Abstract.–The recent age valida-tion of the tropical snappers *L. adetii* and *L. quinquelineatus* has facilitated the comparison of growth, mortality, and age structures for both these spe-cies at the spatial scale of individual reefs. The age structure of both species among reefs within the Great Barrier Reef Marine Park was based on counts of annuli from sectioned otoliths. There was significant variability in growth, mortality, and age structures. Signifi-cant differences in mean length, age, and weight (independent of the sex of the fish) were observed for both species among reefs. Peaks in abundance of year classes were variable from reef to reef. Comparisons of the von Berta-lanffy growth curves indicated that the pattern of growth in individuals of *L. quinquelineatus* was significantly dif-ferent among reefs, whereas the pat-tern of growth in *L. adetii* was not. However, there were no significant dif-ferences in the mean length of the early age classes of either species among reefs. The mortality rates and hence survivorship of both *L. adetii* and *L. quinquelineatus* among reefs were highly variable. It is hypothesized that the varying age structures and mortal-ity rates of both of these species at the spatial scale of individual coral reefs are determined by the nonequilibrial balance of variable recruitment inter-acting with density-independent mor-tality. Hence the effect of good recruit-ment years may persist in the age structure of populations over time.

Variability in the population structure of *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) among reefs in the central Great Barrier Reef, Australia*

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Spatial comparisons of life history parameters of species of the family Lutjanidae have been undertaken only among broad geographic areas (e.g. Nelson and Manooch, 1982). Likewise, the majority of life history studies of species of the Lutjanidae have been based on widespread col-lections of individuals from broad geographic areas (e.g. Druzhinin and Filatova, 1980; Loubens, 1980; Liu and Yeh, 1991; Davis and West, 1992; Sanders et al.[1]; Mees[2]) and not on an individual reef scale. On the Great Barrier Reef in Austra-lia, the fishing industry and other resource users (e.g. tourists, rec-reationalists, etc.) are managed under a system which protects ma-rine areas of which individual coral reefs are the primary management unit.[3] To date, a comparison of age and growth parameters of lutjanids among individual reefs within a single geographic area has not been undertaken.

Comparisons of the age structure of lutjanids among a number of

reefs within a single geographic area of the Great Barrier Reef have been published for only two species: the damselfishes *Pomacentrus moluccensis* and *P. wardi* (Doherty and Fowler, 1994, a and b). A number of studies have compared the abundance and size structure of the serranid *Plectropomus leopardus* between reefs open to fishing and those closed to fishing.[4,5,6] More recently, Ferreira and Russ (1995) have examined the size, age, and sex structure of populations of *P. leopardus* on closed and open reefs in the central Great Barrier Reef region.

The hussar, *Lutjanus adetii*, and the five-line snapper, *L. quinquelineatus*, are both widely distributed along the entire length of the Great Barrier Reef (10°S–24°S) and occur as far as 34°S (Kuiter, 1993). The habitats of both species vary, although they are most commonly associated with hard bottom areas. In the central Great Barrier Reef region, *L. adetii* is common at depths greater than 30 m within the midshelf group of reefs and is known to occur on the outershelf at depths up to at least 99 m, whereas *L. quinquelineatus* is common in both shallow and deep waters on both midshelf and outershelf reefs to a depth of at least 128 m (Newman, 1995). Loubens (1980) has demonstrated that both species are relatively long lived and slow growing in New Caledonia; similar conclusions have been obtained from the central Great Barrier Reef (Newman et al.[7]).

Neither of these lutjanids forms a significant portion of the commercial catch in the central Great Barrier Reef, and they form only a nominal contribution to the recreational catch in this region (Higgs, 1993; Newman, 1995). However, in the southern Great Barrier Reef, *L. adetii* contributes a significant proportion to the commercial lutjanid catch (Newman, 1995) and may become of increasing significance to the recreational line fishery in future years.[8] Relatively little information is available concerning the ecology of these species in Australian waters.

The recent validation (Newman et al.[7]) of age and growth for both *L. adetii* and *L. quinquelineatus* has facilitated the comparison of demographic parameters of both these species at the spatial scale of individual reefs. The aims of this study are to examine spatial variability in growth, mortality, and age structures of populations of *L. adetii* and *L. quinquelineatus* among reefs within the central Great Barrier Reef region (Fig. 1).

Materials and methods

Sampling procedures

Specimens of *L. adetii* (*n*=355) and *L. quinquelineatus* (*n*=573) were obtained between October 1991 and December 1993 from fish traps (O-trap design with 40-mm galvanized hexagonal wire mesh [Newman, 1995]) used during a research program investigating the distribution and abundance of lutjanids among reefs in the central Great Barrier Reef region (Newman, 1995; Newman and Williams, 1995). Samples of both species were obtained from four reefs (Rib [RI], John Brewer [JB], Lodestone [LO], and Kelso [KL]); additional samples of *L. quinquelineatus* were obtained from two other reefs (Davies [DV] and Myrmidon [MR]) (Fig. 1). Individual *L. adetii* <17 cm fork length (FL) and *L. quinquelineatus* <10 cm FL were usually not vulnerable to trap fishing and specimens in this size range were therefore not obtained for analysis.

Individuals of each species were measured (FL and standard length [SL]) and weighed (clean weight after removal of the gills and viscera), and sexes were determined by macroscopic examination of the gonads. The sagittal otoliths of individuals were removed and sectioned laterally through the focus with a Beuhler Isomet low-speed jewelry saw, and ages were determined according to the methods described in Newman et al.[7]

Analysis of data

Because a previous study (Newman et al.[7]) indicated significant differential growth between sexes in both species, two-way factorial analyses of variance were used to compare the mean length (FL, mm), age (years), and clean weight (g) of each species both among reefs and between sexes (in order to prevent

[4] Ayling, A. M., and A. L. Ayling. 1984. Distribution and abundance of coral trout species (*Plectropomus* spp.) in the Swain group of reefs. Capricorn section of the Great Barrier Reef Marine Park. Unpubl. report to the Great Barrier Reef Marine Park Authority (GBRMPA; Project 171), Australia.

[5] Ayling, A. M., and A. L. Ayling. 1986. A biological survey of selected reefs in the Capricornia section of the Great Barrier Reef Marine Park. Unpubl. report to the Great Barrier Reef Marine Park Authority (GBRMPA; Project 243 and 269), Australia.

[6] Ayling, A. M., and B. P. Mapstone. 1991. Unpublished data collected for GBRMPA from a biological survey of reefs in the Cairns section of the Great Barrier Reef Marine Park. Unpubl. report to the Great Barrier Reef Marine Park Authority (GBRMPA), Australia.

[7] Newman, S. J., D. McB. Williams, and G. R. Russ. Age validation, growth, and mortality rates of the tropical snappers (Pisces: Lutjanidae), *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the central Great Barrier Reef, Australia. Submitted to Mar. Freshwater Res. (1996).

