 1995 during the Effects of Line Fishing (ELF) Experiment structured research fishing surveys (Mapstone *et al.*, 2004) (Figure 1). Samples of *L. nebulosus* and *L. atkinsoni* from reefs closed to fishing (green reefs) were analysed to explore patterns in biological characteristics from relatively unexploited populations. Samples sizes of *L. olivaceus* and *L. lentjan* were too small to use samples from green reefs only, so all samples collected were used. Since these two species were rarely encountered and seldom retained by the CRFFF the effect of fishing on biological characteristics was probably small. An additional two *L. lentjan* individuals were obtained from research trawling in Cleveland Bay Townsville, for age and length estimates.

Sample Processing

For all samples, fork length (*FL*) was measured to the nearest millimetre and whole wet weight (*W*) measured to the nearest 10 g. Sagittal otoliths were removed, cleaned of any residual material, and stored dry in paper envelopes. *Lethrinus nebulosus* and *L. lentjan* otoliths were kept whole, whilst for ease of interpretation *L. atkinsoni* and *L. olivaceus* otoliths were embedded in clear casting polyester resin and cut transversely at 300-400 µm through the core using twin diamond blades on a low speed diamond-blade saw. Sections for these species were mounted on slides using the resin and covered with cover slips. These otoliths and whole otoliths (placed in immersion oil) were viewed under reflected light and opaque increments were counted from the nucleus to the edge of the otolith along the ventral margin of the *sulcus acousticus* using a stereo dissecting microscope at 40x magnification. 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. All otoliths were read by experienced readers, qualified against reference sets for each species, with a minimum of 24 hours between reads of the same otolith. For species with large sample sizes (*L. nebulosus* and *L. atkinsoni*) otoliths were read once followed by 25% reread as a subsample. This ensured accuracy and precision of interpretation, with the Index of Average Percent Error (IAPE) determined for the first and second reads and bias plots graphed for each species to test for differences between reads (Appendices 1 and 2). Using this protocol, the first count was accepted as the final age. For *L. lentjan* and *L. olivaceus* three reads were conducted, with final age assigned when any two counts agreed. IAPE was also calculated to ensure precision (Appendix 1). For the remaining otoliths for which there was no agreement among three counts, the median count was assigned as the final age estimate.

Gonads from fish were either removed at sea and stored in 10% phosphate buffered formalin or immediately frozen whole for processing back in the laboratory, where they were removed, thawed and similarly preserved in formalin. After fixation, each pair of ovaries or testes was dried of excess fixative, and gonad weight was measured to the nearest 0.01 g. Where only one gonad lobe was available, due to damage during processing, gonad weight was estimated by multiplying the mass of the single complete lobe by two. It was assumed that this provided a reasonably accurate measure of gonad weight, as the two gonad lobes are generally equal in size for other lethrinids (Bean *et al.*, 2003). Histological sections were taken from all gonads following the procedures outlined by Adams (2003). The stage of ovary development was 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 Ferreira (1995) and Adams (2003). Females were

classified into five stages: Immature, Resting, Ripe Running Ripe and Spent. Males were classified into three stages: Resting, Ripe and Spent.

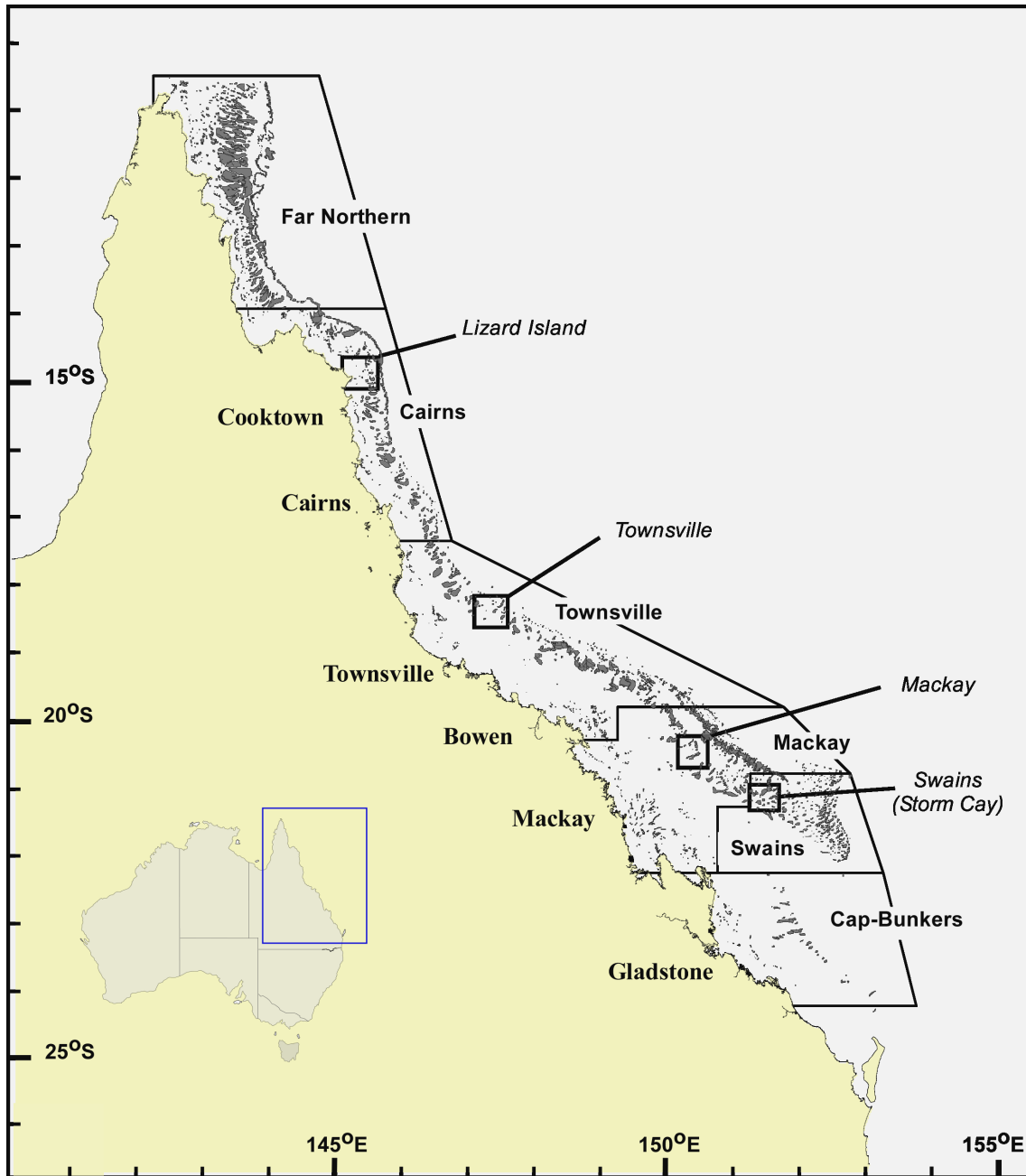


Figure 1: Location of reefs sampled for lethrinids within four regions of the Great Barrier Reef as part of the Effects of Line Fishing (ELF) Experiment. Samples were collected from six reefs within each of the four sites indicated by small squares.

Table 1: Number of monthly sample numbers for four lethrind species used in the analysis of biological characteristics in Great Barrier Reef waters. Samples of *L. nebulosus* and *L. atkinsoni* were only from closed reefs, while samples of *L. olivaceus* and *L. lentjan* were from both open and closed reefs.

Month	<i>L. nebulosus</i>	<i>L. atkinsoni</i>	<i>L. olivaceus</i>	<i>L. lentjan</i>
January	1	11	-	-
February	9	56	2	2
March	24	44	4	11
April	38	83	3	21
May	30	112	2	16
June	-	-	-	2
July	-	-	-	-
August	17	58	1	7
September	20	47	2	4
October	243	566	25	60
November	79	421	9	8
Decemeber	32	194	2	13
Total	493	1592	50	144

Length-weight relationship and length and age frequency distributions

The relationship between FL and W was described using a power function of the form,

$$W = a \times FL^b$$

where a is the coefficient of the power function and b is the exponent. This relationship was plotted for each species for comparison.

Length and age frequency distributions were constructed separately for each lethrind species.

Growth

The von Bertalanffy growth function (VBGF) was fitted by nonlinear least-squares regression of FL on age for each species. The form of the VBGF used to model length-at-age data was,

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)} \right)$$

where L_t is the length at age t , L_∞ is the mean asymptotic fork length, K is the growth coefficient or rate at which L_∞ is approached, t is the age of the fish and t_0 is the age at which the fish have a theoretical length of zero.

