Article

Latitudinal and cross-shelf patterns of size, growth and mortality of a tropical damselfish *Acanthochromis polyacanthus* on the Great Barrier Reef

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Abstract:

Patterns of age and growth of a sedentary damsel fish *Acanthochromis polyacanthus* were tested over a latitudinal range of approximately 10 degrees (1,200 km) on the Great Barrier Reef, Australia. Within latitudes these patterns were also compared on reefs across a continental shelf that ranged in width from 52 to 128 km.   Although variation in length-max, growth, age-max and the von-Bertalanffy metrics of L_∞, and K were found within and among latitudes, greatest variation in some demographic characteristics were found across the shelf regardless of latitude.   Fish were always smaller at inner shelf reefs and grew more slowly when compared to mid and outer shelf reefs.   The oldest fish collected was 11 years old and, there were no consistent variation in age-max among distances from shore. On outer reefs, there was a linear relationship with age-max and latitude.   This 'tropical gradient' of age only explained 34% of the variation, further this was not found when the oldest 10% of fish were considered.   Fish only reached an age-max of 6 years on the southern-most reefs. There was a trend for a smaller L^∞ with latitude but, it was not significant and L^∞ did not vary predictably with water temperature.   The sampling of MPAs did not confound the resultant patterns. Instantaneous mortality rates were 0.245-0.685, highest at inner reefs and showed no consistent MPA-related patterns.   Our study suggested that the mid and outer shelf waters of the GBR appeared best suited for growth of *A. polyacanthus.*   In conclusion, position on continental shelves and related local environmental conditions needs to be considered in spatial models of growth.

Keywords: reef fish, age, growth, mortality, Great Barrier Reef, Pomacentridae, cross-shelf, MPA, latitudinal gradients.

1. Introduction

Patterns of age, growth and mortality are critical to understanding the population dynamics of fishes.   These patterns are influenced by internal factors such as genetics and, related physiological tolerances (Conover 1997) [1] as well as environmental factors [2].   Further, growth and mortality can be influenced by fishing effort (e.g., growth compensation [3]) and related variation in fishing effort in an out of Marine Protected Areas (MPAs [4]).

Environmental factors have often been correlated with demographic characteristics. There are a number of models that relate to latitude and sea water temperature.   Tropical Gradient Models (TGM) state that one or a combination of age-max, length-max, growth and growing season decrease from low latitude to high latitude [1, 2, 5].   This pattern closely aligns with the Temperature Size Rule (TSR) where reduced growth rate correlates with a drop in temperature. In some cases, however, this is the pattern for growth whilst length to infinity can increase with
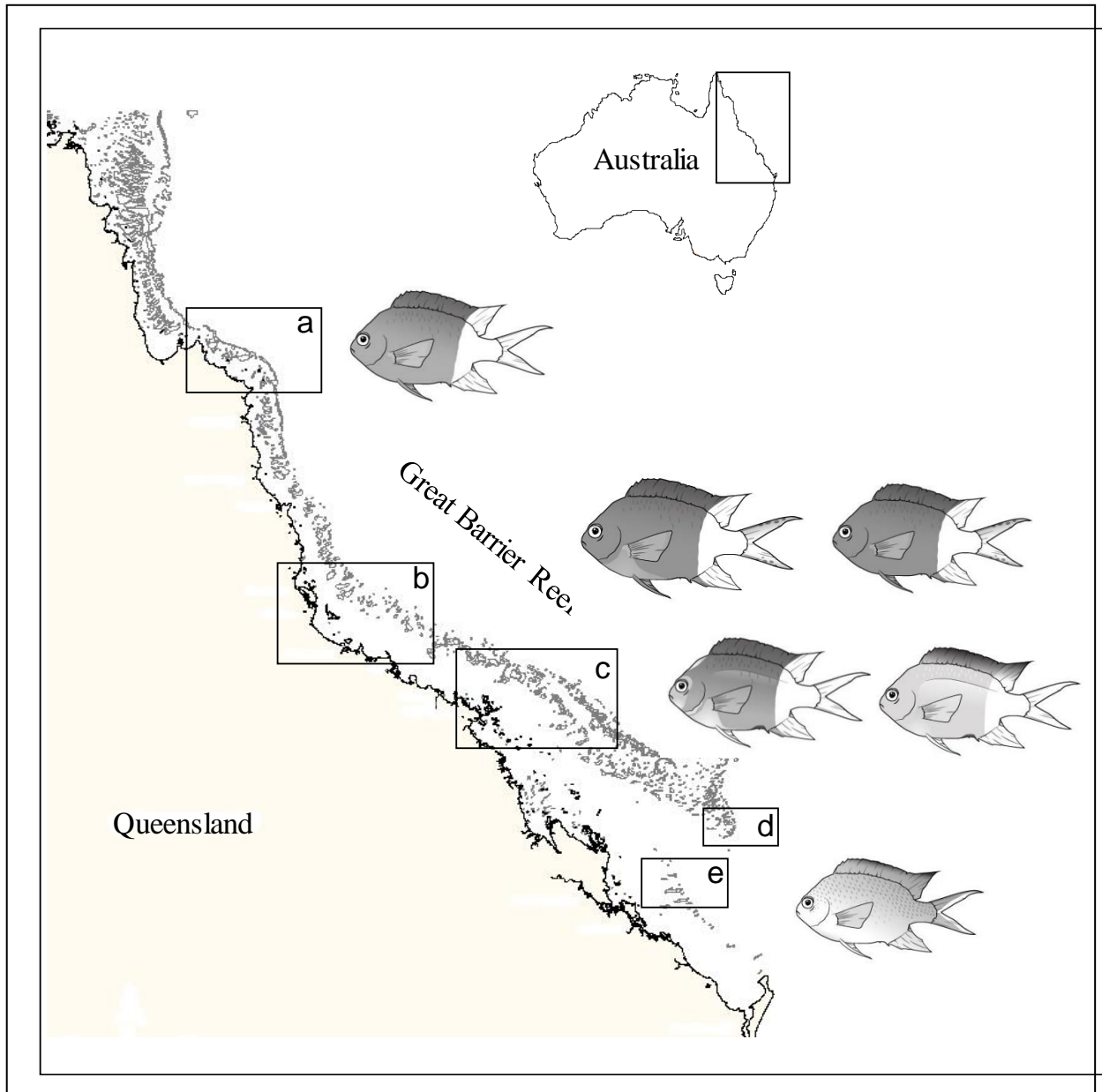
latitude [6]. Counter Gradient models (CGM) state that age-max, length-max or growth will increases from low latitude to high latitude (e.g., [5, 7]). In the case of some surgeon fishes, age-max increases with a decrease in temperature but, due to variation in oceanography does not increase as predictably with latitude[8]. Bergmann's Rule and 'James Rule' refer to an increase in body size with latitude [9, 10]. At some spatial scales regional differences in demographics are not been found to vary predictably over many degrees of latitude (e.g., 12°, *Cromileptes altivelis* [11]). For any correlative study it is often challenging to provide a strong case any of these patterns without sampling a wide latitudinal range and having multiple sampling sites.

The Great Barrier Reef (GBR) is about 2000 km long; accordingly, it covers a broad latitudinal range of approximately $14°$. Furthermore, the width of the continental shelf ranges from 60 km to 300 km wide. A concern is that latitudinal variation could be confounded by position across the shelf. It is well documented that there is more variation in the abundance of and species richness cross-shelf than over long distances latitudinally [12-15]. Moreover, it is well known that with position on the continental shelf there will be differences in environmental drivers. For example, coastal process such as riverine runoff and related sediment loads [16, 17]) and, on the outer shelf proximity to upwelling [18]; by deduction these factors could also have a great influence on the supply of planktonic food. These processes could have a great influence of patterns of size/age and growth [13] that are independent to latitude. Gust et al. [19] demonstrated such differences for the size max, growth and mortality for some species of scarids and one acanthurid at replicate reefs positioned mid shelf or outer shelf on the GBR.

The level of protection of reefs from fishing can also have an impact on demographic metrics and mortality that could confound the interpretation of broad spatial patterns. Protection generally results in greater abundance as well as larger and older fish [20-22]. Furthermore, a high abundance of predatory fishes could affect patterns abundance of prey and the size/age and growth characteristics of reef based populations (e.g., [4]). Kingsford & Hughes [23] found great differences in size maxima and von-Bertalanffy characteristics of fish across the shelf, where fish from inner reefs were much smaller. However this project did not test for variation in demographic characteristics with latitude and did not consider the confounding effects of levels of marine protection.