[8] Williams, D. McB., and G. R. Russ. 1994. Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef, Vol. 1. Great Barrier Reef Marine Park Authority Research Publication 33, 106 p.
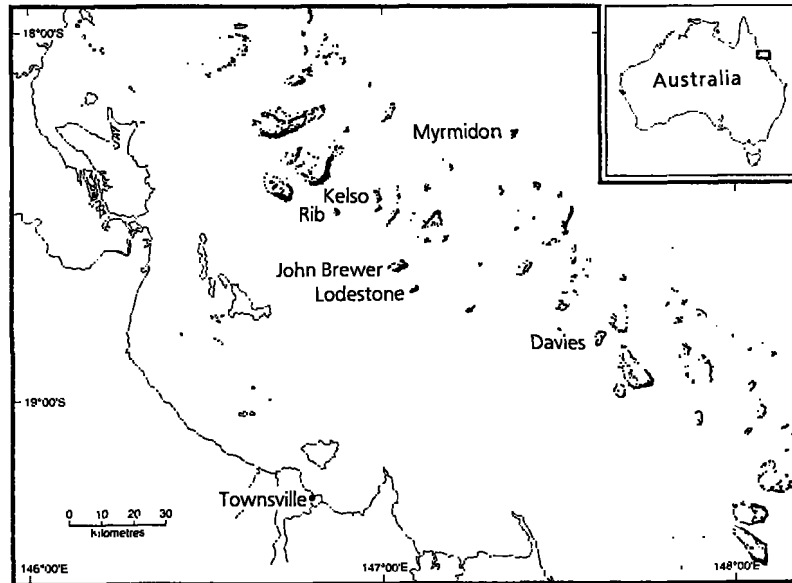
Figure 1

The locations of the reefs sampled for *Lutjanus adetii* and *L. quinquelineatus* from October 1991 to December 1993 in the central region of the Great Barrier Reef, Australia.

confounding differences among reefs with differences between sexes). Both reefs and sexes were treated as fixed and orthogonal factors in the analysis. Multiple comparisons were performed with Tukey's honestly significant difference (HSD) test (α=0.05).

The Kruskal-Wallis one-way analysis of variance by ranks was used to test for differences in the age structures of each species among reefs (Siegel and Castellan, 1988). Multiple pair-wise comparisons were performed, by using Kolmogorov-Smirnov (K-S) tests, to determine differences in the age structure of each species between individual reefs (Zar, 1984).

Growth rates for each species at each reef were also examined. The von Bertalanffy growth function (VBGF) was fitted to lengths at age for each species from each reef by using nonlinear least-squares estimation procedures.[9] The VBGF is defined as follows:

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

where L_t = length at time t;
L_∞ = asymptotic length;
K = Brody growth coefficient;

t = age of the fish; and
t_0 = theoretical origin of the growth curve.

Von Bertalanffy growth curves were compared by using the likelihood-ratio test (Kimura, 1980), considered the most robust measure (Cerrato, 1990). A modified analysis of the residual sum of squares (ARSS) was also employed to compare VBGF's among reefs (Zar, 1984; Chen et al., 1992). Further, one-way analysis of variance was used to determine whether there were significant differences in the mean length (FL) of the early age classes of each species among reefs (α=0.05).

Analysis of covariance was used to determine whether there were significant differences in the clean weight at length (FL) relationships among reefs and between sexes for each species. Length and weight data were transformed to a natural logarithm function ($\log_e x$) to satisfy assumptions of normality and homogeneity as detected by Cochran's test (Winer, 1971). Both reefs and sexes were treated as fixed and orthogonal factors in the analysis. Again, multiple comparisons were performed by using Tukey's honestly significant difference (HSD) test.

Estimates of the annual instantaneous rate of total mortality (Z) for each species among individual reefs were obtained by using the age-based catch-curve method of Beverton and Holt (1957) and Ricker (1975). The natural logarithm of the number of fish

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[9] Prager, M. H., S. B. Saila, and C. W. Recksiek. 1989. FISHPARM: a microcomputer program for parameter estimation of nonlinear models in fishery science, 2nd ed. Old Dominion University Oceanography Technical Report 87-10.

in each age class (N_t) was plotted against their corresponding age (t), and Z was estimated from the descending slope, b. Estimates of the survival rate of both species on different reefs were then calculated from the Z that was derived from catch curves, because $Z = -\log_e S$ (Ricker, 1975).

Results

There were significant differences in mean length, age, and weight of both species among reefs, and these differences were independent of the sex of the fish (Tables 1 and 2). Tukey (HSD) comparisons showed that, in general, mean length and weight were larger and mean age greater for both species at KL, although the multiple comparisons among reefs were not all definitive (Tables 1 and 2). Significant differences in mean length, age, and clean weight of both species between sexes were the same as those

described in Newman et al.,[7] with males larger than females in species (Tables 1 and 2).

Age structures

Age structures of *L. adetii* differed significantly among reefs (Kruskal-Wallis statistic: H=13.85, P<0.01), with the greatest difference being that between RI and JB (Table 3). The relative abundance of older fish (year classes 10–22) at RI was greater than that at JB (Fig. 2). This pattern was seen also at LO and KL, although the overall age structures were not significantly different (Table 3). The pattern of peaks in abundance of year classes was not consistent across all reefs. The small sample size taken from KL may have biased results; however, the sample covered a range of 10 age classes and was similar to the age structure at RI. The age structure at KL was significantly different from that of both JB and LO, and the age structure at JB was significantly dif-
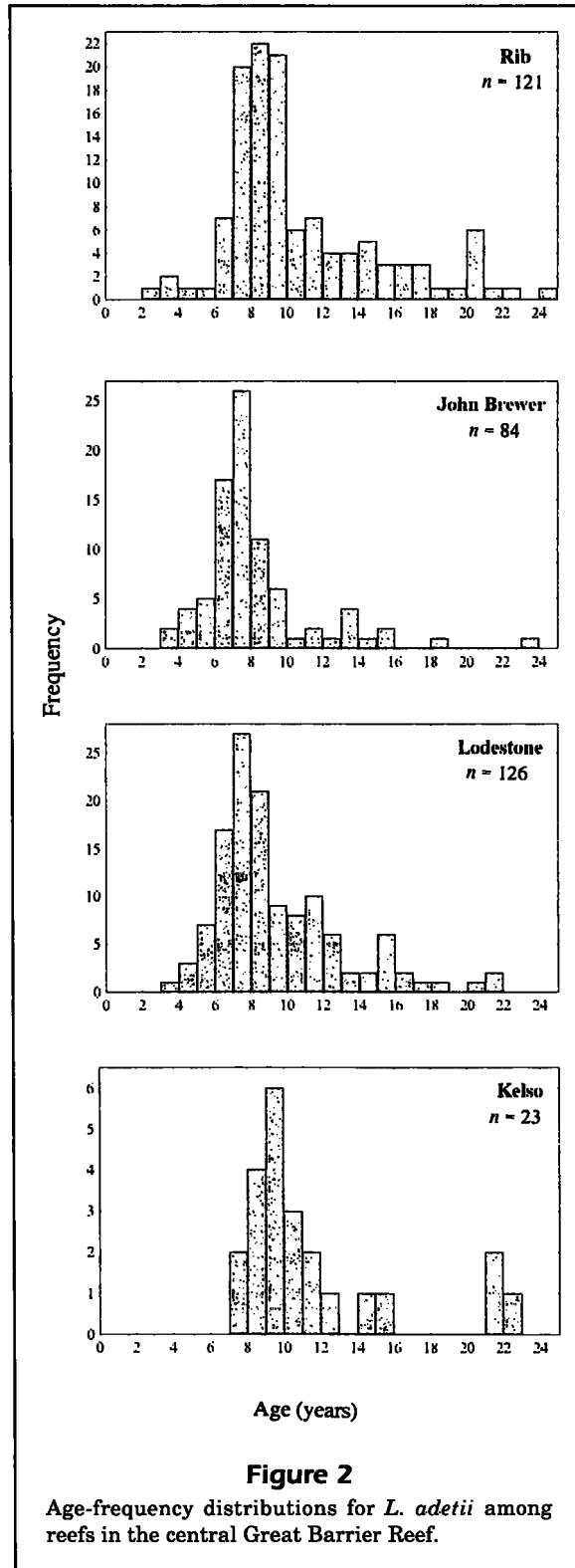

Table 1

Analyses of variance comparing mean length, age, and weight among reefs and between sexes for *Lutjanus adetii* (significant P values are in bold type) and a posteriori multiple comparison of means using Tukey (HSD) analysis (α=0.05; reefs are presented in order of decreasing magnitude). MS = mean square.

