The Comparative Biology of Lutjanid Species on the Great Barrier Reef

Project Milestone Report

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Introduction

The Lutjanidae family comprises a wide array of species of varying size and body form. This family contains approximately 103 species, making it one of the largest and most diverse families of fish. Lutjanids are found in tropical waters around the globe and are often associated with reef habitats (Allen 1985). These small to medium sized fish are of high commercial value throughout the world and are regularly taken in artisanal, recreational and commercial fisheries (Newman *et al.* 1996; Kaunda-Arara and Ntiba 1997; Marriott and Mapstone 2006; Amezcua *et al.* 2006). Due to their high fisheries value, concerns are being raised about the level of harvest and sustainability of fishing lutjanid populations. Their aggregative behaviour and reef based distribution make lutjanids particularly vulnerable to exploitation.

Little is known about the distribution and life history characteristics of many lutjanid species (Newman *et al.* 1996, 2000; Kaunda-Arara and Ntiba 1997; Marriott and Mapstone 2006; Amezcua *et al.* 2006; Marriott *et al.* 2007). Although research has covered much of the family's range, including Mexico (Arreguín-Sánchez and Manickchand-Heileman 1998; Amezcua *et al.* 2006), Kenya (Kaunda-Arara and Ntiba 1997), the United States (Meyer *et al.* 2007), Japan (Shimose and Tachihara 2005), the Great Barrier Reef (Newman *et al.* 1996, 2000; Marriott and Mapstone 2006; Marriott *et al.* 2007), the Arabian Gulf (Grandcourt *et al.* 2006) and the central Indian Ocean (Pilling *et al.* 2000), many species remain unstudied and comparisons between species are limited. The little data that does exist suggests that at least some lutjanid species are long-lived with lifespans over thirty years (Newman *et al.* 1996; Marriott and Mapstone 2006; Marriott *et al.* 2007).

Life-history characteristics among families of coral reef fish are diverse (Sale 1991; Gust *et al.* 2002). This is also true within the highly varied lutjanid family. Some lutjanid species grow to a large size (e.g. *Lutjanus sebae*, *L. malabaricus*), while others are small (e.g. *L. adetii*, *L. vitta*) with variable life spans and distributions. In addition to differences within the family, lutjanids also vary from most other reef fish by being gonochoristic (i.e. they do not change sex), and may mean that they require different management scenarios to other species. Variability in the life history characteristics of coral reef fish means that anthropogenic effects, such as fishing, may produce unpredictable responses within a population causing some species to be more vulnerable to exploitation than others. Thus, management cannot assume uniform life history characteristics, particularly when considering a family as diverse as the lutjanids.

The harvest of lutjanids on the Great Barrier Reef (GBR) is managed by the Queensland Department of Primary Industries and Fisheries (QDPI&F) by a number of input and output controls including species-specific minimum legal size limits, recreational possession limits and a Total Allowable Commercial Catch (TACC). Most lutjanids are managed under the single "other species" TACC within the Coral Reef Fin Fish Fishery (CRFFF), which also includes species of lethrinid, serranid, labrid and scarid, 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, some common species (e.g. *Lutjanus johnii* and *L. argentimaculatus*) occur primarily in inshore waters and are not managed as part of the CRFFF.

This research was designed to examine and compare the biology of several lutjanid species occurring on mid and outer shelf reefs of the GBR. The species examined included the chinaman *Symphorus nematophorus*; green jobfish *Aprion virescens*; blackspot seaperch *Lutjanus fulviflamma*; hussar *L. adetii*; paddletail *L. gibbus*; striped seaperch *L. vitta*; and stripey *L. carponotatus.* Characteristics of the biology of each species were examined including size, age, growth, mortality and reproductive patterns. Comparisons between biological parameters were completed where possible to define differences between species, examine their resilience to fishing pressure and determine whether current management measures are appropriate.

Methodology

Sample collection

A total of 7,307 lutjanids (Table 1) were sampled from reefs in four regions of the GBR (Lizard Island, Townsville, Mackay and Storm Cay) over eleven years from 1995 to 2005 during the Effects of Line Fishing (ELF) Experiment structured research fishing surveys (Mapstone *et al.* 2004) (Figure 1).

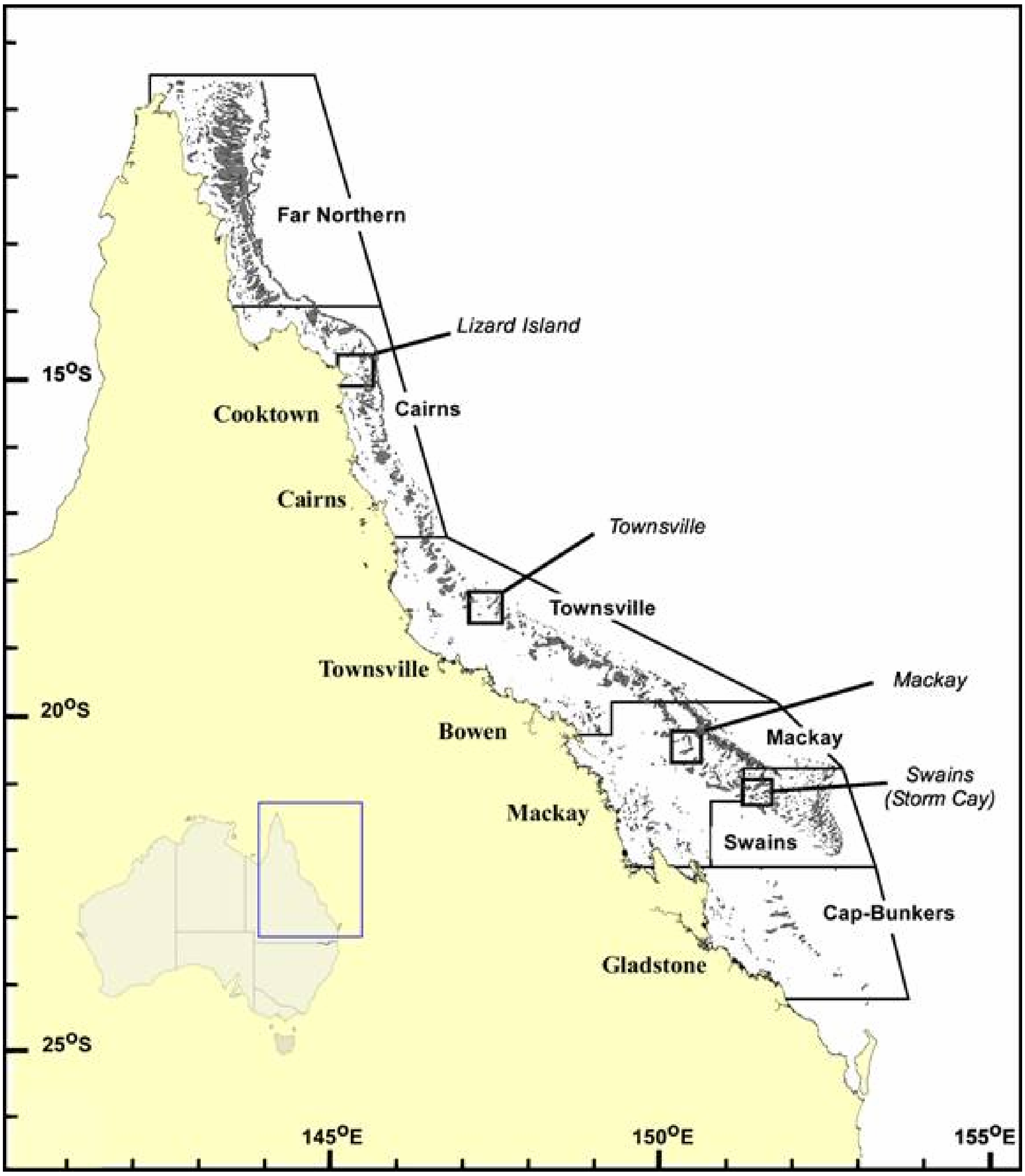

Figure 1: Location reefs sampled for lutjanids within four regions of the Great Barrier Reef as part of the Effects of Line Fishing Experiment. Samples were collected from six reefs within each of the four sites indicated by small squares.

