

Abstract—Demographic parameters from seven exploited coral reef lutjanid species were compared as a case study of the implications of intra-family variation in life histories for multispecies harvest management. Modal lengths varied by 4 cm among four species (*Lutjanus fulviflamma*, *L. vitta*, *L. carponotatus*, *L. adetii*), which were at least 6 cm smaller than the modal lengths of the largest species (*L. gibbus*, *Symphorus nematophorus*, *Aprion virescens*). Modal ages, indicating ages of full selection to fishing gear, were 10 years or less for all species, but maximum ages ranged from 12 (*L. gibbus*) to 36 years (*S. nematophorus*). Each species had a unique growth pattern, with differences in length-at-age and mean asymptotic fork length (L_{∞}), but smaller species generally grew fast during the first 1–2 years of life and larger species grew more slowly over a longer period. Total mortality rates varied among species; *L. gibbus* had the highest mortality and *L. fulviflamma*, the lowest mortality. The variability in life history strategies of these tropical lutjanids makes generalizations about lutjanid life histories difficult, but the fact that all seven had characteristics that would make them particularly vulnerable to fishing indicates that harvest of tropical lutjanids should be managed with caution.

Manuscript submitted 5 November 2009.
Manuscript accepted 7 July 2010.
Fish. Bull. 108:420–432 (2010).

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Demographic characteristics of exploited tropical lutjanids: a comparative analysis

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Knowledge of the life history characteristics of an exploited species can help elucidate inherent resilience to anthropogenic effects such as fishing (Parent and Schriml, 1995; Jennings et al., 1998; Musick et al., 2000). Interspecific variation in life history characteristics may indicate that some species are more susceptible to overfishing than others. Life history characteristics vary widely among families of coral reef fish (Sale, 1991; Gust et al., 2002)—a feature particularly evident within the Lutjanidae. Some lutjanid species grow to sizes in excess of 1 m (e.g., cubera snapper [*Lutjanus cyanopterus*], red snapper [*L. sebae*]) and others reach smaller maximum sizes of less than 30 cm (e.g., two-spot banded snapper [*L. biguttatus*], bluestriped snapper [*L. notatus*]). Variable life spans and spatial distributions also have been recorded within the family. Lutjanids are typically gonochoristic (i.e., do not change sex) and often exhibit sex specific variation in life history traits (Polovina and Ralston, 1987). A high degree of variation in life history strategies among reef fish species within a family would suggest

it is inappropriate to apply the same management strategy to all those species. Here we consider the lutjanids as a case study.

The Lutjanidae comprises approximately 103 species with a wide array of size and body form, making it one of the largest and most diverse families of fish (Carpenter and Niem, 2001). Lutjanids are found in tropical waters around the globe and are often associated with reef habitats (Carpenter and Niem, 2001). Lutjanids are of high commercial value throughout the world and are taken regularly in artisanal, recreational, and commercial fisheries (Newman et al., 1996; Kaunda-Arara and Ntiba, 1997; Marriott et al., 2007; Amezcua et al., 2006). The propensity of lutjanids to aggregate, particularly for spawning, and their predictably reef-associated distribution, make them potentially susceptible to overfishing. Concerns have been raised about the level of harvest and sustainability of fishing for lutjanid populations in some regions (Kamukuru et al., 2005; Amezcua et al., 2006).

Little is known about the specific spatial distribution and demograph-

ic characteristics of many lutjanid species (but see Newman et al., 1996, 2000a; Kaunda-Arara and Ntiba, 1997; Kritzer, 2002, 2004; Amezcua et al., 2006; Marriott et al., 2007). Many species remain unstudied and comparisons among species are few, even though research has covered much of the family's geographic range, including Mexico (Arreguín-Sánchez and Manickchand-Heileman, 1998; Amezcua et al., 2006), Kenya (Kaunda-Arara and Ntiba, 1997), the United States (Wilson and Nieland, 2001; Meyer et al., 2007), Japan (Shimose and Tachihara, 2005), the Great Barrier Reef (Newman et al., 1996, 2000a; Marriott et al., 2007), Arabian Gulf (Grandcourt et al., 2006), and the Indian Ocean (Newman and Dunk, 2003; Pilling et al., 2000). The few data that do exist indicate that at least some lutjanid species are long lived with life spans over 30 years (Newman et al., 1996; Wilson and Nieland, 2001; Newman and Dunk, 2003; Marriott et al., 2007).

In this study we compared the demographic characteristics of seven lutjanid species on mid and outer shelf reefs of the Great Barrier Reef (GBR), Australia, as a case study of the implications for intra-family demographic diversity for managing multispecies fisheries. The species examined included the following: chinamanfish [*Symphorus nematophorus*]; green jobfish [*Aprion virescens*]; dory snapper [*Lutjanus fulviflamma*]; yellow-banded snapper [*L. adetii*]; humpback red snapper [*L. gibbus*]; brownstripe red snapper [*L. vitta*]; and spanish flag snapper [*L. carponotatus*]. These species are among the most common lutjanids caught on the GBR after the highly valued red snappers (*L. erythropterus*, *L. malabaricus*, *L. sebae*) (Newman et al., 2000b).

Demographic characteristics examined for each species included size, age, growth, mortality, and sex-specific patterns. Demographic parameters were compared to quantify differences in life history strategies among species and to infer the likely resilience of each species to fishing impacts. This information was used to assess whether common management measures would be appropriate across species within the lutjanid family. Such descriptive field studies also can be useful for providing the data sets to be used in meta-analyses for further developing our collective understanding of life history theory (e.g., Roff, 1984; Molloy et al., 2007). In this study we describe different aspects of biology across these closely related species. Samples from the same shallow coral reef habitats allowed us to control for taxonomic, geographic, and environmental effects to provide insight into the similarities or differences in life history strategies and thus theoretical trade-offs in evolved traits for moderate-size gonochoristic teleosts.

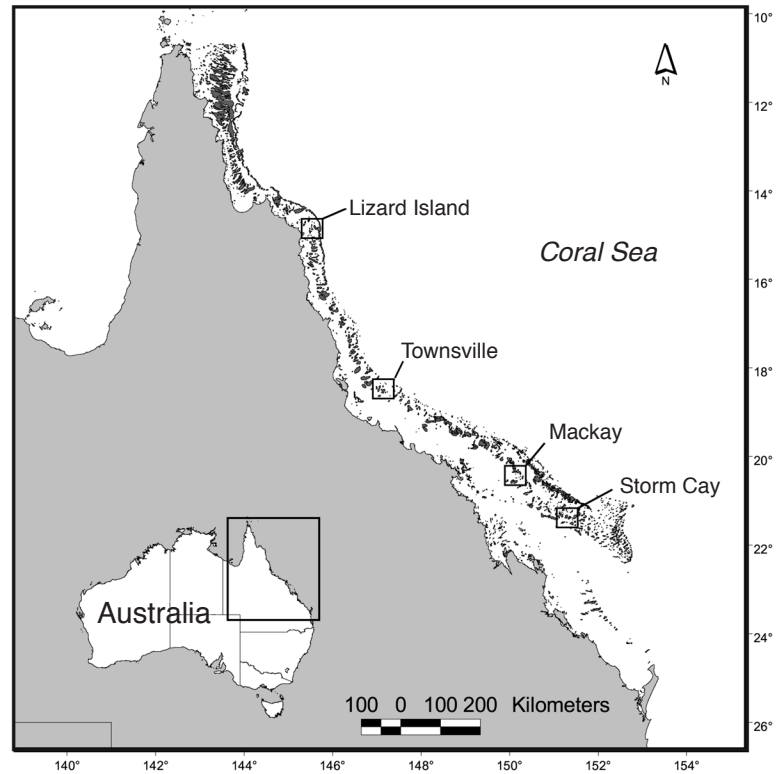


Figure 1

Map of the Great Barrier Reef region off the east coast of Australia showing the four sampling regions where lutjanids were collected for use in this study.

