

Inter-oceanic analysis of demographic variation in a widely distributed Indo-Pacific coral reef fish

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ABSTRACT: The surgeonfish *Ctenochaetus striatus* is abundant and widely distributed on reefs throughout the Indian and Pacific Oceans. Population samples at 15 sites that spanned 158° of longitude and 40° of latitude across both hemispheres of the Indian and Pacific oceans allowed us to examine geographic variation in longevity, growth rate and adult size of this species. Samples from 5 sites in the Indian Ocean, 6 in the western Pacific and 4 in the central Pacific provided otolith-based estimates of size-at-age for 1537 individuals. All populations displayed rapid growth to a distinct asymptotic size, a pattern characteristic of many acanthuroid fishes. In both oceans, fish lived longer at higher latitudes; in addition, Indian Ocean populations tended to be shorter-lived than those in the Pacific Ocean. In contrast, growth rate and adult size did not differ between the 2 oceans, and were not related to temperature (as a proxy for latitude) in either the Pacific or the Indian Ocean. Further, we found no relationship between fishing pressure and longevity, growth or adult size across our set of sampling sites, among which fishing pressure on this species varied from intense to zero. We hypothesize that (1) growth and adult size are most responsive to local environmental features unrelated to latitudinal (temperature) effects; and (2) variation in longevity reflects a combination of responses to latitudinal (temperature) gradients and as yet unidentified environmental differences between the Indian and Pacific oceans.

KEY WORDS: Longitudinal and latitudinal gradients · Longevity · Body size · Growth rate · Asymptotic growth · Coral reef fish · Acanthuridae

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INTRODUCTION

Coral reef fishes display substantial demographic variation over their distributional ranges. This is most obvious in body size, growth rates and age structure. Demographic variation occurs at a number of scales ranging from different habitats of the same reef system (Choat & Axe 1996, Gust et al. 2002, Robertson et al. 2005a), to geographic trends manifested over thousands of kilometers (Robertson et al. 2005a). Establishing the causes of demographic variation is a challeng-

ing task, as 4 sources of variation will all play a part: the physical environment, biological assemblages, evolutionary histories of reef habitats and human impacts. Sampling over latitudinal gradients, where trends in temperature are associated with predictable patterns of demographic variation in many organisms, is a useful starting point.

Increasing body size with latitude has been recorded for both temperate (Yamahira & Conover 2002) and tropical fish species (Meekan et al. 2001, Choat et al. 2003, Robertson et al. 2005a, Ruttenberg et al. 2005).

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This conforms to a general relationship between body size and temperature in ectotherms (Ashton & Feldman 2003, Kingsolver & Huey 2008). Somatic growth rates may also be sensitive to differences in temperature. An example is provided by counter-gradient growth patterns in which individuals at higher latitudes grow faster than those at lower latitudes (Conover 1990, Conover & Present 1990). However, there are still relatively few examples of examinations of systematic trends in body size and growth rates in tropical fishes, even though their distributions make them ideal subjects for such studies.

In a comprehensive analysis of demographic variation in the Caribbean coral reef fish *Acanthurus bahianus*, Robertson et al. (2005a) identified 3 major demographic trends over a latitudinal gradient of 5500 km. Size, growth rate and longevity all displayed a positive relationship with latitude (temperature), with the strongest effect seen on the distribution of maximum life spans. However, these authors also identified pronounced local scale (habitat) variation in size and growth of *A. bahianus*, and concluded that this was a pervasive aspect of reef fish demography that required standardized sampling of habitats in comparative analyses. The configuration of reef systems within the tropical Atlantic allowed sampling of *A. bahianus* within a relatively narrow longitudinal range, and permitted demographic analyses without the confounding effects of divergent reef and ocean histories that may be associated with inter-ocean comparisons.

In contrast to those in the Atlantic, Indo-Pacific reefs extend over a longitudinal range of 20000 km and 2 ocean basins. Although latitudinal gradients of similar magnitude to that in the *Acanthurus bahianus* study can be accessed in the Indo-Pacific, sampling must also incorporate the longitudinal component of species distribution. Sampling Indo-Pacific taxa at large geographic scales raises 2 problems. While latitudinal sampling across systematic gradients in temperature allows interpretation of demographic trends in the context of a well established body of observational and experimental data (Kingsolver & Huey 2008), longitudinal sampling can incorporate different ocean basins with distinct evolutionary histories, regional oceanographic environments and geographical patterns of reef distribution. How this will impact on demographic variables is presently unclear. In addition, different patterns of reef distribution in each ocean basin make it difficult to achieve balanced geographic sampling with respect to latitudinal and longitudinal sources of variation. Consequently, the sampling program for the present study was exploratory, and designed to facilitate the development of more informative hypotheses concerning broad-scale demographic variation in Indo-Pacific reef fishes.

The present study evaluates patterns of demographic variation in a widely distributed Indo-Pacific reef fish over significant latitudinal and longitudinal gradients. The target species, the surgeonfish *Ctenochaetus striatus* (Quoy and Gaimard), has a wide distribution extending across ~190° of longitude from the Red Sea and the eastern coast of Africa (~29° E) to the central Pacific region (~140° W), and across 60° of latitude from 26° N to 34° S (Randall & Clements 2001). A number of demographic variables can be extracted from sectioned sagittal otoliths of this species, for which the annular nature of growth-increment formation has been validated (Choat & Axe 1996). Preliminary information indicates variation in size structure and maximum ages among localities in this species (Choat & Axe 1996, Choat & Robertson 2002).

We examined demographic traits (size, growth rate and longevity) of this species over a gradient spanning 20° of latitude across both oceans, to determine (1) the nature of the relationship between temperature, somatic size and growth rates; and (2) whether there was a positive relationship between latitude and life span, as is seen in tropical Atlantic *Acanthurus*. In addition, we sampled across 158° of longitude (17360 km) in both the Indian and Pacific oceans to explore the magnitude and pattern of demographic variation within a species whose range spans much of both ocean basins that constitute the Indo-Pacific reef system.

