

Abstract—Spatial variation in demographic parameters of the red throat emperor (*Lethrinus miniatus*) was examined among 12 coral reefs in three geographic regions (Townsville, Mackay, and Storm Cay) spanning over 3° of latitude of the Great Barrier Reef, Australia. Estimates of demographic parameters were based on age estimates from counts of annuli in whole otoliths because there was no significant difference in age estimates between whole and sectioned otoliths. There were significant regional differences in age structures, rates of somatic and otolith growth, and total mortality. The Townsville region was characterized by the greatest proportion of older fish, the smallest maximum size, and the lowest rates of otolith growth and total mortality. In contrast the Mackay region was characterized by the highest proportion of younger fish, the largest maximum size, and the highest rates of otolith growth and total mortality. Demographic parameters for the Storm Cay region were intermediate between the other two regions. Historic differences in fishing pressure and regional differences in productivity are two alternative hypotheses given to explain the regional patterns in demographic parameters. All demographic parameters were similar among the four reefs within each region. Thus, subpopulations with relatively homogeneous demographic parameters occurred on scales of reef clusters. Previous studies, by contrast, have found substantial between-reef variation in demographic parameters within regions. Thus spatial variation in demographic parameters for *L. miniatus* may differ from what is assumed typical for a coral-reef fish metapopulation.

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Scales of spatial variation in demography of a large coral-reef fish—an exception to the typical model?

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Estimates of demographic parameters, such as growth and mortality rates, are fundamental to the understanding of a species population dynamics and for predicting responses of populations to exploitation. Processes affecting population dynamics operate at a number of spatial and temporal scales (Levin, 1992) and can result in subpopulations with distinct demographics. Differences in demography between populations may suggest geographic or reproductive isolation (or both) and as such have been used in stock identification for fisheries assessment and management purposes (e.g. Begg et al., 1999).

Identifying the “unit stock” has been the primary focus of studies of spatial structure of harvested populations in most fisheries. Knowledge of spatial structure within a unit stock is important for both fisheries management, because potential yields may vary spatially within a population (Caddy, 1975), and for conservation, in order to maintain intraspecific diversity (Nielson, 1998). Hence, it is important to estimate demographic parameters over a range of temporal and spatial scales to determine the scale(s) at which the parameters vary significantly (Caley et

al., 1996) and, therefore, to infer which scales are of greatest importance for assessment and management purposes (Sale, 1998).

Most coral-reef fish exist as metapopulations of sedentary adult populations linked by pelagic larval dispersal (Sale, 1998). Consequently, adult populations of reef fish are commonly spatially segregated and may be exposed to different environmental, biological, and ecological processes, resulting in spatial differences in demographic parameters at a range of spatial scales. Relatively few studies, however, have focussed on spatial variation in demographic parameters of harvested species of coral-reef fish. Those that have, have generally focussed on spatial scales within individual reefs or among reefs within a single region (e.g. Ferreira and Russ, 1995; Hart and Russ, 1996; Newman et al., 1996). Comprehensive multiscale approaches are rare (but see Adams et al., 2000; Meekan et al., 2001).

The spatial structure of coral-reef populations has generated considerable interest in terms of the use of spatial closures, or marine protected areas (MPAs), as an effective tool for their management (Roberts and Polunin,

1991). However, the lack of information about the stock structure of, and connectivity among, adult populations has hindered MPA design (Walters and Bonfil, 1999). Conservation management of the Great Barrier Reef (GBR) has included the use of spatial closures of areas to activities, including fishing, for more than 15 years. The majority of spatial closures to line fishing are of individual coral reefs or groups of reefs. This spatial management strategy is underpinned by the assumption of the metapopulation model of coral-reef fish described above. That is, closing individual reefs to fishing will protect the adult populations on those reefs, and potentially provide a source of larvae to areas open to fishing. Management of line fishing on the GBR currently includes bag limits for recreational fishermen and minimum-size restrictions that are uniform for all fishermen and across the entire area of the fishery. Such management regulations are based on the assumption that the demography of target species does not vary substantially over the species range and on the assumption that that populations on the GBR represent a single, homogeneous stock.

The red throat emperor (*Lethrinus miniatus*) (also known as the trumpet emperor) is a relatively long-lived (>20 years) (Loubens, 1980; Brown and Sumpton, 1998) member of the Lethrinidae and has a restricted distribution in the western Pacific and eastern Indian Oceans (Carpenter and Allen, 1989). On the GBR it is the second most important demersal species in a multispecies line fishery, contributing up to 1000 metric tons annually to the combined commercial and recreational catch (Mapstone et al.¹; Higgs²). As with many tropical lethrinids, information on the biology and ecology of *L. miniatus* is scarce. The limited data available indicate that *L. miniatus* is usually associated with coral reefs, but that it is also commonly caught in deeper water, in sand, and rubble areas between reefs (Carpenter and Allen, 1989; Newman and Williams, 1996; Williams and Russ³). The habitat of juvenile *L. miniatus* is unknown, but Williams and Russ³ have suggested that juveniles may occupy the deeper rubble areas adjacent to reefs. Like some other coral-reef fish, *L. miniatus* is thought to form large aggregations associated with spawning

(Russell⁴). These available data suggest that *L. miniatus* adults have the capacity to move among individual reefs on the GBR. This movement pattern contrasts with information on movement patterns of other large coral-reef species such as the coral trout (*Plectropomus leopardus*) (also known as the leopard coral grouper, Heemstra and Randall, 1993) where adults show limited movement within a single reef and very restricted movements between reefs (Davies, 1995). It also contrasts with movement patterns of the majority of coral-reef fish, where adults are known to have very restricted home ranges and display little, if any, movement between reefs (Lewis 1997; Sale, 1998). Therefore the relevant spatial scale affecting demographic parameters of *L. miniatus* may be larger than an individual reef and thus is different from that for most "typical" coral-reef fish.