Materials and methods

Sample collection

Individuals of the seven lutjanids considered here were collected during the effects of line fishing (ELF) experiment¹ (Campbell et al., 2001) between 1995 and 2005 from four regions of the GBR spanning 7° of latitude: Lizard Island, 14°S; Townsville, 18°S; Mackay, 20°S; and Storm Cay, 21°S (Fig. 1). All fishing was done by hand-line with the same gear as that used in the operational commercial fishery, but survey effort was stratified to ensure roughly equal distribution around each reef and over two depth strata (above 12 m and below 15 m). Otoliths (sagittae) and gonads of fish were either dissected on the day of capture and processed as described below or fish heads were removed from filleted fish carcasses in the field, frozen, and otoliths were dissected upon return to the laboratory. Otoliths of five of the seven species were examined for age analysis (*A. virescens*, *S. nema-*

¹ Mapstone, B.D., C. R. Davies, L. R. Little, A. E. Punt, A. D. M. Smith, F. Pantus, D. C. Lou, A. J. Williams, A. Jones, A. M. Ayling, G. R. Russ, and A. D. McDonald. 2004. The effects of line fishing on the Great Barrier Reef and evaluations of alternative potential management strategies. CRC Reef Research Centre Technical Report no 52, 205 p. CRC Reef Research Centre, Townsville, Australia.

tophorus, *L. carponotatus*, *L. gibbus*, *L. fulviflamma*). Sufficient specimens were collected for comparisons among regions for only one species (*L. carponotatus*) and specimens for all other species were pooled across regions and years for analyses.

Fish processing

All fish were measured to the nearest millimeter fork length (FL) and weighed to the nearest gram before dissection. Otoliths were dissected from a subsample of specimens, cleaned, and stored dry in paper envelopes. Otoliths were embedded in epoxy resin and cut transversely through the primordium with a diamond-tipped blade on a low-speed saw to produce a thin section of 300–400 μm . Sections were mounted on glass slides by using Crystalbond adhesive (Aremco Products Inc., New York). Otoliths were read under reflected light at 40 \times magnification and opaque growth increments were counted from the primordium to the proximal (*in situ*) margin along the ventral ridge of the sulcus acousticus. Sectioned otoliths were read by one or more individuals. Where more than one reader was used, otoliths were read at least once by each of two independent readers and the age was accepted if these first two counts agreed. A third count was made by one of the two readers if the first two counts did not agree and a match between this third count and either of the previous two was accepted as the age of the fish or, if the third count did not match either of the first two counts, the median count was assigned as a final age estimate. The remaining otoliths were read by a single, experienced reader who counted each otolith at least twice with a minimum of 24 hours between consecutive counts. If the first two counts did not agree, a third count was completed to assign a final age through count agreement or to assign a median age, as described above.

Opaque increments were assumed to be annuli for the five species examined. Supportive evidence for annual periodicity in opaque increment deposition in otoliths has been demonstrated for the majority of tropical reef fish (Fowler, 1995; Choat and Robertson, 2002), lutjanids (e.g., Cappelletti et al., 2000), and for most of the study species: *L. vitta* (Davis and West, 1992; Newman et al., 2000a), *L. carponotatus* (Newman et al., 2000a; Kritzer, 2002), *L. adetii* (Newman et al., 1996), *L. fulviflamma* (Grandcourt et al., 2006), and *A. virescens* (Pilling et al., 2000). Age estimates derived from the otoliths for *L. gibbus* and *S. nematophorus* have not been validated hitherto, but we assumed that increment deposition also occurs on an annual basis for these species, as has been demonstrated for the majority of other tropical lutjanids. A violation of this assumption is likely to result in biases in the parameter estimates we present, such as for the von Bertalanffy parameter K and the instantaneous total mortality coefficient, Z . The magnitude of bias would likely inflate estimates for older-age species, and these estimates would vary among parameters, with a likely smaller influence on estimates of L_∞ (mean asymptotic fork length) (Choat et al., 2009). Gonads were

examined to define the sex and maturity of individuals, but low sample sizes prevented meaningful analysis of detailed histological staging or gonadosomatic index analyses. Gonads were dissected and either frozen or preserved in FAACC (formaldehyde 4%, acetic acid 5%, calcium chloride 1.3%) or 10% buffered formalin immediately after removal. Tissues were preserved in FAACC before May 1999 and 10% buffered formalin thereafter. The sex and maturity of *L. carponotatus* was established by macroscopic methods (Kritzer, 2004). The sex and maturity for a subset of individuals of other species were further assessed by histological analysis. Transverse histological sections were taken from the medial region of all gonads after the procedures outlined by Adams (2003). Female maturity was determined by the presence of vitellogenic oocytes, and the presence of brown bodies, atretic oocytes, vascularization, and the relative thickness of the gonad wall, all of which may indicate prior spawning (Sadovy and Shapiro, 1987; Ferreira, 1995; Adams, 2003). Male maturity was determined by the presence of sperm in the sperm sinuses.

Estimation of demographic parameters

Length- and age-frequency distributions were constructed from pooled samples and compared among species qualitatively. Differences in length and age frequencies by sex were assessed by using two-sample Kolmogorov-Smirnov tests where the largest of absolute discrepancies between relative cumulative frequency distributions (d_{max}) was compared with an approximate two-tailed critical value (D : Sokal and Rohlf, 1995). Growth was modeled with the von Bertalanffy growth function (VBGF) fitted by using a nonlinear least-squares regression of FL on age. The form of the VBGF was

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

where L_t = the length at age t ;

L_∞ = the mean asymptotic fork length;

K = the growth coefficient or rate at which L_∞ is approached; and

t_0 = theoretical age at zero length.

The VBGF model was fitted to L_t on t data groups where t_0 was either constrained to zero ($t_0=0$) or unconstrained (estimated). This was done to examine the effects of the absence of smaller individuals in the sample and (for $t_0 = 0$) to allow biologically sensible comparisons of growth among species if lengths at age of younger fish (not sampled) extrapolated by the model were biologically unrealistic. VBGFs for *L. carponotatus* for all regions were compared by likelihood ratio tests.

Analysis of covariance (ANCOVA) was used to compare log-transformed length data from individuals across a common age range (5–12 years) among the five species with age as a covariate. A Tukey's *post hoc* test ($P=0.05$) was used to test for differences among species when a significant difference among the groups was detected by the ANCOVA.