Source of variation	df	MS	F	P
Dependent variable: fork length (mm)				
Reefs	3	3106.15	12.912	**< 0.001**
Sex	1	462.23	1.92	> 0.15
Reefs × Sex	3	54.45	0.23	> 0.85
Residual	321	240.56		
Dependent variable: age (years)				
Reefs	3	128.85	8.57	**< 0.001**
Sex	1	43.67	2.90	> 0.05
Reefs × Sex	3	7.24	0.48	> 0.65
Residual	320	15.04		
Dependent variable: clean weight (g)				
Reefs	3	31684.62	14.70	**< 0.001**
Sex	1	23013.95	10.68	**< 0.01**
Reefs × Sex	3	799.39	0.37	> 0.75
Residual	288	2154.85		

Tukey HSD analysis among reefs				
Fork length:	Kelso	Lodestone	Rib	John Brewer
Age:	Kelso	Rib	Lodestone	John Brewer
Clean weight:	Kelso	Lodestone	Rib	John Brewer

Tukey HSD analysis between sexes		
Clean weight:	Males	Females

ferent from that of LO. JB and LO had strong modes in year class 7, whereas KL suggested a mode in year class 9 (Fig. 2). The abundance of year classes 10–22 at LO was greater than that at JB (Fig. 2).

Age structures of *L. quinquelineatus* also differed significantly among reefs (Kruskal-Wallis statistic: $H=21.41, P<0.001$). Kolmogorov-Smirnov tests (Table 4) showed that MR and LO were significantly differ-

Figure 2

Age-frequency distributions for *L. adetii* among reefs in the central Great Barrier Reef.

Table 2

Analyses of variance comparing mean length, age, and weight among reefs and between sexes for *Lutjanus quinquelineatus* (significant *P* values are in bold type) and a posteriori multiple comparison of means using Tukey (HSD) analysis (α=0.05; reefs are presented in descending order). MS = mean square.

Source of variation	df	MS	F	P
Dependent variable: fork length (mm)				
Reefs	5	5944.89	25.70	**< 0.001**
Sex	1	19962.29	86.31	**< 0.001**
Reefs × Sex	5	166.94	0.72	> 0.60
Residual	551	231.29		
Dependent variable: age (years)				
Reefs	5	547.00	17.03	**< 0.001**
Sex	1	40.95	1.27	> 0.25
Reefs × Sex	5	41.13	1.28	> 0.25
Residual	550	32.11		
Dependent variable: clean weight (g)				
Reefs	5	28723.22	35.83	**< 0.001**
Sex	1	98157.42	122.45	**< 0.001**
Reefs × Sex	5	1524.81	1.90	> 0.05
Residual	551	801.60		

Tukey HSD analysis among reefs

Fork length:	Kelso	Davies	Rib	John Brewer	Myrmidon	Lodestone

Age:	Kelso	Rib	John Brewer	Davies	Myrmidon	Lodestone

Clean weight:	Kelso	Davies	Rib	John Brewer	Myrmidon	Lodestone

Tukey HSD analysis between sexes

Fork length:	Males	Females
Clean weight:	Males	Females

Table 3

Differences in the distribution of age structures of *Lutjanus adetii* between reefs were determined by using the Kolmogorov-Smirnov test (values of D_{max} are shown, significance level α=0.05, significant results are marked with an asterisk [*]).

	Reef		
Reef	John Brewer	Lodestone	Kelso
Rib	0.38*	0.17	0.19
John Brewer		0.21*	0.56*
Lodestone			0.35*

i.e.   John Brewer   Lodestone   Rib   Kelso

ent from all other reefs. KL was not significantly different from RI, but was significantly different from all other reefs. JB was not significantly different from either DV or RI, whereas DV was significantly different from RI. MR showed a peak in year class 5 and relatively strong year classes 6, 7, and 8 (Fig. 3). However, few fish older than 8 years were represented in catches. LO had relatively strong year classes 2, 3, 4, and 5, but abundance per age class declined rapidly to year 26, except for a strong mode in year class 14 (Fig. 3). DV was somewhat similar, with strong modes in year classes 5 and 6 but with the abundance of subsequent year classes declining approximately exponentially to year 22 (Fig. 3). Data were more limited for KL, which showed relatively even distribution from year classes 2–30 and peaks in year classes 5 and 14. Compared with those from

Table 4

Differences in the distribution of age structures of *Lutjanus quinquelineatus* between reefs were determined by using the Kolmogorov-Smirnov test (values of D_{max} are shown, significance level α=0.05, significant results are marked with an asterisk [*]).

	Reef				
	John Brewer	Lodestone	Davies	Myrmidon	Kelso
Rib	0.14	0.31*	0.23*	0.43*	0.14
John Brewer		0.27*	0.20	0.43*	0.27*
Lodestone			0.35*	0.30*	0.41*
Davies				0.28*	0.36*
Myrmidon					0.54*
i.e.	Myrmidon	Lodestone	Davies	John Brewer	Rib	Kelso

other reefs, older year classes were relatively dominant at KL. JB and RI had relatively flat age distributions for year classes 2–24 compared with those for LO, DV, and MR. The only pattern that was consistent across all reefs was the strong mode of 5-year-old individuals (Fig. 3), and this may have reflected the age at which these fish attained full recruitment to the sampling gear (fish traps).

Growth models

The von Bertalanffy models of the length-age relationship among reefs for *L. adetii* are shown in Figure 4; the coefficients of determination among reefs ranged from 0.177 to 0.462. The low coefficients of determination were attributable to the absence of younger and smaller fish in the samples. Therefore no point of inflexion was evident in the growth models among reefs. As a result, the parameters of the von Bertalanffy models for *L. adetii* among individual reefs were characterized by large asymptotic standard errors (Table 5), with LO having the best-fitting model. The von Bertalanffy model from LO was similar to that derived from all reefs pooled within the central Great Barrier Reef (Table 5). Despite the absence of small and younger fish caused by the bias in sampling, the von Bertalanffy growth function was the best empirically based assessment of growth in *L. adetii* (Fig. 4). The von Bertalanffy growth curves for *L. adetii* were not significantly different among reefs (likelihood-ratio test, $P \gg 0.05$; ARSS:F=1.13, $P \gg 0.05$), and the resulting growth curves (Fig. 4) appeared to be similar. Additionally, there were no significant differences in the mean length (FL) of the early age classes (6+, 7+, 8+, and 9+) of *L. adetii* among reefs (Table 6).