The objective of this study was to compare the demographic characteristics of *A. polyacanthus* cross-shelf and over a latitudinal range of ~9 degrees (about 1200 km). Our approach was to sample with high spatial resolution at replicate reefs and multiple latitudes from the northern to southern GBR. Where geomorphology allowed, we sampled at multiple distance strata from shore (inner, mid and outer shelf). The specific aims of this study were to: (1) describe patterns size, age and growth of reef-based populations of *A. polyacanthus* with latitude and within and among sampling strata at different distances from shore; (2) calculate the instantaneous mortality rates (Z) of populations of *A. polyacanthus* with latitude and within and among distance strata; (3) we also tested a hypothesis that the level of marine protection could confound broad scale spatial patterns. *A. polyacanthus* was an ideal species for the study of patterns of size, age and growth as it is found over a broad latitudinal range and on reefs at inner, mid and outer distances across the continental shelf [12, 24]. Furthermore, the distribution and abundance of the species allowed for high spatial resolution of the aforementioned patterns.

Figure 1. Location of sampling sites for *Acanthochromis polyacanthus* on the Great Barrier Reef with inserts indicating latitudinal positions as follows. Lizard (a), Townsville (b), Whitsunday (c), Swains (d) and Capricorn/Bunker (e). Outlines of the colour morphs of *Acanthochromis polyacanthus* by latitude are provided, larger images in colour are provided in Figure S1.

2. Materials and Methods

2.1 Study Sites and Sampling Design

Spatial variation in demographics and structures of cross-shelf populations of *A. polyacanthus* was determined using a partially hierarchical sampling design. Individuals of a wide range of sizes were collected from two or three sites from two or three replicate reefs within each of three distance strata (inner, mid- and outer-shelf) spanning the width of the continental shelf at three latitudes, Lizard Island, Townsville and the Whitsundays (Townsville data are from [23]. Additional outer shelf sites were located in the Swains, and the Capricorn section in the GBR (Figure 1, Table 1). At each site, a minimum of 40 fish were collected using hand spears from 2001-2006 (Table 1). The environmental gradient of temperature with latitude with was as follows. Seawater temperatures were up to 4 ^{o}C lower in the Capricorn Bunker Group in winter and about 2 degrees cooler in summer when compared with Lizard. Further, temperatures were about 1 ^{o}C lower on outer reefs of the Townsville latitude in winter and similar in summer when compared with Lizard (Fig. S2). Hobo data loggers were used to collect these data at 10 and 30m deep at outer reefs of each latitude over a period of two years.

Although *Acanthochromis polyacanthus* is considered as single species on the GBR, there is variation in color morphs by latitude and distance from shore (see [25].   In some sections of the GBR *A. polyacanthus* are of the same color morph and these morphs can be genetically isolated (Central GBR, [26], while more than one colour morph were was found at some latitudes (Whitsundays Section). Accordingly, we were careful to note the colour morph of *A. polyacanthus* by distance from shore and latitude in case incipient speciation could explain some of the differences in demographic characteristics that we detected Fig. 1.

2.2. Processing of samples

All fish were measured to the nearest mm (Standard Length, SL). Sagittal otoliths were extracted, cleaned in MQ water to remove the sagittal membrane and allowed to dry overnight. One otolith from each fish was then sectioned using a Gemmasta GF4 Faceting Machine using a 1200 grit diamond disc and Crystal bond thermoplastic glue.

2.3. Analysis of growth increments

The opaque zones visible in the internal structure of the otolith were counted along a radius from the primordium to the outer edge of the largest sagittal lobe of the otolith using a compound microscope (Leica DMLB) and white incident light source. Alternating translucent and opaque increments were interpreted as annuli. This has previously been validated by Kingsford and Hughes [23]. Sections were coded and examined in random order and the opaque increments counted on two occasions by the same observer separated by four days. Counts of annuli were compared between these two occasions in order to assess the confidence that could be placed in the interpretation of otolith structure. If increment counts differed then the otoliths were re-examined. If, following a third reading, agreement was not reached then the otolith was not included in the analysis; 6.6% of otoliths were rejected on this basis (*n*=186 fish). Fish that could not aged were still included in the results relating to standard length only.

Spatial patterns of oldest age (10%) and largest fish SL (10%) over a latitudinal range of 10 degrees were tested with a fully hierarchical ANOVA as follows: Latitude (a=5), reefs (latitude), b=2; n = 7 fish.   So that distance across the shelf and latitude were not confounded this analysis was only done on 13 outer shelf reefs. Sample size was determined by the smallest n at a reefs, this allowed us to do a more robust balanced ANOVA (Underwood 1997)[27].   Data were tested for normality, in the case of SL (10%) the data were still heterogeneous after transformation; because ANOVA is

robust to heterogeneity we continued with the analysis.   Linear relationships between latitude and demographic variables were done with least squares regressions.

Table 1. Location and numbers of *Acanthochromis polyacanthus* collected from September 2001 to January 2006.

Latitude	Shelf	Total n	Reef	N	Dates Collected
Lizard	Inner	279	Martin	162	Nov 2004
			Linnet	116	Nov 2004
	Mid	237	Eagle Ilet	99	Dec 2001
			North Direction Is.	57	Dec 2001
			MacGillivray	111	Dec 2001
	Outer	293	Yonge	155	Dec 2001
			Day	138	Dec 2001
Townsville	Inner	156	Havannah Island	70	Sep 2001
			Orpheus Island	41	Sep 2001
			Pandora	45	Sep 2001
	Mid	286	Britomart	88	Oct 2001
			Bramble	105	Oct 2001
			Slashers	93	Oct 2001
	Outer	298	Barnett Patches	116	Oct 2001
			Pith	100	Oct 2001
			Myrmidon	82	Oct 2001
Whitsunday	Inner	232	Hook Island	105	Sep 2003
			South Mole	127	Sep 2003
	Mid	173	Line	84	Sep 2003
			Net	89	Sep 2003
	Outer	169	Elizabeth	79	Sep 2003
			Ellen	90	Sep 2003
Swains	Outer	215	Hixson Cay	82	Jan 2006
			Sweetlips	70	Jan 2006
			Sandshoe	66	Jan 2006
Cap/Bunker	Outer	245	One Tree Island	97	Jan/Feb 2002
			Lamont	73	Jan/Feb 2002, Feb 2006
			Heron Island	86	Jan/Feb 2002

2.4. Growth

It was hypothesized that patterns of growth would vary with distance from the coast and between different latitudes. Growth was described using the von Bertalanffy growth function (VBGF) which provided the best fit to size-at-age data when compared with estimates of the Schnute growth function [28].

The von Bertalanffy expression for length at age t (L_t), as a function of time is:

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

where L_t = length at age t *(years)*; L_∞ = the mean asymptotic standard length; K = the rate at which the growth curve approaches L_∞, and t_0 = the age at which the fish have a theoretical length of zero. Kingsford and Hughes [23] demonstrated that variation in growth for *A. polyacanthus* off Townsville on the GBR was greater among distance strata than within distance strata. Accordingly, we tested the robustness of this pattern among the regions where all distance strata could be sampled.

An orthogonal design was used to test for spatial patterns in size, age, growth and mortality across the shelf (Distance strata: inner, mid and outer-) and among three latitudes as follows: Lizard Island, Townsville and Whitsunday. We did find significant differences in demographic characteristics across the shelf. So that distance and latitude were not confounded a further analysis was done on outer reef only. Further, to increase latitudinal coverage in addition to Lizard Island, Townsville, Whitsunday, additional samples were taken from the Swains and the Capricorn-Bunkers (Table 1). Spatial patterns for the top 10% of fish by length and age were tested using balanced ANOVA designs as follows: (1) A partially hierarchical design for comparisons among distances from shore (Factor Distance, Fixed), at three latitudes (Factor Latitude, Fixed) with two sites at each distance (nested in L*D). (2) Comparisons were made with a fully hierarchical design among five random latitudes (Factor Latitude, random) and there were two reefs nested in latitude. (3) To determine if the GBR marine zoning plan consisting of fully fished and unfished reefs could confound our interpretation of spatial patterns of age and size we selected fished and unfished reefs that were close. Pairs of reefs with the two different types of zones (Factor Zone, fixed) were available at Inner and Outer distances from shore (Factor Distance, fixed), there were two locations at each distance stratum that had this pairing and therefore 'location' was nested in distance [Factor Loc(distance), random]. All analyses were done according to Underwood [27]. Data were analyzed for heterogeneity with Cochran's tests.