Age-based catch curves (Ricker, 1975) were used to estimate the instantaneous rate of total mortality (Z) for each species. The natural log-transformed number of fish in each age class was regressed against the corresponding age on the descending slope of the age-frequency distribution to provide an estimate of total mortality, Z . Regressions were fitted from the first modal age class, presumed to be the first age class fully selected by the sampling gear, through the oldest age class that was preceded by no more than two consecutive zero frequencies. An ANCOVA was used to determine whether there were differences in mortality among regions for *L. carponotatus*. Z also was estimated by using the Hoenig (1983) estimator for fish populations from $\log_e Z = 1.46 - 1.01 \log_e t_{max}$, where t_{max} was the maximum observed age in years.

Sex ratios and size- and age-frequency distributions were examined to describe sex-specific aspects of population structure. Departure from a 1:1 sex ratio was tested with a chi-squared test by using Yates's correction for continuity (Zar, 1999).

Results

A total of 7307 individuals of the seven lutjanid species were sampled, of which *L. carponotatus* was the most abundant. The modal length in the sampled distributions differed among species (Fig. 2) and was largest for *S. nematophorus* (400–449 mm FL) and *A. virescens* (450–499 and 600–649 mm FL) and smallest for *L. fulviflamma* (260–279 mm FL). *Symphorus nematophorus* and *A. virescens* had the largest maximum fork lengths of 885 mm and 810 mm FL, respectively. Of the seven species, the sampled length ranges of *L. carponotatus*, *L. fulviflamma*, and *L. adetii* were most similar, with 72%, 89%, and 81% coming from the size range of 200–300 mm FL, respectively.

Age-frequency distributions varied considerably among the five species for which age was estimated. The modal

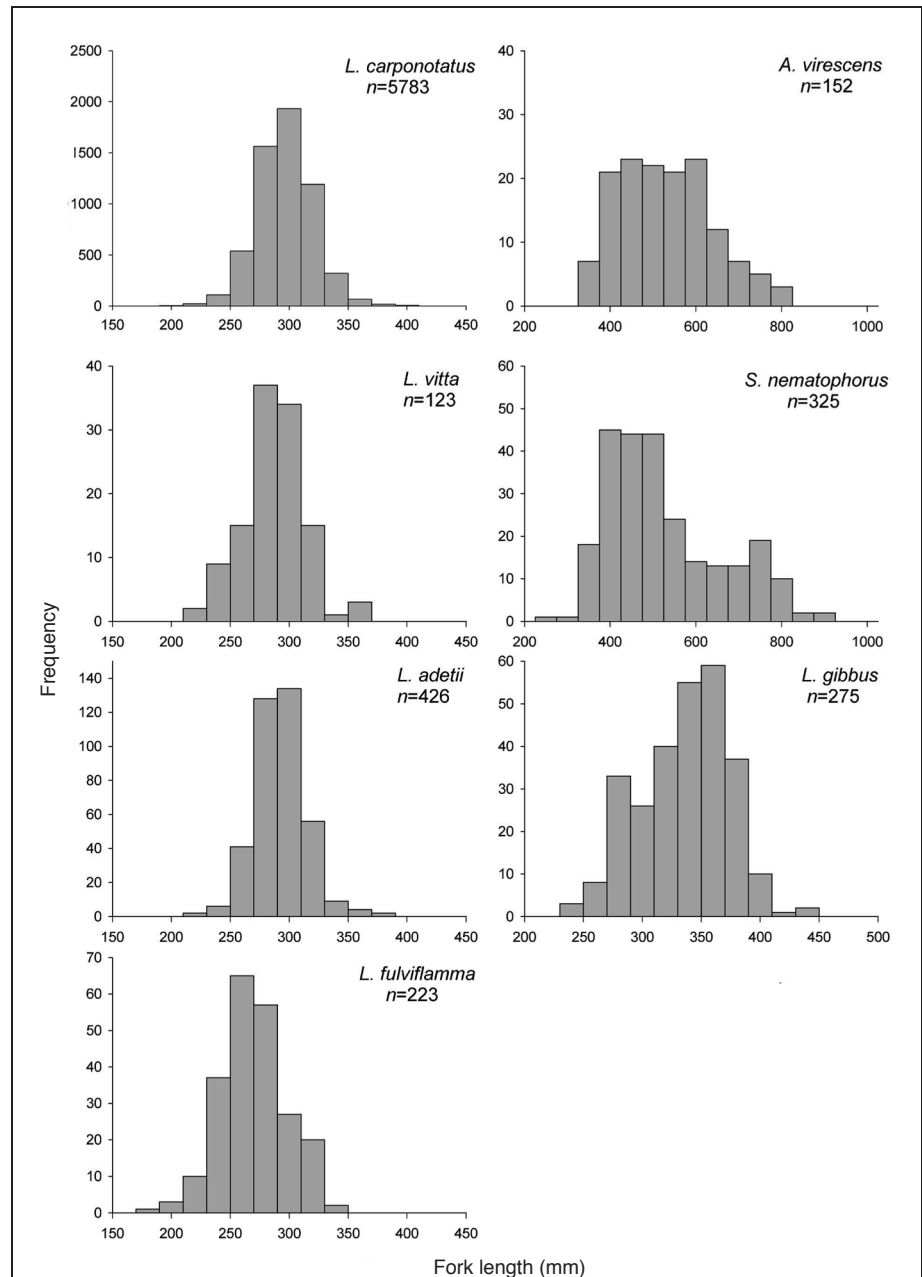


Figure 2

Length-frequency distributions for seven lutjanid species on the Great Barrier Reef between 1995 and 2005 (note difference in y axes).

age in the catch was 2 years for *A. virescens*, 3 years for *S. nematophorus*, 7 years for *L. carponotatus*, 8 years for *L. gibbus*, and 10 years for *L. fulviflamma* (Fig. 3). The catch of the two largest species (*S. nematophorus* and *A. virescens*) consisted predominately of younger age classes (<6 yr), whereas the catch of smaller species (*L. carponotatus*, *L. gibbus*, *L. fulviflamma*) included a higher proportion of fish sampled from older age classes (>8 yr; Fig. 3). The maximum age in the catch also

differed among species (Fig. 3) and the oldest fish was a 36-year-old *S. nematophorus*.