MATERIALS AND METHODS

Data collection. Samples were collected in the western, northern and central Indian Ocean, and the western and central South Pacific Ocean. At all but one site, sampling was standardized by habitat with fish collected from the crests and outer slopes of reefs. The exception was Samoa, where all samples were collected in back reef habitats. In the Indian Ocean, fish were sampled on the reefs fringing the granitic northern islands of the Seychelles (55° 4' E, 4° 3' S), the coral reefs of the Amirantes Island group (53° 1' E, 6° S, 230 to 1150 km southwest of the Seychelles), the Al Halaaniyaat Islands off the south coast of Oman (56° E, 17° 3' N), which are in a productive upwelling region supporting a mixture of rocky, algal and coral reefs, and at the Cocos Keeling Islands (96° 5' E, 12° 3' S) in the eastern Indian Ocean. At Cocos Keeling, independent samples were collected in 2 habitats: (1) the lagoon and (2) the reef crest. In the western South Pacific Ocean, samples were collected from Papua New Guinea (PNG) in Kavieng (152° 5' E, 3° 7' S) and in Kimbe Bay (151° E, 5° S), and along the Great Barrier Reef, Australia (GBR) from Lizard Island at the northern end of the GBR (145° 3' E, 14° 4' S), from the mid-

shelf reefs off Townsville in the central GBR ($146^{\circ} 5' E$, $19^{\circ} 1' S$), and from One Tree Island at the southern end of the GBR ($152^{\circ} 3' E$, $23^{\circ} 4' S$). At Lizard Island 2 independent samples were collected on reefs separated by an average distance of 20 km: (1) on the fringing reef fronts surrounding Lizard Island and (2) on the exposed reef fronts of 3 reefs on the outer shelf (No Name, Day and Hicks reefs). In the central South Pacific Ocean, samples were collected in American Samoa from the fringing coral reefs of Ofu-Olosega, Ta'u and Tutuila Islands ($170^{\circ} W$, $14^{\circ} 2' S$), and in Moorea in French Polynesia ($149^{\circ} 6' W$, $17^{\circ} 5' S$). Sampling locations are shown in Fig. 1.

A total of 1537 individuals of *Ctenochaetus striatus* were speared on scuba and snorkel. On collection, individuals were either processed immediately or placed in an ice-slurry until return to the laboratory for processing on the same day. For each individual, fork length (FL) was measured to the nearest mm. The sagittal pair of otoliths was removed following sectioning of the skull, cleaned and stored dry in lidded 96-well trays.

Otolith preparation and determination of age. All age estimates were based on sectioned sagittal otoliths. The annual pattern of increment formation has been validated for a number of acanthurid species,

including *Ctenochaetus striatus* (Choat & Axe 1996). Daily ring formation has been previously validated for juvenile acanthurids of the same genus (*Ctenochaetus binotatus*, Lou & Moltschanivskyj 1992).

One sagitta of each pair of otoliths was chosen randomly and weighed to the nearest 0.1 mg for adults, and to the nearest 0.01 mg for juveniles. These weights were used to establish the relationship between otolith weight and age. Site-specific regressions of otolith weight on age allowed rapid checking of the precision of reading of the number of annuli and daily increments (Boehlert 1985). A transverse section was obtained by grinding down both rostral and distal ends of the otolith using wet and dry sandpaper or lapping film, resulting in a thin section containing the nucleus. Each section was then covered with clear Crystalbond thermoplastic cement (Aremco) for reading. Annual increments were counted under a stereo dissector, and daily rings under a high-power microscope. Age was estimated as the mean of 3 separate readings provided that the 3 counts did not differ by more than 10%. When readings deviated by more than 10%, the second otolith was processed when available, or else the individual was not included in the age-based analyses. All otolith-increment readings were performed by E. L. Trip.

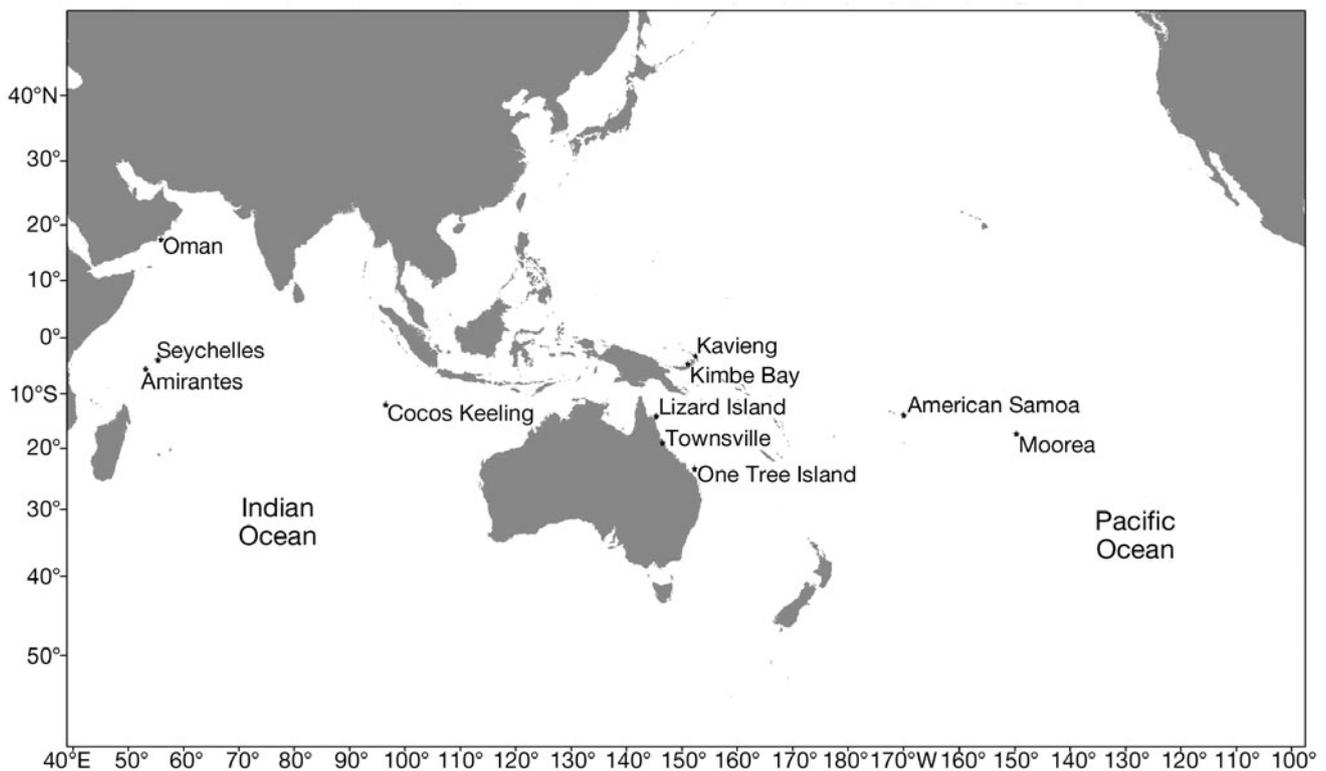


Fig. 1. Sampling locations of *Ctenochaetus striatus* across the Indo-Pacific region. Two independent samples were collected at Cocos Keeling and Lizard Island, and 3 islands were sampled separately in American Samoa (Tutuila, Ta'u and Ofu-Olosega)

Modelling of somatic growth and estimation of growth rate. Comparing growth trajectories between populations—limitations of the VBGF equation:

Growth in fish is traditionally described using the generalized equation of the von Bertalanffy growth function (VBGF), which adequately describes growth in fish (Cerrato 1990, Chen et al. 1992). The generalised VBGF equation is as follows:

$$L(t) = L_{\infty} \{1 - \exp[-K(t - t_0)]\} \quad (1)$$

where $L(t)$ is estimated mean size-at-age t , L_{∞} is mean asymptotic size, K is a curvature parameter and t_0 is the age at which the fish have a theoretical size of zero. However, the biological interpretation of the VBGF parameters L_{∞} , K and t_0 has often been questioned, and many uncertainties have been raised as to the statistical properties of the parameters when comparing them between populations (Knight 1968, Roff 1980, Ratkowsky 1986, Moreau 1987, Cerrato 1991, Mulligan & Leaman 1992, Craig 1999). Additionally, the curvature parameter K is not a true growth rate (Cerrato 1991): K is a measure, as a reciprocal of time, of the time taken before the asymptote is (or would be) reached, and a high value of K does not necessarily imply a high rate of growth. These limitations to the VBGF equation were of primary concern for 2 key aspects of the present study: the assessment of early somatic growth, and the statistical comparison of demographic parameters among populations. Therefore, the VBGF equation was re-parameterized after Francis (1988), Moulton et al. (1992), Ewing (2003), and Welsford & Lyle (2005).

Re-parameterized version of the VBGF equation:

The re-parameterized version of the VBGF equation (rVBGF) describes growth in a similar fashion as the traditional VBGF, and is based on 3 parameters, $L(\tau)$, $L(\omega)$ and $L(\mu)$, which express expected average body size at 3 arbitrary ages τ , ω and μ . As a result, the biological significance of the parameters allows for a direct comparison of mean size-at-age data between populations. Ages τ and μ are chosen arbitrarily within the range of the dataset so as to represent the general form of growth, and ω is determined by the average age of τ and μ . The re-parameterized equation of the VBGF is as follows:

$$L(t) = L(\tau) + \frac{(L(\mu) - L(\tau)) \left[1 - r \left(2 \frac{t - \tau}{\mu - \tau} \right) \right]}{1 - r^2} \quad (2)$$

where $r = \frac{L(\mu) - L(\omega)}{L(\omega) - L(\tau)}$, and $L(t)$ is the average size-at-age t to be predicted by the model, provided that $L(\tau) < L(\omega) < L(\mu)$ and $(L(\mu) - L(\omega)) \neq (L(\omega) - L(\tau))$, limitations that affect both the generalised and the re-parameterized VBGF.

Ctenochaetus striatus is characterized by rapid growth in the first year, followed by attainment of asymptotic size by the fifth year in all populations examined to date. In order to compare growth of the study species across geographical scales and locations, 2 key points along the growth trajectory were selected. These were mean size achieved at the end of the first year of growth as an estimate of growth rate, and mean size achieved by year 5 as an estimate of adult body size. In the context of the rVBGF model, age τ was chosen as year 1, generating an estimate $L(1)$ of mean size-at-year 1, hereafter referred to as 'age-1 size' or $L(1)$; and age μ was set at 5 yr old generating an approximation for mean size-at-age 5, the asymptotic size for all populations, hereafter referred to as 'adult size' or $L(5)$. Age ω was then calculated to be 3 yr old. Thus, the parameters for the rVBGF model in the present study were $L(1)$, $L(3)$ and $L(5)$; however, we focused on the parameters $L(1)$ and $L(5)$.

The rVBGF model was fitted through the observed data of each sample, and the best-fit model describing each dataset was determined by minimizing the negative log of the likelihood given a probability density function with a Poisson distribution (Kimura 1980, Haddon 2001). For each sample, the rVBGF model was fitted by constraining the y-intercept of the curve to approximate size at settlement L_0 (Kritzer et al. 2001), with $L_0 = 47$ mm FL (based on estimates from Stobutzki & Bellwood 1997).

Estimation of longevity. Mean maximum age, mean T_{\max} , was calculated as the average age of the oldest 10% of individuals in each sampled population (modified from Choat & Robertson 2002).

Mean sea surface temperature. Mean sea surface temperature (SST, °C) was used to describe the latitudinal environmental gradient (see Table 1). SST was calculated based on long-term NOAA data from 1971 to 2000 (January to December) by estimating the average annual temperature observed at each location (www.cdc.noaa.gov/cgi-bin/DataAccess.pl?DB_dataset=NOAA+Extended+Reconstructed+SST&DB_variable=Sea+Surface+Temperature&DB_statistic=Long+Term+Mean&DB_tid=3955&DB_did=63&DB_vid=1294). Years were selected so as to cover the life spans of the longest lived individuals across all sampled populations.

Analysis of spatial variation in longevity, age-1 size and adult size. The latitudinal distribution and area of reef habitats differs substantially between the Indian and Pacific oceans (Spalding & Grenfell 1997). This confounded attempts to develop separate comparative analyses of demographic variation over geographically equivalent latitudinal gradients in each ocean basin. Therefore, a multiple regression analysis was used to detect trends in growth, size and longevity across the entire sampled range of the study species including

Table 1. Locations and demographic information of *Ctenochaetus striatus* populations sampled across the Indo-Pacific region. Habitat type, fishing pressure, mean SST (°C), sample size n, size range (Fork length, FL, mm), generalised (VBGF) and re-parameterized (rVBGF) von Bertalanffy growth parameters, mean maximum age (mean T_{max} in years) and maximum age (in years) are presented. See Appendix 2 for additional data on fishing. Total n = 1537

Ocean	Location	Habitat type	Fishing pressure	SST (°C)	n	Size range (FL, mm)	VBGF parameters			rVBGF parameters			Longevity	
							L_{∞}	K	t_0	L(1) (FL,mm)	L(5) (FL,mm)	Mean T_{max} (yr)	Max age (yr)	
Central South Pacific	Tutuila	Back reef	Heavy ^{a,c}	29.05	263	80–214	172	0.75	-0.4	114	169	17.9	34	
	Ta'u	Back reef	Heavy ^{a,c}	29.05	162	140–220	182	0.5	-0.6	100	171	16.8	26	
	Ofu-Olosega	Back reef	Heavy ^{a,c}	29.05	238	90–214	176	1.4	-0.2	153	175	17.6	36	
Western South Pacific	Moorea	Outer reef slope/crest	Light ^c	27.99	93	125–205	178	0.7	-0.4	121	175	18.3	21	
	Kavieng	Outer reef slope/crest	Light ^c	29.26	36	99–178	159	0.5	-0.7	92	150	10.2	17	
	Kimbe Bay	Outer reef slope/crest	Light ^{b,c}	29.27	119	33–158	128	0.6	-0.7	82	123	12.6	28	
Lizard Island	Back reef	Back reef	None	27.07	117	86–230	194	1.0	-0.3	143	193	17.8	37	
	Lizard Island outer reef	Outer reef slope/crest	None	27.07	80	133–202	171	0.9	-0.4	120	170	18.1	29	
	Townsville	Outer reef slope/crest	None	26.36	85	121–228	201	0.8	-0.3	133	198	26.7	32	
Indian Ocean	One Tree Island	Outer reef slope/crest	None	24.75	116	150–233	199	0.3	-0.8	92	173	26.6	34	
	Oman	Outer reef slope/crest	None	24.82	45	179–259	232	1.3	-0.2	180	232	12.5	28	
	Mahe Plateau, Seychelles	Outer reef slope/crest	Light ^c	28.19	36	177–238	205	2.1	-0.1	184	204	11.7	19	
Cocos Keeling lagoon	Amirantes, Seychelles	Outer reef slope/crest	Light ^c	28.32	72	107–209	185	1.1	-0.3	140	184	12.3	21	
	Cocos Keeling lagoon	Lagoon	None ^c	27.82	40	84–252	188	0.4	-0.6	108	178	18.1	27	
	Cocos Keeling	Outer reef slope/crest	None ^c	27.82	35	123–210	194	0.4	-0.7	95	172	13.3	20	