The VBGFs were compared between species using likelihood ratio tests (Kimura, 1980), which are considered the most reliable procedure for such comparisons (Cerrato, 1990). A common range of age classes (2-15 years) was used to assure validity of the comparisons (Haddon, 2001).

Mortality

Age-based catch curves (Ricker, 1975) were used to estimate the instantaneous rate of total mortality (Z) for each species. The log-transformed number of fish in each age class was regressed against the corresponding age, and the descending slope provided an estimate of Z . Regressions were fitted from the first age class that was fully selected by the sampling gear through to the oldest age class that was preceded by no more than two consecutive zero frequencies. Z approximated natural mortality (M) for species for which only samples from green reefs were used, assuming that the movement of adults between reefs was limited.

Spawning seasonality

The spawning season for each species was examined using samples collected in different months throughout the year. A gonadosomatic index ($GSI = \text{gonad weight} / W \times 100$) was calculated for each sample, which provided a relative measure of reproductive stage. Measurements of W were not always available. Consequently, W was estimated for some samples using the species-specific length-weight relationship. It was assumed that estimates of W would suffice for use in estimating GSI because only the temporal patterns in GSI, rather than the absolute values of GSI, were required to determine the spawning season. The proportion of samples in each mature female and male reproductive stage in each month were plotted for each location to examine the ovarian and testicular development patterns throughout the year, and the degree of spawning activity occurring in each month for each species.

Sex change

A logistic function was fitted to the proportion of males (relative to females) in each length and age class to estimate the length and age at which each species of lethrinid changes sex. The length and age at sex change was estimated for each species 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 in age or 10 mm length class s , and s_{50} and s_{95} are the age or length at which 50% and 95% of the population are males for each species, respectively.

Results

Length-weight relationship

The relationship between FL and W was approximately isometric ($b \approx 3$) for each lethrinid species (Figure 2; Table 2). The slope of the FL - W relationship indicated that all species except *L. nebulosus* becomes more heavy-bodied with increasing size (FL), with *L. olivaceus* becoming slightly more rotund with age when compared to the other species.

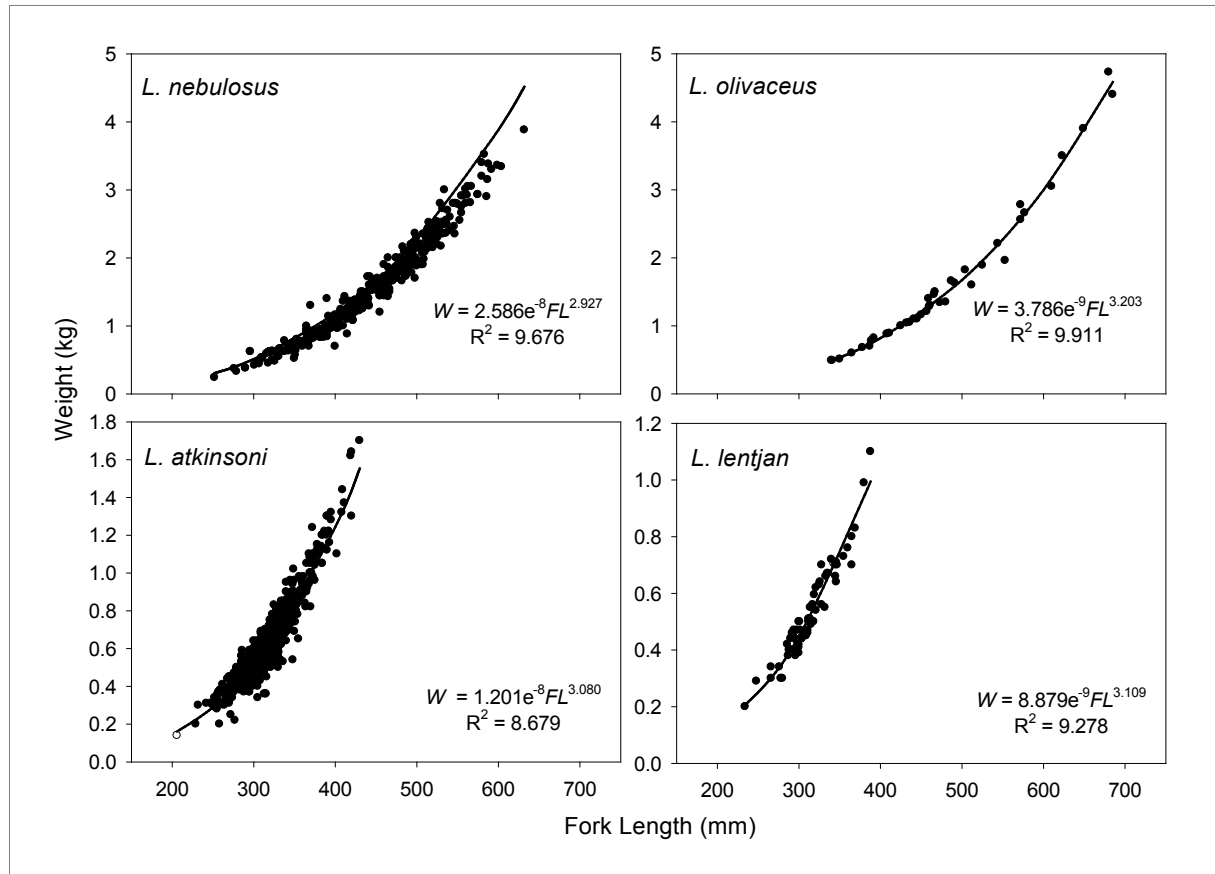


Figure 2: Length at weight data and fitted power curves for the four lethrinid species on the GBR.

Table 2: Parameter estimates for the length-weight relationship, VBGF and rates of total mortality for four lethrinid species from the Great Barrier Reef: a and b are parameters of the allometric relationship ($W = a \times FL^b$) between fork length (FL) and weight (W); L_∞ is the mean asymptotic fork length; K is the von Bertalanffy growth coefficient; t_0 is the theoretical age at length zero; and Z is the instantaneous rate of total mortality.

Species	$a(\times 10^{-8})$	b	$L_\infty(\text{mm})$	$K(\text{yr}^{-1})$	$t_0(\text{yr})$	$Z(\text{yr}^{-1})$
<i>L. nebulosus</i>	2.59	2.93	556	0.13	-6.46	0.21
<i>L. atkinsoni</i>	1.20	3.08	339	0.11	-10.84	0.25
<i>L. olivaceus</i>	0.38	3.20	755	0.16	-3.20	0.17
<i>L. lentjan</i>	0.88	3.11	313	0.42	-0.29	0.18

Length and age frequency distributions

The modal length in the catch differed among lethrinid species (Figure 3) and was largest for *L. nebulosus* (460 mm FL) and *L. olivaceus* (440 mm FL) and smallest for *L. lentjan* (300 mm FL) and *L. atkinsoni* (320 mm FL). *L. olivaceus* and *L. nebulosus* were generally larger in size in comparison to the other two species, with maximum fork lengths of 734 mm and 640 mm observed respectively. The maximum lengths observed for the smaller species were 478 mm for *L. atkinsoni* and 388 mm for *L. lentjan*.