The von Bertalanffy model provided a better description of the length-age relationship among reefs for *L. quinquelineatus* (Fig. 5), with coefficients of determination among reefs ranging from 0.267 to 0.752. The younger and smaller fish were underrepresented in the catch samples from some reefs and this was reflected in the coefficients of determination (Table 5; Fig. 5). The parameters of the von Bertalanffy models for *L. quinquelineatus* among individual reefs were characterized by relatively small asymptotic standard errors (Table 5). The growth curves for *L. quinquelineatus* were significantly different among reefs (likelihood-ratio test, $P < 0.01$; ARSS:F=8.401, $P < 0.001$). Differences among reefs were observed in values of L_∞, K, and t_0 (Table 5). However, there were no significant differences in the mean length (FL) of the early age classes (2+, 3+, 4+, 5+, and 6+) of *L. quinquelineatus* among reefs (Table 7).
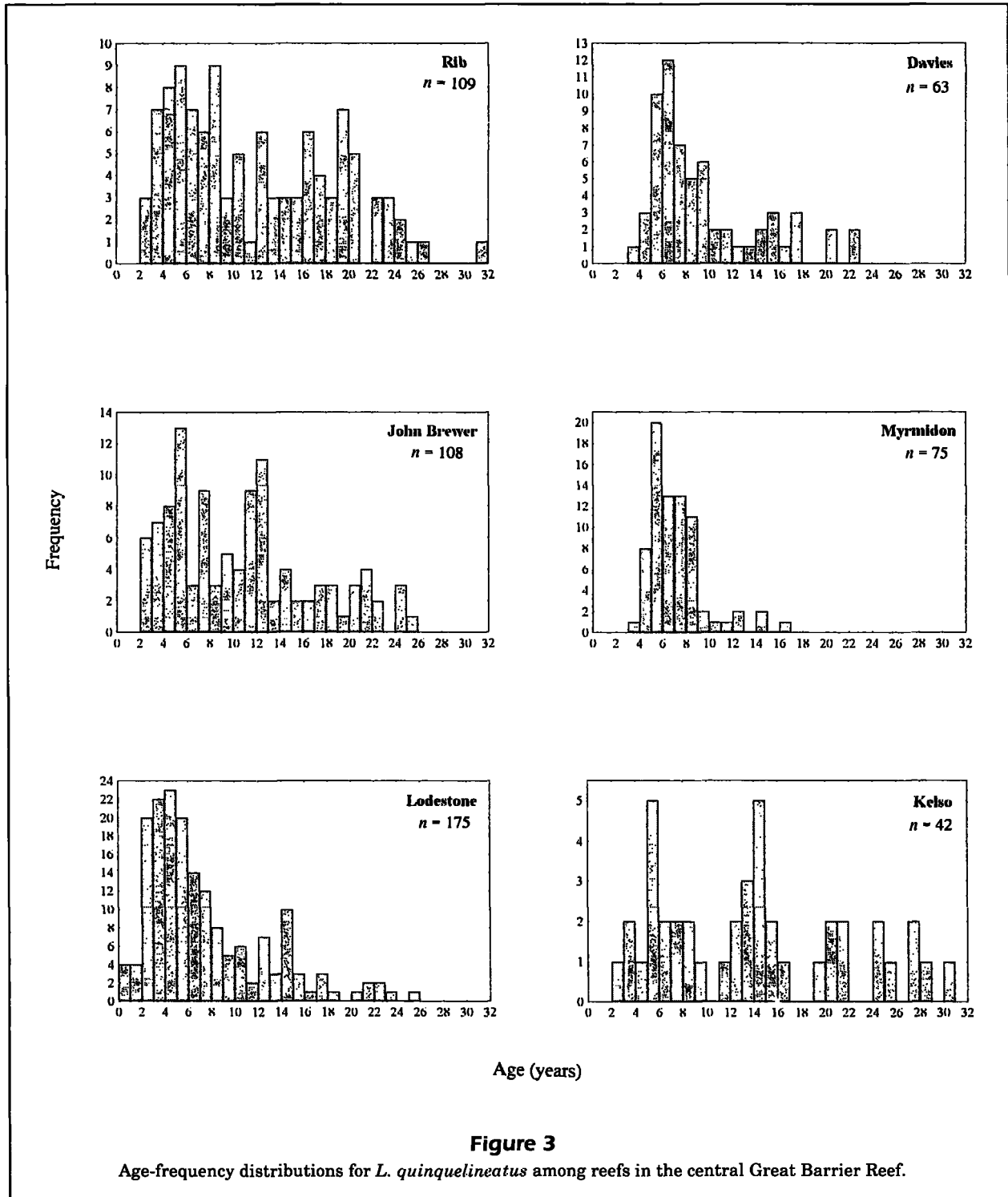
Analysis of covariance (ANCOVA) demonstrated that the relationship between weight and length in *L. adetii* was significantly different both among reefs and between sexes and that the among-reef differences were independent of the sex of the fish (Table 8). Similarly, ANCOVA demonstrated that the relationship between weight and length in *L. quinquelineatus* was also significantly different both among reefs and between sexes (Table 8). However, the significant among-reef differences were not independent of the sex of the fish (a significant interaction effect occurred between reefs and sex). The differences among reefs were different for each sex (Table 8).

Mortality

In general, individual *L. adetii* less than 7 years of age did not appear to be fully recruited in the sampled

population and were excluded from the mortality estimates derived from catch curves. For RI, JB, LO, and KL, the reef-specific total annual rate of mortality, Z, of $L.$ $adetii$, was 0.179 (fish aged 8–24 years, r^2=0.729, SE=0.0292), 0.304 (fish aged 7–15 years, r^2=0.512, SE=0.1123), 0.225 (fish aged 7–21 years,

r^2=0.781, SE=0.0344) and 0.286 (fish aged 9–15 years, r^2=0.795, SE=0.0726), representing an annual survivorship of approximately 83%, 74%, 80%, and 75%, respectively (Fig. 6). The mortality rates of $L.$ $adetii$ among reefs were significantly different (homogeneity of slopes test, $P<0.01$), and a multiple com-

Figure 3

Age-frequency distributions for $L.$ $quinquelineatus$ among reefs in the central Great Barrier Reef.

parison of slopes indicated that the mortality rate at Rib Reef was significantly lower than that at all other reefs (RI<[JB=LO=KL]).