The spatial hierarchy of growth patterns was visualised by generating cross sections of the approximate 95% confidence regions around L_∞ and K, by constraining t_0 to a common value by fitting a VBGF to all size-at-age data for the curves being compared. We formally tested the visual separation of 95% confidence intervals among regions and distance strata using likelihood ratio tests (Kimura, 1980). This test is considered the most reliable procedure for comparing non-linear curves (Cerrato, 1990). These tests were done on paired comparisons among reefs at different latitudes; these results are compared in Table SP1. Comparisons of size at age were also made for two and three year olds as this corresponded to the fastest period of growth before fish reached L_∞.

2.5. Mortality

The instantaneous rate of mortality (Z) was calculated using log-linear regression analyses of age-frequency data sets for *A. polyacanthus* populations from each reef sampled [29]. This method assumes that recruitment is consistent over time at each reef. The natural logarithm of the number of fish sampled from each age class was compared with their corresponding age. Year classes to the left of the age-frequency mode were excluded from the analysis because our sampling technique was biased against small *A. polyacanthus*. Fish greater than 60 mm were collected representatively, ie as they were encountered. The slope of the regression line between year classes estimated the instantaneous mortality rate (Z):

$$Z = F + M,$$

where F is fishing mortality and M is natural mortality [19]. Since there is not a fishery for *A. polyacanthus* on the GBR, F equals zero and therefore Z estimates natural mortality only. Annual survival rate estimates were then calculated according to the equation $S = e^{-Z}$ [30] and are presented
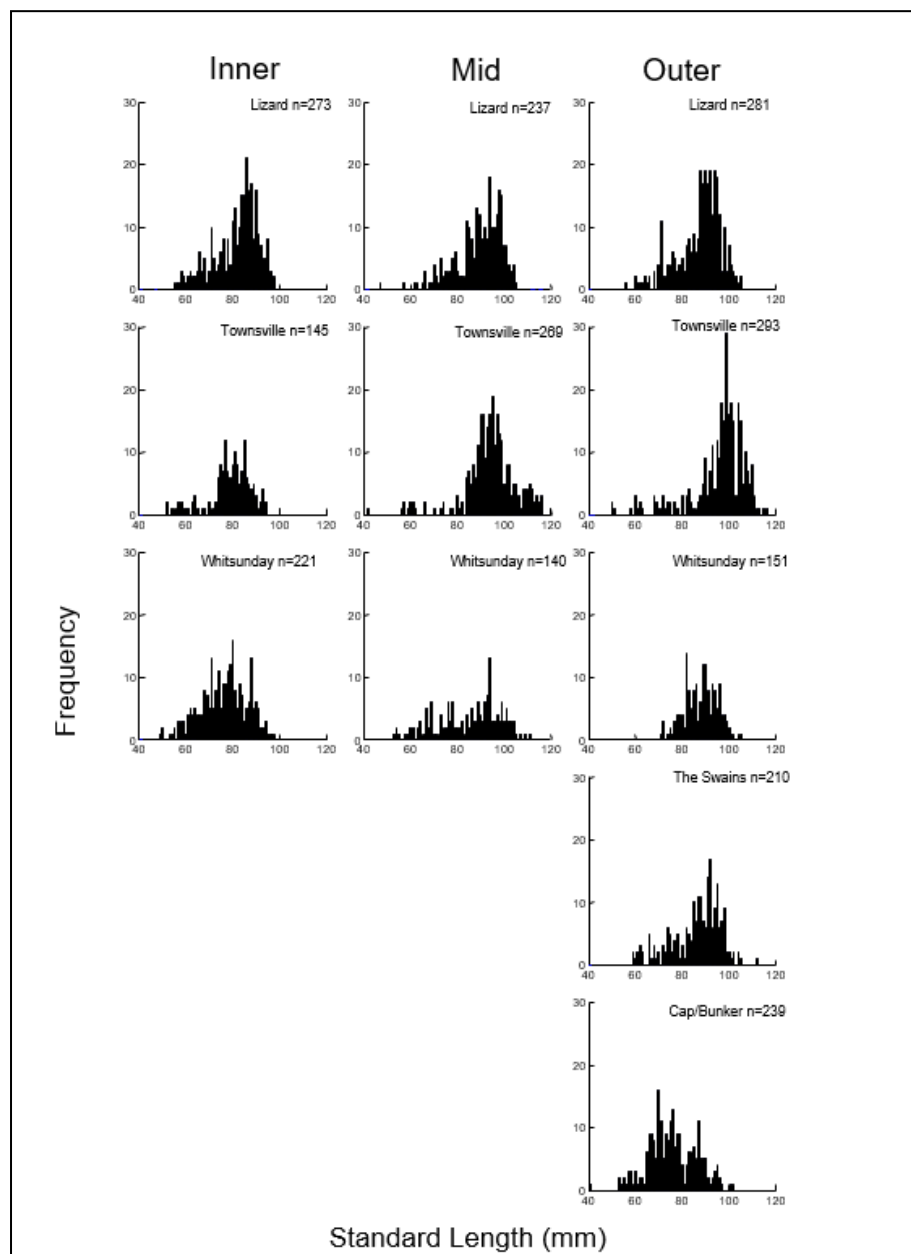
as percentages. Data from each site were pooled for each reef because in many cases sample sizes were too small to provide reliable estimates of mortality at the site level. Similarities in mortality rates among replicate reefs within distance strata allowed pooling of data at the strata level so that comparisons of mortality between shelf positions could be made.

3. Results

3.1. Colour morphs

The colour morph of *A. polyacanthus* varied by latitude and on some occasions with distance within a latitude. Fish collected either of the brown and white colour morph for the Cairns; brown and white colour at the Townsville latitude and sometimes with a gold-yellow chin at inner sites; brown and white colour, with a gold-yellow chin and similarly coloured head, with a purple/blue vent for inner Whitsundays and at mid and outer reefs a pale greenish anterior and white posterior with purple/blue vent. In contrast, at the Swains and Capricorn/Bunker group fish were a slaty grey with darker highlights on the distal end of scales and on the edges of the fins (Colour images – Figure 1, S1).

Figure 2. Length-frequency distributions for *A. polyacanthus* collected from the 13 positions on the GBR (reefs pooled within distances) LOW RESOLUTION IMAGE.

3.2. Size,age and growth

There were consistent patterns of length frequency and maximum length (LMAX) across the continental shelf at three latitudes (Figure 2, Table 2).   Fish were generally shorter at all inner reefs and it was rare for fish to be over 95mm SL.   In contrast, *A. polyacanthus* were over a 100 mm SL at mid and outer reefs where this was most obvious at the Townsville latitude (Max lengths of fish were 6-20 mm shorter at inner reefs when compared to maxima recorded at mid and outer reefs).   Max lengths of the largest 10% of fish showed a similar trend to SLmax.   Although there was a clear pattern for the largest fish on reefs to be small at inner strata, a significant interaction between Distance and latitude indicated that the magnitude of differences varied between inner reefs and those at mid and outer strata (Table 3).   The differences across the shelf were least obvious on reefs of the Lizard island latitude and were greatest at reefs of the Townsville latitude. Local variation in growth between sites within distance strata was also found [Site(L*D), Table 3], but this did not obscure the broad differences found across the shelf.

Among latitudes of outer reefs fish the only clear pattern was that the size max of *A. polyacanthus* was at outer reefs off Townsville. Although 29% of the variation in SL10% was explained by latitude this factor was not significant (Table 4). Fifty-eight percent of the variation was explained by differences, on a scales of kilometres to tens of kilometres, between reefs within latitudes and only 13% at the level of replication.   When the top 10% of fish was considered there was no relationship between SL and latitude. Further, there were no significant linear relationships between SL max or SL10% and latitude for fish from all latitude and nested reefs (n=13); in both cases ANOVA indicated that the slopes for these linear comparisons were not significantly different from zero. There was little evidence that temperature was a primary driver in patterns of SL with latitude as SLmax10% was much larger at Townsville when compared to Lizard, but seawater temperatures were similar between these latitude.   In contrast, SLmax10% was similar at Lizard and the Capricorn Bunker group where the latter was up to 4 C° cooler (Figure S2).

Table 2. Parameters from von Bertalanffy growth models and instantaneous mortality on the fishes collected from different distances across the shelf and latitude strata.   The maximum age and size (SL) is provided as well as mean age and size for the top 10% of fish.