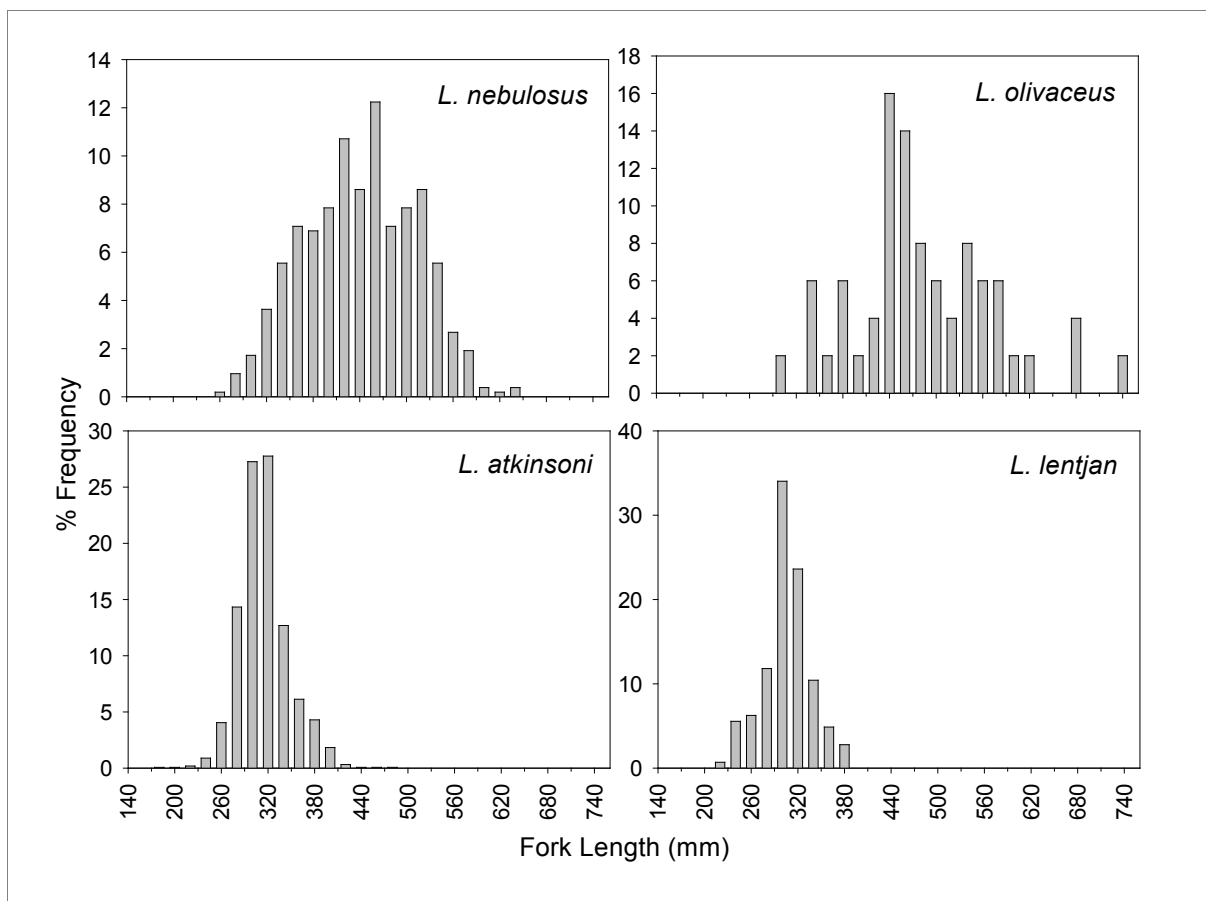


Figure 3: Length frequency distributions for four lethrinid species on the Great Barrier Reef (note difference in y-axes). Data for *L. nebulosus* and *L. atkinsoni* are from closed reefs only, data for *L. olivaceus* and *L. lentjan* are from open and closed reefs combined (*L. nebulosus*, n = 523; *L. atkinsoni*, n = 1585; *L. olivaceus*, n = 50; *L. lentjan*, n = 144).

Age frequency distributions varied considerably for each of the four species. The modal age in the catch was three years for *L. olivaceus*, four years for *L. nebulosus*, eight years for *L. lentjan* and 16 years for *L. atkinsoni* (Figure 4). The catch of the two larger species (*L. nebulosus* and *L. olivaceus*) were predominately in younger age classes (<6 years), whilst those smaller lethrinids (*L. atkinsoni* and *L. lentjan*) had an older modal age and greater proportion of samples at older ages. The maximum age in the catch was also different among species, with the oldest fish being a 36 year old *L. atkinsoni* (Figure 4). The most noticeable difference among species was the older modal age for *L. atkinsoni* and the normal distribution of ages, including a large number of older individuals (>16 years) (Figure 4).

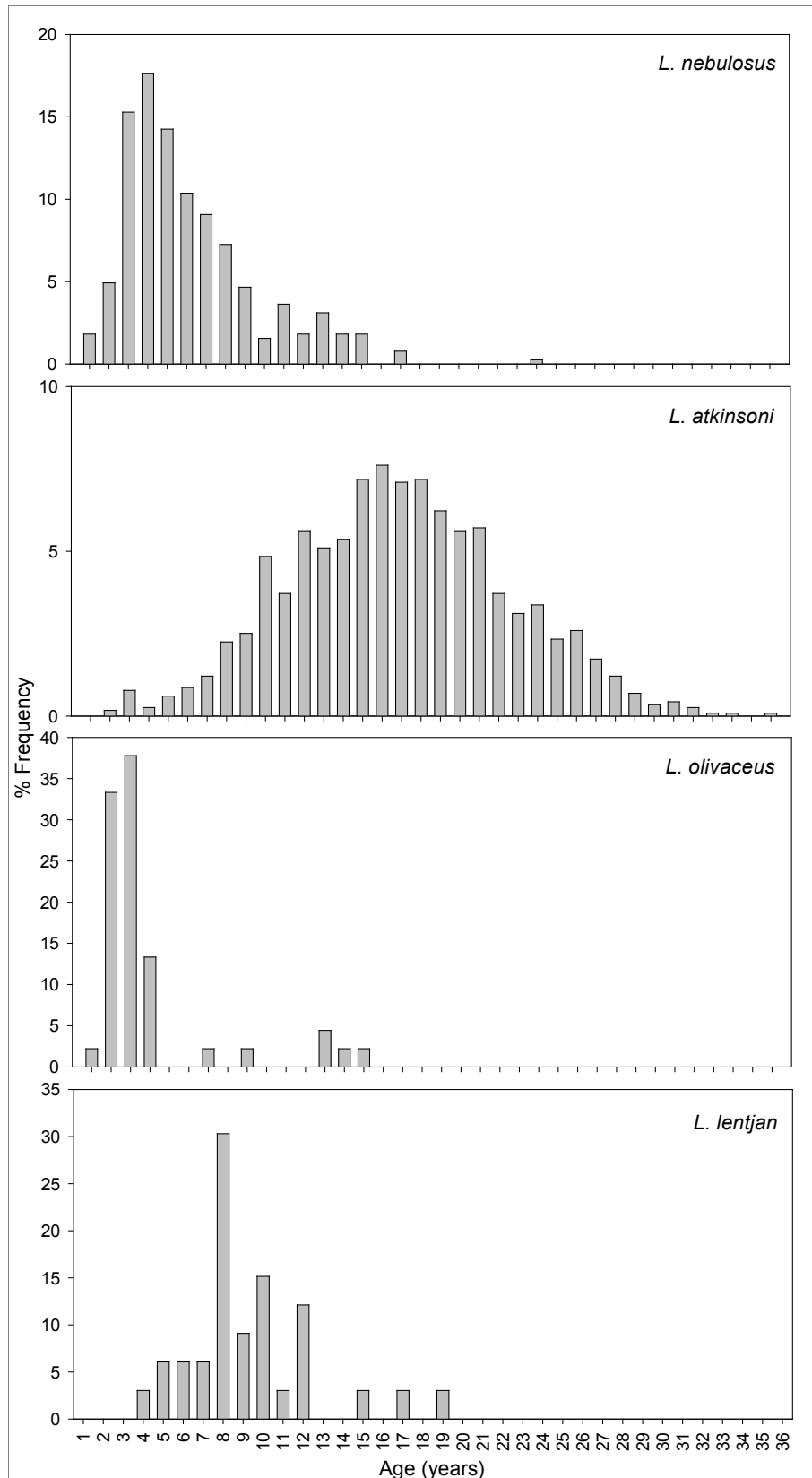


Figure 4: Age frequency distributions for four lethrind species on the Great Barrier Reef (note difference in y-axes). Data for *L. nebulosus* and *L. atkinsoni* are from closed reefs only, data for *L. olivaceus* and *L. lentjan* are from open and closed reefs combined (*L. nebulosus*, n = 386; *L. atkinsoni*, n = 1156; *L. olivaceus*, n = 45; *L. lentjan*, n = 33).

Growth

The length-at-age data and fitted growth curves differed substantially among species. *Lethrinus olivaceus* grew quickly to longer lengths, was longer for any given age (<15 years) and reached a larger average maximum length (L_{∞}) than all other species (Figure 6). *Lethrinus nebulosus* displayed intermediate growth and *L. atkinsoni* was the slowest growing and oldest species (Figure 6). *Lethrinus lentjan* displayed similar growth pattern to *L. atkinsoni* beyond four years of age (Figures 6).