Regional and sex-specific differences in length- and age-frequency distributions could only be analyzed for *L. carponotatus* because of low sample sizes for all other species. There was a significant effect of sex on lengths (Kolmogorov-Smirnov test: $n_1=1279$, $n_2=399$, $d_{\max}=0.336$, $D=0.078$, $P<0.05$) and ages ($n_1=1279$, $n_2=399$, $d_{\max}=0.281$, $D=0.078$, $P<0.05$) for the frequency distributions and a greater proportion of males than females in the larger size classes and younger age classes (Fig. 4). Differences in growth by sex were significantly different ($\chi^2=68.34$, $P<0.0001$), with males reaching a significantly greater maximum size than females

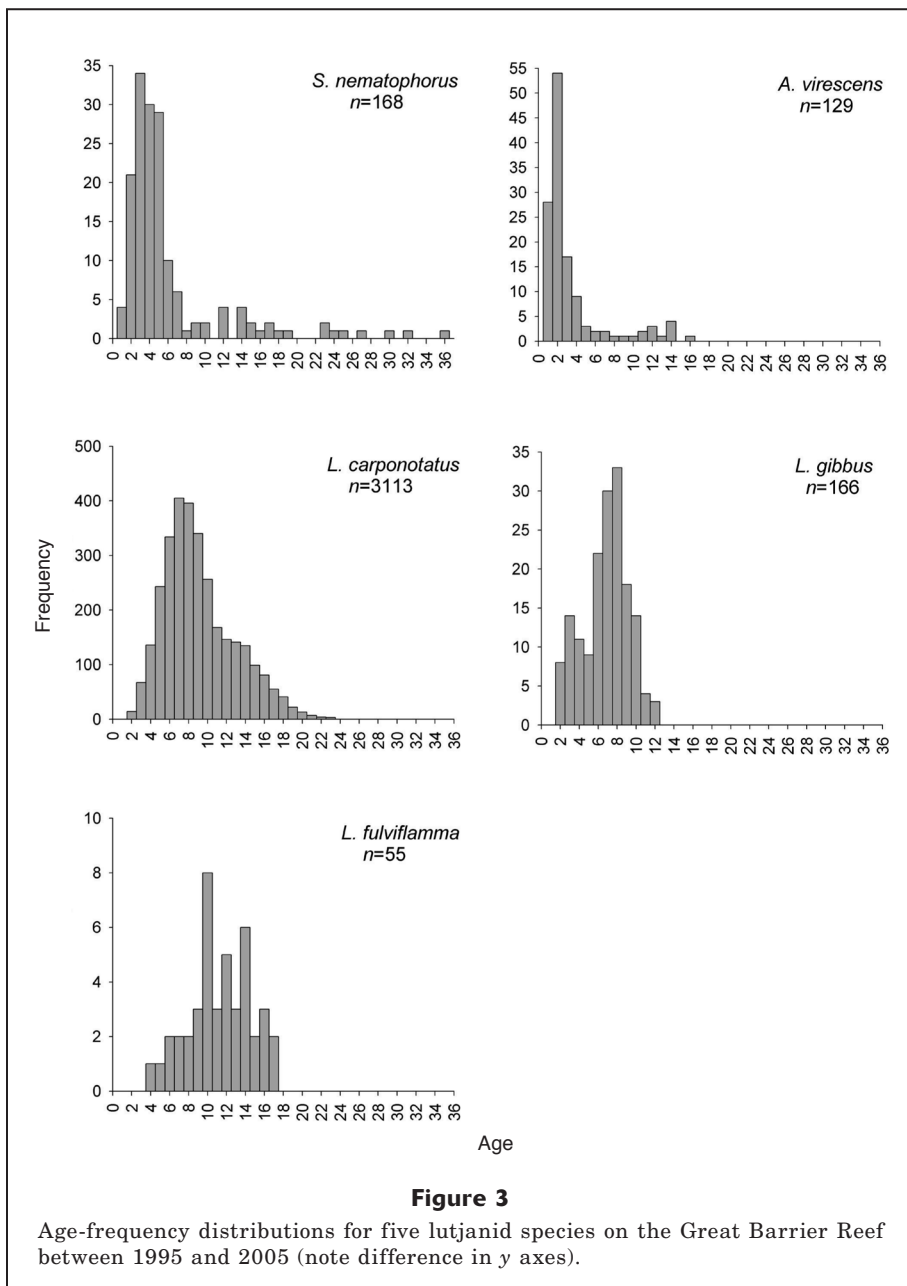
(female: $L_{\infty}=278$, $K=0.43$, $t_0=-2.55$; male: $L_{\infty}=293$, $K=0.55$, $t_0=-1.43$).

The unconstrained fits of the VBGF differed substantially among species with *L. carponotatus*, *A. virescens*, and *L. fulviflamma* reaching a maximum size relatively early in life (Fig. 5). *Symphorus nematophorus* reached a maximum size somewhat later in life, and the growth curve for *L. gibbus* was not asymptotic. The lack of juvenile fish collected for all species, but particularly for *L. carponotatus*, *L. fulviflamma*, and *L. gibbus*, resulted in relatively flat fits of the unconstrained VBGF. The nonasymptotic growth pattern for *L. gibbus* indicates that under-sampling of larger individuals may also have occurred. VBGF parameter estimates for all

species from the unconstrained fit are likely to be biased and should be interpreted with some caution.

Constraining the VBGF by setting $t_0=0$ produced similar estimates of K and L_{∞} to those for the unconstrained estimates for *L. carponotatus* and *L. fulviflamma*. Despite limited sampling of the youngest individuals, this similarity indicates that a sufficiently wide range of age classes were sampled in these populations to produce biologically reasonable estimates of growth without the need to constrain t_0 . Constraining t_0 resulted in faster initial growth estimates (greater estimate of K) and smaller asymptotic length (L_{∞}) than the unconstrained fits for *S. nematophorus*, *A. virescens*, and *L. gibbus*. The constrained fit produced a more asymptotic growth curve for *L. gibbus*, indicating that constraining t_0 may have provided a more biologically realistic estimate of length-at-age for this species.

Both constrained and unconstrained growth curves differed across species. These species showed distinct differences in the rate of growth at young ages and the age at which they reached average maximum length: smaller species grew fast in the first couple of years and reached asymptotic length early, whereas larger species grew slightly slower in the first few years to reach an asymptotic FL later. The lack of small-size individuals resulted



in a lack of definition of early growth in the unconstrained curves when compared to constrained estimates. Both constrained and unconstrained growth curves for *L. carponotatus* and *L. fulviflamma* were relatively “square-shaped” (Choat and Robertson, 2002), revealing little growth over most of their life spans. Several species had K values $>0.30/\text{yr}$, indicating rapid growth to maximum size at a young age.

Comparison of growth rate among 5–12 year olds revealed significant differences among species ($F_{4,2503}=1543.8$, $P<0.0001$). *Post hoc* tests indicated that each species had a unique growth rate. Examination of age at 50% L_{∞} indicated some differences between constrained and unconstrained fits (Table 1), but in all cases, 50% of asymptotic length was reached at relatively young ages compared with estimated longevity, and only *L. gibbus* took longer than 10% of expected longevity to reach 50% of asymptotic size (Table 1).

Lutjanus carponotatus was the only species with a sample size sufficient for regional analysis of growth data. Likelihood ratio tests indicated that patterns of growth differed significantly between Lizard Island, Mackay, and Storm Cay regions ($\chi^2=68.34$, $P<0.001$) but there were similar L_{∞} values among regions, and quite variable K values (Table 1). The most notable difference was the greater L_{∞} (and lower K) in the Storm Cay region (Table 1).