Table 1: Sample numbers for lutjanid species used in the analysis of biological characteristics in the project.

Species	Age	Repro	Length (mm)
Blackspot (*L. fulviflamma*)	-	44	223
Chinaman (*S. nematophorus*)	168	73	325
Green jobfish (*A. virescens*)	129	82	152
Hussar (*L. adetii*)	-	40	426
Paddletail (*L. gibbus*)	166	56	275
Striped seaperch (*L. vitta*)	-	25	123
Stripey (*L. carponotatus*)	3113	2242*	5783

* Macro sex only.

Sample processing

All specimens were measured to the nearest millimeter fork length (FL) and weighed to the nearest gram prior to dissection. Sagittal 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 centrum 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 using Crystalbond adhesive. Otoliths were read under reflected light at 40× magnification and opaque increments counted from the nucleus to the edge along the ventral margin 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 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 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. Where one reader was used, 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 assignment of median age as described above.

Gonads were dissected and frozen immediately after removal. Thawed tissues were preserved in a solution of FAACC (Formaldehyde 4%, Acetic Acid 5%, Calcium Chloride 1.3%; Winsor 1984) prior to May 1999 and ten percent buffered formalin thereafter[1]. Paired gonads were dried of excess fixative and weighed to the nearest 0.01 gram after fixation. The weights of single lobes were measured and doubled to represent a total gonad weight for both lobes if one of the lobes was lost or damaged during processing. This procedure has been previously used and is assumed to provide reliable estimates of whole gonad weight (Adams 2003; Williams *et al.* 2008).

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[1] This change in fixative was prompted by the discovery of deleterious effects of FAACC on the staining properties of histological sections after long term storage.

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 data were used to produce length frequency distributions for all sampled populations. This allowed comparison of size and frequency of individuals encountered. Age frequency distributions were also constructed and similarly compared.

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, t_0 is the age at which the theoretical length at age zero. VBGF estimates were calculated using a constrained ($t_0 = 0$) and unconstrained (no value set for t_0) approach to look for differences in growth parameters.

Analysis of covariance (ANCOVA) was used to compare log transformed (x+1) length data from individuals aged five to twelve years in each of the five aged species with age as a covariate. A Tukey's post hoc test ($p = 0.05$) was used to test for differences among species.

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* was also estimated using the Hoenig (1983) estimator for fish populations where $\log_e Z = 1.46 - 1.01 \log_e t_{max}$ (where t_{max} is the maximum age in years).

Reproductive status and sex ratios

Size and age by sex and sex ratios were examined to define any patterns within the population. The gonadosomatic index (GSI = gonad weight / $W \times 100$) was calculated for each sample, providing a relative measure of reproductive stage. The reproductive stage of each individual was assessed by macrosexing or histological analysis. 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.

Results

Length-weight relationship

The relationship between fork length and weight was approximately isometric (*b* ≈ 3) for three of five lutjanid species where relationships were fitted (Figure 2; Table 2), with no evidence of individuals becoming more heavy bodied with increasing size. Growth of paddletail and stripey was allometric, with the former becoming more heavy-bodied and the latter more thin-bodied.

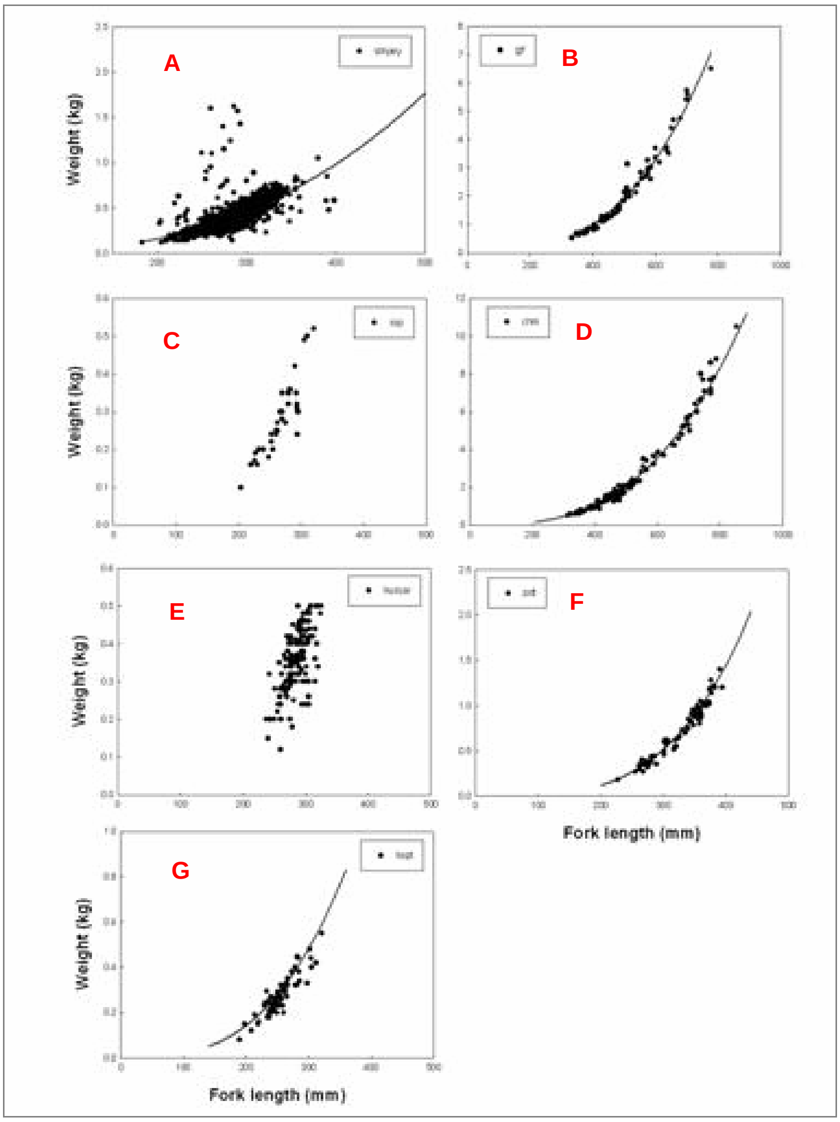

Figure 2: Length-weight data and fitted power curves (where possible) for seven lutjanid species on the Great Barrier Reef. Species include: stripey (A), green jobfish (B), striped seaperch (C), chinaman (D), hussar (E), paddletail (F) and blackspot seaperch (G).

Table 2: Parameter estimates for the length-weight relationship, VBGF, age at 50% L_∞ and percent longevity at 50% L_∞ for five lutjanid species from the Great Barrier Reef. *a* and *b* are parameters of the power 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, and t_0 is the theoretical age at length zero. 1 indicates unconstrained estimate, 2 indicates estimate constrained by $t_0 = 0$.

Species	**a**	**b**	**L_∞ (mm)**	**K (yr^{-1})**	**t_0 (yr)**	**Age at 50% L_∞**	**Percent longevity at 50% L_∞**
Chinaman 1	2.23×10^{-8}	2.95	820	0.12	-2.83	3	8.33
Chinaman 2			732	0.26	0	3	8.33
Green jobfish 1	2.12×10^{-8}	2.95	683	0.35	-1.53	0.5	3.13
Green jobfish 2			623	0.85	0	1	6.25
Paddletail 1	7.00×10^{-10}	3.58	544	0.06	-9.48	2	16.67
Paddletail 2			352	0.51	0	3	25.0
Stripey 1	1.47×10^{-7}	2.62	295	0.37	-2.58	0	0
Stripey 2			291	0.66	0	1	4.35
Blackspot 1	2.0×10^{-8}	2.98	265	1.66	0.61	1	5.88
Blackspot 2			267	0.41	0	1	5.88

Length and age frequency distributions

The modal length in the catch differed among lutjanid species (Figure 3) and was largest for chinaman (750 mm FL) and green jobfish (380 mm FL) and smallest for blackspot seaperch (250 mm FL). Chinaman and green jobfish reached larger sizes in comparison to the other sampled species, with maximum fork lengths of 789 mm and 778 mm FL respectively.