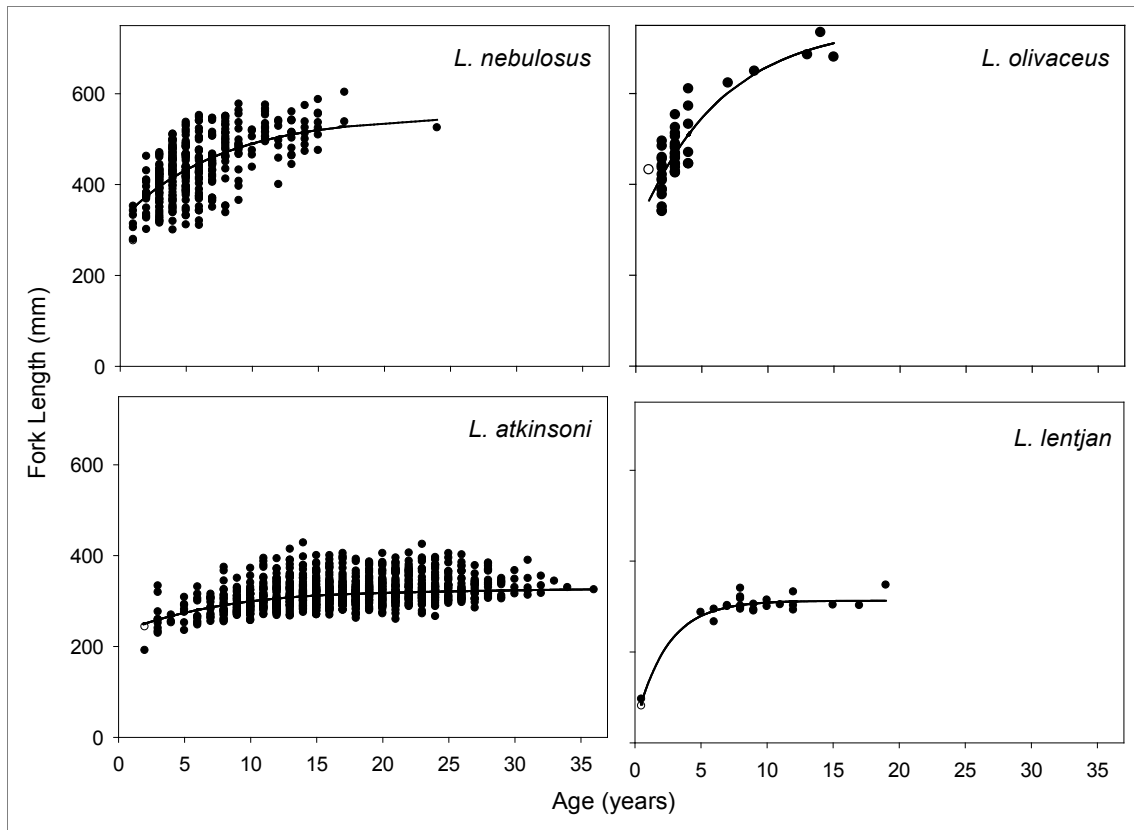


Figure 5: Length-at-age data and fitted VBGF curves for four lethrinid species from the Great Barrier Reef. Data for *L. nebulosus* and *L. atkinsoni* are from closed reefs only, data for *L. olivaceus* and *L. lentjan* are from open and closed reefs combined (*L. nebulosus*, $n = 382$; *L. atkinsoni*, $n = 1155$; *L. olivaceus*, $n = 45$; *L. lentjan*, $n = 28$).

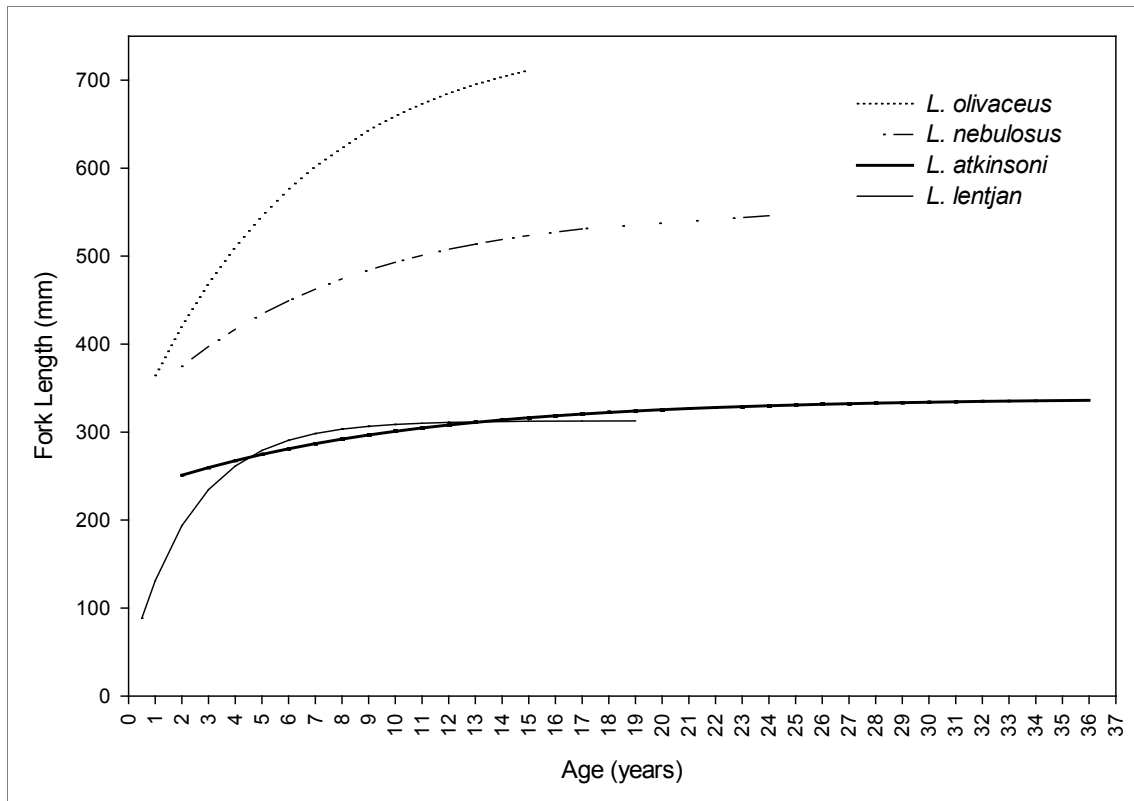


Figure 6: Comparison of the fitted VBGF curves without length-at-age data for four lethrinid species from the Great Barrier Reef (*L. nebulosus*, $n = 382$; *L. atkinsoni*, $n = 1155$; *L. olivaceus*, $n = 45$; *L. lentjan*, $n = 28$).

Statistical comparisons of growth curves among species assumed the selectivity bias is similar for all species and were made across the same age range. Likelihood ratio tests confirmed that patterns of growth differed significantly among species ($\chi^2 = 1230.20$, $p < 0.001$). Evidently, differences in growth patterns were seen between the larger species group compared with the smaller lethrinids. *Lethrinus nebulosus* and *L. olivaceus* continued to grow in length; however growth reached a plateau for *L. atkinsoni* and *L. lentjan*. The presence of *L. lentjan* juveniles sampled was the likely reason for a high K value, depicting the fast initial growth rate. The other lethrinids lacked these smaller younger juveniles; therefore K may be underestimated for these three species, and in turn produced an overestimation of L_{∞} .

Mortality

Total mortality (Z) estimates differed between species (Figure 7) and was highest for *L. atkinsoni*, lowest for *L. olivaceus* and intermediate for *L. nebulosus* and *L. lentjan* (Table 2). Low sample sizes for *L. lentjan* and *L. olivaceus* resulted in a high level of uncertainty in estimates of Z .