Total mortality (Z) estimates calculated from catch curves varied significantly among the five species examined ($F_{4,41}=5.61$, $P=0.001$) (Fig. 6). Z was highest for *L. gibbus* and *A. virescens* and lowest for *L. fulviflamma* (Table 2). Mortality rates calculated by the Hoenig method resulted in more homogeneous estimates, of which highest rates were for *L. gibbus* and lowest for *S. nematophorus*. Mortality estimates calculated from catch curves were higher than those estimated by Hoenig’s method for all species except *L. fulviflamma* (Table 2). Z for *L. carponotatus* did not vary significantly among the three regions ($F_{2,29}=2.24$, $P=0.15$) and therefore a single catch curve was fitted to data pooled across regions.

All except one of the individuals sampled (282-mm *L. gibbus*) were sexually mature, making analysis of size and age at maturity impossible. Adult sex ratios in a few of the sampled populations differed from a 1:1 sex ratio (Table 3), despite the expected gonochoristic nature of these species. Sex ratios of *L. carponotatus*, *L. gibbus*, and *L. vitta* were biased significantly toward males.

Discussion

Many coral reef fish species have overlapping spatial distributions, are found in similar habitats, and grow to roughly similar sizes. It might be expected that superficially similar species from the same family would have

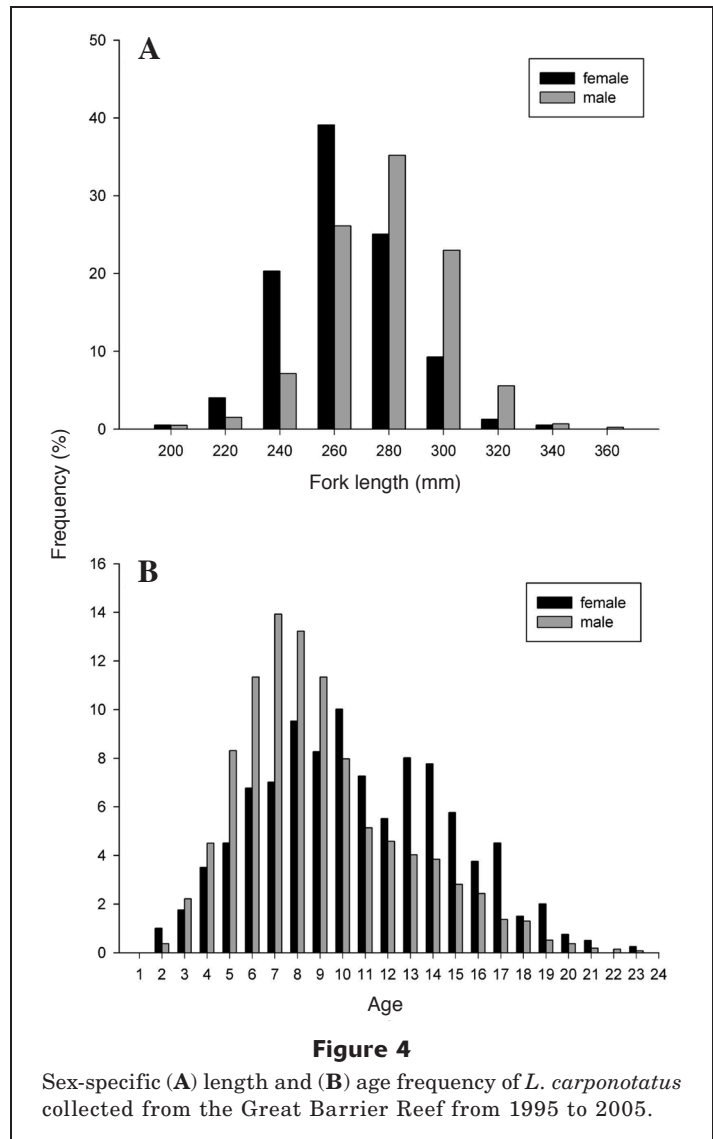
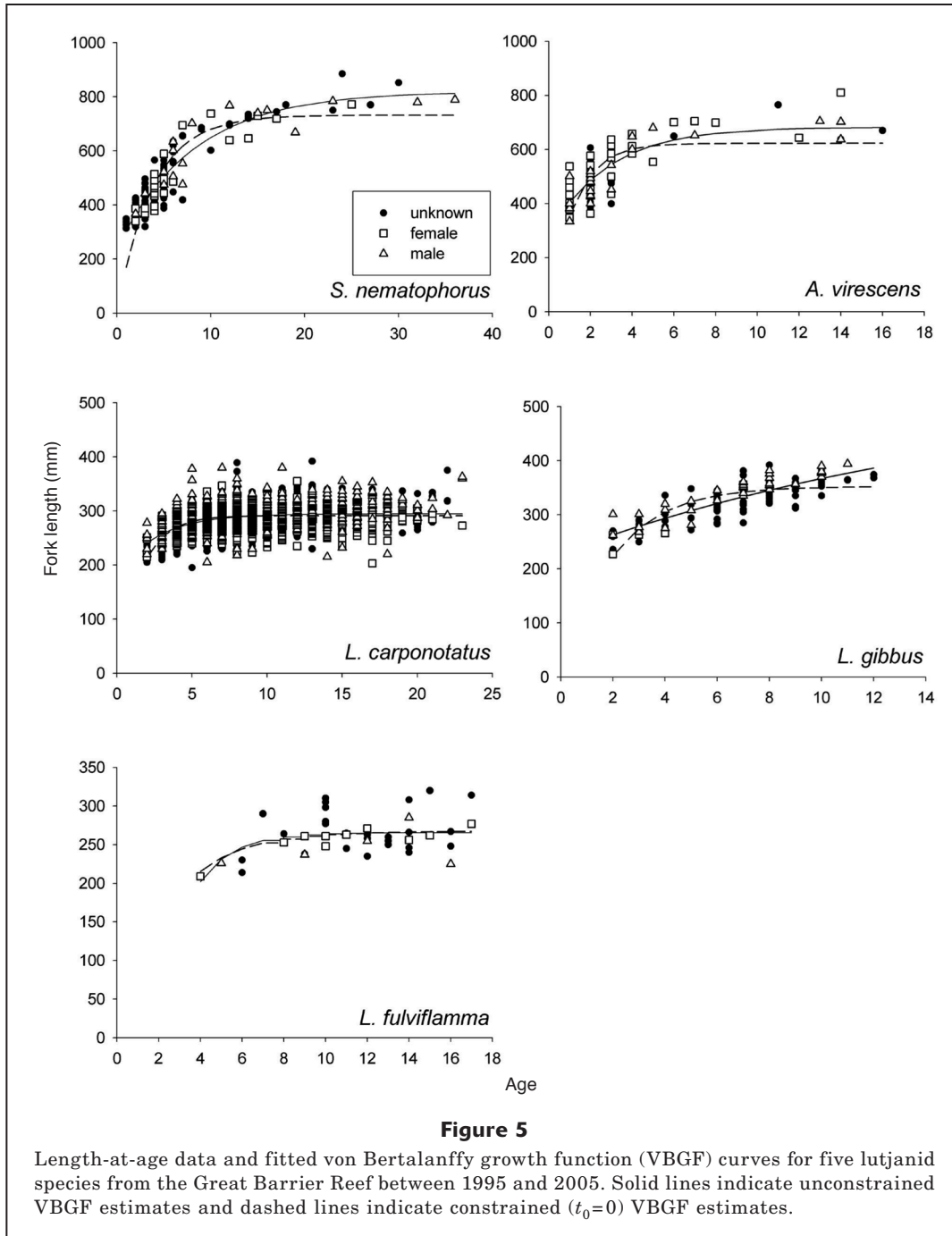


Figure 4
Sex-specific (A) length and (B) age frequency of *L. carponotatus* collected from the Great Barrier Reef from 1995 to 2005.

similar demographic characteristics and life history strategies. The results of this case study of lutjanid species, however, indicate that it is impossible to make generalizations about the life histories of members of a family, even where they grow to similar sizes and coexist in the same habitats. Even this small subset of seven lutjanid species had quite different growth, mortality, and longevity characteristics. Our results support previous findings for individual species but also provide evidence of the considerable differences among species in this family and highlight the need for careful, and potentially species-specific, approaches to managing the harvest of lutjanid assemblages.