Individual *L. quinquelineatus* <5 years of age were usually not fully recruited in the sampled population and were excluded from the mortality estimates

derived from catch curves. Estimates of mortality with high coefficients of determination were obtainable from only two reefs, LO and MR. The other reefs had a poor fit to the catch-curve regressions (Fig. 7), and hence mortality rates were not obtained either because there was a persistence of numerous strong

Figure 4

Von Bertalanffy growth curves and observed length at age for *L. adetii* among individual reefs in the central Great Barrier Reef.
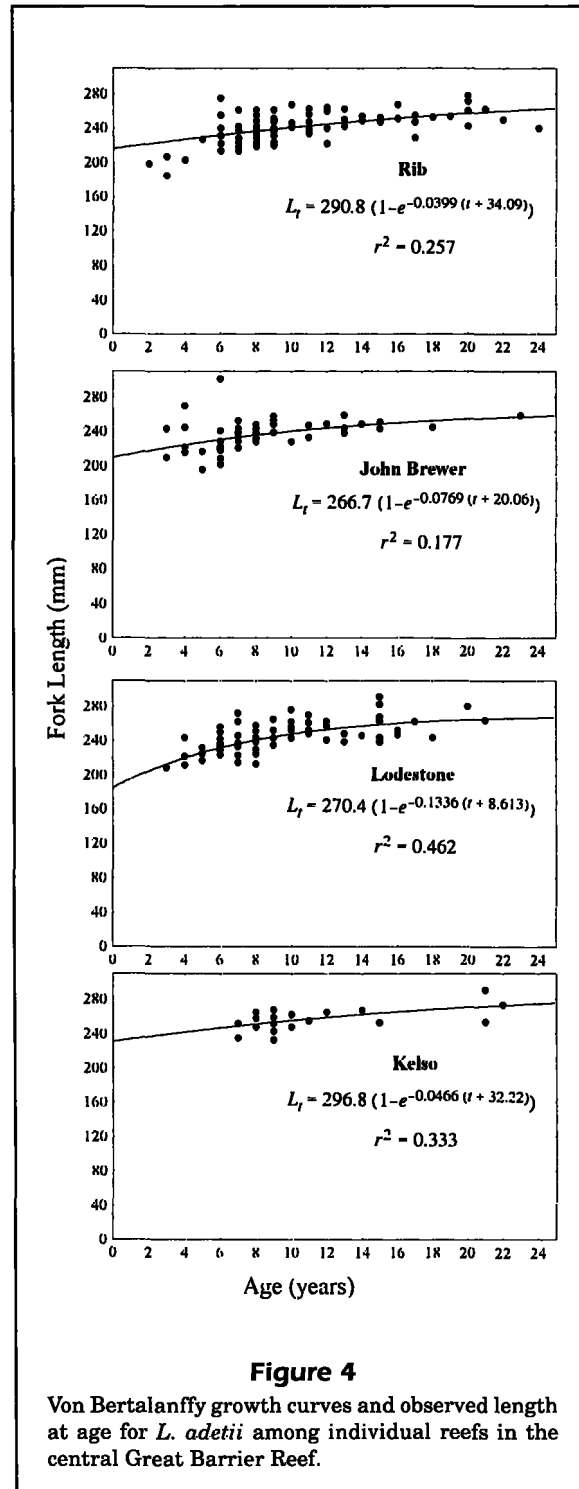
Table 5

Growth parameters and asymptotic standard errors (ASE) calculated from the von Bertalanffy growth function, mean fork length (FL, mm), and age (years) for *Lutjanus adetii* and *L. quinquelineatus* among reefs in the central Great Barrier Reef (GBR).

Lutjanus adetii

Parameters	Reefs				All reefs pooled central GBR (n=369)
	Rib (n=122)	John Brewer (n=84)	Lodestone (n=126)	Kelso (n=23)	
L_∞ (FL)	290.8	266.7	270.4	296.8	265.2
ASE	59.95	34.27	8.93	119.4	4.229
K	0.0399	0.0769	0.1336	0.0466	0.1454
ASE	0.0511	0.0959	0.0484	0.1638	0.0285
t_0	−34.09	−20.06	−8.613	−32.22	−8.077
ASE	31.26	22.10	3.961	94.31	2.132
r^2	0.257	0.177	0.462	0.333	0.390
FL_{mean} (SE)	240.3 (1.48)	234.6 (1.67)	242.0 (1.39)	256.7 (2.59)	241.1 (0.88)
FL_{min}	185	196	209	233	185
FL_{max}	285	301	291	291	301
t_{mean} (SE)	10.24 (0.397)	7.79 (0.350)	8.93 (0.314)	11.17 (0.934)	9.27 (0.206)
t_{min}	2	3	3	7	2
t_{max}	24	23	21	22	24

Lutjanus quinquelineatus

Parameters	Reefs						All reefs pooled central GBR (n=577)
	Rib (n=110)	John Brewer (n=108)	Lodestone (n=175)	Davies (n=63)	Myrmidon (n=75)	Kelso (n=42)	
L_∞ (FL)	214.1	204.1	198.1	211.5	208.0	220.4	206.9
ASE	5.221	1.665	1.697	2.417	11.26	2.72	0.979
K	0.1125	0.3138	0.4665	0.3048	0.1711	0.2182	0.3064
ASE	0.0433	0.0506	0.0367	0.0694	0.1290	0.0474	0.0174
t_0	−14.12	−2.789	−1.108	−2.313	−8.238	−3.978	−2.587
ASE	5.774	0.8787	0.1942	1.456	7.443	1.588	0.2708
r^2	0.421	0.652	0.745	0.603	0.267	0.752	0.638
FL_{mean} (SE)	198.5 (1.5)	193.2 (1.5)	180.3 (1.9)	199.3 (1.6)	190.5 (1.3)	207.0 (2.8)	191.6 (0.8)
FL_{min}	148	146	60	163	170	155	60
FL_{max}	231	230	230	224	219	233	233
t_{mean} (SE)	11.6 (0.66)	10.2 (0.59)	6.9 (0.39)	9.06 (0.60)	6.65 (0.28)	13.43 (1.21)	9.12 (0.25)
t_{min}	2	2	<1	3	3	2	<1
t_{max}	31	25	25	22	16	30	31

year classes or because there were age-varying mortality rates (Fig. 7). The estimates of total mortality rate, Z, of *L. quinquelineatus* at LO and MR were 0.153 (fish aged 4–22 years, r^2=0.711, SE=0.0245) and 0.335 (fish aged 5–16 years, r^2=0.661, SE=0.0703), representing an annual survivorship of approximately 86% and 72%, respectively. Mortality rates of *L. quinquelineatus* between LO and MR reefs were significantly different (homogeneity of slopes test, $P<0.01$). Figure 7 shows that mortality rates and hence survivorship of *L. quinquelineatus* among reefs is highly variable.

A comparison of mortality rates among successive years (with a relatively large sample size) could be determined only for *L. quinquelineatus* at LO. The total rate of mortality, Z, of *L. quinquelineatus* at LO in 1992 was 0.176 (fish aged 4–17 years, r^2=0.615, SE=0.0402, n=109), representing an annual survivorship of approximately 84% (Fig. 8), whereas the total rate of mortality, Z, of *L. quinquelineatus* at LO in 1993 was 0.155 (fish aged 3–14 years, r^2=0.409, SE=0.0621, n=64), representing an annual survivorship of approximately 86% (Fig. 8). The mortality rates of *L. quinquelineatus* at LO were not significantly different between successive years (homogeneity of slopes test, $P>0.05$; Fig. 8). The natural mortality rate, M, of both species among reefs is considered equal to total mortality owing to the negligible amount of fishing mortality.