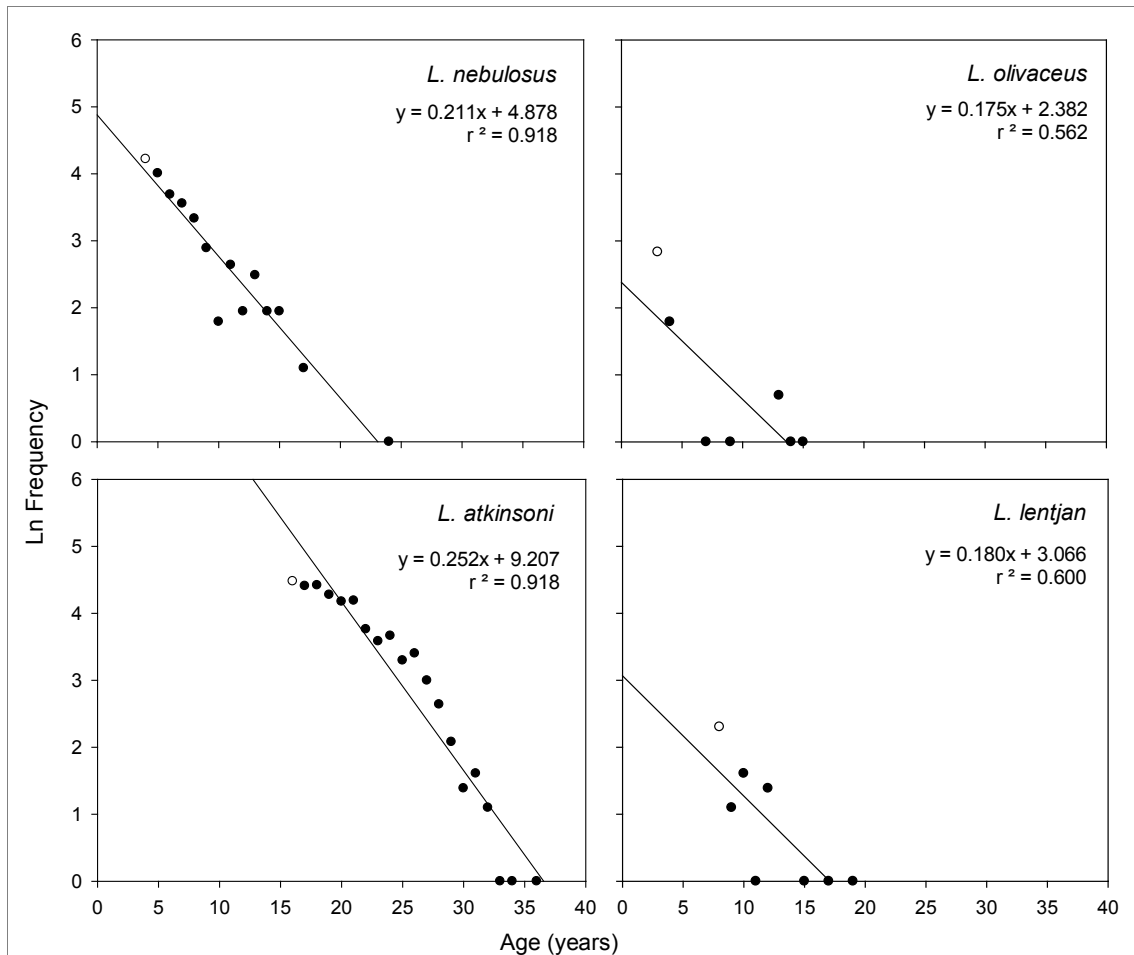


Figure 7: Catch curves for four lethrinid species from the Great Barrier Reef. The slopes of the regressions are an estimation of the rate of total mortality (Z) for each species. Data for *L. nebulosus* and *L. atkinsoni* are from closed reefs only, other species are from open and closed reefs combined.

Spawning seasonality

Monthly trends in mean GSI and developmental stages of ovarian and testicular tissue indicated differences in the timing of reproduction between the four lethrinid species. Mean monthly values of GSI corresponding to peak spawning period were highest for females in July-August for *L. nebulosus*, September-October for both *L. olivaceus* and *L. lentjan* and November-December for *L. atkinsoni* (Figure 8, Table 3). Males followed a similar pattern in GSI for *L. olivaceus* and *L. lentjan*, however male *L. nebulosus* showed greater GSI later than the females, in November-December (Figure 9). Insufficient data was available for male *L. olivaceus* to make conclusions on reproductive status.

The temporal pattern in spawning activity based on ovarian stages followed a similar pattern to the monthly GSI values for all species (Figure 8). Ripe females were observed in periods of high mean GSI, however the presence of hydrated (running ripe) females are key indicators of peak periods of spawning activity. Few females in this developmental stage were observed, but those present for *L. atkinsoni* coincided with the peak spawning months of November-December and the two months previous, also represented by high mean GSI. Hydrated gonads were also identified during the peak spawning months of September-October for *L. lentjan* however one running ripe female was identified in March-April suggesting perhaps a protracted spawning for this species (Figure 8). Ripe males were found in almost all periods, with generally higher frequencies of this developmental stage corresponding to peaks in mean GSI (Figure 9).

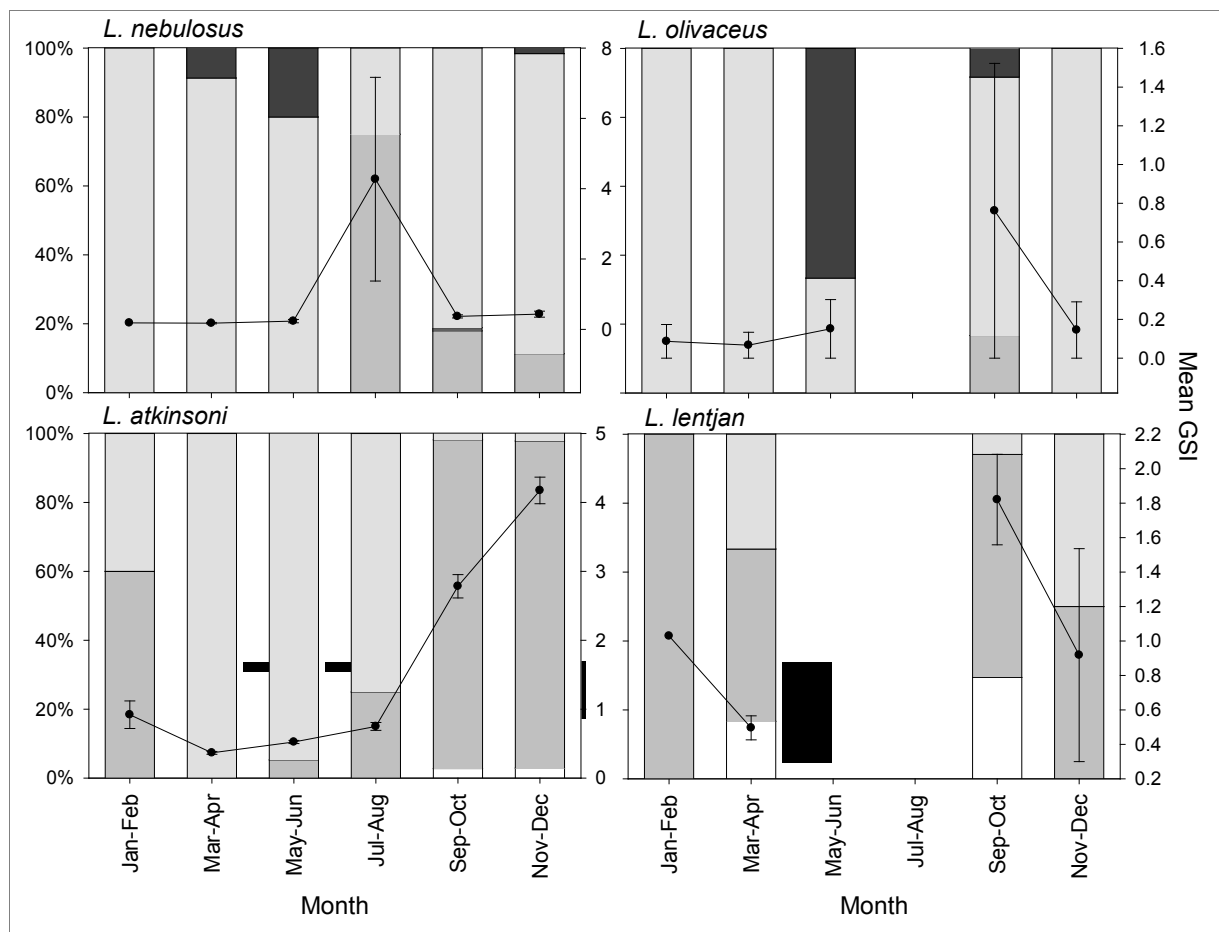
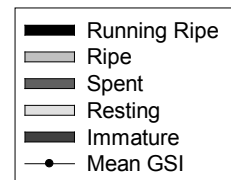


Figure 8: Catch curves for four lethrinid species from the Great Barrier Reef. The slopes of the regressions are an estimation of the rate of total mortality (Z) for each species. Data for *L. nebulosus* and *L. atkinsoni* are from closed reefs only, other species are from open and closed reefs combined.