Latitude	Shelf	LAT (°S)	*n*	L_∞	*K*	T_0	*Mortality* m(r^2)	*Max age*	*Mean age 10%*	*Max SL*	*Mean SL 10%*
Lizard Island	**Inner**	14°	273	88.64	1.38	-0.04	0.681 (0.61)	7	5.9	98	94
	Mid	14°	237	94.53	1.52	-0.04	0.578 (0.52)	8	6.0	105	102
	Outer	14°	281	93.13	1.55	-0.04	0.536 (0.54)	9	5.8	105	100
Townsville	**Inner**	18°	145	82.01	1.06	-0.06	0.506 (0.55)	10	8.0	100	92
	Mid	18°	269	97.85	1.06	-0.05	0.398 (0.47)	10	8.5	120	112
	Outer	18°	293	101.16	1.16	-0.04	0.432 (0.65)	11	8.3	116	110
Whitsundays	**Inner**	19°	221	83.17	1.77	-0.04	0.438 (0.35)	11	7.6	98	92
	Mid	19°	140	94.96	1.14	-0.05	0.245 (0.55)	8	7.4	111	104
	Outer	19°	151	90.40	1.64	-0.03	0.398 (0.41)	9	6.6	104	99
Swains	**Outer**	22°	210	94.05	1.45	-0.04	0.617 (0.64)	8	5.7	112	100
Cap/ Bunker	**Outer**	23°	239	80.84	1.58	-0.04	0.414 (0.49)	6	5.5	102	93

Table 3. Partially hierarchical ANOVA, testing for differences among Distances across the shelf and three latitudes n=4 fish; dependent variable Standard Length top 10% and Age top 10%; * p< 0.05; *** p< 0.001.   Distance and latitude were tested as fixed and site as random. C = Cochran's Test for heterogeneity of the data, k=18, df = 3.

Source of variation	df	SL 10% C=0.21, ns		Age 10% C=0.14, ns	
		MS	F	MS	F
Latitude	2	15.7	0.35	18.0	19.6***
Distance	2	874.4	19.3***	1.43	1.55
L*D	4	264.5	5.8*	5.0	5.4*
Site(L*D)	9	45.2	10.3***	0.92	1.15
Residual	60	4.4		0.79	

There was no evidence for variation in the agemax or age 10% for *A. polyacanthus* at reefs across the shelf and this was consistent at all three latitudes (Figure 3, Table 2). Among latitudes, the agemax of *A. polyacanthus* at outer reefs was greatest at Lizard, Townsville and the Whitsundays (range 9-11 years), while no fish was older that six years at the Capricorn Bunker Group. Twenty one percent of variation in the age of fish was explained by differences between latitudes, but as for SL, this factor was not significant.   There were significant differences between reefs within latitudes, but greatest variation was found at the residual level (63%).   There was a significant negative linear relationship between agemax and latitude (Tropical Gradient) that explained 34% of the variation; ANOVA for slopes was significantly different from zero (Figure 4). Rather than a counter gradient the relationship was strongly influenced by highest values of agemax on Townsville and Whitsundays reefs.

In some cases replicate reefs within distance strata had different levels of protection, but this did not influence the broad patterns we described for age or size (Table 5).   For example, the two inner reefs (Pandora, Havannah; one green one blue) had similar SL max to each other, but both reefs had much smaller fish than two outer reef with different zones where the fish were much larger (Barnett Patches and Myrmidon). Inner reefs at Lizard had very similar agemax regardless of zone as did the two outer reefs compared in the Capricorn Bunker group. Changes in rank were detected for largest and oldest fish with zone indicating that there was no consistent pattern that could be explained by level of protection. There were also no consistent differences in von-Bertalanffy parameters between zones in any of the pairs of fished and unfished zones (Table SP3). In all cases the green zones had been in place for close to the age-max of *A. polyacanthus* or twice that.

Figure 3. Age-frequency distributions for *A. polyacanthus* collected from the 13 sites reefs pooled within distances at each latitude (LOW RESOLUTION IMAGE).
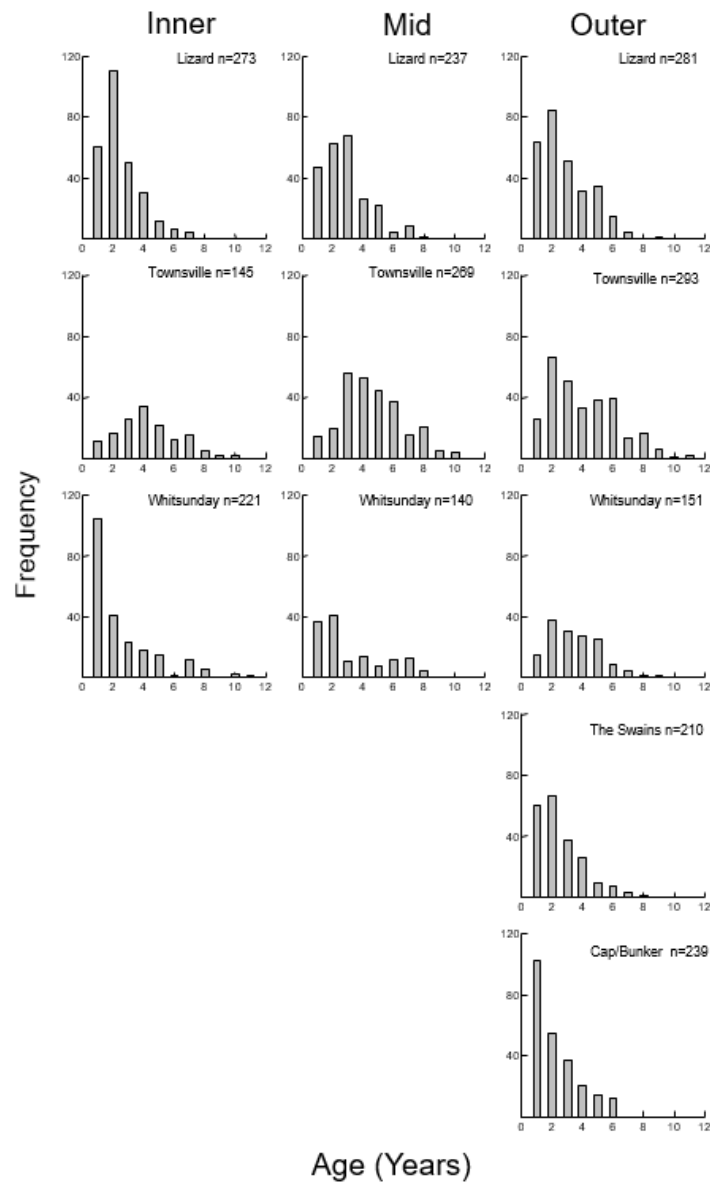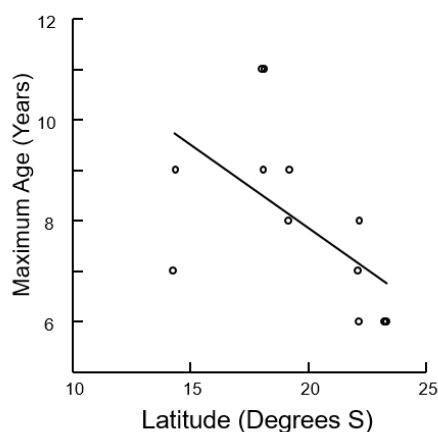
Table 4. Nested ANOVA, testing for differences among five latitudes with two reefs nested per latitudes and n=7; dependent variable Standard Length top 10% and Age top 10%; * p< 0.05; *** p< 0.001. Variance components describe the variation contributed to each factor as a percentage. The denominator MS for Latitude is Reef (Lat) and that of Reef (Lat) is the residual.

Source of variation	Df	SL 10%		Age 10%	
		MS	Variance Comp.%	MS	Variance Comp.%
Latitude	4	486.7 ns	29	12.95 ns	21
Reef (Lat)	5	247.3 ***	58	4.67 *	15
Residual	60	7.9	13	1.76	64

Figure 4. The relationship between age-max and latitude for *A. polyacanthus* from outer reefs only. Collections from all reefs are included in this analysis with a minimum of 66 fish (range 66-155) collected at anyone reef, n=13 reefs. R^2 = 0.34, ANOVA for slopes, $F_{1,1}$=5.74, P<0.03.

Acanthochromis polyacanthus grew quickly to L∞ at two to three years old (Figure 5). The L∞ of fishes at different distances across the shelf concurred with our comparisons of length frequency in that L∞ was consistently smallest at inner reefs regardless of latitude. The confidence ellipses shown in the Kimura plots also showed consistently small L∞ for fish from inner reefs (Figure 6). Although multiple differences among different distances and latitude were detected according to chi-square tests the effect size was always greatest for inner versus mid and outer reefs (Figure 6 A, Table S1). The rate at which fish grew to L∞ (K, Table 2; Figure 5) was highly variable and not consistent patterns were detected either across the shelf or when comparison were made among the five latitudes with outer reefs. Differences were also detected among reefs with Chi-square tests (Table S1). There was no significant correlation between K and latitude for 13 reefs over the full latitudinal range of the study (10 degrees).