^aCraig et al. 2008; ^bJones et al. 2004; ^cNewton et al. 2007

the longitudinal and latitudinal elements of the sampling program.

A separate multiple linear regression analysis was performed for each of the following 3 dependent variables: longevity (mean T_{max}), age-1 size [$L(1)$] and adult size [$L(5)$]. In each analysis, the following 2 continuous predictor variables were included: longitude, and mean SST. SST was a proxy for latitudinal location, as temperature varied systematically along this gradient. These analyses were designed to detect trends in longevity, growth rate and body size in relation to longitude and varying temperature. In order to avoid redundancy in samples at the same location (Lizard Island and Cocos Keeling each have 2 samples), and in an effort to standardise by habitat as far as possible, the following samples were excluded from these 3 analyses: Lizard Island inner reefs and Cocos Keeling lagoon. The model tested was of the form:

$$Y = a_0 + a_1(\text{longitude}) + a_2(\text{SST}) + \text{error} \quad (3)$$

where Y is the dependent variable tested (longevity, age-1 size or adult size, respectively), and a is the corresponding partial regression coefficient; a_0 represents the intercept, a_1 the effect of longitude when SST remains constant, and a_2 the effect of SST when longitude remains constant.

For each analysis, the null hypothesis tested was that each partial regression coefficient equalled zero. Assumptions of colinearity, homogeneity of variances and normality were checked. Firstly, a matrix of correlation coefficients showed that, in each case, the 2 predictor variables longitude and SST were not correlated ($r^2 = 0.2953$, $p = 0.327$, tolerance = 0.9128). Secondly, observed values of each dependent variable were normally distributed and spread of the residuals was reasonably constant across predicted values. In each of the 3 analyses the regression model chosen to best represent the data was linear, as the adjusted r^2 value did not increase significantly when using non-linear models.

The mean and variance in longevity and body size were estimated at 2 spatial scales, between oceans and between locations within oceans. The comparisons were made using 2-way nested ANOVAs with oceans treated as a fixed factor, and locations a random factor nested within oceans. Maximum age data used in the analysis were the 10% oldest individuals at each location sampled. Size data used in the analysis were individuals aged 5 to 7 yr. Adult size was achieved by

5 yr in all populations sampled; 5 to 7 yr old age classes were well sampled at all locations. As in the regression analyses, Lizard Island inner reefs and Cocos Keeling lagoon were excluded from the analyses so as to avoid redundancy in samples at the same location. The 2 nested ANOVAs showed an unbalanced design, with unequal numbers of levels of the nested factor (location) within each level of the higher factor (ocean) for both analyses, and an unequal number of replicates across groups. The missing cells were taken into account by using a Type V sum of squares for calculation of the F -ratio, and nested ANOVA is relatively robust to unbalanced designs (Quinn & Keough 2002). Care was taken to comply with assumptions of normality and homogeneity of variance, the latter being particularly important in the analysis of unbalanced nested designs (Quinn & Keough 2002).

There are relatively few reefs in the Indian Ocean compared to the Pacific Ocean, which resulted in an unbalanced sampling design with 4 locations in the Indian Ocean and 9 in the Pacific. In addition, logistics on isolated Indian Ocean reefs made it difficult to collect large samples at each location. To guard against comparisons being compromised by unbalanced sampling designs, 2 subsampling procedures were used to check for (1) the effect of an unequal number of locations sampled in each ocean, and (2) the effect of differing sample sizes across locations sampled in both oceans. The results were consistent with those found in the original nested analyses (Appendix 1).

Variance components were then calculated (from the nested ANOVAs based on a balanced sampling design) to estimate the relative proportion of the overall variation in longevity and adult body size that could be explained by each spatial scale (ocean, location). Locations included in the Pacific Ocean were Tutuila, Moorea, Townsville and Kimbe Bay (one of the combinations in Pacific Ocean locations was randomly picked; there was no effect on the results of the combination of locations included, Appendix 1). Variance components were calculated following Quinn & Keough (2002).

Impact of fishing pressure and habitat type on demographic variables. To examine the potentially confounding effect of diverse fishing pressures of our study species and habitat types across our sampling sites on our results, each location was assigned a level of fishing pressure and habitat type (see Table 1, Appendix 2).

Fishing levels: Separate 1-way ANOVAs were used to test for the effect of the categorical factor 'fishing level' on each of the 3 dependent variables: longevity (mean T_{\max}), age-1 size [$L(1)$] and adult size [$L(5)$]. There was no significant difference in homogeneity of variance for $L(1)$ or $L(5)$, and residuals were normally distributed. The dependent variable mean T_{\max} was

log₁₀-transformed to meet assumptions of normality of variance and normality of distribution of the residuals.

Habitat types: Habitat types were assigned as in Connolly et al. (2005) based on on-site inspection of the structure of the reefs where samples were collected and on literature reports. Three habitat categories were assigned: (1) outer reef slope/crest, where reefs are exposed to ocean conditions and prevailing winds; (2) back reef, which are reef slopes but on the sheltered side of reefs; and (3) lagoonal environments, which are enclosed and sheltered (see Table 1). A separate 1-way ANOVA was performed for each of the 3 dependent variables, mean T_{\max} , $L(1)$ and $L(5)$, to examine the effect of the categorical factor 'habitat type'. In each case there was no significant difference in homogeneity of variance across groups for both size variables, $L(1)$ and $L(5)$, and residuals were reasonably normally distributed. Mean T_{\max} was power-transformed to meet the assumptions of homogeneity of variance and normal distribution of the residuals. All analyses were performed using Statistica 6.1 (StatSoft).

RESULTS

Analysis of the relationship between size and age in 15 populations of *Ctenochaetus striatus* from the Indian Ocean (5 populations), the western Pacific Ocean (6 populations) and the central Pacific Ocean (4 populations) revealed that asymptotic growth was consistent across locations and geographical scales (Fig. 2). In all sampled populations there was a fast initial growth, which reduced sharply with an increase in age. In most populations, asymptotic size was achieved within the first 10 to 20% of the life span, resulting in a decoupling of size and age in adults. This form of growth is characteristic of many coral reef fishes, including acanthurid species (Choat & Robertson 2002), a number of lutjanids (Newman et al. 2000) and some chaetodontids (Berumen 2005).