The central objective of this study was to determine how the spatial patterns in demography of large, more mobile reef fish differ from smaller site-attached reef-fish species. To achieve this we used validated age estimates to examine spatial variation in demographic parameters of populations of *L. miniatus* across two spatial scales most relevant to assessing and managing the species on the GBR: 1) among individual reefs within regions and, 2) among geographic regions. Specifically, we estimated age structures, growth, mortality, and otolith growth rates for among four reefs (all closed to fishing) within each of three geographic regions spanning over 500 km (over 3° of latitude) of the GBR.

Materials and methods

Collection methods

Samples of *L. miniatus* were collected from three geographic regions of the GBR as part of a large-scale manipulative experiment to examine the effects of line fishing on the GBR (Davies et al.⁵; Mapstone et al.⁶). The three regions cover most of the distribution of *L. miniatus* on the GBR (Fig. 1), which is restricted to the southern 50% of the GBR. Within each region *L. miniatus* were collected from six individual reefs. Four of these reefs were zoned "Marine National Park B" and were closed to all forms of fishing (referred to as "closed reefs" in this article) whereas the other two reefs were zoned "General Use B" and were

¹ Mapstone, B. D., J. P. McKinlay, and C. R. Davies. 1996. A description of commercial reef line fishery logbook data held by the Queensland Fisheries Management Authority. Report to the Queensland Fisheries Management Authority from the Cooperative Research Centre for the Ecologically Sustainable Development of the Great Barrier Reef, and the Department of Tropical Environmental Studies and Geography, James Cook University, Queensland, Australia, 480 p. [Available from the Queensland Fisheries Service, G.P.O. Box 46, Brisbane, Queensland, Australia 4001.]

² Higgs, J. 2001. Experimental recreational catch estimates for Queensland residents. Results from the 1999 diary round. RFISH technical report no. 3. Queensland Fisheries Service, Australia, 62 p. [Available from the Queensland Fisheries Service, G.P.O. Box 46, Brisbane, Queensland, Australia 4001.]

³ Williams, D. McB., and G. R. Russ. 1994. Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef. Report to the Great Barrier Reef Marine Park Authority, 103 p. [Available from the Great Barrier Reef Marine Park Authority, P.O. Box 1379, Townsville, Queensland, Australia, 4810.]

⁴ Russell, M. 2001. Spawning aggregations of reef fishes on the Great Barrier Reef: implications for management. Report from the Great Barrier Reef Marine Park Authority, 37 p. [Available from the Great Barrier Reef Marine Park Authority, P.O. Box 1379, Townsville, Queensland, Australia, 4810.]

⁵ Davies, C. R., B. D. Mapstone, A. Ayling, D. C. Lou, A. Punt, G. R. Russ, M. A. Samoily, A. D. M. Smith, D. J. Welch, and D. McB. Williams. 1998. Effects of line fishing experiment 1995–1997: project structure and operations. Supplementary to progress report. CRC Reef Research Centre, Townsville, Australia, 28 p. [Available from the CRC Reef Research Centre, P.O. Box 772, Townsville, Queensland, Australia 4810.]

⁶ Mapstone, B. D., C. R. Davies, D. C. Lou, A. E. Punt, G. R. Russ, D. A. J. Ryan, A. D. M. Smith, and D. McB. Williams. 1998. Effects of line fishing experiment 1995–1997: progress report. CRC Reef Research Centre, 86 p. [Available from the CRC Reef Research Centre, P.O. Box 772, Townsville, Queensland, Australia 4810.]

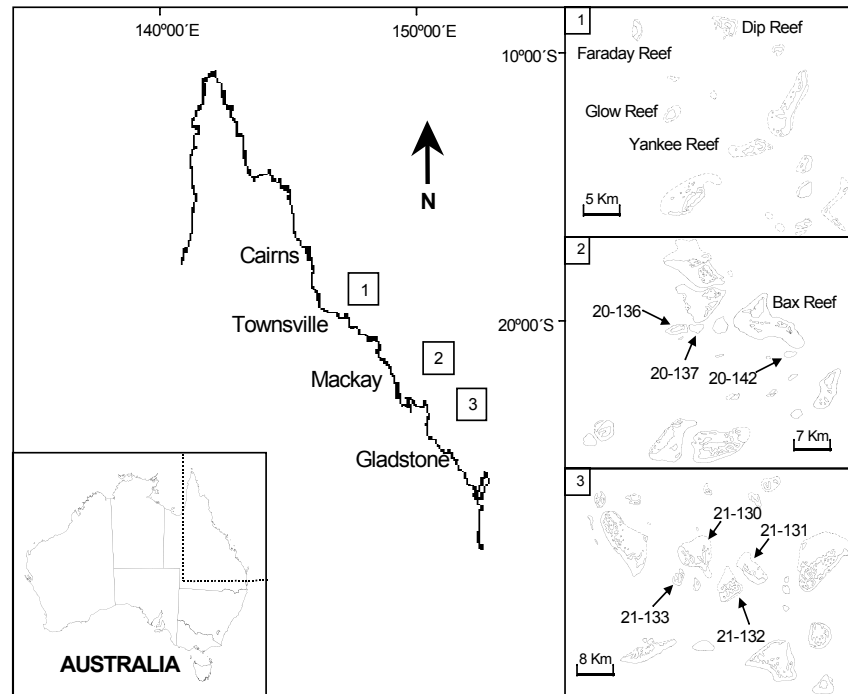


Figure 1

Location of reefs sampled for *L. miniatus* from October 1995 to January 1996 in the 1) Townsville, 2) Mackay, and 3) Storm Cay regions of the Great Barrier Reef, Australia. Reefs maps indicate the relative position of the four reefs closed to fishing that were sampled in regions 1, 2, and 3.