Length at age varied with position across the shelf and it was clear that although fish from all reefs grew quickly to L∞ by about 3 years old, growth rate to that L∞ varied with position on the shelf (Figure 5, Table SP4).   For example, cross-shelf at the Townsville latitude at age two were about 71 mm SL compared to 86 and 93 mm SL at mid and outer shelf reefs. By age three, fish were on average 79 mm SL at inner reefs and 97 and 100 SL respectively at mid and outer shelf reefs. Significant differences in size at age were detected with distance from shore and this was true for fish aged two and three (Table SP5). There was a consistent pattern of smallest sizes at ages 2 and 3 years nearshore at all latitudes but, the magnitude of size differences between inner reefs and those at mid and outer shelf positions varied with latitude and this resulted in significant interaction between the factors shelf and latitude (Table SP4).

Table 5. The influence of marine protection form fishing on demographic characteristic of *Acanthochromis polyacanthus*. Summary statistics for both SL and age date are presented as mean (SE) range.   Three way partially hierarchical ANOVA are presented with the factors Shelf, Zone, S*Z. location (Shelf) and location (Shelf)*S in **Table SP2;** significant factors are listed here. Factor Zone: treatments MPA and Fished. Details of von Bertalanffy parameters by reef and zone are provided in Table SP3.

(a) The top 10% by size; the interaction location (Shelf)*S was significant.

Shelf	Latitude	MPA	Fished
Inner	Lizard	95.3(0.7)3	97.5(1.3)6
Inner	Townsville	87.5(0.9)4	91.5(0.6)3
Outer	Townsville	111.3(1.3)5	113(1.1)5
Outer	Capricorn Bunker	82(0.9)4	99(1.5)6

(b) The top 10% of fish by age; the interaction S*Z was significant.

Shelf	Latitude	MPA	Fished
Inner	Lizard	6(0)0	6.8(1)2
Inner	Townsville	6.8(0.3)1	7.8(1)2
Outer	Townsville	9.5(0.6)3	9(0.7)3
Outer	Capricorn Bunker	6(0)0	6(0)0

Figure 5. Von Bertalanffy growth curves for *A. polyacanthus* collected with distance across the shelf and with latitude (reefs pooled within distances at each latitude). LOW RESOLUTION IMAGE
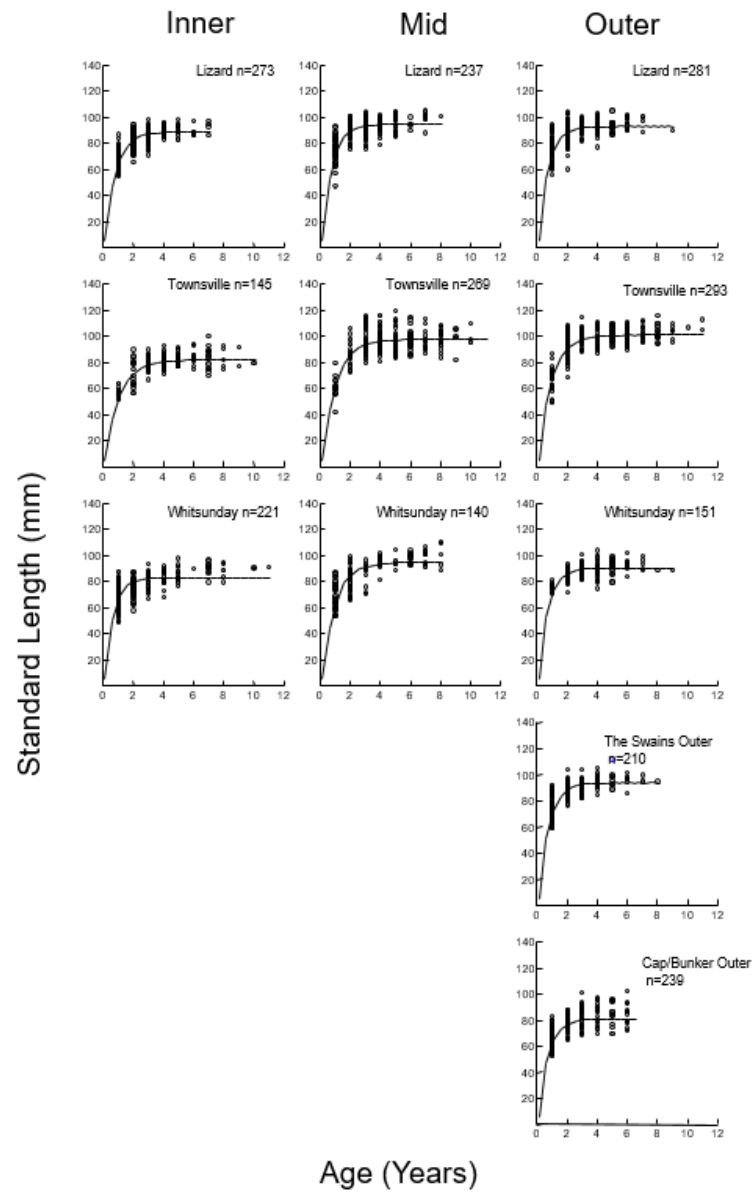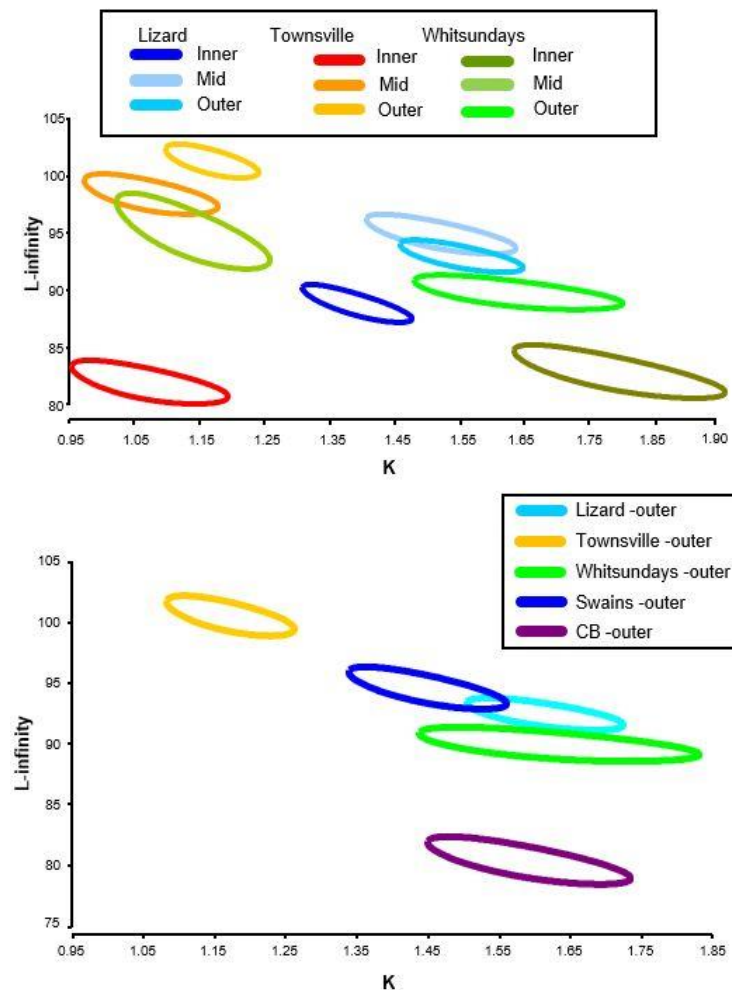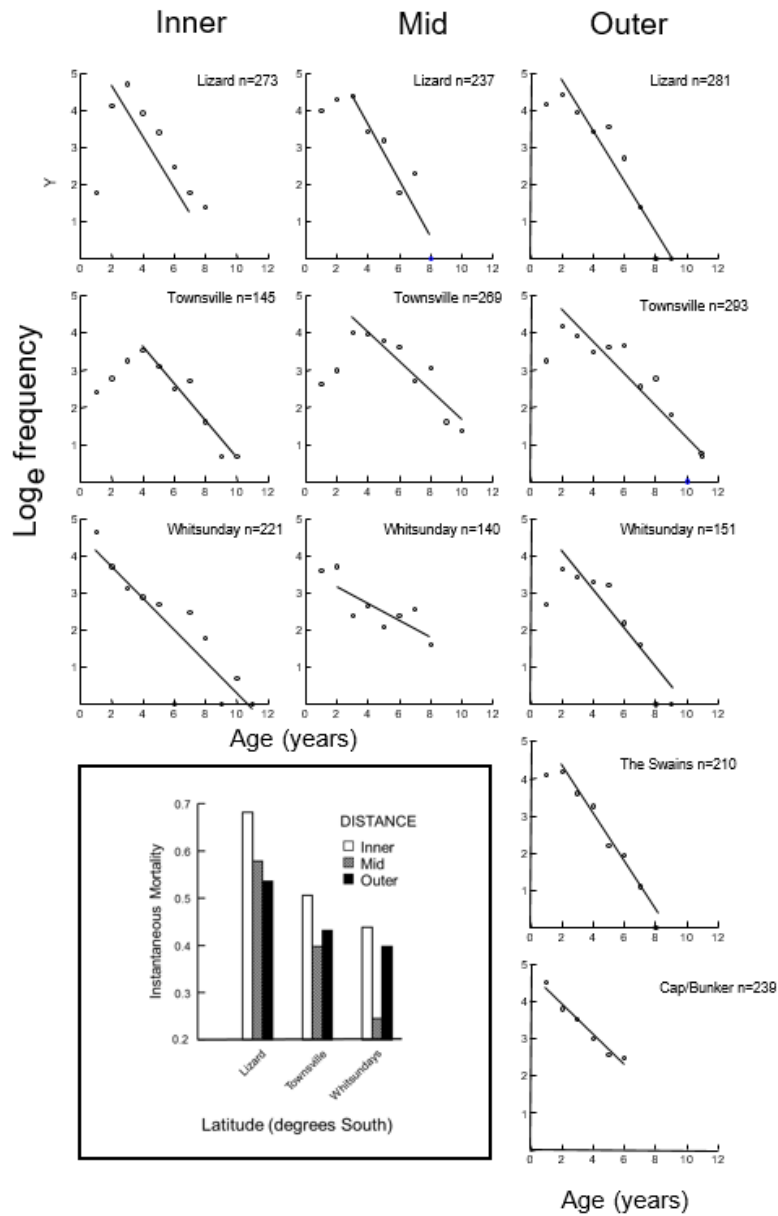
Figure 6. Kumara plots showing a 95% confidence ellipses for the parameters K (growth coefficient) and L_∞ (mean asymptotic length) for A Latitudes with inner mid and outer collection sites and B latitudes where collections where only made at outer reefs (LOW RESOLUTION IMAGE).