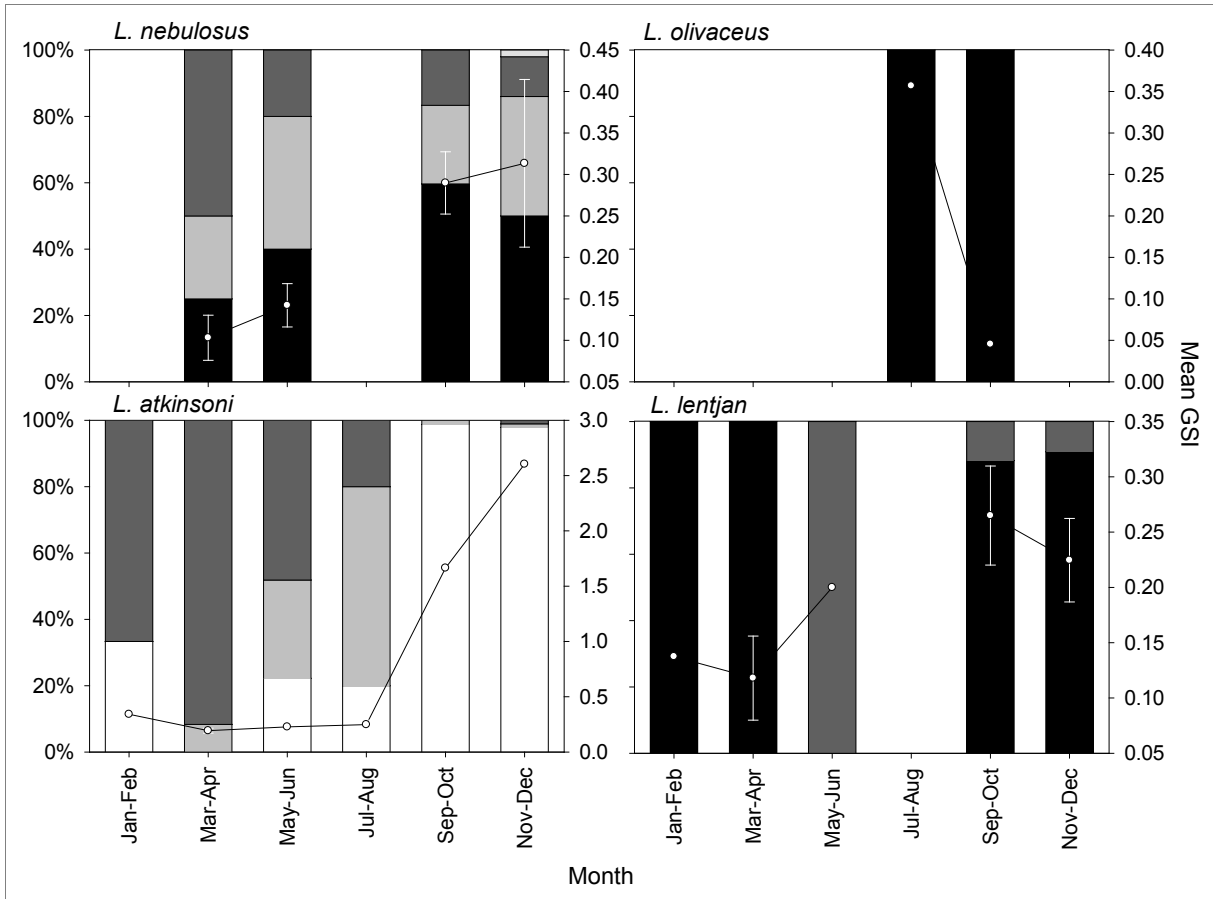


Figure 9: Monthly frequencies of mature testicular stages (bars) and mean monthly gonadosomatic index (GSI) values (lines) for male lethrinids from the Great Barrier Reef. Error bars are standard errors. (*L. nebulosus*, n = 186; *L. atkinsoni*, n = 219; *L. olivaceus*, n = 2; *L. lentjan*, n = 46).



Table 3: Season of peak spawning for each of the four lethrinid species represented by periods of highest mean GSI.

Species	Female	Male
<i>L. nebulosus</i>	July – August	November – December
<i>L. atkinsoni</i>	November – December	November – December
<i>L. olivaceus</i>	September – October	September – October
<i>L. lentjan</i>	September – October	-

Sex change

Investigations into sex change for the four lethrinid species showed varied results. All male testes displayed a central cavity, a remnant ovarian lumen, indicating individuals developed from females. However, these species did not conform to the typical trend displayed by other protogynous hermaphrodite lethrinids. More small young females and more large old males are usually expected in populations that change sex from females to males. For both length (Figure 10) and age (Figure 11), the proportion of females and males was variable for each species. *Lethrinus lentjan* showed an increase in proportion of males with increasing length, with 50% and 95% of the population male by 309.71 mm FL (L_{50}) and 460.85 mm FL (L_{95}), respectively (Figure 10). However, for *L. atkinsoni*, an inverse relationship was apparent, with a greater proportion of males at smaller lengths (Figure 10). No discernible trend was observed for *L. nebulosus* (Figure 10). There were insufficient samples of *L. olivaceus* to determine length or age at sex change.

Trends in the proportion of the sexes at age were similarly unclear and the logistic function could not be fitted to the proportion of males, relative to females for *L. nebulosus* or *L. atkinsoni* (Figure 11). Sample size was too small for *L. lentjan* to display any trend.

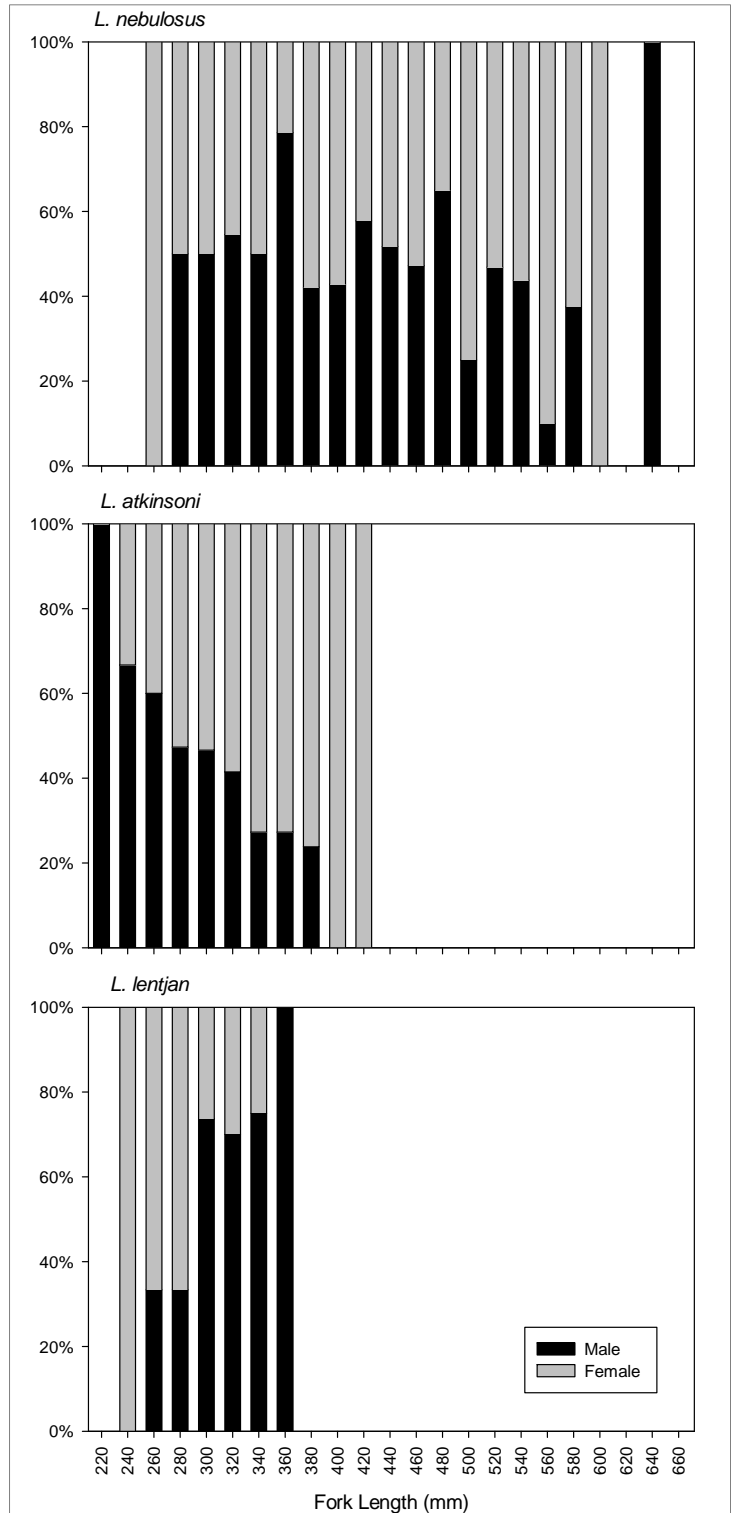


Figure 10: Proportion of males and females in each size class for three lethrinid species from the Great Barrier Reef.