Demographic characteristics of the lutjanid species described here must be considered in the context of the limitations of size selectivity of the fishing gear used to sample populations. No individuals below 200 mm FL were collected for any species, meaning the youngest age classes were not fully selected, resulting



in an absence of immature individuals for all, but one species. However, some individuals of most species were sampled in their first or second year indicating that these species mature at a very early age. The fact that full recruitment to the gear occurred at age 2 for *S. nematophorus* and at age 3 for *A. virescens*, the largest species sampled, illustrated the rapid early growth characteristic of many lutjanid species (Newman et al., 1996, 2000a; Kritzer, 2004; Grandcourt et al., 2006). It is important to note that the same sampling gear

was used in this project as that most commonly used by commercial and recreational fisheries on the GBR and therefore the biological characteristics described here should reflect those characteristics of individuals of these species harvested by the fishery. Importantly, the sampled age distributions revealed the age range of these populations susceptible to fishing gear. It is also likely that many fish were not sampled because sampling was constrained to depths shallower than 30 m and to daylight hours, which are the most common

Table 1

Parameter estimates for the von Bertalanffy growth function parameters age at 50% L_{∞} (mean asymptotic fork length) and percent longevity at 50% L_{∞} for five lutjanid species from the Great Barrier Reef. K is the von Bertalanffy growth coefficient, and t_0 is the theoretical age at length zero. "U" indicates an unconstrained estimate, "C" indicates an estimate constrained by $t_0=0$. Region-specific growth curves for *L. carponotatus* were not constrained.

Species	L_{∞} (mm)	K (/yr)	t_0 (yr)	Age (yr) at 50% L_{∞}	% longevity at 50% L_{∞}
<i>S. nematophorus</i> —U	820	0.12	-2.83	3	8.33
<i>S. nematophorus</i> —C	732	0.26	0	3	8.33
<i>A. virescens</i> —U	683	0.35	-1.53	0.5	3.13
<i>A. virescens</i> —C	623	0.85	0	1	6.25
<i>L. gibbus</i> —U	544	0.06	-9.48	2	16.67
<i>L. gibbus</i> —C	352	0.51	0	3	25.0
<i>L. fulviflamma</i> —U	265	0.61	1.66	1	5.88
<i>L. fulviflamma</i> —C	267	0.41	0	1	5.88
<i>L. carponotatus</i> —U	295	0.37	-2.58	0	0
<i>L. carponotatus</i> —C	291	0.66	0	1	4.35
<i>L. carponotatus</i> —Lizard Is	293	0.67	-0.17	—	—
<i>L. carponotatus</i> —Mackay	292	0.47	-1.68	—	—
<i>L. carponotatus</i> —Storm Cay	302	0.16	-9.35	—	—

Table 2

Estimates of mortality for five lutjanid species using catch curve and Hoenig (1983) estimators. Maximum age and age range used in mortality estimation are indicated.

Species	Maximum age (yr)	Age range (yr)	Catch curve Z (/yr) [SE]	Hoenig Z (/yr)
<i>S. nematophorus</i>	36	3–17	0.20 [0.05]	0.11
<i>A. virescens</i>	16	2–9	0.56 [0.07]	0.26
<i>L. gibbus</i>	12	8–12	0.63 [0.08]	0.35
<i>L. carponotatus</i>	23	7–23	0.30 [0.02]	0.18
<i>L. fulviflamma</i>	17	10–17	0.14 [0.06]	0.25

depth and time fished by commercial and recreational fishing crews. A small number of fishing crews fish during the night in deeper water (>50 m) where a greater proportion of larger lutjanids are caught (Marriott, personal commun.).

Limited sample sizes prevented the statistical analyses of sex- and region-specific variation in life history characteristics except for *L. carponotatus*. As with previous findings, *L. carponotatus* displayed sex-specific differences in these characteristics, with males reaching larger maximum sizes than females. Reasons for sex-specific size and age distributions may be due to a wide array of factors, including regional conditions and physiological costs of sperm and egg production. Kritzer (2004) also found male *L. carponotatus* to be larger than females and suggested that this is an Indo-Pacific trait within the lutjanids because it does not always occur in other geographic areas. Such sex-specific differ-

ences in lutjanid populations also may vary by region, although the magnitude of any sex-dependent variation within a geographic area remains poorly understood. Hence, our parameter estimates for the remaining species from samples pooled over regions of the GBR may not be as informative as we would like, but they nevertheless provide a good starting point for comparison and applicability to other regions where data remain scarce or absent.

Age and growth

Five of the seven species examined grew to similar sizes, but three of these demonstrated different longevities and the two largest species showed a twofold range in longevity for roughly similar maximum sizes, again illustrating the lack of a relationship between length and age across tropical lutjanids. High maximum ages

Table 3

Number and size of male and female lutjanid individuals sampled from the Great Barrier Reef between 1995 and 2005 for reproductive analysis. Size range is included in parentheses; values in bold indicate significant difference from an even sex ratio.

Species	Female		Male		Sex ratio F/M
	<i>n</i>	Mean size (mm FL)	<i>n</i>	Mean size (mm FL)	
<i>L. fulviflamma</i>	28	263 (209–315)	16	250 (219–285)	1.75
<i>S. nematophorus</i>	32	533 (340–772)	41	485 (320–789)	0.78
<i>A. virescens</i>	50	511 (332–810)	32	509 (334–778)	1.56
<i>L. adetii</i>	18	284 (254–374)	22	290 (243–341)	0.82
<i>L. gibbus</i>	8	277 (227–356)	48	330 (262–418)	0.17
<i>L. vitta</i>	7	266 (204–307)	18	270 (226–310)	0.39
<i>L. carponotatus</i>	520	274 (203–355)	1722	292 (205–405)	0.30