Table 6

Mean length (FL, mm) of early age classes of *Lutjanus adetii* among reefs and analyses of variance comparing the mean lengths of individual age classes among reefs. Number of samples per age class is in parentheses. ns = not significant.

| | Reefs | | | | | |
| | Rib | John Brewer | Lodestone | | | |
Age class	Mean FL	Mean FL	Mean FL	df	F	P
2+	199.0 (1)	— (0)	— (0)	—	—	—
3+	196.0 (2)	226.5 (2)	209.0 (1)	—	—	—
4+	203.0 (1)	238.3 (4)	226.0 (3)	—	—	—
5+	227.0 (1)	212.2 (5)	226.3 (7)	—	—	—
6+	237.1 (7)	228.5 (17)	234.1 (17)	2, 38	0.744	ns
7+	231.3 (20)	233.2 (26)	234.4 (27)	2, 70	0.507	ns
8+	235.3 (22)	239.6 (11)	238.9 (21)	2, 51	0.920	ns
9+	238.3 (21)	245.5 (6)	243.9 (9)	2, 33	1.825	ns

Table 7

Mean length (FL, mm) of early age classes of *Lutjanus quinquelineatus* among reefs and analyses of variance comparing the mean lengths of individual age classes among reefs. Number of samples per age class is in parentheses. ns = not significant.

| | Reefs | | | | | | | | |
| | Rib | John Brewer | Lodestone | Davies | Myrmidon | Kelso | | | |
Age class	Mean FL	Mean FL	Mean FL	Mean FL	Mean FL	Mean FL	df	F	P
1+	—	—	113.0 (8)	—	—	—	—	—	—
2+	163.0 (3)	160.5 (6)	154.3 (20)	—	—	155.0 (1)	3,26	0.523	ns
3+	179.9 (7)	167.6 (7)	166.8 (22)	163.0 (1)	174.0 (1)	172.0 (2)	5,34	1.171	ns
4+	185.0 (8)	179.1 (8)	179.1 (23)	180.0 (3)	181.1 (8)	173.0 (1)	5,45	0.360	ns
5+	188.7 (9)	187.2 (13)	186.8 (20)	191.7 (10)	187.8 (20)	193.6 (5)	5,71	0.984	ns
6+	193.4 (7)	195.7 (3)	188.6 (14)	193.4 (12)	189.4 (13)	193.0 (2)	5,45	0.754	ns

Discussion

The significant differential growth in length and weight of both species among reefs and between sexes indicates that rates of growth in terms of weight at length of both species was variable at the spatial scale of individual reefs. However, statistical and visual comparisons of the VBGF for *L. adetii* indicate that the pattern of growth in individuals among reefs with increasing age was relatively similar. Because only one gear type was used and the distribution of juvenile *L. adetii* was not determined and is presently not known, it was not possible to obtain a sufficient range of sizes to describe the first few years of growth. The growth patterns of *L. quinquelineatus* described by the VBGF were significantly different among reefs. However, no significant differences were detected in the mean lengths of individuals in age classes 2–6 among reefs (Table 6). These results indicate that initial growth rates among reefs were not significantly different and that the significant differences in the overall growth rates among reefs probably reflected the number of young fish available for capture at each reef.

The necessary pooling of size-at-age data over two different years may have biased the resulting growth patterns, if growth was variable among years. There was, however, no evidence to suggest that growth of either species was variable among years. The pooling of data over a number of years was necessary in order to sample a wide cross section of age classes. The inclusion of size-at-age data over a number of years has the advantage of providing a general description of the growth patterns of each species at each reef. However, large sample sizes covering a

range of age classes from a number of consecutive years would be needed to determine if growth rates were variable between years.

The age structures for populations of *L. adetii* and *L. quinquelineatus* among reefs usually showed several strong year classes that were variable among reefs. The occurrence of strong year classes is well docu-

mented in the commercial catches of many temperate species (Hjort, 1914; Sissenwine, 1984; Rothschild, 1986) and has recently been observed in a number of tropical species (Doherty and Fowler, 1994b; Ferreira and Russ, 1995). Year-class strength in both temperate and tropical species has been linked to early life history processes (e.g. Hjort, 1914; Sissenwine, 1984;
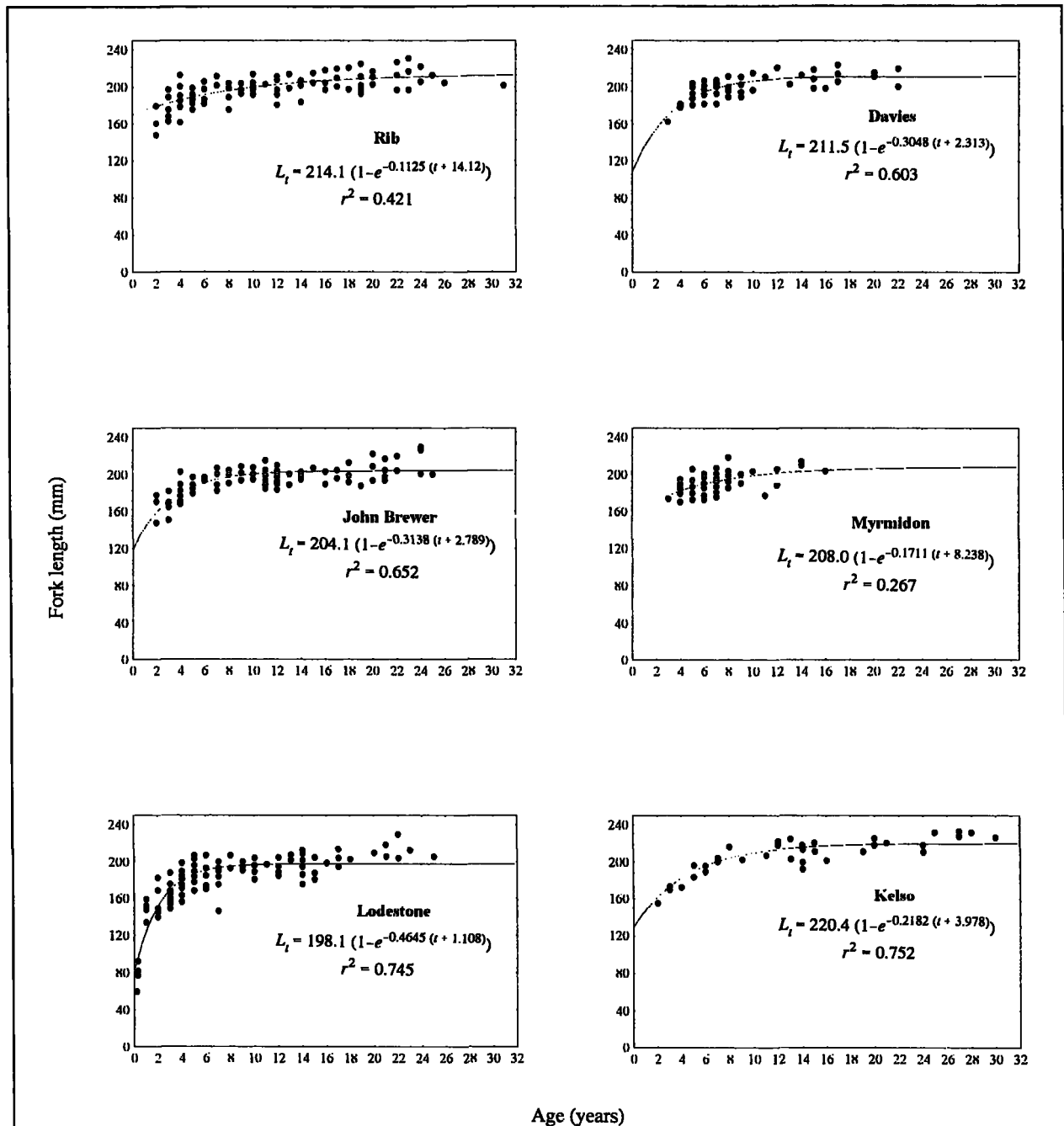

Figure 5

Von Bertalanffy growth curves and observed length at age for *L. quinquelineatus* among individual reefs in the central Great Barrier Reef.