open to line and spear fishing (referred to as “open reefs”). Fishing had been prohibited from the closed reefs for at least seven years prior to sampling. Each reef was sampled for two days by the same four commercial line fishermen using gear and sampling designs standardized across all reefs (Davies et al.⁵). Fork length (FL) was measured to the nearest millimetre immediately upon capture. Sagittal otoliths were removed from frozen frames in the laboratory, cleaned of any residual material, dried, and weighed to the nearest 0.1 mg.

A total of 1015 *L. miniatus* were collected from the four closed reefs in each region between October 1995 and January 1996. Sample sizes from the open reefs were small and mortality and growth estimates from these reefs were unreliable. Therefore, these samples were used only to increase the sample size of older fish for a comparison of the two methods for reading otoliths (whole and sectioned).

Comparison of otolith reading methods

The annual periodicity of opaque increment formation in *L. miniatus* otoliths has been validated (Brown and Sumpton 1998). A subsample of 355 *L. miniatus* otoliths from both open and closed reefs was used to assess whether readings of whole otoliths provided age estimates similar to those from sectioned otoliths, but at substantially lower cost (in time). Otolith weight was used to select a broad range of age classes for this assessment on the assumption that

otolith weight was a coarse indicator of age, thus avoiding the need to preread otoliths to obtain a sample covering all age classes. Each otolith in the subsample was read, both whole and sectioned, on three separate occasions in random order with no prior knowledge of collection date, location, or fish size. For consistency, the right otolith was chosen to estimate the age of all fish unless it was missing or damaged, in which case the left one was used. Otoliths to be read whole were placed in a small black dish of immersion oil and examined under reflected light with a stereo dissecting microscope. Counts of opaque increments were made from the nucleus to the dorsoposterior edge on the convex face of the otolith. For otoliths from older fish it was necessary to rotate the otolith approximately 45° to clearly observe increments on the otolith margin.

Otoliths to be sectioned were embedded in epoxy resin and cut transversely, adjacent to the anterior side of the nucleus with a Buehler Isomet low-speed saw. The posterior portion of the otolith was retained and mounted on a glass microscope slide with Crystalbond adhesive. A second transverse cut adjacent to the posterior side of the nucleus resulted in a thin section, incorporating the otolith nucleus, remaining on the slide. Otolith sections were then ground on 800- and 1200-grade sandpaper to remove saw marks and a single drop of immersion oil was placed on sections to fill surface irregularities. Otolith sections were examined under a stereo dissecting microscope with reflected light and a black background. Counts of opaque increments were

made from the nucleus to the proximal surface, along the dorsal margin of the sulcus acousticus.

The precision of age estimates from whole and sectioned otoliths was calculated by using the index of average percent error (Beamish and Fournier 1981). The estimates of age from whole and sectioned otoliths were compared by a paired *t*-test. Difference in bias between the two reading methods was observed by plotting the difference between the two readings (sectioned age minus whole age) against sectioned age, based on the assumption that sectioned age provided the best estimate of true age (Beamish 1979). The results from this comparison indicated no significant difference between whole and sectioned otolith readings and there was no discernible difference in bias in the plot. As a result, all remaining otoliths were read whole for greater efficiency. Age estimates from whole otoliths were accepted and used in subsequent analyses when counts from the first two readings agreed. If the counts differed, otoliths were read a third time. The otolith was excluded from subsequent analyses if no two counts agreed, but included if any two counts agreed.

Comparison of demographic parameters

The central objective of this study was to estimate the variation in demographic parameters of *L. miniatus*, specifically otolith and somatic growth rates, age structure, and mortality, at different spatial scales. In the first instance, parameters were compared among the four reefs within each region to estimate the magnitude of variation at the inter-reef scale. Data were then pooled from individual reefs within each region to generate regional parameter estimates, which were used to estimate the magnitude of variation at the regional spatial scale.

The relationship between otolith weight and age (representing otolith growth) was examined for each reef by least-squares regression analysis, with otolith weight as the dependent variable. The relationship was compared among reefs within each region and among regions by using analysis of covariance (ANCOVA).

Reef-specific age-frequency distributions were constructed for all reefs. Multidimensional contingency tables were used to compare age frequencies among reefs within regions and among regions. Age classes 4 years and younger and age classes 10 years and older were pooled into 4 and 10+ age classes, respectively, because of low frequencies in the tails of the age distributions. As a result, the analyses included a total of seven age classes.

Age-based catch curves (Ricker, 1975) were used to estimate the instantaneous rate of total mortality (*Z*) at each reef expressed on an annual basis. The 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. As a result, the age range used to estimate mortality varied slightly among reefs. Mortality rates were compared among reefs within regions and among regions by using ANCOVA.