3.3. Mortality

Instantaneous mortality rates ranged from 0.69 at Lizard, Inner to 0.245 at Whitsundays mid (Table 2, Figure 7). Mortality rates were consistently higher at inner shelf reefs (Figure 7). This pattern was also apparent from age frequency where the representation of fish greater than 4 years old was relatively low when compared to mid and outer reefs at the same latitude (Figure 3). Although there was a strong trend for mortality rates to drop with latitude, among outer reefs (13 reefs); this relationship, however, was not significant (ANOVA for slopes ns). The relationship was largely derailed by high mortality rates that were detected at the Swains. When all instantaneous mortality relationships were considered, they explained 41 to 65% of the variation in these relationships. The dependency of the relationships on young and small fish under 3 year old varied with sites within reefs, but there was no consistency with latitude or distance that could have confounded the conclusions relating to spatial differences.

Figure 7. Age-based instantaneous mortality rates for *A. polyacanthus* collected with distance across the shelf and with latitude (reefs pooled within distances and latitude). The lower left panel presented instantaneous mortality by distance for each of the three latitudes sampled in this orthogonal combination. LOW RESOLUTION IMAGE

Discussion

The robustness of this study is in the spatial resolution by distance from shore and latitude that is hard to achieve.   In short, we could sample large numbers of fish and that has allowed us to test hypotheses relating to distance across the shelf and with latitude.   The data are unequivocal in that position on the continental shelf of the GBR had a substantial influence on the growth and size of *A. polyacanthus*. The findings of this study concur with our earlier study that focused on one latitude, that of Townsville [23].   There is only one other study we are aware of that addresses this source of variation. Gust et al. demonstrated differences in the demographic characteristics of scarids between mid and outer shelf reefs of the GBR [19]. In this study significant differences in L^∞, growth and mortality were found. Of course, fish have to be found over the full extent of the GBR, or similar geomorphological features, for distance across the shelf to be an issue. For many species they may only be found at one or two distance strata (e.g. [12]) and the danger of confounding latitudinal trends with cross shelf differences would be minimized.

We sampled 13 reef positions over a distance of 1200 km and ~ 9 degrees of latitude and based on this we could test hypotheses concerning variation in demographic characteristics with latitude. Even with this unusually high spatial resolution, few latitudinal gradients were detected. Gradients have been detected for other species over a similar spatial range for size, growth and age-max (e.g. [9, 31]).   For example, Cappo et al. [9] found that the body size of *L. johnii* increased with latitude (=counter gradient) on the GBR and therefore distance from the equator, which concurred with James rule. In contrast, we often only found differences between latitudes on a spatial scales of a few hundreds of kilometers, but not between reefs separated by over 1000 kilometers.   For example, one of the greatest differences in size max was found from between the two northern most latitudes, Lizard Townsville.   These locations are bathed in similarly warm waters, so perhaps at this spatial local factors such as the supply of planktonic food may play a major role on patterns of growth as at least one of our offshore sites Myrmidon reef is well known for upwelling [32, 33].

We found variation between reefs within a latitude, both for the largest and oldest fish.   Fry and Milton [34] also found variation in demographic metrics within a location that 'made it difficult to detect differences with latitude'. They did, however, find variation in *L. malabaricus* in size and age over a broad longitudinal range (Western to eastern Australia).   In contrast, to the small scale variation we found, Williams et al [35] did not detect differences the growth and age-max of *Lethrinus miniatus*; among reefs within locations. However, there were different among regions separated by hundreds of kms or up to 4 degrees; these patterns were consistent when they were compared five years later [36]. Variation in demographics among reefs within a latitude may be due to factors such as the density of conspecifics, availability of prey and predatory regimes.   Ong et al [37] examined differences between *Lutjanus bohar* populations at the same latitude from the and west coast of Australia.   They argued that the differences they found local factors such as oceanography and ecological differences were the primary drivers of differences in demographics.   Our findings across the continental shelf of the GBR and big differences in SLmax at some sites such as Myrmidon (Townsville) align with this view.

Although most of the latitudinal trends we tested for SL, growth and age were not significant (=Tropical gradient), we did find a variable, but significant, negative relationship between the agemax of *A. polyacanthus* and latitude. Piddocke et al., (2015) also found a negative relationship between agemax and temperature and growth for *Lutjanus argentimaculatus*.   There was no relationship *A. polyacanthus* between growth to $L\infty$ (K) with latitude. Although seasonal cycles in temperature between 14 and 24° S were about four degrees (Fig. SP2), greatest latitudinal differences were found between Lizard and Townsville latitudes where seasonal temperature cycles were similar.   Latitude is clearly a rough proxy for a temperature gradient given the complexities of oceanography [8]. We also found that SLmax was similar at the latitudinal extremes in our study where seasonal difference in temperature were greatest; this does not align with the Temperature Size Rule [6].   Of course, differencs in growth may manifest itself at the more extreme ends of the temperature and food availablilty spectrum. For example, experiments on *A. polyacanthus* have

demonstrated that the growth potential of fish can be inhibited regardless of how much food is available at high temperatures (e.g., 31°C, [38]).

The consistency of relatively small size of fish at inner reefs of the GBR suggests some similarity of the biophysical drivers influencing growth and size maxima. Shallow waters of the GBR can get very warm in summer and this area is notorious for coral bleaching when reefs further from shore are below the bleaching threshold of 31°C [39]. It is highly likely the growth potential of *A. polyacanthus* can be inhibited at these times, as has been shown experimentally [38]. Sediment loads are generally higher on inshore reefs [40] and this could reduce the intake of food of a planktivore [41]). We also have some evidence from unpublished cross shelf plankton samples that the abundance of small plankton (i.e., copepodites etc retained by 100 micron mesh) is about a quarter that of mid and outer reefs. A combination of these factors, therefore are most likely drivers for the patterns we found. Further, the patterns are unequivocal because we had an orthogonal; design with distance across the shelf and three latitudes that showed similar patterns.

Our findings concur with other studies that variation in environmental conditions within a latitude can have a strong influence on demographic characteristics and in some cases this variation can be a great as some purported 'gradient models'.   For example, Ong et al [37] studied spatial patterns in the growth variability of *Lutjanus bohar* over a similar latitudinal range in tropical waters, they concluded that the major drivers were variation in local climatic patterns (e.g., oceanography) and biological factors. Similarly, Gust et al [19] found differences in size and age-maxima of scarids between mid and outer reefs of the GBR over a narrow latitudinal range. Gillanders [42] also found great differences in patterns of growth of a large subtropical labrid over spatial scales of kilometres. These studies further emphasize the importance of local factors in determining demographic characteristics.