Doherty and Fowler, 1994b). Further, the suggestion that recruitment variability is a major factor influencing both the distribution and local densities of coral reef fishes has been recognized for a number of years (Williams, 1980; Doherty, 1981, 1983, 1991; Victor, 1983; reviews of Doherty and Williams, 1988). Subsequently, Doherty and Fowler (1994b) have shown that for the common tropical damselfish *Pomacentrus moluccensis*, age structures from individual reefs have preserved major temporal variations in the recruitment patterns over at least 10 years, providing empirical evidence of a strong effect of recruitment history on subsequent year-class strength. It is therefore conceivable that the various age structures of both lutjanid species among reefs is a consequence both of variability in recruitment at the localized scale of individual reefs and of good recruitment years persisting in the age structure of populations over time.

Estimates of the rate of natural mortality in fish populations are essential to fishery management (see Ricker, 1975; Gulland, 1983; and Russ, 1991). The mortality rate for *L. adetii* was significantly different among reefs, although these differences were small. The mortality rates for this species in general were low and the rates of survivorship were correspondingly high. Mortality rates for *L. quinquelineatus* were not obtainable from all reefs owing to either the persistence of strong year-class modes, (possibly to nonconstant mortality rates at a number of reefs (although these were not detected among years at Lodestone Reef), or differential mortality of cohorts (as opposed to interannual variability in mean [cross-cohort] mortality rates). The results observed here suggest that interannual variation in recruitment may be retained in the age structure at each reef as found for *P. moluccensis* (Doherty and Fowler, 1994b). Mortality rates derived with the catch-curve method of Beverton and Holt (1957) and Ricker (1975) are based on the assumption that recruitment is constant in the population under con-
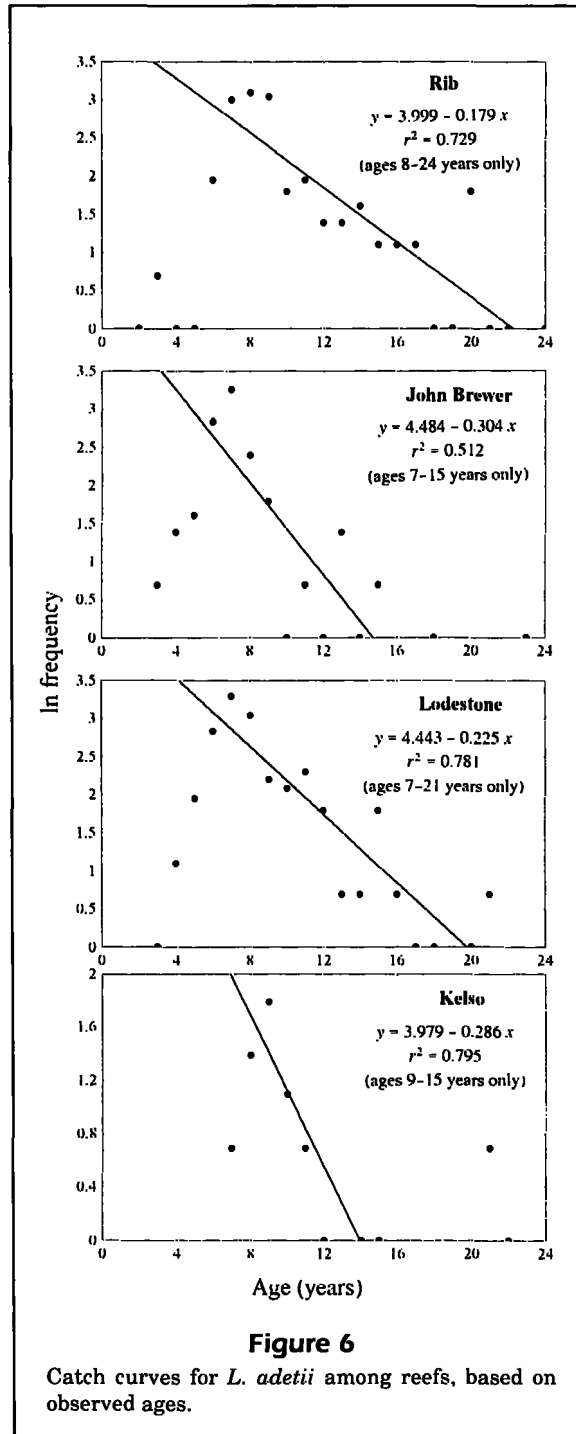
Table 8
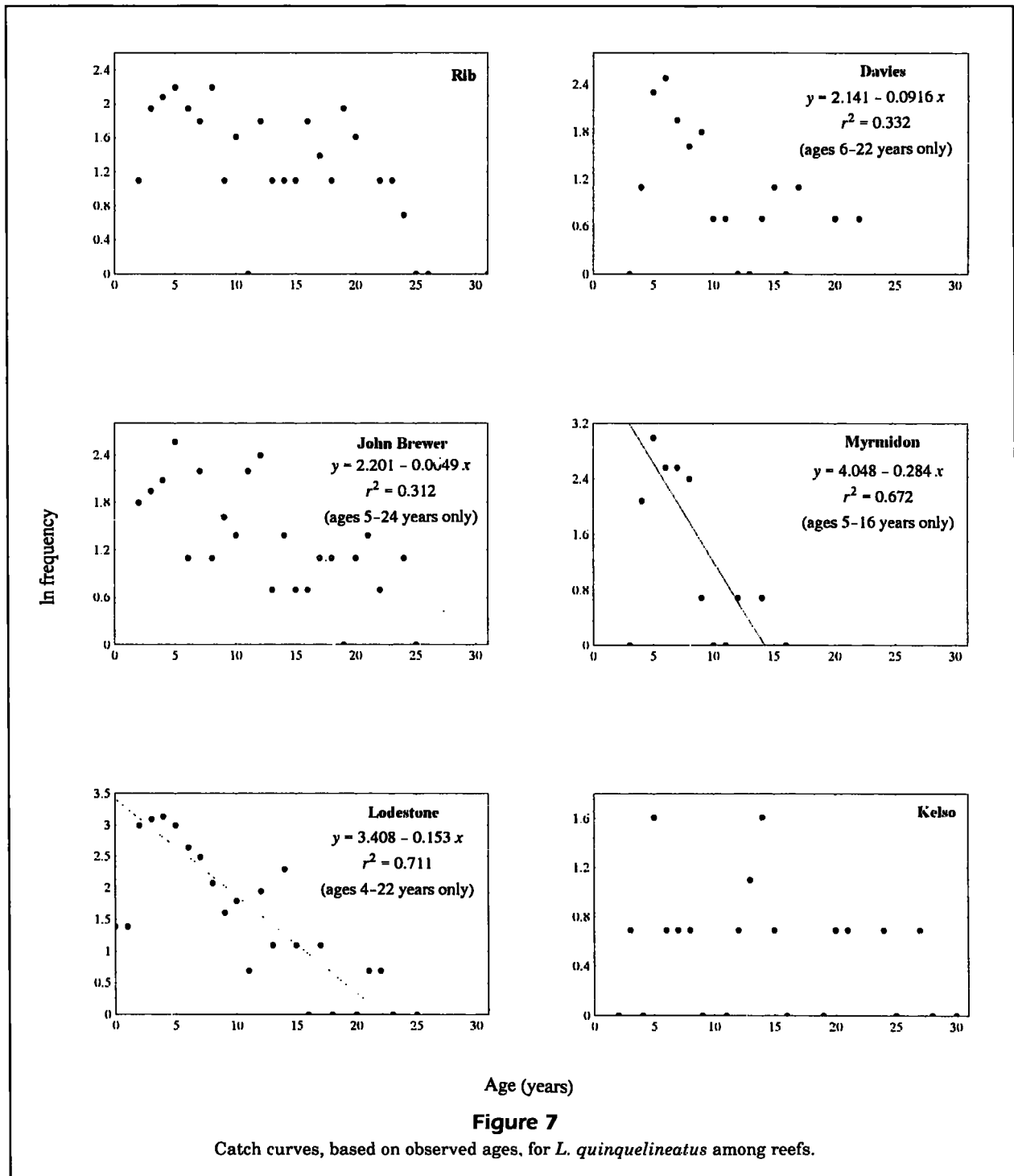
Analyses of covariance comparing weight at length (transformed to $\log_e$, covariate = length) among reefs and between sexes for *Lutjanus adetii* and *L. quinquelineatus* (significant *P* values are in bold type; note Kelso Reef was not included in the analyses because of the small sample size) and a posteriori multiple comparison of means using Tukey (HSD) analysis ($\alpha=0.05$).