Age frequency distributions varied considerably for the five aged lutjanid species. The modal age in the catch was two years for green jobfish, three years for chinaman, seven years for stripey, eight years for paddletail and ten years for blackspot seaperch (Figure 4). The catch of the two larger species (chinaman and green jobfish) were predominately in younger age classes (less than six years), whilst those of smaller lutjanids (stripey, paddletail and blackspot seaperch) included more samples from older age classes. The maximum age in the catch was also different among species, with the oldest fish being a 36 year old chinaman (Figure 4).

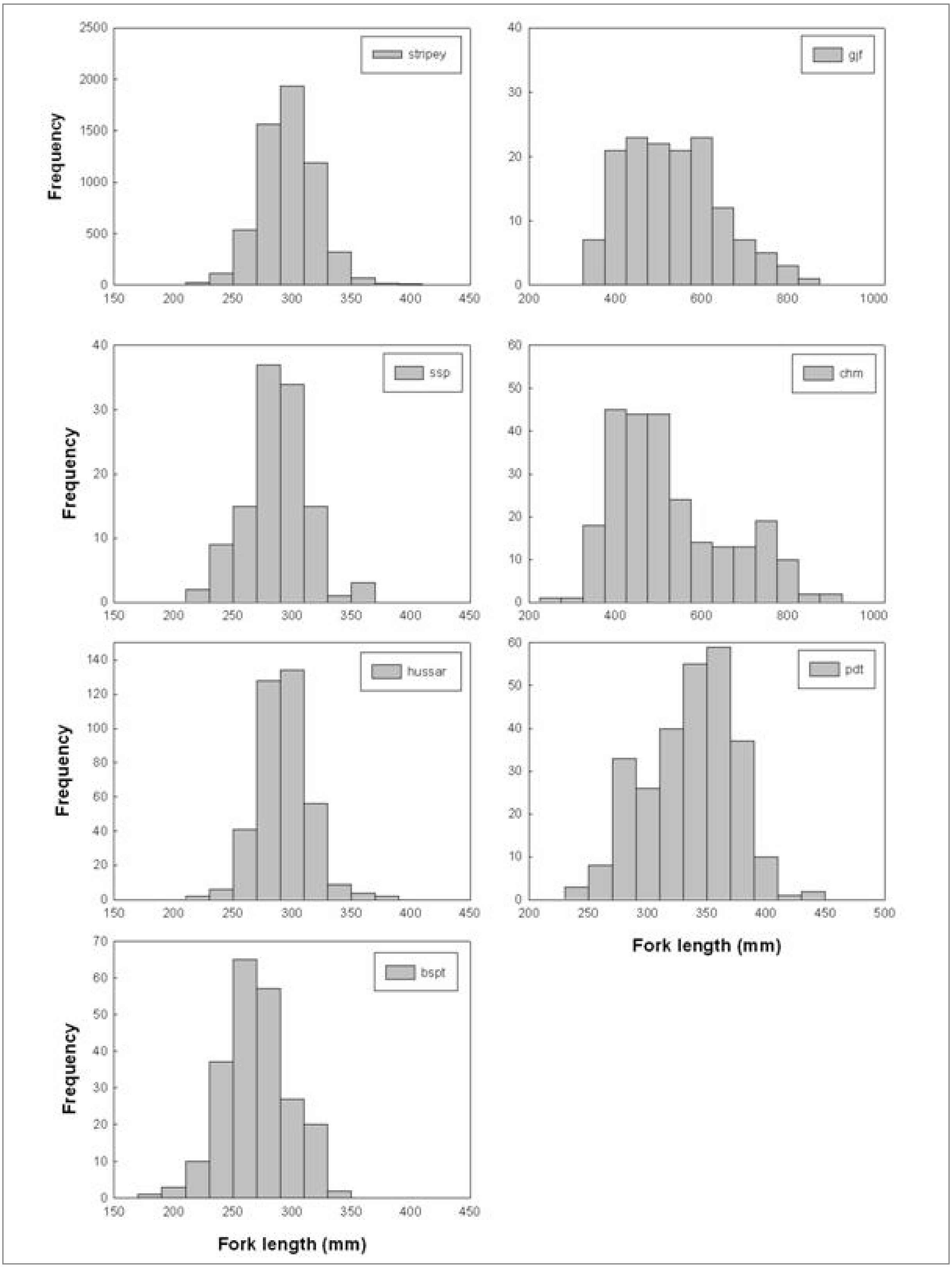

Figure 3: Length frequency distributions for seven lutjanid species on the Great Barrier Reef (note, differences in y-axes). Species include stripey, green jobfish (gjf), striped seaperch (ssp), chinaman (chm), hussar, paddletail (pdt) and blackspot seaperch (bspt).

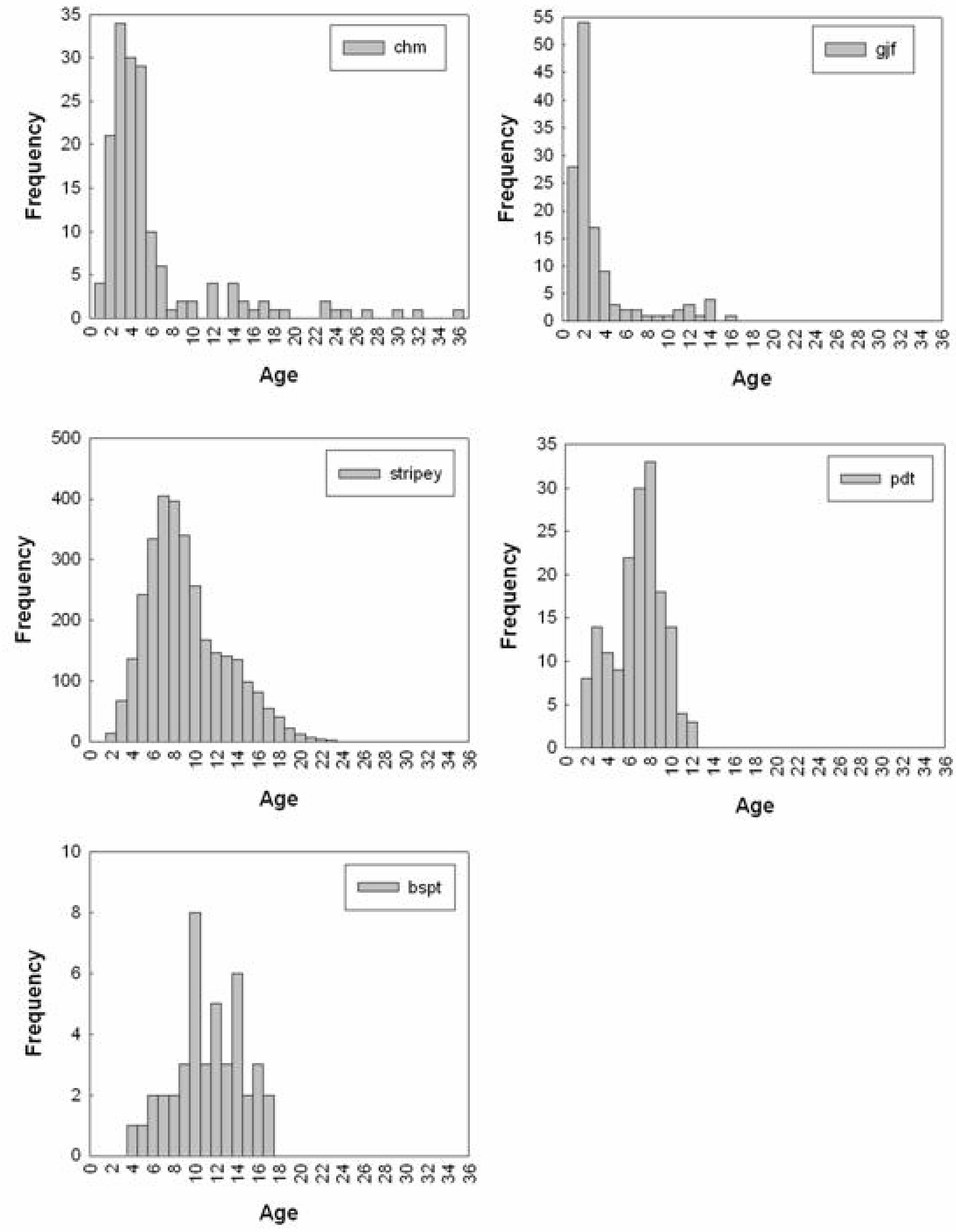

Figure 4: Age frequency distributions for five lutjanid species on the Great Barrier Reef (note, differences in y-axes). Species include chinaman (chm), green jobfish (gjf), stripey, paddletail (pdt) and blackspot seaperch (bspt).