The von Bertalanffy growth function (VBGF) provided the best fit to length-at-age data for most reefs according to the parameter estimates of the Schnute (1981) growth function. For consistency, and to enable spatial comparisons of growth, the VBGF was used to estimate growth parameters for each reef and region:

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

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

It was difficult to obtain a reliable estimate of initial growth because the youngest fish collected was 2 years old. There are also no published size-at-age data for larval or juvenile *L. miniatus*, or any other letrhinid. We constrained the VBGF parameter t_0 to zero to provide a better description of the likely early growth of *L. miniatus*. This procedure also allowed growth curves to be compared among reefs within regions and among regions by using 95% confidence regions of the VBGF parameters L_∞ and K described by Kimura (1980).

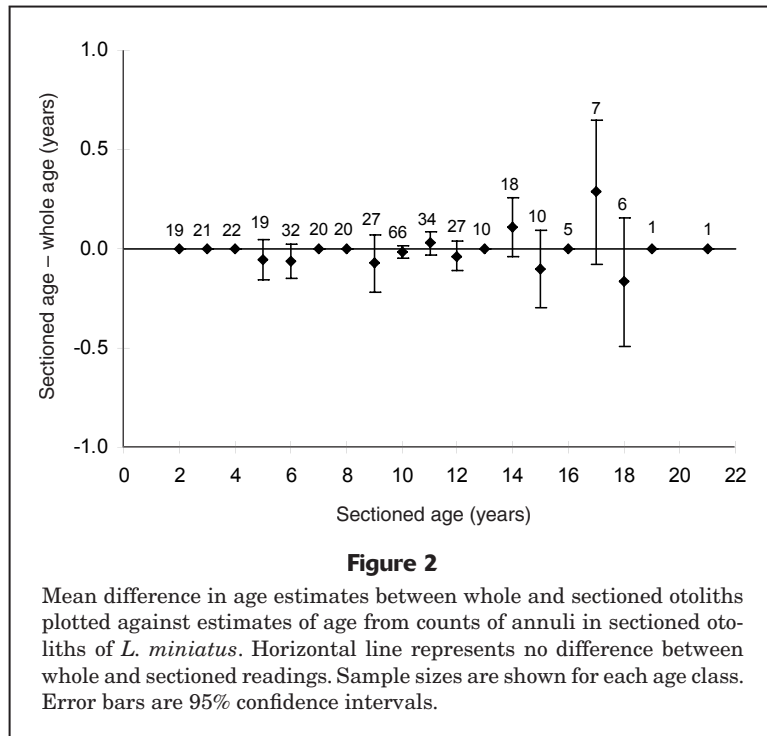
Results

Comparison of otolith reading methods

Age estimates from whole and sectioned otoliths did not vary significantly over the range of ages between 2 and 21 years ($t_{0.05, 2, 354} = 0.46$, $P = 0.73$). That is, for each age class estimated from sectioned otoliths, the average difference between whole and sectioned otolith readings did not differ significantly from zero (Fig. 2). The index of average percent error was very low for whole (1.6%) and sectioned (1.4%) otolith readings, indicating that otolith readings for both methods were highly repeatable. This low index was reflected in the agreement of at least two age estimates for all whole otoliths, and hence no otoliths were excluded from analyses.

Otolith growth

There was a significant positive linear relationship between otolith weight and age for all reefs, with regression coefficients ranging from 0.64 to 0.90. ANCOVA revealed that the slope of this relationship was not significantly different among reefs within each region (Townsville: $F_{3,328} = 1.91$, $P = 0.13$; Mackay: $F_{3,341} = 1.02$, $P = 0.38$; Storm Cay: $F_{3,267} = 1.55$, $P = 0.20$). Thus, otolith weight and age data were pooled for each region to compare the region-specific relationships between otolith weight and age (Fig. 3). The slopes of the region-specific relationships differed significantly among all regions ($F_{2,946} = 28.9$, $P < 0.001$). The average growth in otolith weight was greater in the Mackay region (26.91 mg/yr) than in the Storm Cay region (24.48 mg/yr), and was least in the Townsville region (19.50 mg/yr).