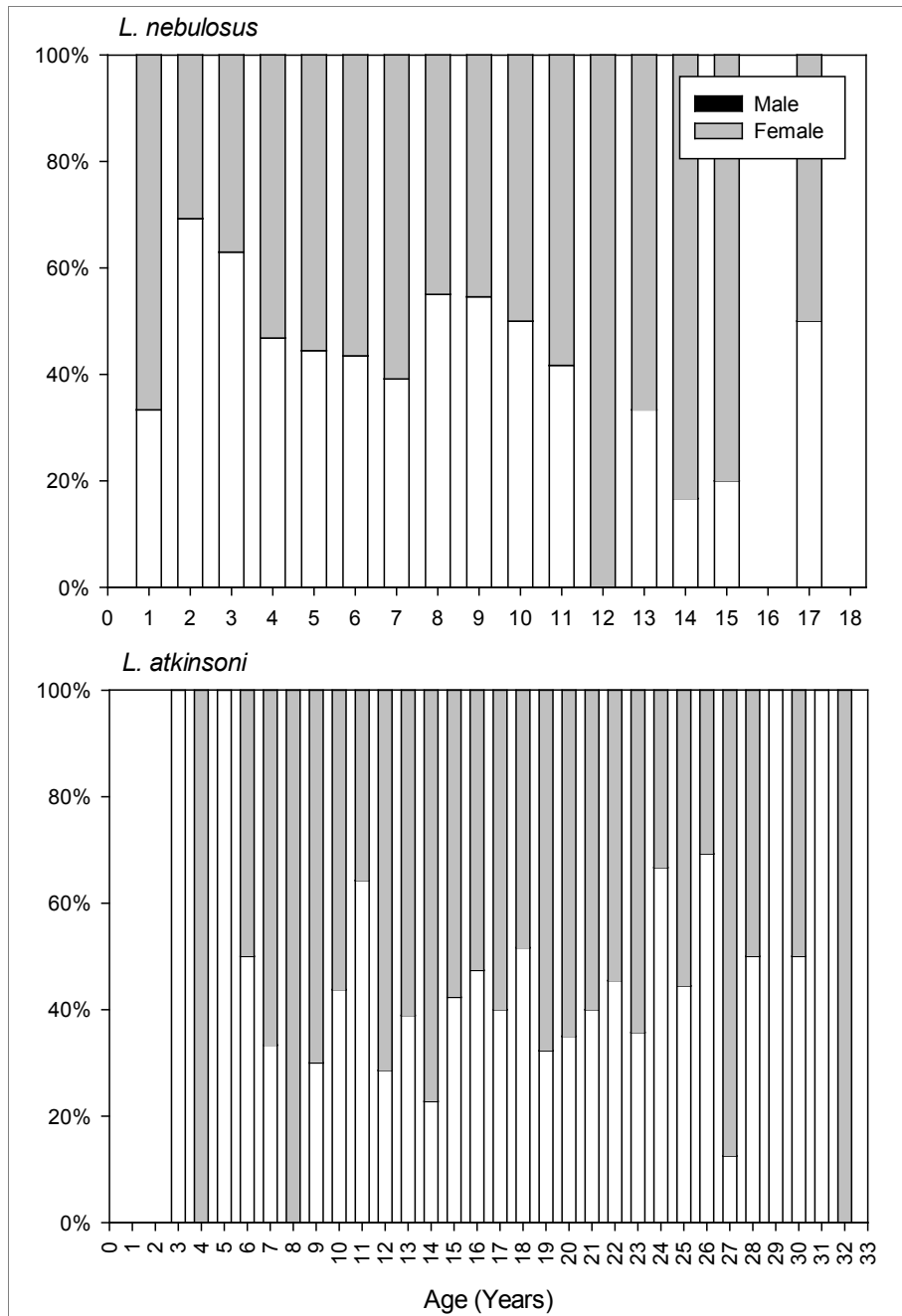


Figure 11: Proportion of males and females in age classes of two lethrinid species from the Great Barrier Reef.

Discussion

Coral reef fishes from the Family Lethrinidae are common on the Great Barrier Reef (Newman and Williams, 2001) and thus make up an important component of catches from the CRFFF (Simpfendorfer *et al.* 2008). The most abundant species, the red-throat emperor (*L. miniatus*) has its own annual catch quota, and is the second most commonly landed species after the coral trout (*Plectropomus* spp.) (Mapstone *et al.*, 1996a, 1996b; Williams *et al.*, 2003). The four species investigated in this report are all managed as part of the 'Other Species' quota group. Although regularly captured in both the commercial, charter and recreational sectors of the reef line fishery, there is limited data available on their life history for most of these species, making management more difficult.

The lethrinids species examined in this report can be separated into two groups based on their size and life span: larger species (*L. nebulosus* and *L. olivaceus*) that grow to over 600 mm and have relatively short life spans, and small species (*L. atkinsoni* and *L. lentjan*) that grow to a maximum of approximately 400 mm but have longer life spans. To achieve the larger sizes, the former group must have considerably higher growth rates than the latter, especially in the first few years of life. This was not necessarily supported by the reported growth rate data from the von Bertalanffy growth functions because of the limited number of very young individuals collected due to the selectivity of the sampling gear used in the ELF project. It is clear from the growth curves that all four species increase in size at a relatively high rate during the first year or two of life, but that the smaller species reach an asymptotic size at a relatively young age, while the larger species continue to grow. This same pattern has been observed in most other groups of coral reef fish, including the serranids (Grandcourt, 2002a), lutjanids (Newman *et al.*, 1996) and acanthurids (Choat and Robertson, 2006).

The differences observed in life history between the species do not appear to be related to the systematic relationships. For example, although *L. olivaceus* is evolutionarily less related to the other three species examined, as evidenced by its different dentition (Lo Galbo *et al.*, 2002) and has a more elongated body shape, it shares similar life-history characteristics with *L. nebulosus*. These larger species grow at a consistently faster rate to larger maximum sizes, and the catches were dominated by younger age classes. Research is lacking for *L. olivaceus*, however other studies have found similar results for *L. nebulosus*. For example, Grandcourt and others (2006a) reported a modal age of five years and considerable variability in growth from the Arabian Gulf. Our longevity estimate of 24 years for *L. nebulosus* was older than estimated by Grandcourt *et al.* (2006a) (14 years), yet Edwards and others (1985) observed a maximum age of 21 years in the Gulf of Aden.

Alternatively, the smaller species, *L. atkinsoni* and *L. lentjan* grew to much smaller maximum lengths of less than 340 mm *FL*, and reached a plateau in growth at a similar length and age. The catches of these more rotund, deep-bodied lethrinids were mostly in older age classes with *L. atkinsoni* spread normally over age classes and exhibited relatively high longevity (36 years). Loubens (1980b) reported a maximum age of only 24 years for *L. atkinsoni*. However, the same maximum age of 19 years was reported by Grandcourt (Grandcourt, 2002b) for *L. lentjan*. The higher modal age found for these lethrinids as compared to those from the large sized group could suggest a habitat or diet shift from juveniles to adults, as juveniles for these species occur in shallow seagrass and sandy areas then shift to reefs and deeper waters (Carpenter and Niem, 2001, Wilson, 1998). This change in habitat is the likely cause of the dominance of older age classes in the current study, since collections were only made in reefal environments. Alternatively, the lack of these fish and smaller individuals caught may be due to fishing selectivity with younger fish less vulnerable to the fishing gears used.

Estimates of total mortality for the lethrinid species in this study were quite variable, ranging between 0.25 for *L. atkinsoni* and 0.17 for *L. olivaceus*. Since the samples for *L. nebulosus* and *L. atkinsoni* were taken from reefs closed to fishing, the estimates of mortality should approximate natural mortality. Despite being the longest lived of the four species examined, *L. atkinsoni* had the highest estimated mortality level. This is even more puzzling given that this is an estimate of natural mortality. 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 (i.e. seagrass to reef). This is further supported by the age structure of the catch, which was normally distributed, with the mode at 16 years. There are no previous estimates of mortality available for *L. atkinsoni* with which to compare these results. However, previous estimates of total mortality are available for *L. nebulosus* (0.44 yr⁻¹, Edwards *et al.* 1985; 0.20 yr⁻¹, Grandcourt *et al.* 2006a) and *L. lentjan* (0.142 yr⁻¹, Grandcourt 2002b). Comparison of these previous estimates to the current study is difficult because each is dependent upon the level of fishing in the specific study. However, the estimate for *L. lentjan* is lower than for the current study, possibly due to differences in fishing mortality.