Growth

Unconstrained length-at-age data and fitted growth curves differed substantially among species, with the chinaman reaching greatest lengths and ages (Figure 5). Chinaman grew to longest lengths and ages, but green jobfish appeared to grow more quickly to their maximum size. Despite the large sample size for stripey, the growth curve was relatively flat, suggesting sampling omitted smaller, fast growing stages (i.e. 0-1 year olds). Data from paddletails may have also been limited by a lack of sampling of smallest and largest individuals suggested by the inability to reach asymptote with these data. This led to a presumably biologically unrealistic curve for this species which should be interpreted with caution. A limited number of blackspot seaperch were aged and similar to other species the data indicated rapid initial growth followed by asymptote at a relatively small size.

Constraining VBGF estimates by setting $t_0 = 0$ produced similar results to unconstrained estimates for stripey and blackspot seaperch. This suggests a wide range of age classes were sampled in these populations, producing biologically reasonable length-at-age estimates. For chinaman, green jobfish and paddletail, constraining t_0 resulted in faster initial growth estimates followed by asymptote at smaller sizes than those from unconstrained data. Constrained estimates produced an asymptote for paddletail data, which was not produced in unconstrained estimates. This suggests constraining t_0 may provide a more biologically realistic estimate of length-at-age for this species from the data used in this analysis.

Comparison of growth curves across species reveals that size selectivity in sampling probably played a role in the amount and type of individuals collected. Both constrained and unconstrained growth curves were different across species (Figure 6) with chinaman and green jobfish showing the most complete curves. Despite their similar size, these species show distinct differences in the rate of growth at young ages and the age at which they reach maximum size. Differences between the smaller and larger individuals are evident and indicative of lack of sampling over the full size range for these species with smallest individuals lacking from samples. Both constrained and unconstrained growth curves for stripey and blackspot seaperch were relatively flat revealing little growth in older age classes. Despite the flattened curve presented for stripey this species has the highest K value (0.37yr^{-1}) of any of the species examined, suggesting rapid growth to maximum size at a young age. Differences between unconstrained and constrained estimates for paddletail are probably due to limited sampling of small and large sizes as stated previously. Thus forcing the data through the origin produces an asymptotic curve that may be more realistic for this population.

Comparison of growth rate among five to twelve years olds of each species revealed significant differences (ANCOVA, $F_{4,2503} = 1543.8$, $p<0.0001$). Post hoc tests indicated that each species had a unique growth rate. Examination of age at 50% L_∞ revealed differences in length-at-age data between constrained and unconstrained analyses (Table 2). In unconstrained data stripey and green jobfish both reached age at 50% L_∞ in less than one year, while blackspot seaperch, paddletail and chinaman reach 50% L_∞ after one, two and three years respectively. In contrast, data from constrained estimates resulted in stripey, green jobfish and blackspot seaperch all reaching 50% L_∞ after one year with paddletail and chinaman reaching 50% L_∞ after three years. Analysis of percent longevity at 50% L_∞ for constrained and unconstrained data also revealed differences for most species (Table 2). Constrained estimates were similar for most species ranging from 4.3-8.3%, except for paddletail which were much higher at 25%. Percentage longevity at 50% L_∞ for unconstrained growth curves were variable ranging from 0-16.7%.

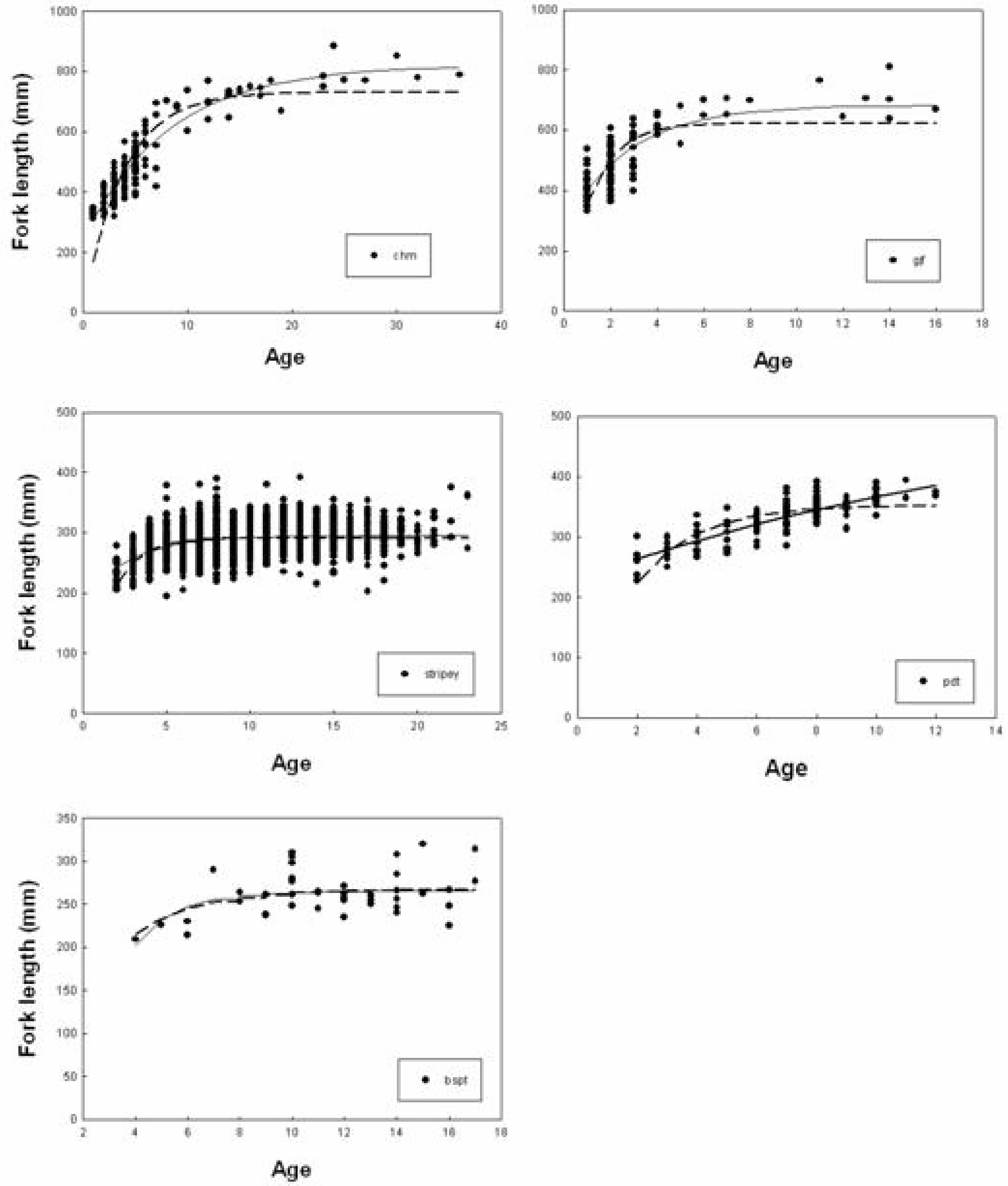

Figure 5: Length-at-age data and fitted von Bertalanffy Growth Function (VBGF) curves for five lutjanid species from the Great Barrier Reef. Species include chinaman (chm), green jobfish (gjf), stripey, paddletail (pdt) and blackspot seaperch (bspt). Solid lines indicate unconstrained VBGF estimates and dashed lines indicate constrained (t_0 = 0) VBGH estimates.