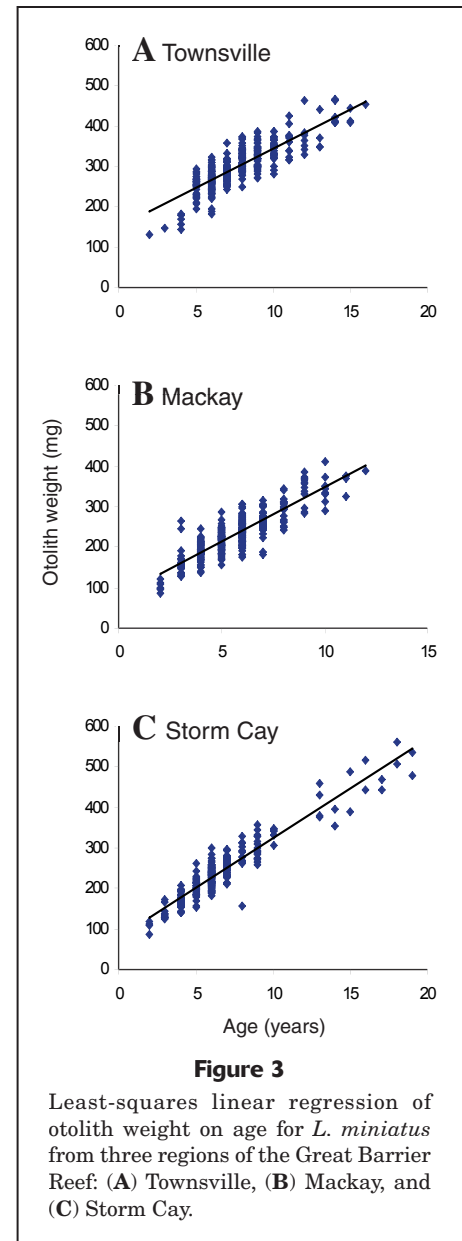


Age structure

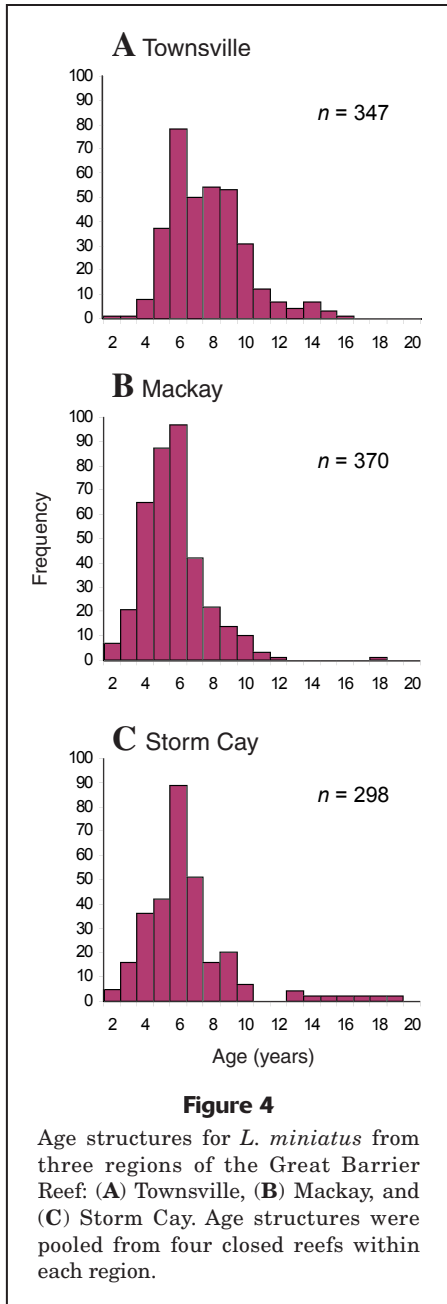
The youngest fish sampled from any reef was two years of age, suggesting that *L. miniatus* becomes vulnerable to standard line fishing gear at this age. All age-frequency distributions for individual reefs were unimodal and the most common mode was 6 years of age. This age is thus assumed to represent the age at which *L. miniatus* is fully recruited to the sampling gear. The relative frequencies of the seven age classes 4 to 10+ were not significantly different among reefs within each region (Townsville: $\chi^2=23.59$, $P=0.17$; Mackay: $\chi^2=27.97$, $P=0.06$; Storm Cay: $\chi^2=20.29$, $P=0.32$). As a result, age structures from individual reefs were pooled for each region (Fig. 4) and multidimensional contingency tables were used to test for regional differences in age structures. The relative frequencies of the seven age classes were significantly different among all three regions (all regions: $\chi^2=193.31$, $P<0.0001$, Townsville vs. Mackay: $\chi^2=172.70$, $P<0.0001$; Townsville vs. Storm Cay: $\chi^2=91.88$, $P<0.0001$; Mackay vs. Storm Cay: $\chi^2=22.27$, $P=0.001$). The most obvious difference among regions was the greater relative abundance of older fish (>6 years) in the Townsville region than in the Mackay and Storm Cay regions (Fig. 4). However the oldest fish were from the Storm Cay region, where a small number of fish persisted in the older age-classes up to 19 years of age. The relative abundances of age classes 4 and 5 were greater in the Mackay region than in the Townsville and Storm Cay regions (Fig. 4).

Mortality

Estimates of annual total mortality rates (Z) for individual reefs were generally similar among reefs within each

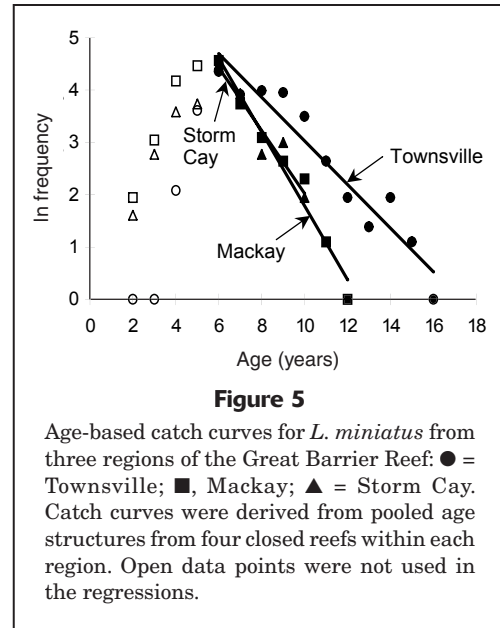


region, with the exception of the Storm Cay region where the estimated Z appeared much lower for reef 21-131 than for other reefs in that region (Table 1). ANCOVA indicated no significant difference in mortality among reefs in any region (Townsville: $F_{3,30}=0.80$, $P=0.50$; Mackay: $F_{3,20}=0.08$, $P=0.97$; Storm Cay: $F_{3,15}=1.14$, $P=0.37$). Therefore mortality rates were estimated for each region from the pooled age structures for all reefs within each region (Fig. 5). A comparison among regions of the regression slopes from the pooled age structures indicated significant differences among regions ($F_{2,18}=7.11$, $P=0.005$). Tukey's multiple comparison tests revealed that the estimated Z for the Townsville ($Z=0.42$) and Mackay ($Z=0.71$) regions differed significantly, whereas the estimate from the Storm Cay region ($Z=0.60$) did not differ significantly from either Townsville or Mackay.