While all populations displayed a consistent form of growth, there was considerable variation in the relationship between size and age among locations. Shifts among populations could be observed along both the x - and y -axes of the size-at-age relationships, reflecting variation in longevity, mean maximum size and steepness of the ascending part of the growth trajectory or growth rate (Fig. 2). Variation in the structure of these curves identified differences among populations in the parameters of longevity, age-1 size and adult (age-5) size.

Regression analyses on longevity (mean T_{\max}), age-1 size [$L(1)$] and adult size [$L(5)$] revealed contrasting effects of longitude and mean SST. Both longitude and SST significantly influenced longevity, while

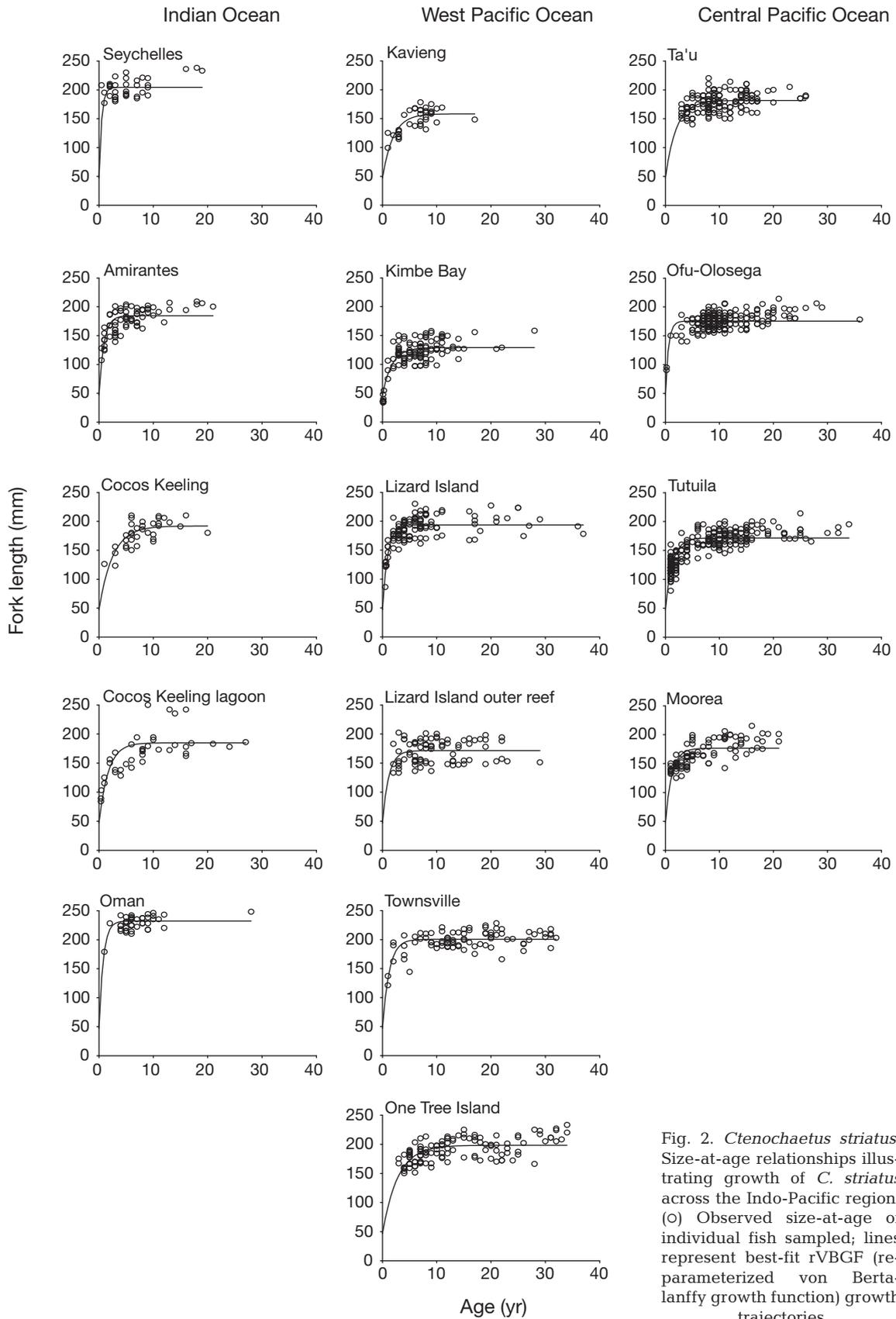


Fig. 2. *Ctenochaetus striatus*. Size-at-age relationships illustrating growth of *C. striatus* across the Indo-Pacific region. (o) Observed size-at-age of individual fish sampled; lines represent best-fit rVBGF (re-parameterized von Bertalanffy growth function) growth trajectories

Table 2. Results of linear multiple regression analyses performed on *Ctenochaetus striatus* longevity (mean T_{\max}), age-1 size [$L(1)$] and adult size [$L(5)$], to examine the effect of longitude ($^{\circ}\text{E}$) and mean SST ($^{\circ}\text{C}$, as a proxy for latitude). $n = 13$ for each analysis performed. t shows value of the t -test statistic. Semi-partial correlation coefficients indicate the unique contribution by the respective predictor variable to explaining the total variance. Multiple R^2 represents the amount of variation explained by the overall regression model fitted for each dependent variable. Bold p-values are significant at the 0.05 level

Variable tested	Predictor variable	Regression coefficient \pm SE	t	p	Semi-partial correlation coefficient	Tolerance	Multiple R^2
Mean T_{\max}	Intercept	71.46 \pm 16.72	4.27429	<0.01			
	Longitude	0.075 \pm 0.020	3.71602	<0.01	0.66	0.912	
	SST	-2.33 \pm 0.62	-3.75181	<0.01	-0.67	0.912	0.62
$L(1)$	Intercept	229.67 \pm 150.08	1.53028	0.1569			
	Longitude	-0.38 \pm 0.18	-2.10648	0.0614	-0.53	0.912	
	SST	-2.01 \pm 5.59	-0.35923	0.7268	-0.091	0.912	0.22
$L(5)$	Intercept	424.79 \pm 97.37	4.36275	<0.01			
	Longitude	-0.24 \pm 0.12	-1.99968	0.0734	-0.42	0.912	
	SST	-7.82 \pm 3.62	-2.15696	0.0563	-0.46	0.912	0.46

there was no significant effect of either predictor variables on age-1 size or adult size (Table 2). There was a significant linear relationship between longevity and longitude (t -test; $t = 3.71602$, $p < 0.01$), indicating that longevity increased linearly on a gradient from the western Indian Ocean to the central Pacific Ocean in the populations sampled (Table 2, Fig. 3a). There was also a significant negative linear relationship between longevity and SST (used as a proxy for latitude) ($t = -3.75181$, $p < 0.01$) (Table 2, Fig. 3a). Together, longitude and SST explained 62% of the total variance in longevity in the populations sampled (Table 2).