Mortality may also have a role in the cross shelf patterns that we found (e.g. [19]). Mortality rates were consistency highest at inner reefs and the numbers of fish over 4 years old were less inshore when compared to mid and outer reefs. Interestingly the age-max of inner reefs was similar to mid and outer, it is just that few fish reached ages over. Accordingly, mortality alone does not explain the patterns in age-maxima that we found with distance across the GBR.   There can be temporal variation in mortality rates [36]) and, this is highly likely where the size of pulses in recruitment alter values of Z. The methods for calculating instantaneous mortality assume even recruitment among years.   However, this is unlikely to alter the consistency of the pattern of highest mortalities nearshore though more information on temporal patterns of recruitment with distance from shore would help to resolve this issue.

Although there was a strong trend for mortality rates to drop with latitude this was not significant.   The relationship was largely derailed by high mortality rates that were detected at the Swains.   Similarly, no clear latitudinal trend in mortality was also found by Williams et al [35] for *Lethrinus miniatus*.

Although *A. polyacanthus*   is still considered a single species [24], the variation in colouration that is well known suggests that insipient speciation is likely. A contributing factor to variation in demographic parameters, therefore, could be due in part to phenotypic plasticity relating to genetic differences [1, 43]. However, the cross shelf patterns found were robust regardless of latitude and colour morph.   Fish were smallest inshore at Lizard where all fish were the brown and white colour morph (Figure S1a); the Townsville latitude was again brown and whites with some additional golden colouration on the chin at inner reefs (Figure S1b). Two different morphs were collected on the Whitsundays transect (Figure S1c) while the dark colour morph were only found from the southern two latitudes of the GBR (Figure S1d).   Although the Age-max for Capricorn Bunker fish was six years, oldest fish of the same colour morph from the Swains were up to eleven years old; this equated with the highest value found at any latitude and distance.

A concern for many ageing studies that deal with commercial species such as lutjanids and lethrinids is that natural patterns, be they by distance across the shelf or latitude can be confounded by differences in fishng pressure that could affect differences in SLmax, L∞, agemax, and of course mortality (ie a combination of fishing mortality F and natural mortality M [3]). In contrast, the small damselfishes in this study are not subject to a fishery and they don't attract much attention from the

aquarium trade.   Furthermore, although top-down effects from large predators have the potential to alter density of small prey and affect mortality rates.   Inverse relationships between the numbers of predators and numbers of prey have been detected when comparisons have been made between marine sanctuary zones and fishes areas at the same latitude [4]. Further, Gust et al [19] concluded that differences in age-maxima cross shelf were drivern by predation.   However we found no evidence for such patterns in our study.

5. Conclusions

In conclusion, we found that demographic characteristics of *A. polyacanthus* varied greatly across the continental shelf of the Great Barrier Reef; this pattern was consistent within three latitudes. SLmax was smallest and growth slowest at inner reefs and, mortality rates were also greatest at this distance.   A comparison among outer reefs over 10° of latitude detected a 'Tropical Gradient of decreased agemax with an increase in latitude. No other latitudinal trends in L, K and age were detected, but there was significant variation between outer reefs at the same latitude. We suggest that local environmental factors had the greatest effect on patterns of size and growth and this should be has been considered in latitude-based gradient models of fish demographic characterietics.

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Supplementary material 1

Figure S1 Colour morphs of *A. polyacanthus* from different latitudes and distances across the shelf (ie inner, mid and outer). Lines indicate where a colour morph was found at more than once distance across the shelf. Where there are two fish at a latitude the line refers to fish two.
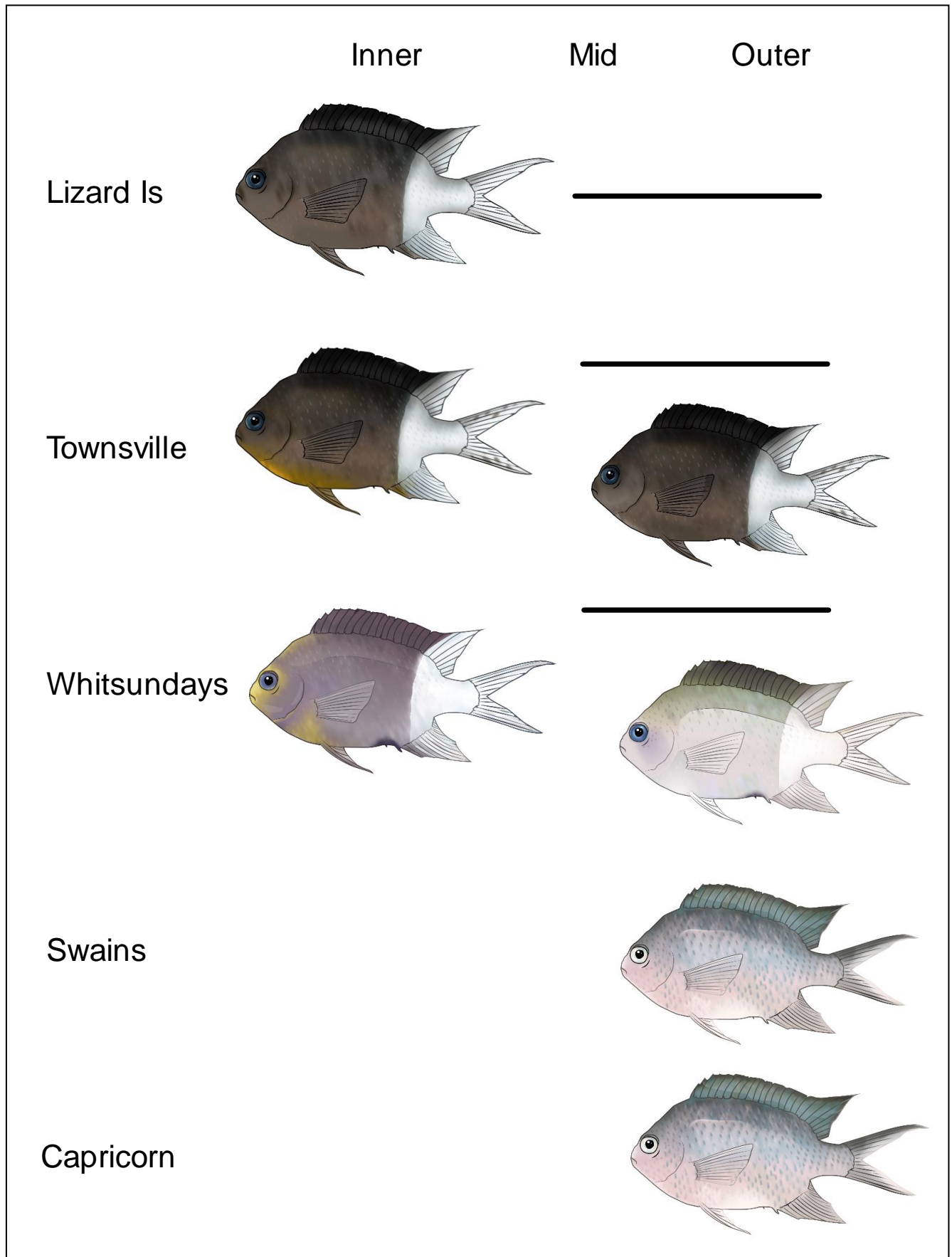
Figure S2 Temperature data collected from loggers in shallow (10 m) and deep (30m) water at offshore three latitudes (Lizard – Yonge Reef; Townsville-Myrmidon Reef, Capricorn Bunker, One Tree Island) that encompassed the latitudinal range of the study.   The x-axis is presented in two month increment for the years 2007 – 2009.
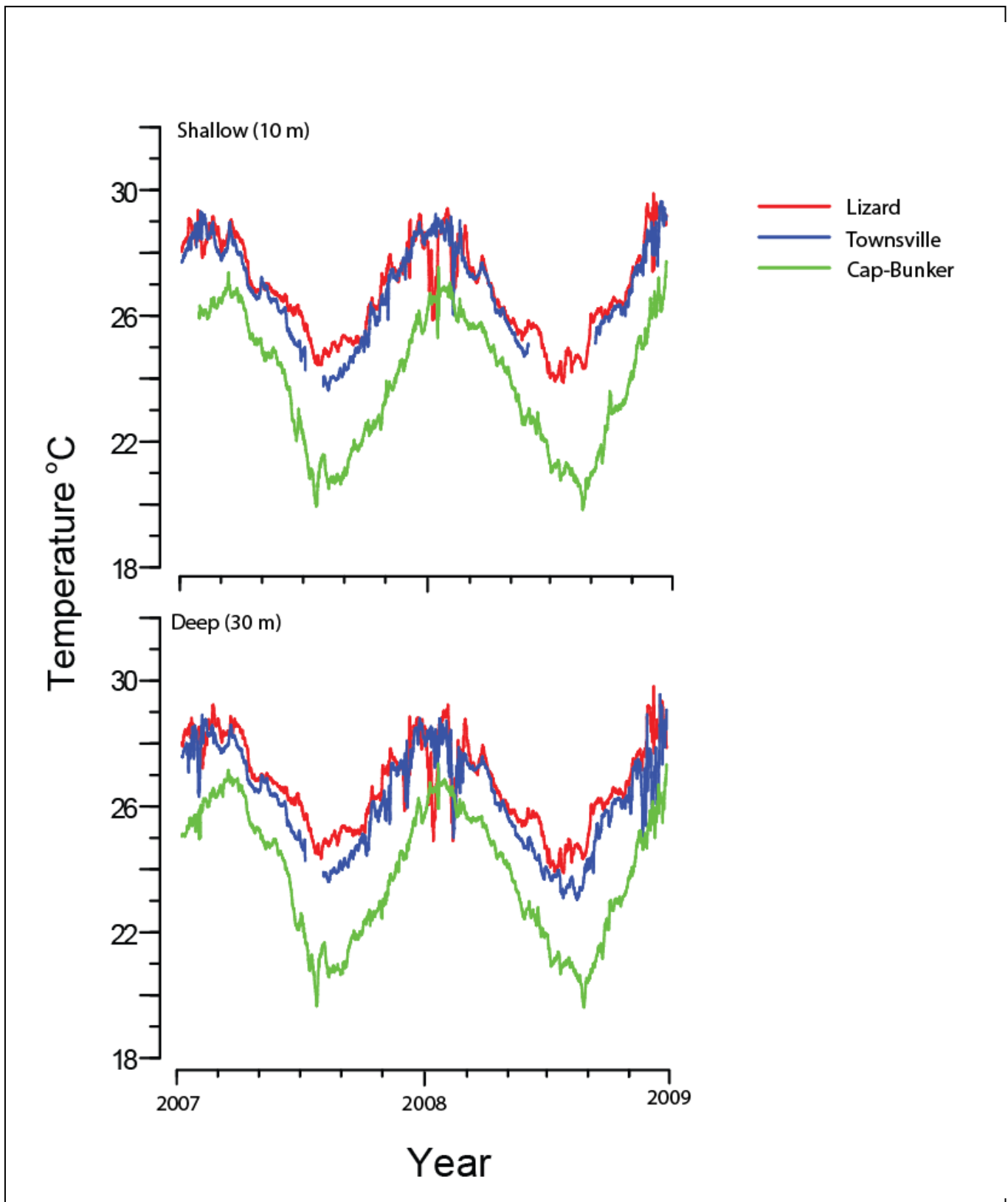
Table SP1 results of chi-square tests from Kimura plots (Figure 6) Likelihood ratio tests showed that patterns in growth differed among regions and distance strata ($X^2_{,24}$ = 931.78, p < 0.001). Post hoc tests indicated that this significant result was due to significant differences in growth between almost all combinations of region and shelf position. In general the effect within each region was explained by differences in the value of the estimated L_∞ rather than K or t_0, however this result was variable. The estimate of L_∞ was generally lower for inner-shelf distance strata for all regions however this wasn't consistent statistically. Growth patterns for the inner-shelf distance strata were different among all regions. For the outer-shelf distance strata across the regions Lizard Island, Townsville, Whitsundays, Swains and the Capricorn-Bunkers significant differences in growth patterns were detected ($X^2_{,12}$ = 464.92, p < 0.001). This difference was due to a higher L_∞ for the Townsville region and a lower L_∞ for the Capricorn-Bunker region, than all other regions. The outer-shelf strata for the Lizard Island, Whitsundays and Swains regions were generally similar. Estimates of the K parameter among regions were generally similar except for Townsville where it tended to be lower.