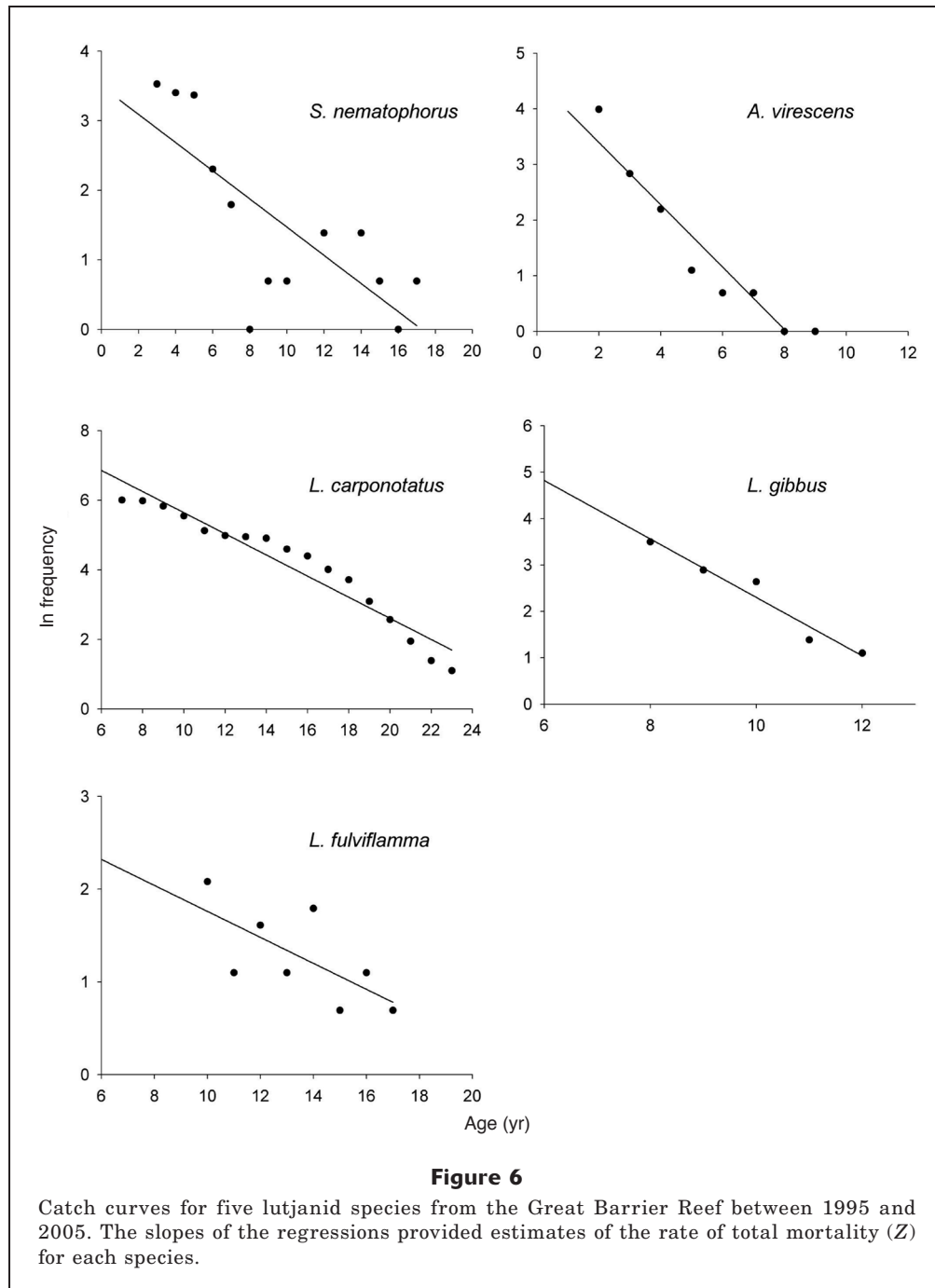
of 36 and 23 years were evident in *S. nematophorus* (the largest species) and *L. carponotatus* (the second smallest species), respectively, despite their different maximum sizes. *Lutjanus gibbus*, *A. virescens*, and *L. fulviflamma* had shorter life spans and maximum ages of 12, 16, and 17 years, respectively. *Lutjanus carponotatus* have previously been reported to have maximum ages of 18 and 20 years (Newman et al., 2000a; Kritzer, 2002, 2004) which are consistent with the 23 year maximum obtained here. Shorter longevities recorded for *L. gibbus*, *A. virescens*, and *L. fulviflamma* align with those from other lutjanid species such as *L. vitta* (12 years, Newman et al., 2000a), *L. guttatus* (rose snapper, 11 years, Amezcua et al., 2006), and *L. fulviflamma* (14 years, Grandcourt et al., 2006). In contrast, *L. adetii*, a small species similar in size and appearance to *L. vitta*, has a reported maximum age of 24 years (Newman et al., 1996), further demonstrating the variability in life histories of similar size lutjanid species.

This and most previous studies reveal that these species have rapid initial growth despite differences in size and longevity; however, they reach asymptotic sizes at relatively young ages (Newman et al., 1996, 2000a; Kritzer, 2002, 2004; Grandcourt et al., 2006). Newman et al. (1996) suggested that size could not be used to infer age for *L. adetii* beyond five years of age. This principle is probably applicable for many lutjanid species and is supported by the growth patterns for four of the five species for which growth was analyzed, the exception being *L. gibbus*. All five species reached 50% of L_{∞} before reaching 4 years of age. Caution should be used when generalizing, however, because red bass (*L. bohar*) and goldband snapper (*Pristipomoides multidens*) have been shown to be slow growing, long lived, and

late maturing, showing a classic K-selected life history (Newman and Dunk, 2003; Marriott et al., 2007). That result contrasts with the fast growth observed in most other lutjanid species so far examined.

Lutjanus gibbus was the only species that did not reach an asymptote in the unconstrained growth curve. This may have been the result of the gear excluding smaller and younger individuals, a proposition supported by the fact that the constrained VBGF curves did produce an asymptote and the unconstrained functions produced an unrealistic t_0 value of -9.48. Observations that larger individuals were collected from deeper water indicate that the largest size and oldest age classes of *L. gibbus* and *S. nematophorus* may have been under-sampled. Alternatively, these species may indeed have a long growth period and not stop growing throughout life, as does *L. bohar* (Marriott et al., 2007). The largest reported *L. gibbus*, however, was 50 cm total length (TL) (Carpenter and Niem, 2001)—only 5 cm larger than the largest individual sampled in this study (418 mm FL, \approx 500 mm TL). *Lutjanus gibbus* was also the species with the highest mortality estimates from both catch curve and Hoenig's estimators, indicating that it had the highest turnover rates. Further sampling will be required to gain a better understanding of the age and growth characteristics of this species and resolve whether the differences in characteristics between *L. gibbus* and the other species examined were attributable to different life history strategies or to the effects of species-specific sampling biases.