ANOVA of raw maximum age data confirmed the presence of significant differences in longevity among ocean basins (Table 3). Differences in longevity between the Indian and Pacific oceans (on an oceanic scale) explained 47% of the variation in longevity among populations sampled (Fig. 4). Longevity also varied significantly among locations independently of ocean, with this accounting for a further 16% of the variation in longevity (Fig. 4).

Table 3. Results of nested ANOVAs comparing longevity (maximum age, in years) and adult body size (fork length of 5 to 7 yr olds, in mm) of *Ctenochaetus striatus*, based on raw age and size data across spatial scales (ocean, location). Location was nested within ocean. Bold p-values are significant at the 0.05 level

Variable	Effect	SS	MS	df	F	p
Longevity	Intercept	22646.85	22646.85	1	164.0748	<0.001
	Ocean	683.92	683.92	1	5.1132	<0.05
	Location (Ocean)	2766.03	251.46	11	17.8139	<0.001
	Residual	1835.05	14.12	130		
Adult size	Intercept	5623339	5623339	1	750.2943	<0.001
	Ocean	35894	35894	1	4.7694	0.0512
	Location (Ocean)	109410	9946	11	51.1590	<0.001
	Residual	48411	249	194		

In contrast, no significant trends in growth or adult size were observed in relation to either longitude or latitude (temperature) (Table 2). Longitude and SST explained 22% of the variation in age-1 size and 46% of the variation in adult size (Table 2). ANOVA of raw adult body size data confirmed that there was no significant difference in adult body size between the Indian and the Pacific oceans, and revealed that variation in size across populations sampled was explained primarily by differences among locations (Table 3), which explained 58% of the variation (Fig. 4).

Analysis of potential confounding effects on our results included those of differing fishing intensities and habitat types across populations sampled. Separate 1-way ANOVAs were performed on each of the 3 demographic variables of age-1 size, adult size and longevity, testing for the effects of fishing level and habitat type, respectively. We found no significant effect of fishing pressure on age-1 size [$L(1)$: 1-way ANOVA, $F_{2,10} = 0.0017$, $p > 0.05$], adult size [$L(5)$: $F_{2,10} = 0.9445$, $p > 0.05$] or longevity (log₁₀ mean T_{\max} : $F_{2,10} = 2.612$, $p > 0.05$), suggesting that differences found in body size across locations, and differences in longevity across longitudinal and latitudinal scales, were not affected by differences in fishing intensity across our sampling locations. Similarly, we found no significant effect of habitat type on any of the 3 demographic variables. There was no significant difference in age-1 size ($F_{1,11} = 0.0032$, $p > 0.05$), adult size ($F_{1,11} = 0.1335$, $p > 0.05$) or longevity (exp mean T_{\max} : $F_{1,11} = 0.6338$, $p > 0.05$), confirming that the patterns of differences in body size and longevity found for *Ctenochaetus striatus* were not the result of differing habitat types across sampling sites.

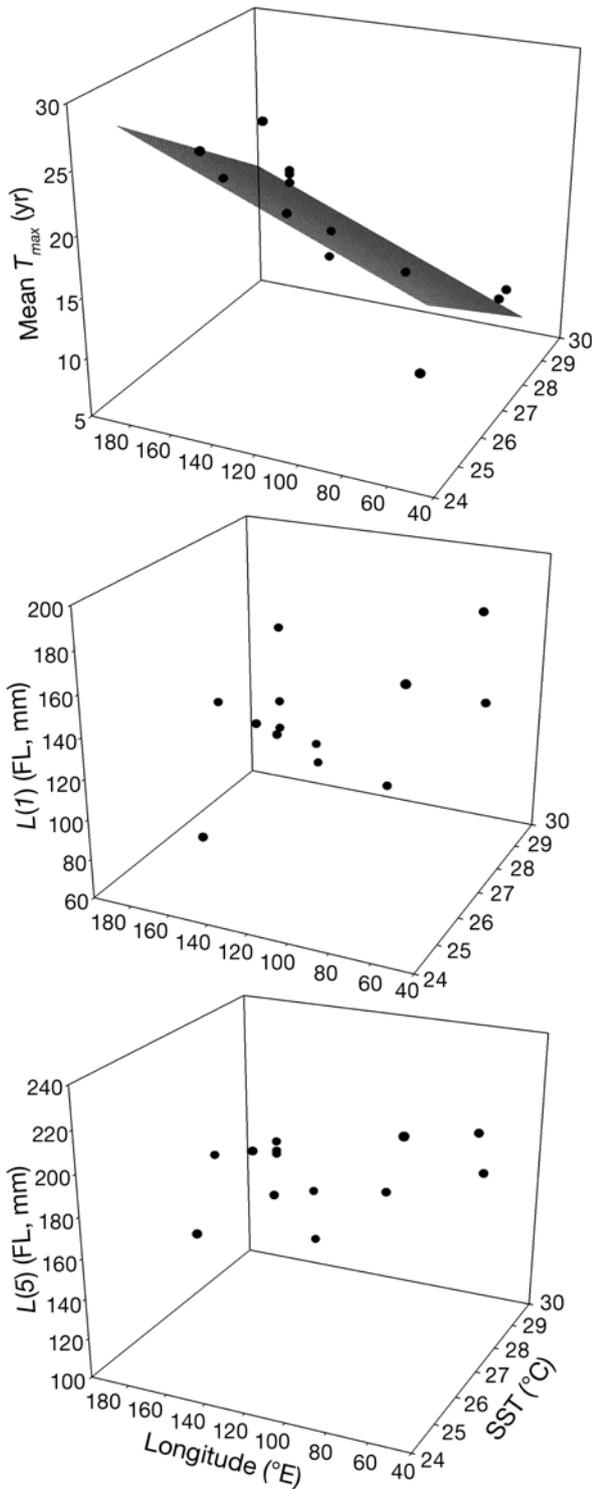


Fig. 3. *Ctenochaetus striatus*. (a) Relationship between longitude ($^{\circ}$ E), mean SST ($^{\circ}$ C, as a proxy for latitude) and longevity (mean T_{max}) of *C. striatus* across the Indian and Pacific Ocean basins. Regression model fitted is mean $T_{max} = 71.46 (\pm 16.72) + 0.075 (\pm 0.020) (\text{Longitude}) - 2.33 (\pm 0.62) (\text{SST})$, $R^2 = 0.62$. (b) Relationship between longitude, mean SST and age-1 size ($L(1)$). (c) Relationship between longitude, mean SST and adult size ($L(5)$). FL = fork length