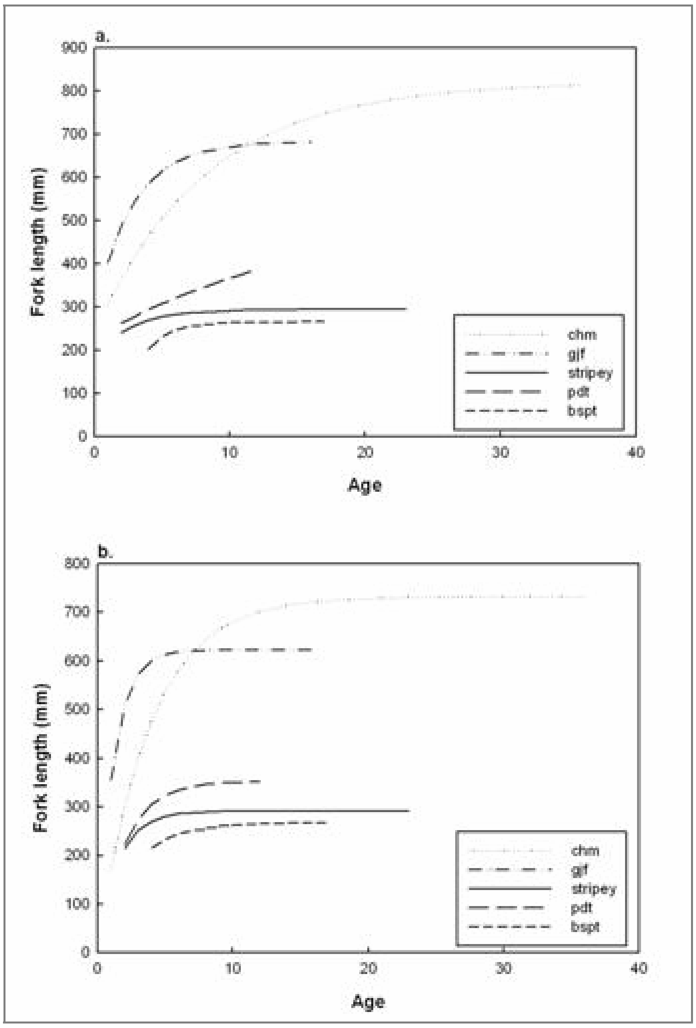

Figure 6: Comparison of the fitted VBGF curves without length-at-age data for five lutjanid species from the Great Barrier Reef. Species include chinaman (chm), green jobfish (gjf), stripey, paddletail (pdt) and blackspot seaperch (bspt), with (*top*) unconstrained VBGF estimates, and (*bottom*) constrained (t_0 = 0) VBGF estimates.

Stripey was the only species with a large enough sample size to conduct regional analysis of growth data. Comparison of growth among Lizard Island, Mackay and Storm Cay regions revealed similar VBGF parameters among regions (Table 3). However, likelihood ratio tests indicated that patterns of growth differed significantly among all regions (Table 4). The most notable difference was the greater L_∞ (and lower K and t_0 due to the correlation among VBGF parameters) in the Storm Cay region. Although statistically significant, the difference in growth may have less biological significance since likelihood tests are sensitive to subtle differences, especially when applied to large data sets.

Table 3: Von Bertalanffy growth parameters for stripey by region within the Great Barrier Reef. L_∞ is the mean asymptotic fork length, K is the von Bertalanffy growth coefficient, and t_0 is the theoretical age at length zero.

Region	L_∞	K	t_0
Lizard Island	293	0.67	-0.17
Mackay	292	0.47	-1.68
Storm Cay	302	0.16	-9.35

Table 4: Results of pairwise likelihood ratio tests comparing VBGF of stripey between regions.

Comparison	**Age classes (yr)**	***df***	x^2 ***(L)***	***p (L)***
All regions	2-20	6	68.34	<0.001
Lizard Island vs. Mackay	2-20	3	9.82	0.02
Lizard Island vs. Storm Cay	2-20	3	59.82	<0.001
Mackay vs. Storm Cay	2-20	3	47.71	<0.001

Mortality

Total mortality (*Z*) estimates calculated form catch curves differed between species (Figure 7) and were highest for paddletail and lowest for blackspot seaperch (Table 5). Mortality rates calculated via the Hoenig method resulted in highest rates for paddletail and lowest for chinaman. Levels of mortality calculated by both methods differed with catch curve calculations resulting in higher estimates for all species except blackspot seaperch.

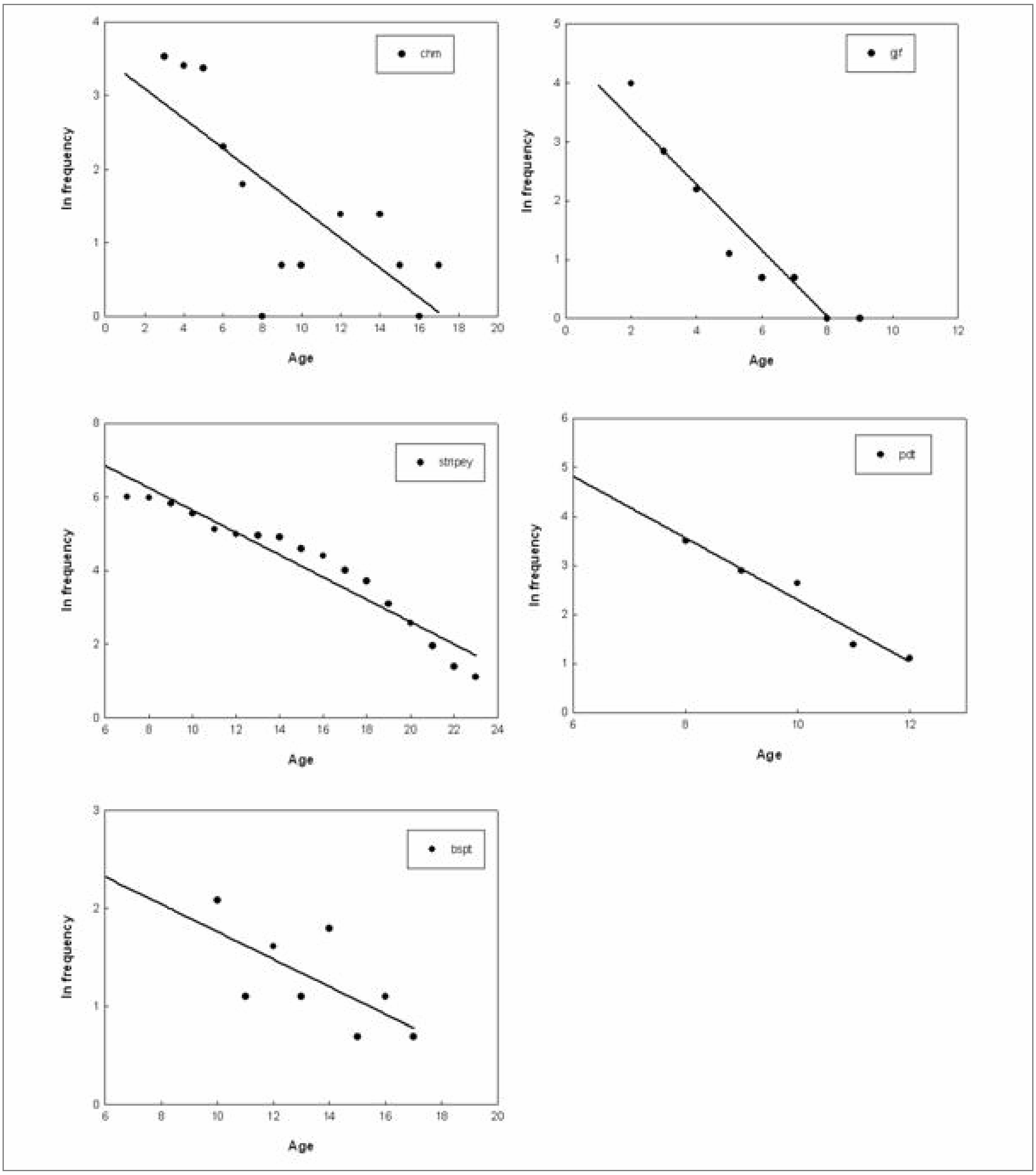

Figure 7: Catch curves for five lutjanid species from the Great Barrier Reef. The slopes of the regressions are an estimation of the rate of total mortality (*Z*) for each species. Species include chinaman (chm), green jobfish (gjf), stripey, paddletail (pdt) and blackspot seaperch (bspt).