It would be assumed that reproductive development should be similar for these four related lethrinids, or at least comparable between the larger and smaller species. This was not the case, with a number of differences observed. There was substantial variation between species for peak spawning periods (mean female GSI), with *L. nebulosus* in July-August (winter), both *L. olivaceus* and *L. lentjan* in September-October (spring) and *L. atkinsoni* in November-December (spring-summer). Mean male GSI followed a similar pattern, except for *L. nebulosus* which displayed highest mean GSI later (November-December) than for the females, however ripe individuals were present in all months. Furthermore, GSI is not a reliable indicator of annual spawning activity neither for males nor for comparing among species, because unlike female oocytes which gain weight prior to spawning (higher GSI), male testes become lighter with onset of spermiogenesis (lower GSI) (Stoumboudi *et al.*, 1993). Thus, there was considerable difference in the season of peak female spawning for these species in other locations. Spawning activity for *L. nebulosus* has been reported in all seasons with autumn-winter peaks in the Arabian Sea (McIlwain *et al.*, 2006) whilst for northwestern Australia (Kuo and Lee, 1990), Okinawan waters (Ebisawa, 1990) and the Arabian Gulf (Grandcourt *et al.*, 2006b) peaks in activity were seen in spring-summer months. Ebisawa (1999) investigated *L. atkinsoni* in Okinawan waters and reported spawning peaked in spring, which corresponds to the current study. In contrast, previous work has suggested that *L. lentjan* spawn almost year-round with two main peaks in GSI identified (Mobiha, 1991). Two peaks were similarly found in this study (January-February and September-October), despite the small sample size, suggesting they may have a protracted spawning season or spawn more than once each year. Spawning information was lacking for *L. olivaceus*, therefore no conclusions regarding peak spawning period can be made due to the variability identified among species in the present study.

Detailed information on the reproductive development mode of most lethrinids is lacking, and variation exists between species and regions (Ebisawa, 1990). Research has suggested protogynous hermaphroditism is the general reproductive pathway for lethrinids, in which fish begin life as females and change sex to become males later in life (Grandcourt, 2002b, Young and Martin, 1982). However, discrepancies exist between studies, due to differences in species, sampling locations and limitations of drawing conclusions based on gonads identified macroscopically (Grandcourt *et al.*, 2006b). According to Sadovy and Shapiro (1987) strong indicators for protogyny include transitional individuals and presence of a female lumen in male testes. Although transitional individuals were absent for all species in this study they have been observed for other lethrinid species (Bean *et al.*, 2003, Sumpton and Brown, 2004). Studies on *Lethrinus miniatus* concluded sex transition is a rapid process and not all individuals change sex (Bean *et al.*, 2003, Williams *et al.*, 2006), justifying the low frequency of transitional individuals observed in general. Testes for each species in the

current study possessed a central cavity formed from a female ovarian lumen, substantiating males were derived from females through sexual transition (Ebisawa, 1990).

The typical mode of protogynous hermaphroditic development, involves the generation of males from mature females changing sex. Young and Martin (1982) identified this strategy for lethrinids including *L. lentjan*, similarly to the current study, with sex change from females to males illustrated by the dominance of females at the smaller lengths and ages, whilst males predominate the larger sizes and ages. However, the presence of young small males for other species in the current study, particularly for *L. atkinsoni*, was unexpected for protogynous hermaphrodites. The proportions of males did not increase with increased length or age for all species, and length and age at sex change in this study did not clearly show when (or if) fifty percent of a species changed into males. *Lethrinus atkinsoni* and *L. nebulosus* both displayed different proportions of males with size and age, and generally did not conform to the usual hermaphroditic trend. In these cases, other authors have concluded that this pattern is the result of juvenile hermaphroditism, in which individuals change sex from female to males before maturity (immature females), thus producing a population which appears to have separate sexes (Ebisawa, 1990). Ebisawa (1990, 1999), and Loubens (1980a) confirmed *L. nebulosus*, *L. atkinsoni* and *L. lentjan* males developed from females prior to sexual maturation. However, another population of *L. atkinsoni* (Ebisawa, 1999) and *L. lentjan* (present study) have also been observed to develop via protogynous hermaphroditism. This variation within species suggests that plasticity exists in reproductive development for lethrinids and neither protogynous nor juvenile hermaphroditism is fixed to species, but perhaps more dependent on environmental factors or population densities (Ebisawa, 1999, Ebisawa, 2006).

The results of this study demonstrate the diversity of life histories observed in the 'Other species' TACC quota group in the CRFFF on the GBR. The lethrinids, like other families, have evolved a range of life histories to take advantage of the many niches available in these complex tropical habitats. The management of such a large number of species with a single quota group represents some risk to those species that have less resilience to fishing pressure. In particular those species that grow slowly and have long life spans (e.g. *L. atkinsoni*), are potentially less resilient. The use of a single quota group for a variety of species can potentially mask the loss of these less resilient species, while the more resilient species become proportionally more important. As such it is important that management of these populations also include species-specific regulations that take account of the variability in resilience. Although such regulations including size limits and bag limits for recreational fishers exist for the more desired species, *L. nebulosus* and *L. olivaceus*, it is important that these management strategies are based on biological data (e.g. size at maturity) to protect the least resilient species.

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Appendix 1

Table A1: Index of Average Percent Error (IAPE) of successive otolith reads for each lethrinid species in this study.

Species	Common name	IAPE
<i>Lethrinus nebulosus</i>	Spangled emperor	4.42
<i>Lethrinus atkinsoni</i>	Yellow-tailed emperor	2.70
<i>Lethrinus olivaceus</i>	Long-nosed emperor	16.20*
<i>Lethrinus lentjan</i>	Pink-eared emperor	9.05

* Note, IAPE is substantially high for this species due to the low sample size of 21 individuals.

Appendix 2

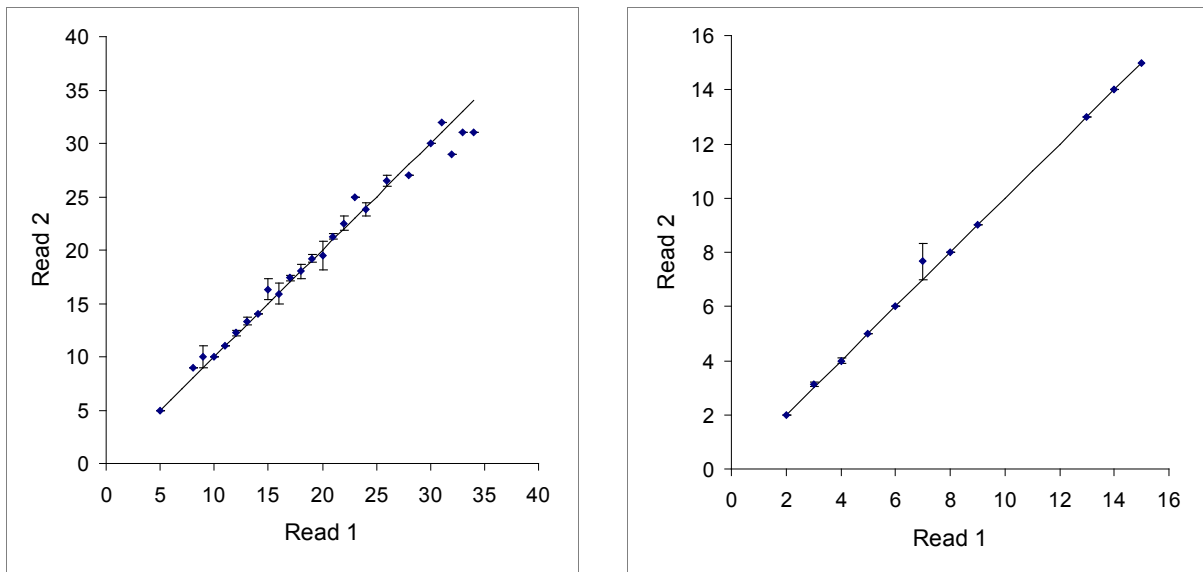


Figure A1: Bias plots of otolith Read 1 vs. Read 2 for (left) *L. atkinsoni* and (right) *L. nebulosus*. Reads for each species is plotted against the straight line representing no difference in reads (i.e. both reads identical).