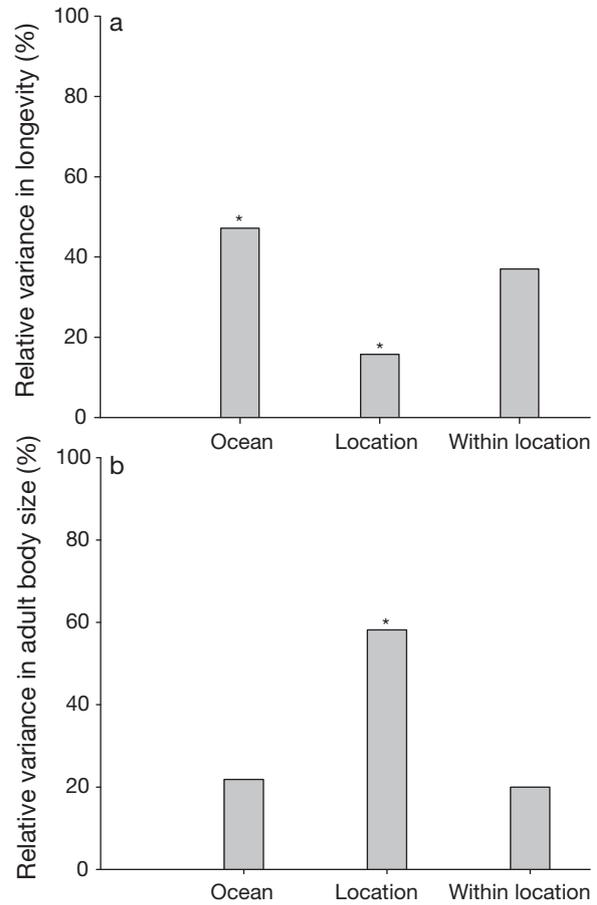


Fig. 4. *Ctenochaetus striatus*. Percentage of relative variance in (a) longevity and (b) adult size at 2 spatial scales: between ocean basins and across locations sampled within the Pacific and Indian Oceans. Within location represents the unexplained residual error within each level of the nested factor. *: Significant result of 2-way ANOVA performed for each of the 2 variables, $p < 0.05$

DISCUSSION

The analysis of 15 populations of *Ctenochaetus striatus* sampled across 17 360 km, or 83 % of its longitudinal range, and 2280 km, or 66 % of its latitudinal range, revealed several distinct trends in age structure, growth rate and size. These were manifested at different spatial scales. At the greatest (longitudinal) spatial scale, the most consistent signal in the dataset was a trend in mean maximum age (longevity). Analysis over the longitudinal gradient revealed a trend in longevity from the western Indian Ocean to the central Pacific Ocean, with Indian Ocean populations tending to be shorter lived than Pacific populations. Latitudinal large-scale sampling revealed a negative relationship between longevity and mean SST. This pattern is consistent with that observed in a tropical Atlantic acan-

thurid (Robertson et al. 2005a), where longevity was correlated with decreasing SST and increasing seasonality. In contrast, we detected no large-scale longitudinal or latitudinal patterns in either growth rate or adult size. Growth and size varied primarily at the scale of locations within each ocean, with all populations displaying a strongly asymptotic growth pattern typical of acanthurids.

Robertson et al. (2005a) detected a negative relationship between growth of the Atlantic surgeonfish *Acanthurus bahianus* and SST on a large geographic scale. While consistent with latitudinal counter-gradient variation (Conover et al. 2006), the effect was only manifested in early growth phases. There was also evidence of more localized variation in growth associated with habitat structure, with the extent of differences in growth between 2 habitats on one reef spanning much of the latitudinal range of variation in growth. Localized variation in growth rates and size structures might be pervasive in reef fishes. Indeed, the present study detected no latitudinal trend in growth rate in *Ctenochaetus striatus*. Most of the variation in adult size in this species was related to locality (58%), the only factor to show a significant effect, and within-location (20%); variation in body size between oceans accounted for only 22% of the variation. Although the sampling habitat was standardized as far as possible, subtle differences in habitat structure may have contributed to the variation in size and growth rate observed in different locations in the present study.

While variation in growth rate and size structure of *Ctenochaetus striatus* was localized, variation in longevity occurred at a large geographical (latitudinal) scale. A number of factors could drive this latitudinal trend including temperature, seasonality, productivity and prevailing mortality regimes. For some teleosts, increases in life span are associated with increasing variation in annual reproductive outputs and recruitment, so that long-lived species manifest a highly uneven distribution of age classes (Murphy 1968). At high latitudes there are reduced seasonal windows for spawning compared with low latitude populations of the same species (Robertson 1991, Kokita 2004, Srinivasan & Jones 2006). At present the relationship between reproduction, recruitment and life span is unclear for reef fishes. Robertson et al. (2005a) examined variation in longevity of an Atlantic acanthurid with respect to recruitment variation and found no evidence for such a relationship. However, Robertson et al. (2005a) did identify a relationship between the seasonality of reproductive output and longevity suggesting a trade-off between longevity and reproduction (Stearns 1992).

Longer spawning periods will increase reproductive costs, leading to reduced allocations of energy for

growth and somatic maintenance (Robertson et al. 2005a, Ruttenberg et al. 2005). Ruttenberg et al. (2005) demonstrated that, for a subtropical reef fish, temperature explained a significant proportion of reproductive output per unit of biomass, with fish from warmer temperature habitats manifesting increased reproductive outputs, lower growth rates and shorter life spans relative to those from colder water habitats. However, establishing the relationship between reproductive output and other demographic characteristics will be complex, as increased reproductive outputs may be both a response to and a cause of increased mortality (Stearns 1992, Ruttenberg et al. 2005). Ruttenberg et al. (2005) concluded that temperature-mediated reproductive output was a cause of increased mortality, arguing that populations with shorter reproductive seasons would allocate less of their annual energy budgets to reproduction, resulting in larger, older animals. The complexity of the relationship between life-span and relative investments in somatic maintenance versus reproduction and the impact of feeding regimes have been recently explored by Inness & Metcalfe (2008). In addition, lower temperature populations will experience reduced metabolic rates and maintenance costs (Clarke & Johnston 1999). This explanation is consistent with the limited number of studies that focus on age-based approaches to reef fish life histories.

The emerging picture of reef fish demographic variation identifies the importance of integrating reproductive, growth and mortality schedules. However, estimates of annual or life-time reproductive outputs for most reef fishes will be difficult to obtain. Many populations, including acanthurids, manifest extended seasonal spawning periods with daily spawning migrations and episodes of group spawning. Estimating individual contributions to both seasonal and life-time fecundities has been accomplished in only a few cases with tropical reef fishes (Doherty 1983, Ross 1983, Hoffman & Grau 1989, Warner et al. 1995). Such analyses will be further complicated by the possibility that reduced seasonal opportunities for reproduction may lead to compensatory increases in reproductive output in high-latitude populations (Kokita 2004).