Table 5: Estimates of mortality for five lutjanid species using catch curve and Hoenig (1983) estimators.

Species	Catch curve *Z* (yr $^{-1}$) [std err]	Hoenig *Z* (yr $^{-1}$)
Chinaman	0.20 [0.04]	0.11
Green jobfish	0.56 [0.06]	0.26
Paddletail	0.63 [0.02]	0.35
Stripey	0.30 [0.01]	0.18
Blackspot seaperch	0.14 [0.02]	0.25

Reproductive status

All but one of the individuals sampled in this project were sexually mature (Table 4) making analysis of size and age at maturity impossible. Despite the gonochoristic nature of these species, sex ratios in these samples most of the sampled populations did not display a 1:1 sex ratio (Table 4). Variability in sex ratio by size class can be seen in Figure 8. Examination of sex by age also revealed a variable pattern in male to female ratios (Figure 9).

Histological stage and GSI of individuals from all dissected species (except stripey) were examined, but sample numbers were low. Ripe females were observed in periods of high mean GSI. No hydrated (running ripe) females were observed, although this stage is a key indicator of peak periods of spawning activity (Table 7a). Ripe males were also found with highest GSI values and most individuals were in this stage (Table 7b). There were not enough data to examine monthly or seasonal trends in mean GSI and developmental stages of ovarian and testicular tissue, thus no estimates of spawning seasonality could be completed.

Table 6: Number and size of male and female individuals sampled for reproductive analysis. The number of mature individuals in each sample and overall sex ratio are also listed.

Species	Female			Male			Sex ratio F/M
	N	No. mature	Mean size (mm FL)	N	No. mature	Mean size (mm FL)	
Blackspot seaperch	28	28	263 (209-315)	16	16	250 (219-285)	1.75
Chinaman	32	27	533 (340-772)	32	32	485 (320-789)	0.78
Green jobfish	50	48*	511 (332-810)	32	32	509 (334-778)	1.56
Hussar	18	18	284 (254-374)	22	22	290 (243-341)	0.82
Paddletail	8	7*	277 (227-356)	48	47#	330 (262-418)	0.17
Striped seaperch	7	2#	266 (204-307)	18	7#	270 (226-310)	0.52
Stripey	520	-	274 (203-355)	1,722	-	292 (205-405)	0.30

* One immature paddletail, no other immature animals.

[#] Missing individuals = macro sex only, no maturity data.

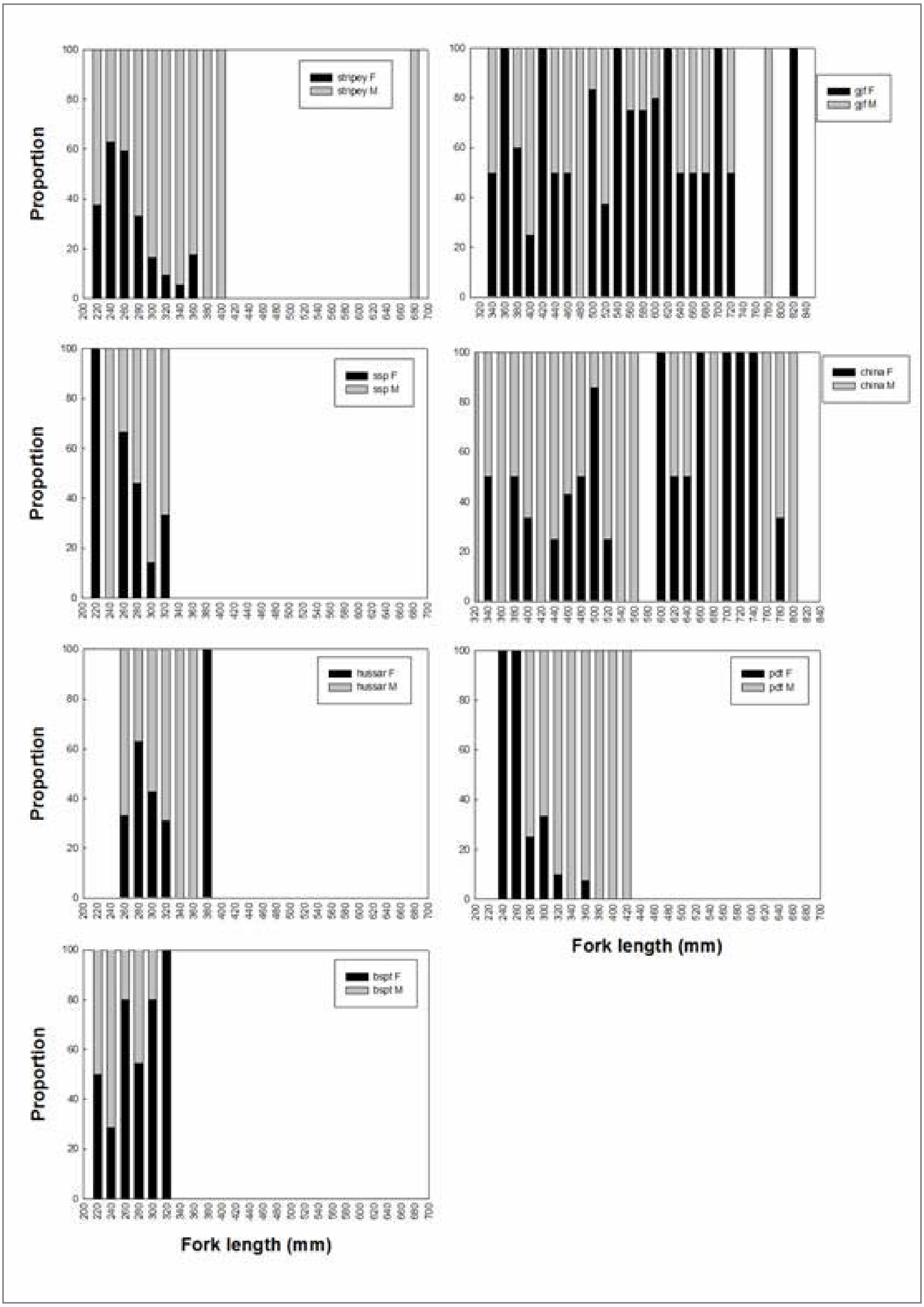

Figure 8: Proportion of males and females in each size class for lutjanid species from the Great Barrier Reef.