Source of variation	df	MS	F	P
L. adetii				
Reefs	2	0.0328	11.917	**< 0.001**
Sex	1	0.0484	17.577	**< 0.001**
Reefs × Sex	2	0.0004	0.127	> 0.85
Residual	266	0.0028	—	—

Tukey HSD analysis among reefs	Lodestone	Rib	John Brewer	
Tukey HSD analysis between sexes	Males	Females		

Source of variation	df	MS	F	P
L. quinquelineatus				
Reefs	4	0.0683	15.647	**< 0.001**
Sex	1	0.0258	5.907	**< 0.05**
Reefs × Sex	4	0.0129	2.948	**< 0.05**
Residual	510	0.0044	—	—

Tukey HSD analysis among reefs

Male:	Rib	Davies	John Brewer	Myrmidon	Lodestone
Female:	Rib	Davies	John Brewer	Myrmidon	Lodestone

Tukey HSD analysis between sexes

Rib:	Males	Females
John Brewer:	Males	Females
Lodestone:	Males	Females
Davies:	Males	Females
Myrmidon:	Males	Females

sideration. Mortality estimates derived with the catch-curve regression method are least sensitive to minor violations of this assumption (Ricker, 1975) and this is particularly evident in L. quinquelineatus. Despite this, it is evident from Figure 7 that mortality rates of L. quinquelineatus are variable among reefs and are similar to those for populations of L. adetii in that they are characterized by low rates of

total mortality and high rates of survivorship. However, mortality estimates cannot be derived with great confidence from populations where significant recruitment variability is retained in the age structure (e.g. Ferreira and Russ, 1995), and although Ricker (1975) has suggested that irregularities in catch curves caused by variable recruitment can be reduced by combining samples over successive years,

Figure 6

Catch curves for L. adetii among reefs, based on observed ages.

Figure 7

Catch curves, based on observed ages, for *L. quinquelineatus* among reefs.

this method was not expected to reduce variability among age classes in the present study.

However, the mortality rates of *L. quinquelineatus* at Lodestone Reef were not significantly different between successive years (Fig. 8). This result suggests that the variable mortality rates and hence survivorship of these species among reefs may be relatively consistent through time. Similarly, Doherty and Fowler (1994a) suggested that mortality schedules were consistent (not constant) across space and time for two damselfish species from the positive correlations that were present between spatial and temporal variation in recruitment and subsequent abundance. Therefore, the observed differences in mor-

Figure 8

Catch curves for *L. quinquelineatus* from Lodestone Reef between successive years, based on observed ages.
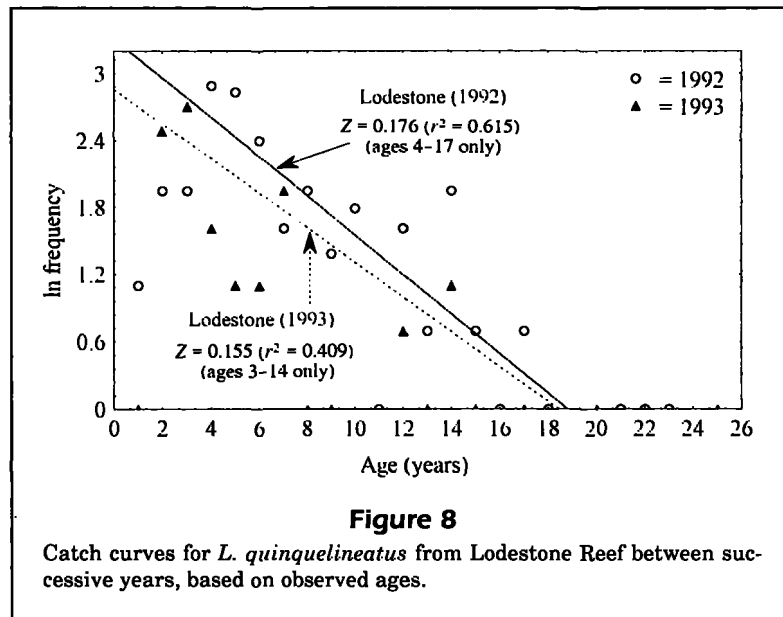
tality rates among reefs for these species are likely to be authentic and not a product of the assumptions inherent in the use of catch curves.

In conclusion, this study demonstrated that significant variability exists in the mortality and age structures of *L. adetii* and *L. quinquelineatus* at the spatial scale of individual reefs. The demography of both these lutjanid species at the spatial scale of individual coral reefs is most likely to be a consequence of the nonequilibrial balance of variable recruitment interacting with density-independent mortality (Doherty and Fowler, 1994b). This spatial variability in demographic parameters among reefs should be considered in the development of management models. The significant differences in mortality rates and age structures for the populations of *L. adetii* and *L. quinquelineatus* among reefs would have more impact on management models than the small differences in growth for these species. Further, greater longevity conveys a selective advantage by increasing the cumulative lifetime fecundity (egg production) of the female parent (see Beverton, 1987). Therefore, in terms of the current management models of the Great Barrier Reef Marine Park, it would be advantageous to protect reefs that are characterized by species with extended longevity and low rates of natural mortality (in comparison with reefs of similar population size but which are characterized by fish with reduced longevity and high rates of natural mortality). The primary advantage of adopting this strategy would be that the spawning biomass of the longer lived fishes would be protected which has the capacity to act as a recruitment source for the surrounding areas that are fished.

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