Somatic growth

Estimates of VBGF parameters varied considerably among reefs within the Townsville and Mackay regions but in the Storm Cay region, estimates of L_{∞} and particularly K were very similar (Table 1). Examination of 95% confidence regions for VBGF parameters for individual reefs (Fig. 6) indicated considerable uncertainty in the estimates of both K and L_{∞} and no clear differentiation among reefs within regions. The similarity in VBGF parameters for individual reefs within the Storm Cay region was particularly evident from the 95% confidence regions. In both the Townsville and Mackay regions, three reefs showed overlap in 95%



confidence regions, whereas only a single reef in each region appeared to have significantly different VBGF parameters from the others (Fig. 6).

Given the lack of differentiation in growth among reefs, the data from individual reefs were pooled for each region to examine regional patterns in growth. VBGF parameters varied significantly among regions (Table 1) with no overlap in the 95% confidence regions (Fig. 7). It appeared that *L. miniatus* in the Mackay region attained a larger average asymptotic size ($L_{\infty}=472.21$ mm FL) than in the Storm Cay region ($L_{\infty}=462.83$ mm FL), where in turn these fish grew larger than fish in the Townsville region ($L_{\infty}=453.36$ mm FL). It should be noted that the constrained fitting of the VBGF (t_0 set to zero) provided a conservative estimate of regional variation in growth, and regional differences were considerably larger when the VBGF parameter t_0 was not constrained to zero.

Discussion

The scale of spatial variation in demography of a large, potentially more mobile reef fish was found to be larger than that reported for smaller site-attached reef-fish species on the GBR. Estimates of otolith and somatic growth, age structure, and mortality of *L. miniatus* all varied more among regions than among reefs within regions. Furthermore, with the exception of mortality estimates, which differed only between the Townsville and Mackay regions, all estimated parameters were significantly different among all three regions. Despite their relative proximity, the Townsville and Mackay regions consistently showed the greatest difference for each demographic parameter. This indicates that the observed differences did not relate simply to a linear latitudinal gradient among the regions.

Table 1

Total mortality (Z) and von Bertalanffy growth parameters for *L. miniatus* collected from four reefs within three regions of the Great Barrier Reef. The von Bertalanffy growth parameter t_0 was constrained to zero for all reefs.

Region	Reef	n	Mortality			Growth	
			Age range (years)	Z	r^2	L_∞ (mm)	K
Townsville	Glow	110	6-14	0.30	0.74	456.21	0.48
	Dip	90	6-15	0.40	0.89	445.77	0.60
	Yankee	96	6-16	0.31	0.86	462.44	0.40
	Faraday	51	6-11	0.29	0.90	442.26	0.59
	Pooled	347	6-16	0.42	0.92	453.36	0.48
Mackay	20-136	92	6-11	0.47	0.93	488.87	0.41
	20-137	93	5-11	0.52	0.97	481.68	0.42
	20-142	92	5-10	0.54	0.67	446.28	0.47
	Bax	93	6-12	0.55	0.85	450.78	0.55
	Pooled	370	6-12	0.71	0.97	472.21	0.43
Storm Cay	21-130	70	6-10	0.76	0.93	466.76	0.38
	21-131	78	6-10	0.43	0.92	463.03	0.39
	21-132	81	6-10	0.66	0.69	453.44	0.38
	21-133	69	6-10	0.77	0.99	467.44	0.38
	Pooled	298	6-10	0.60	0.91	462.83	0.38