Multi-scale sampling has revealed the complexity of demographic variation in reef fishes, especially in longevity. Although significant trends occur over broad spatial scales, variation in longevity may also occur at very localized scales. Gust et al. (2002) and Gust (2004) identified a pattern of consistent differences in longevities, growth rates and sex-specific maturation of reef fishes in genetically connected populations (Dudgeon et al. 2000) separated by 12 km. Individuals of the study populations on exposed outer barrier reefs had both significantly higher mortalities and reduced growth rates as well as a significantly

reduced age at first reproduction. Gust et al. (2002) attributed the higher mortality rates to the greater abundance of predators on exposed reef sites. This resulted in populations with a high turnover rate in which changes in reproductive output were a consequence, not a cause, of increased mortality.

A consistent theme in much of the recent coral reef literature concerns overfishing, and the tacit assumption that locality and regional scale patterns of demographic variation are no more than reflections of the geography of anthropogenic influences. Although fishing has obvious impacts on abundance patterns in coral reef species, it has proved more problematical to demonstrate impacts on longevity (Choat et al. 2003, Robertson et al. 2005b). This is illustrated in the present study in that longevity in American Samoa (16.8 to 17.9 yr), an overfished, collapsed fishery (Newton et al. 2007) that heavily targets *Ctenochaetus striatus* (Craig et al. 2008), is similar to that on the GBR (17.8 to 26.7 yr), where there is no fishery for that species, and greater than that in northern PNG (10.2 to 12.6 yr), an underexploited fishery (Newton et al. 2007) (Appendix 2).

It is clear that the underlying causation of demographic variation in reef fishes will involve both evolutionary and mechanistic processes. Resolution of the relationship between life history features and environmental variation (both biological and physical) will require 2 things. First, an experimental approach employing common-garden experiments that subject individuals of known parentage and provenance to controlled manipulation of environmental variables and resource levels (Conover 1992, Kokita 2003, 2004). However, there are formidable technical obstacles to such experiments, including the development of culturing programs for tropical groups such as acanthurids and scarines, and the substantial life spans of these and other tropical species. Second, better estimates of reproductive outputs including life time fecundities are required, but will be difficult to obtain for long-lived species with multiple spawning episodes. Realistically, the most productive present approach is to obtain better information on the magnitude and direction of multi-scale demographic trends in order to frame more rigorous and testable hypotheses.

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Appendix 1. Subsampling procedures

To guard against comparisons being compromised by unbalanced sampling designs, 2 subsampling procedures were used to check for the following: (1) the effect of an unequal number of locations sampled in each ocean, and (2) the effect of differing sample sizes across locations sampled in both oceans.

(1) The nested analyses for size and longevity were re-run with a balanced sampling design consisting of the 4 Indian Ocean localities and 4 randomly subsampled Pacific Ocean localities. This procedure was repeated 10 times with a new subsample of Pacific Ocean reefs for each analysis. Type III sum of squares was used for all 10 balanced analyses. Results were consistent with those of the unbalanced analysis: nested ANOVAs based on 10 different combinations of 4 random Pacific Ocean locations resulted in a non-significant difference in size across oceans in 100% of all combinations tested, a significant difference in size across locations in 100% of all combinations tested, a significant difference in longevity between oceans in 90% of combinations tested, and a significant difference in longevity across locations in 80% of combinations tested.

(2) The mean sample size of individuals for the analysis of between-ocean differences in longevity and body size was 45 for the Indian and 131 for the Pacific Ocean, with a minimum sample size of 35 individuals in the Indian Ocean

(Cocos Keeling sample). As the oldest ages occurred in the locations with the highest sample sizes, greater mean age could possibly be the product of a greater sample size. To examine this, populations were subsampled randomly to a new sample size of 35 individuals to match the lowest sample size of the Indian Ocean populations. Nested ANOVAs were re-run based on the new sample sizes, as performed in the original nested analyses. Type V sum of squares was used to account for an unbalanced sampling design (all locations were included except Lizard Island inner reefs and Cocos Keeling lagoon). The results were consistent with those found in the original nested analysis. Nested ANOVAs comparing longevity and body size between the Indian and the Pacific oceans, based on subsamples of 35 individuals, showed a significant difference in longevity ($F_{1,39} = 7.8974$, $p < 0.05$) and no significant difference in body size between the 2 ocean basins ($F_{1,52} = 4.5634$, $p > 0.05$).

These results support those found using unbalanced sampling designs, and suggest the presence of real biological effects between the 2 oceans. However, subsampling of the Pacific Ocean populations produced evidence that reducing sample size produced slight declines (by an average of 19%) in mean maximum age, indicating that balanced sample sizes should be an important element of comparative demographic studies.

Appendix 2. Locality-specific description of fishing pressures on *Ctenochaetus striatus* across sampled sites

Attempts to develop proxies for fishing pressure such as population per unit length of coastline were unsuccessful due to differences in fishing practices and culture over the broad geographical gradients samples in the present study. *Ctenochaetus striatus* is harvested primarily by divers through spearing and drive nets. Oman supports 1531 persons per km of coastline while American Samoa 497 per km. However, fishing pressure is much greater in American Samoa, as diving and spearing are traditional fishing practices in Polynesian but not Arab society.

American Samoa: Overexploited to collapsed reef fishery (Newton et al. 2007). Two acanthurids, *Ctenochaetus striatus* and *Acanthurus lineatus*, are targeted in an established spear fishery (Craig et al. 2008). Fishing allocation: Heavy.

Moorea: Underexploited (Newton et al. 2007). *C. striatus* at Moorea is regarded as ciguatoxic (M. Kulbicki pers. comm.). This and other smaller acanthurids are lightly exploited. Fishing allocation: Light.

Papua New Guinea, Kavieng, Kimbe Bay: Underexploited (Newton et al. 2007). *C. striatus* supports a light to negligible fishery (Kaly & Opnai 2005). Both landing and market surveys indicated very low catch rates for small (150–200 mm FL) acanthurids. Fishing allocation: Light.

Oman: No organised reef fishery (www.fao.org/fi/fcp/fcp.asp 2006). *C. striatus* was recorded only from the offshore Al Halaniyatt Islands in southern Oman and were never observed in local markets (J. MacIlwain pers. comm.) Fishing allocation: None.

Seychelles - granitic islands (Mahe Plateau); Amirantes - carbonate reefs: Fully exploited (Newton et al. 2007). Evidence of some net fishing in the Mahe group; no evidence of fishery impacting *C. striatus* in the southern Amirantes. No evidence of *C. striatus* in market surveys (E. Grandcourt pers. comm.) Fishing allocation: Light.

Cocos Keeling and Great Barrier Reef: No fisheries for this species. Fishing allocation: None.