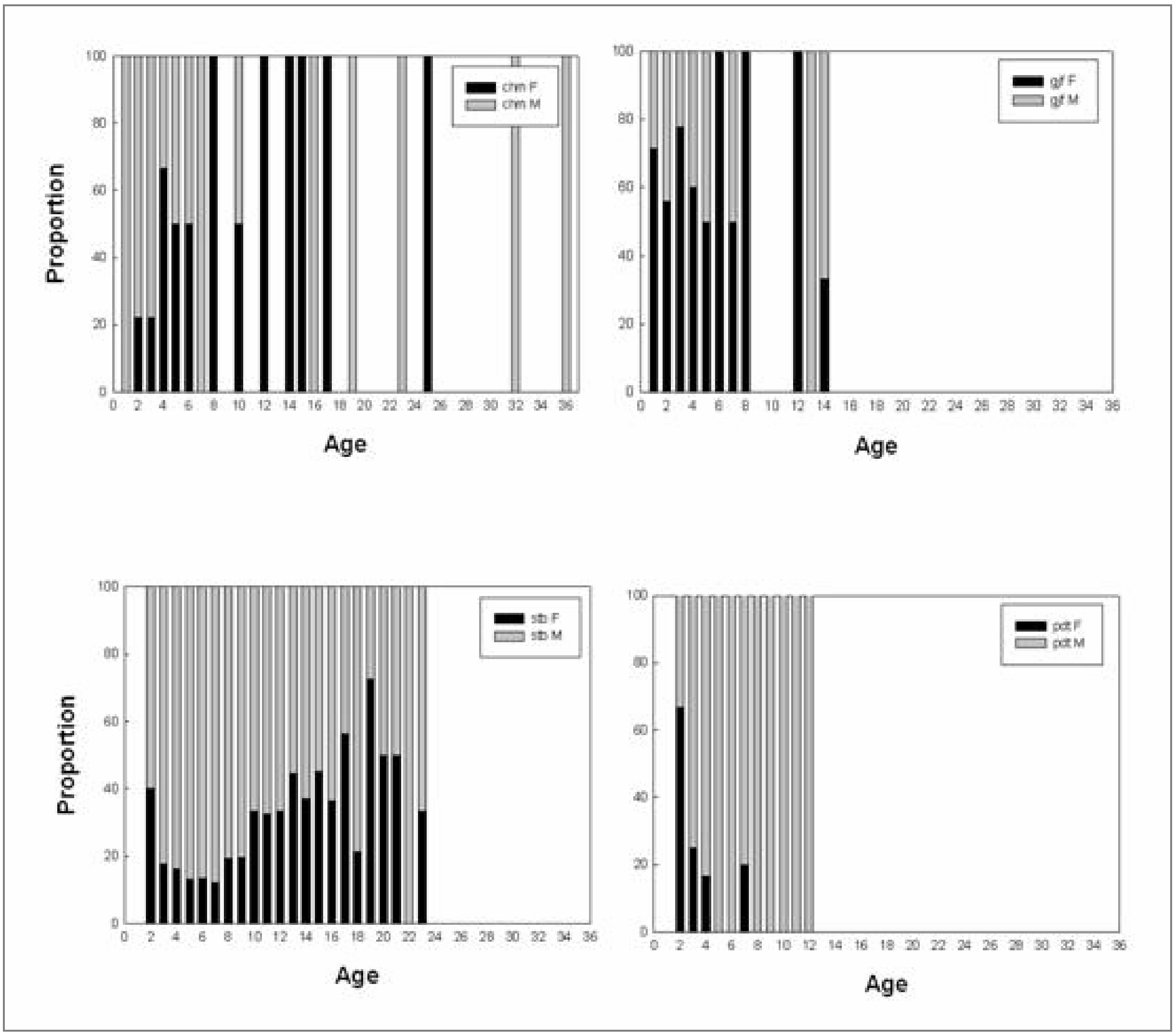

Figure 9: Proportion of males and females in age classes for lutjanid species from the Great Barrier Reef.

Table 7: Female and male reproductive stage data. Numbers indicate sample numbers with GSI range listed in brackets below each sample number if measured.

Females				
Species	**Resting**	**Ripe**	**Ripening**	**Unknown**
Blackspot seaperch	3 (0.48, 0.56)	4 (2.34-6.13)	1 (0.96)	-
Chinaman	18 (0.12-0.93)	4 (1.58, 2.13)	5 (0.44-1.67)	5
Green jobfish	39 (0.12-1.31)	6 (1.23-6.38)	3 (0.51-0.62)	2
Hussar	-	18 (0.3-7.95)	-	-
Paddletail	1 (0.43)	2 (0.22, 0.98)	3 (0.17-0.96)	1
Striped seaperch	1 (0.67)	-	1 (0.76)	5
Males				
Species	**Resting**	**Ripe**	**Ripening**	**Unknown**
Blackspot seaperch	1 (0.23)	4 (0.40-1.84)	-	-
Chinaman	19 (0.05-0.23)	17 (0.09-1.30)	5 (0.06-0.17)	-
Green jobfish	-	30 (0.06-3.68)	2 (0.41)	-
Hussar	-	22 (0.13-6.58)	-	-
Paddletail	5 (0.11-0.56)	33 (0.07-0.91)	9 (0.10-0.71)	1
Striped seaperch	-	7 (0.15-1.17)	-	11

Discussion

Although lutjanid species are found in similar habitats, typically tropical and subtropical marine regions, and many species grow to similar sizes, it is impossible to make generalisations about the life history of members of this family due to their differences in growth and longevity. Examination of seven species of lutjanid within the Great Barrier Reef supports previous findings for individual species, but also provides evidence for the differences present in this family and highlights the need for careful, and potentially individual, management approaches for these species.

Discussion of biological characteristics of the lutjanid species in this study must first consider the limitations of size selectivity of the fishing gear used. No individuals below 200 mm FL were collected resulting in a lack of individuals in smallest and youngest age classes for all species. This is a crucial life stage for species such as lutjanids that are known to be fast growing in their first years of life (Newman *et al.* 1996, 2000; Kritzer 2004; Grandcourt *et al.* 2006). Limitations in sampling can be seen in both the length-weight relationships, and length and age frequency data for all of the sampled species. Length frequency data were normally distributed for four of the five small sized species (stripey, striped seaperch, hussar, blackspot seaperch) but length frequency distributions for larger species (green jobfish, chinaman) revealed small-size biased distributions. The final small species, paddletail, had a distribution biased toward large sizes when compared to the other similar-sized species. Differences in distributions of individuals by size or age within a species (i.e. movement to different habitat by older, larger individuals) may explain the differences in size frequency of the sampled populations. Some evidence for this type of distribution is already evident in studies of several of these species. For example, Newman and others (1997) reported that stripey and blackspot seaperch were more common on mid-shelf reefs than on outer shelf reefs. Both species were present in various locations within mid-shelf reefs (reef slope, lagoon, etc.) but it was unclear whether there were any size or age differences within individuals sampled at within reef locations. Further, within reef distributional differences by species were reported by Newman and Williams (2001) where stripey and blackspot seaperch were found in shallower sampling (0-18m) compared to hussar and striped seaperch which were found more commonly in deeper sampling (30-40m). These differences in distribution among and within reefs possibly played a role in some of the patterns observed in the data collected during this project. Despite the limits in the size of individuals sampled here, it is important to note that this project used the same sampling gear and techniques as those used in the Coral Reef Fin Fish Fishery. Thus the data presented here is representative of catch within the commercial line fishery.

Examination of age and growth data for the five species with adequate biological samples revealed very different ages and rates of growth despite similar sizes. Maximum ages were variable across species, with chinaman and stripey having the greatest longevity at 36 and 23 years respectively, despite their different size ranges. Paddletail, green jobfish and blackspot searperch had shorter life spans with maximum ages of twelve, sixteen and seventeen years respectively. These ages correspond closely with those obtained for other lutjanid species. Stripey sampled within the Great Barrier Reef have previously been reported to have maximum ages of eighteen and twenty years (Newman *et al.* 2000; Kritzer 2004) which agree closely with the 23 year maximum obtained here. Shorter longevities recorded for paddletail, green jobfish and blackspot seaperch align with those from other studies such as striped seaperch (twelve years, Newman *et al.* 2000), rose snapper (eleven years, Amezcua *et al.* 2006) and blackspot seaperch (fourteen years, Grandcourt *et al.* 2006). In contrast, hussar, a small species, very similar in size and appearance to striped seaperch, had a reported maximum age of 24 years (Newman *et al.* 1996), demonstrating the variability in the life history of similar sized lutjanid species. Despite differences in size and age estimates most previous studies of lutjanid species agree that these species have rapid initial growth, usually during the first two years of life, before declining, resulting in length at age curves reaching asymptote at relatively young ages (Newman *et al.* 1996, 2000; Kritzer 2004; Grandcourt *et al.* 2006). In fact, Newman and others (1996) go so far as to suggest that beyond five years of age size cannot be used as a means of age estimation for hussar. This sentiment is probably applicable for most lutjanid species and is supported by the data from the five sampled species here where initial growth was rapid and asymptote reached fairly rapidly for all but paddletail. In fact, all five species examined here reach 50% of L_∞ prior to reaching four years of age.