Test	X^2 coincident	df	p	Linf p	K p	t_0 p
Overall	931.78	24	<0.001	<0.001	<0.001	<0.001
LI inner v LI outer	101.87	3	<0.001	<0.001	0.932	0.501
LI inner v LI mid	115.33	3	<0.001	<0.001	0.908	0.767
LI mid v LI outer	3.871	3	0.276	0.347	0.862	0.795
Tvl inner v Tvl outer	396.45	3	<0.001	<0.001	0.002	0.002
Tvl inner v Tvl mid	233.33	3	<0.001	<0.001	0.012	0.004
Tvl mid v Tvl outer	33.84	3	<0.001	<0.001	0.858	0.712
Whit inner v Whit outer	81.07	3	<0.001	0.401	0.03	0.057
Whit inner v Whit mid	47.16	3	<0.001	0.677	0.242	0.073
Whit mid v Whit outer	28.97	3	<0.001	0.013	0.135	0.634
LI inner v Tvl inner	136.34	3	<0.001	<0.001	0.084	0.497
LI inner v Whit inner	64.54	3	<0.001	0.075	<0.001	<0.001
Tvl inner v Whit inner	47.32	3	<0.001	<0.001	0.001	<0.001

Table SP 2. Partially hierarchical ANOVA, testing for differences among Distances across the shelf and Zone (MPA and fished) n=4 fish; dependent variable Standard Length top 10% and Age top 10%; * $p < 0.05$; *** $p < 0.001$.   Distance and latitude were tested as fixed and site as random. C = Cochran's Test for heterogeneity of the data, k=18, df = 3.

Source of variation	df	SL 10% C= 0.21 ns		Age 10% C=0.14, ns	
		MS	F	MS	F
Distance	1	760.5	0.7	0.03	0.03
Zone	1	312.5	0.3	5.3	5.8
S*Z	1	66.1	0.06	47.5	52.5*
Loc(Shelf)	2	1089	6.33	0.9	1
Loc(Shelf)*zone	2	172.1	39.1***	0.9	1
Residual	24	4.4		0.9	

Table SP3 Reef status comparison of age and growth parameters between Protected zones (Marine National Park Zone B –Green=unfished) with General Use Zones (Blue – fished).

		n	L∞	K	To	r^2	Max age	Time Green (Years)
Havannah	Inner	82	79.98	1.39	-0.05	0.37	10	
Pandora	Inner	43	77.43	1.39	-0.05	0.66	9	14
Myrmidon	Outer	81	103.29	1.27	-0.04	0.53	11	
Barnett Patches	Outer	113	100.073	1.17	-0.04	0.71	11	14
Lamont	Outer	73	92.52	1.36	-0.04	0.61	6	
One Tree Island	Outer	81	77.13	1.46	-0.05	0.60	6	20
Martin	Inner	160	88.49	1.37	-0.04	0.63	7	
Eagle	Inner	92	90.18	1.25	-0.05	0.63	8	9

Table SP4 Mean size of *A. polyacanthus* at ages 2 and 3 collected from different distances across the shelf and latitude strata on the GBR, Australia

Location	Shelf Position	LAT (°S)	*n*	Mean size at 2 (SE)	*n*	Mean size at 3 (SE)
Lizard Island	Inner	14°	110	83 (0.55)	50	86 (0.78)
	Mid	14°	63	90 (0.83	67	93 (0.74)
	Outer	14°	82	88 (0.74)	50	92 (0.54)
Townsville	Inner	18°	16	71 (2.68)	26	79 (1.04)
	Mid	18°	20	86 (2.14)	57	97 (1.26)
	Outer	18°	66	93 (1.11)	51	100 (0.72)
Whitsundays	Inner	19°	41	75 (1.08)	23	81 (1.39)
	Mid	19°	40	80 (1.16)	11	78 (2.79)
	Outer	19°	38	87 (0.71)	31	90 (0.86)
Swains	Outer	22°	67	89 (0.60)	37	91 (0.83)
Cap/ Bunker	Outer	23°	52	78 (0.85)	36	83 (1.30)

Table SP 5 Three factor ANOVA, Factors, distance (F) and latitude with the response variable SL for fish aged 2 and 3.   Heterogeneity of the data were checked with Cochran's C, k= 9 and df = 19; Age 2 C=0.17 NS; Age 3 C=0.23 *.

Source of variation	df	SL at age 2 C= 0.17 ns		SL at age 3 C=0.23, *	
		MS	F	MS	F
Distance	2	1497	27.3***	1393	31.1***
Latitude	2	789.6	14.4***	262.8	5.9**
D*L	4	318.5	318.5***	192.7	4.3*
Residual	143	4.4		44.8	