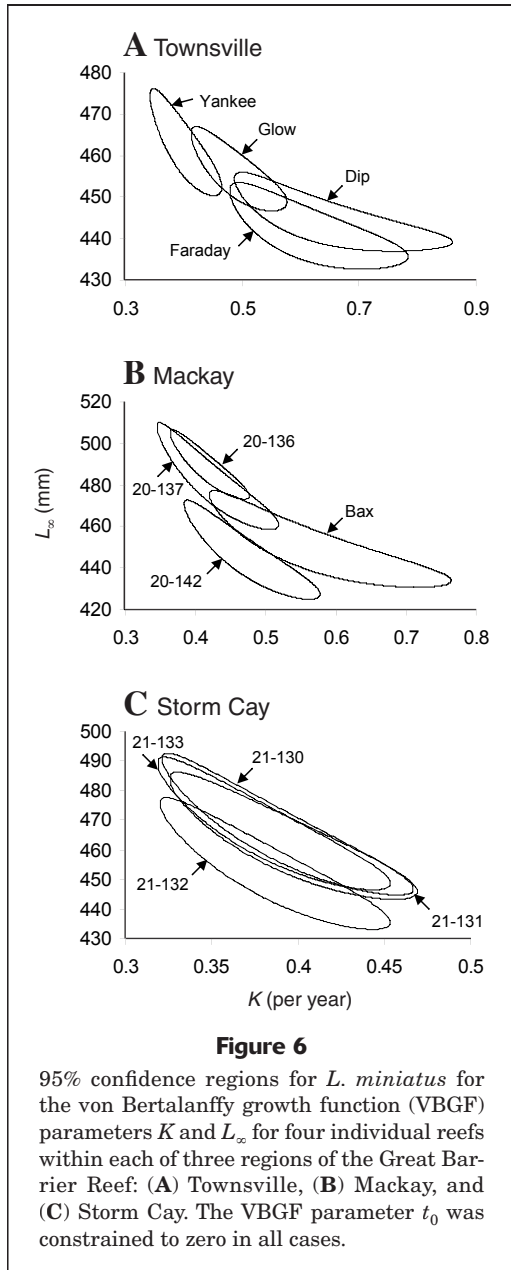
The homogeneity of demographic parameters among reefs within regions presented here is not consistent with a number of studies of other reef fish species on the GBR (e.g. Doherty and Fowler, 1994; Hart and Russ, 1996; Newman et al., 1996). These other studies demonstrated significant differences in age structures, somatic growth, mortality, and otolith growth among individual reefs within a single geographic region for several smaller reef-associated lutjanid, acanthurid and pomacentrid species. The consistency of demographic parameters among reefs within regions found in the present study is consistent with an hypothesis that *L. miniatus* may move over larger distances than “typical” coral-reef fish, including being capable of movements among reefs within a region. There are limited direct data on the movement of *L. miniatus*, and lehrinids in general, or about the range of habitats they occupy. However, *L. miniatus* is frequently found on shoal grounds between reefs and to depths of at least 128 m (Newman and Williams, 1996), suggesting a strong potential for *L. miniatus* to move among reefs. Movements of adults among coral reefs would suggest that *L. miniatus* does not fit the typical metapopulation model for coral-reef fish, in which adults are confined to a single coral reef, and the pelagic larval stage is the only means of dispersal among reefs. Accordingly, differences in conditions among neighboring reefs would be less likely to be manifest in demographic parameters of *L. miniatus* than in the demographic parameters of more sedentary species that inhabit only a single reef for their postsettlement life.

Using microsatellite markers, van Herwerden et al. (in press) examined the genetic structure of *L. miniatus* populations on the GBR. They sampled from two reefs within the Townsville (Dip and Glow) and Mackay (Bax

and 20-137) regions in addition to two other reefs in the far southern GBR (Sweetlip and Sandshoe). They found no evidence of stock structure for *L. miniatus* populations on the GBR indicating that the regional patterns in demographic parameters of *L. miniatus* are not a result of distinct genetic stocks. This is consistent with other genetic studies that have demonstrated a lack of genetic structuring of coral-reef fishes over large spatial scales of hundreds to thousands of kilometers (Doherty et al., 1995; Shulman and Bermingham, 1995; Dudgeon et al., 2000).

The observed regional variation in demography may be the result of regional differences in postsettlement processes, such as competition (Jones, 1987), food and habitat availability (Hart and Russ, 1996), population density (Doherty, 1983), and water temperature (Conover, 1992). Alternatively, the regional variation in demography may have resulted from regional variation in recruitment, coupled with density dependent processes (Doherty and Fowler, 1994), or the factors that influence larval survival and settlement. Unfortunately data for these processes for *L. miniatus* are at best limited, restricting any conclusion on the causative factor(s) driving the observed regional patterns. However, because demographic parameters for *L. miniatus* do not show a linear trend with latitude, factors such as water temperature, which have strong latitudinal gradients on the GBR (Lough, 1994), are unlikely to independently explain the observed differences. Meekan et al. (2001) also found that temperature did not appear to be a causal factor driving spatial differences in demography of damselfishes in the tropical eastern Pacific Ocean.

Estimates of numerical density of *L. miniatus* on the GBR are greater in the southern regions (Mackay and Storm Cay) than on reefs in the Townsville region (Wil-



liams and Russ³). Under the assumptions that demographic parameters are density dependent, and densities are high enough for density-dependent effects to operate, the spatial pattern in densities is consistent with the observed patterns in age structures and mortality. However, the observed patterns in growth are inconsistent with the expected pattern, if density dependence was the dominant influencing mechanism. We would not expect *L. miniatus* to reach a larger size in the southern regions, where densities are higher, compared with the Townsville region, where densities are lower, unless conditions were more favourable in the southern regions. It would be necessary to invoke another mechanism, such as regional differences in food availability, acting in combination with density depen-

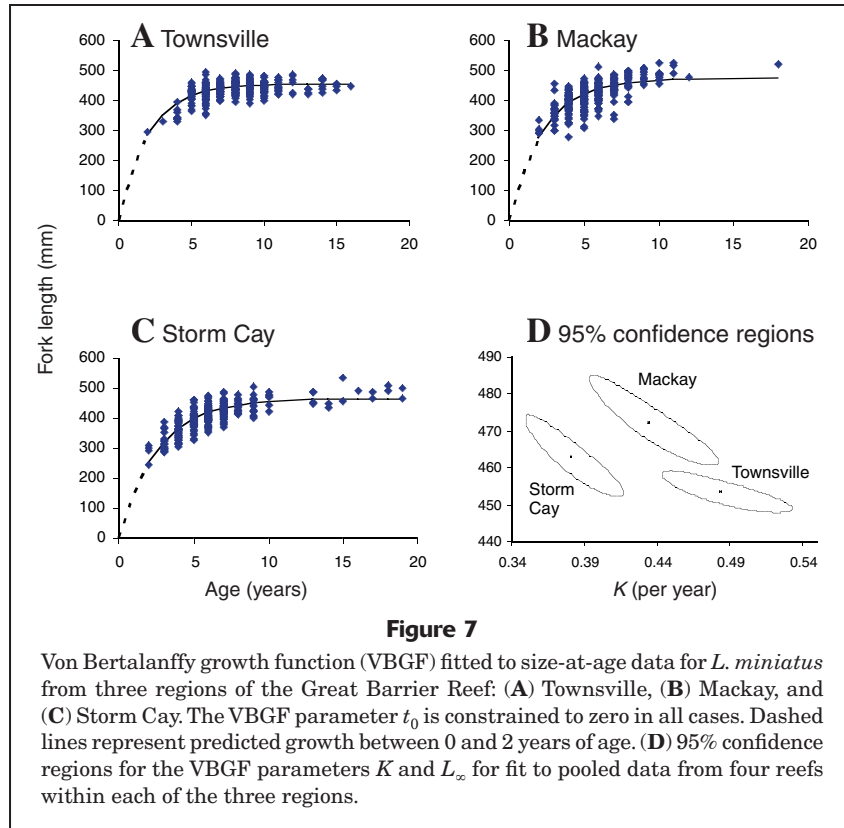
dence, to explain the overall pattern of growth, mortality, and age structure.