All five species for which age was estimated reached 50% of the estimated L_{∞} at young ages in relation to their maximum age. The percentage of longevity at which 50% L_{∞} was reached was similar for most spe-



cies, and *L. gibbus* was the only species taking greater than 10% of its longevity to attain 50% L_{∞} . Growth of *L. carponotatus* varied significantly among regions spanning 7° latitude, growing more quickly to smaller asymptotic lengths in the more equatorial regions than in the south. Although statistically significant, the difference in growth may have little biological significance with L_{∞} varying only about 3% among regions. Regional variation in growth for the other species remains unknown because of a lack of data but results for

L. carponotatus reveal potential environmental influences on observed patterns for these other species.

Mortality

Estimates of mortality were likely biased because of selectivity of the sampling gear. For example, the positively skewed age distributions for *S. nematophorus* and *A. virescens* indicate that older fish were less available to the sampling gear and were likely to be under-

represented in the sample, resulting in overestimates of Z from catch curves. Estimates of Z derived from Hoenig's equation may be more appropriate for these species. Similarly, older individual *L. gibbus* and *L. fulviflamma* may not have been collected by the gear and if so, under-sampling may have resulted in overestimates of Z from the catch curves and Hoenig's method. Notwithstanding these potential biases, comparison of mortality rates revealed that *A. virescens* had a similar mortality rate to that of *L. gibbus*, indicating that *A. virescens* also has a relatively high population turnover rate. *Aprion virescens* grows quickly to a large size but may not live as long as other lutjanid species, despite attaining relatively large sizes. *Symphorus nematophorus*, for example, attained the largest size and had the second lowest mortality rate of the species examined. *Lutjanus fulviflamma* mortality estimates differed most between estimation methods, with catch curve estimates resulting in lowest mortality rates for this species (0.14/yr), but the Hoenig estimate revealed higher mortality rates (0.25/yr), similar to those for *A. virescens* and *L. gibbus*. The Hoenig estimate was also similar to rates previously reported for *L. fulviflamma* (0.29/yr, Grandcourt et al., 2006), indicating some bias in the estimate from catch curves. Like *L. gibbus*, *L. carponotatus* under six years of age could not be used in catch curve estimates of mortality, but the 6–23 year age classes yielded mortality estimates for *L. carponotatus* of 0.30/yr (catch curve) and 0.18/yr (Hoenig), similar to estimates calculated previously for this species (0.20/yr, Newman et al., 2000a; 0.26–0.29/yr, Kritzer, 2004). The range of mortality estimates for the species examined in this analysis agree well with those for other lutjanids (Newman et al., 1996, 2000a; Amezcua et al., 2006) and are another indication of the variability in life history strategies within the family.

Maturity and sex ratio

All except one individual sampled across all species were sexually mature, supporting the conclusion that these lutjanids reach sexual maturity early in life. Biased sex ratios were observed for all of the species sampled although the apparent biases were statistically significant for only three species. Two species (*L. fulviflamma*, *A. virescens*) showed large but nonsignificant female-biased sex ratios, whereas all others showed a male-biased ratio, and three (*L. carponotatus*, *L. vitta*, *L. gibbus*) were not significantly different from 1:1. Lutjanids are gonochoristic species and therefore it may be expected that adult sex ratios would be close to 1:1 in local populations, although at least three other studies have revealed biased sex ratios. Kritzer (2004) found that *L. carponotatus* had a female-biased sex ratio, whereas Newman et al. (2000a) reported a strongly male-biased sex ratio for the same species in similar locations to those that we examined. Studies of *L. fulviflamma* from different locations showed widely variable sex ratios. Kaunda-Arara and Ntiba (1997) reported a male-biased sex ratio in Kenya, and Grand-

court et al. (2006) reported a female-biased sex ratio in the southern Arabian Gulf. It is difficult, therefore, to establish generic patterns of sex ratios across, or even within, lutjanid species given the contradictory patterns in the literature and among the species sampled here. It is possible that sex-ratio bias is a result of a differential survival of males and females or sex-specific patterns in distribution that would result in males and females having different probabilities of capture in the sampling strategies used in various studies, including the present one. Kritzer (2004) was one of the few to have examined mortality by sex, but no difference in mortality by sex was found. This single result may indicate that differential spatial distributions may be a more likely cause of sex-ratio biases in samples of lutjanid populations. It has been suggested that sex ratio may be more even during spawning events (Kritzer, 2004), but no data are available to test this hypothesis.

Implications for management of lutjanid populations

An improved understanding of the demographic parameters of gonochoristic species is crucial to furthering research on the effects of fishing on their populations. Results here clearly demonstrate that all or even superficially similar (e.g., in size) subsets of lutjanid species should not be treated in the same manner in these types of analyses and that vulnerability is likely to be variable within the family. Careful consideration of the inherent life history variability of these species is required in the development of theories and generalizations about this family and others.

This case study of seven lutjanid species clearly indicates that data from one species cannot be applied to another in determining appropriate management measures for these populations. Some species appeared to be more susceptible than others to overexploitation by fisheries because of their longer life spans and lower rates of mortality. *Symphorus nematophorus* is a good example of a species with a long life span, large size, and low mortality. The combination of these factors could make this species a desirable fisheries target (owing to its larger size than other lutjanids), but also one of the most vulnerable because of its life history characteristics. *Symphorus nematophorus* and *L. gibbus* are currently no-take species within the GBR and have historically been avoided because of a potential risk of ciguatera (a form of food poisoning from eating large reef fish), and therefore these species are largely protected from harvest within this region, although this may not be the case in other parts of their range.

In comparison, the longevity of *L. carponotatus* and *L. adetii* in relation to other lutjanid species may make them more vulnerable to overfishing than sibling species (Newman et al., 1996). Despite their small size and fast growth, these populations may be more vulnerable than similar species such as *L. vitta* which have shorter longevities and hence potentially faster population turnover rates (Newman et al., 2000a). Notably, most of the species examined here recruited to the fishing gear at

relatively early ages but also apparently reached sexual maturity before recruitment to the fishery. The existence of early maturity in relation to longevity indicates a life history strategy with high reproductive potential in older individuals—perhaps indicative of adaptation to low-frequency episodic recruitment successes (Kritzer, 2002, 2004). These characteristics may mean that lutjanids are particularly vulnerable to recruitment collapse from sustained harvest at relatively low rates of fishing-induced mortality.

Current management measures for lutjanid species within the GBR are precautionary to protect the widest possible range of lutjanid family members, but this may not be the case in other parts of their range and implications of differences among species should be considered in such situations. The presence of substantial variation in life histories among species would indicate that the data presented here could serve as a benchmark for these species in other regions, but should not be applied to different species that may not have comparable demographic parameters despite morphometric similarities to the species examined here. Failure to recognise differences in life histories when implementing management strategies across species may result in over-exploitation of some species, under-exploitation of others, or both. Furthermore, we recommend that local species-specific estimates of population parameters are obtained wherever possible because significant regional and local variation in population parameters is becoming increasingly apparent for tropical reef fish populations (e.g., Adams et al., 2000; Kritzer, 2002; Williams et al., 2003). Consequently, estimates derived from local populations are likely to significantly improve assessments and advice for the management of particular stocks.

Acknowledgments

Funding for the ELF experiment was provided by the CRC Reef Research Centre, the Fisheries Research and Development Corporation, the Great Barrier Reef Marine Park Authority, Queensland Primary Industries and Fisheries, and James Cook University. The authors would like to thank the many commercial fishermen who participated in the ELF experiment, in particular R. Stewart, M. Petersen, T. Must, K. Holland, and M. Bush. Funding to process and analyze samples from the ELF experiment was provided by the Australian Government's Marine and Tropical Sciences Research Facility through the Reef and Rainforest Research Centre. This manuscript is a contribution from the ELF project.

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