Paddletail are the only sampled species that did not reach asymptote in unconstrained length-at-age data. This may have been the result of the sampling effect discussed earlier and apparent in size frequency data. This is supported by the fact that constrained VBGF estimates did produce an asymptote. However, another possible explanation is that this species has a long growth period, and does not stop growing throughout life. Paddletail was also the species with the highest mortality estimates by both catch curve and Hoenig's estimators suggesting that this population has the highest turnover rates. However, it is important to note that individuals under six years of age could not be used in the catch curve mortality estimates. Given the number of elements in the biology of paddletail that seem contrary to other species it seems most likely that sampling of this species was not as complete as that for other species and that broader distribution patterns may play a role in the type and amount of data collected for this population. Further sampling may be required to gain a fuller understanding of the age and growth characteristics of this species on the Great Barrier Reef.

Comparison of growth among species was difficult due to variation in VBGF estimates. Examination of a limited set of ages, however, revealed some similarities with all species reaching 50% L_∞ at young ages. Percentage longevity was also similar for most species with paddletail the only species resulting in a value over ten percent. Comparison of growth among regions was only possible for stripey, but growth rates, though significant, were very similar. This suggests little variation in growth among regions, at least for this species.

Comparison of mortality rates of the remaining three species reveal that green jobfish had a similar mortality rate to paddletail, suggesting that this species also has a relatively high turnover rate. This result is not surprising given the large size and low age estimates for this population. This would suggest this species grows quickly to a large size, but dies younger than some of the other large species. Chinaman, for example, attained the largest size and had the second lowest mortality rate of the species examined. This suggests chinaman grow quickly to sizes that may make them less vulnerable to predation and therefore increase their survival. Blackspot seaperch mortality estimates differed between methods with catch curve estimates resulting in highest survival rates for this species (0.14 yr $^{-1}$). The Hoenig estimate, however, suggested higher mortality rates (0.25 yr $^{-1}$) similar to those for green jobfish and paddletail. The Hoenig estimate was also similar to rates previously reported for blackspot seaperch (0.29 yr $^{-1}$; Grandcourt *et al.* 2006). Like paddletail, stripey under six years of age could not be used in catch curve estimates of mortality. Based on the 6-23 year age classes mortality in stripey was 0.30 yr $^{-1}$ (catch curve) and 0.18 yr $^{-1}$ (Hoenig), which are similar to estimates calculated previously for this species (0.20 yr $^{-1}$, Newman et al. 2000; 0.26-0.29 yr $^{-1}$, Kritzer 2004). While variable, the range of mortality estimates for the species examined in this analysis agree well with those for striped seaperch (0.34 yr $^{-1}$, Newman *et al.* 2000), rose snapper (0.35 yr $^{-1}$, Amezcua *et al.* 2006) and hussar (0.24 yr $^{-1}$, Newman et al. 1996).

All but one of the individuals sampled in the course of this research were sexually mature. This supported the conclusion that lutjanid species grow quickly and reach sexual maturity early. Biased sex ratios were observed for each of the species sampled. Two species (blackspot seaperch, green jobfish) showed female biased sex ratios while all others showed a male biased ratio. Being dioecious species it would be predicted that sex ratios are close to 1:1 in lutjanid populations. However, at least three other studies have revealed biased sex ratios. Kritzer (2004) found that stripey in the Palm Islands had a female biased sex ratio, while Newman *et al.* (2000) report a heavily male biased sex ratio for this same species in the central GBR. Studies of blackspot seaperch from different locations also contradict one another in relation to sex ratio. Kaunda-Arara and Ntiba (1997) report a male biased sex ratio in Kenya, while Grandcourt *et al.* (2006) report a female biased sex ratio in the southern Arabian Gulf. Given contradictory patterns in the literature and within the species sampled here, there is no apparent pattern of sex ratio within lutjanid species. It is more likely that sex ratio bias is a result of differential survival or distribution patterns. Kritzer (2004) was one of the few studies to have examined mortality by sex with no difference in mortality by sex. This would suggest that distribution may be a more likely cause of the sex ratio differences observed in these and other lutjanid populations. It has been suggested that sex ratio may be more even during spawning events (Kritzer 2004) but no data were available to support or refute that theory.

Similar to sex ratio, no differences in proportions of male and female individuals in size or age classes were expected. However, stripey appeared to have more males in larger age classes, which supports the conclusion by Kritzer (2004) that male stripey grow faster and larger than females. Blackspot seaperch, however, had more, larger females present, which is also consistent with the previous findings of Grandcourt *et al.* (2006) who found females to grow faster and to a larger size and greater age than males. None of the remaining species showed distinct patterns in proportion of sexes by size or age except for paddletail that had more, older males than females. This variation is yet another example of the differences that are apparent in these populations and that generalisations cannot be applied.

Despite the number of samples collected, no conclusions could be drawn regarding the periodicity of spawning within these populations. Data from other lutjanid species show conflicting results with some species reported as having a seasonal spawning period (Kritzer 2004, Grandcourt *et al.* 2006) and others a prolonged discontinuous spawning season (Kaunda-Arara and Ntiba 1997). Further data need to be collected from these species to define seasonality in reproductive patterns in the Great Barrier Reef.

Management implications

This comparison of seven lutjanid species clearly indicated that data from one species cannot be applied to another in determining management measures for these populations. Some species appear to be more susceptible to overexploitation by fisheries due to their longer life spans and lower rates of mortality. Chinaman 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 (due to its larger size than other lutjanids), but also one of the most vulnerable due to its life history characteristics. However, chinaman is a no-take species due to its propensity to carry ciguatera providing it protection from harvest. In comparison, the longevity of stripey and hussar (Newman *et al*. 1996) in relation to other lutjanid species make them more vulnerable to overfishing than sister species. So despite their small size and fast growth, these populations may be more vulnerable than similar species such as striped seaperch which have shorter longevities and hence faster turnover rates (Newman *et al.* 2000).

Despite the potential vulnerability of most lutjanids to overfishing, current management regulations prohibit take of individuals below 250 mm total length (c. 230 mm FL) for all of the species examined here except green jobfish which has a minimum legal size of 380 mm total length. Data regarding sexual maturity collected in this study reveal that all individuals except one paddletail were sexually mature and samples from six of the seven study species contained sexually mature individuals under the size of 250 mm FL. These data suggest all of these species would have an opportunity to spawn at least once prior to exposure to the fishery. The smallest green jobfish captured in this study was 332 mm FL, and this was a mature female. Therefore, individuals of this species also appear to reach sexual maturity prior to exposure to the fishery. Current data for stripey indicate fifty percent sexual maturity at 190 mm FL (Kritzer 2004), suggesting that the minimum of 250 mm would be acceptable for this species. Mean size at first sexual maturity in blackspot seaperch in the Arabian Gulf was reported at 167 and 187 mm for males and females respectively. More precise estimates of size at maturity for the remaining species would be useful, but it seems likely that the current management measures are providing an opportunity for these populations to spawn prior to take in the fishery. The fact that the lutjanids are dioeceous (unlike the other families of major commercial reef fish – Lethrinidae and Serranidae – which change sex) is also an advantage from a management standpoint since it may not be as important to protect larger individuals. Thus, the results of this study suggest that the current management regulations appear to be suitable for these lutjanid populations. However, if current management is changed, differences in the size and longevity of lutjanid species should be taken into consideration in any and all future management.

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