The likelihood that the observed regional variation is due to a response to regional differences in historic (1960s–1980s) fishing pressure bears consideration. *L. miniatus* are vulnerable to standard line fishing gear from approximately two years of age and are fully recruited to the line fishing gear by six years of age. The reefs in this study had been closed to fishing for seven years prior to sampling. Consequently, all cohorts older than 9 years of age could have been fished prior to the reef closures in 1988, and before the availability of spatially referenced catch and effort data for the commercial fishery. Anecdotal evidence on the development of the fishery and its operation suggests that it developed from the southern ports of Gladstone and Mackay (Fig. 1), which have remained the dominant commercial line fishing ports in the fishery (Mapstone et al.¹). It seems plausible, therefore, that potentially higher historic fishing effort in the southern two regions could have modified the population structure of *L. miniatus* sufficiently to produce significant differences in demography. Given the longevity of the species, it is also plausible that current differences in the populations are the result of lagged recovery following the closure of the reefs to fishing.

Brown and Sumpton (1998) found small differences in growth rates, and significantly different total mortality rates, between populations of *L. miniatus* in the Swain Reefs and those in the Capricorn-Bunker regions of the southern GBR (separated by $\sim 1^\circ$ latitude). They attributed the difference in growth estimates to the selectivity of the gear used to obtain samples and to the different mortality rates to differences in fishing pressure between the two regions. They dismissed the possibility that these differences were a result of separate populations with different dynamics. However it is difficult to separate the confounding effects of regional differences in fishing pressure and gear selectivity in sampling; thus variation in growth and mortality between the Swain Reefs and Capricorn Bunker region cannot be dismissed.

The consistency in demographic parameters among reefs within each region suggests that populations of *L. miniatus* may be well mixed at the spatial scale of reef clusters and that any influence of environment on demographics is relatively uniform among reefs within regions. This uniformity may be facilitated by movement of adults among reefs, or by recruitment and postsettlement processes that are relatively uniform within regions. With significant movement of adults among reefs, the benefits of protection from individual reef closures may be limited, depending on the rate of exchange between open and closed reefs, and the level of fishing mortality on open reefs (Russ et al., 1992; DeMartini, 1993; Walters and Bonfil, 1999). In such a scenario, any historical effects of differences in fishing effort among regions would be perpetuated, even though individual reefs were closed to fishing.

In this study whole otoliths of *L. miniatus* provided similar age estimates to those from sectioned otoliths and thus offered a much faster alternative for age estimation for this species, without any apparent loss of precision or



accuracy in relation to those estimated from sectioned otoliths. In contrast, Brown and Sumpton (1998) concluded that whole otoliths from larger and presumably older *L. miniatus* underestimated age by up to 40% with respect to sectioned otoliths. The discrepancy between studies may be due to differences in the techniques used to count increments in whole otoliths. It was noted early in the present study that otoliths from older fish needed to be rotated to reveal a number of increments close to the otolith margin. By not using this technique Brown and Sumpton (1998) may have underestimated ages from whole otoliths of older fish. Readings from whole otoliths have been shown to consistently underestimate the age of a number of reef fish species (e.g. Ferreira and Russ, 1994; Newman et al., 2000) resulting in biased estimates of mortality and subsequent yield estimates (Newman et al., 2000). The results from this study suggest that whole otoliths are adequate for estimating the age of *L. miniatus* and that estimates of demographic parameters presented in the present study were not biased by underestimates of age.

The spatial patterns in the demography of *L. miniatus* described in the present study are based on data collected from a single survey in one year, thus leaving the temporal stability of the patterns open to question. Continued monitoring of the populations will be required to determine the stability of the patterns, and focussed stock structure studies are required to determine the most likely causal mechanism(s) of the patterns. Notwithstanding the need for this work, the significant regional differences in demographic parameters

found in the present study suggest different levels of productivity of *L. miniatus* populations in each region. Consequently, there is the potential for less productive populations to be overfished, even where the fishing effort for the stock as a whole is managed at sustainable levels (Caddy, 1975; Sheperd and Brown, 1993). This argues for assessments and management of *L. miniatus* stocks to explicitly consider the regional structure in demography in order to meet both sustainable use and conservation objectives for the Great Barrier Reef World Heritage Area overall and on a regional basis. Furthermore, this study highlights a more general need for the use of multiscale sampling and analyses of fish populations to understand the relative importance of the processes affecting demographic parameters, and the scales at which these processes operate.

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