Abstract—Age-based analyses were used to demonstrate consistent differences in growth between populations of Acanthochromis polyacanthus (Pomacentridae) collected at three distance strata across the continental shelf (inner, mid-, and outer shelf) of the central Great Barrier Reef (three reefs per distance stratum). Fish had significantly greater maximum lengths with increasing distance from shore, but fish from all distances reached approximately the same maximum age, indicating that growth is more rapid for fish found on outer-shelf reefs. Only one fish collected from inner-shelf reefs reached >100 mm SL, whereas 38–67% of fish collected from the outer shelf were >100 mm SL. The largest age class of adult-size fish collected from inner- and mid-shelf locations comprised 3–4 year-olds, but shifted to 2-year-olds on outer-shelf reefs. Mortality schedules (Z and S) were similar irrespective of shelf position (inner shelf: 0.51 and 60.0%; mid-shelf: 0.48 and 61.8%; outer shelf: 0.43 and 65.1%, respectively). Age validation of captive fish indicated that growth increments are deposited annually, between the end of winter and early spring. The observed cross-shelf patterns in adult sizes and growth were unlikely to be a result of genetic differences between sample populations because all fish collected showed the same color pattern. It is likely that cross-shelf variation in quality and quantity of food, as well as in turbidity, are factors that contribute to the observed patterns of growth. Similar patterns of cross-shelf mortality indicate that predation rates varied little across the shelf. Our study cautions against pooling demographic parameters on broad spatial scales without consideration of the potential for cross-shelf variability.

Patterns of growth, mortality, and size of the tropical damselfish Acanthochromis polyacanthus across the continental shelf of the Great Barrier Reef

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Coral reefs are spatially diverse and heterogeneous marine environments. The Great Barrier Reef (GBR) is the largest reef system and represents a near-continuous matrix of over 2400 individual reefs spanning a distance of some 2000 km along the coast of Queensland, eastern Australia (Fig. 1). Coral reef habitats are subject to the influences of environmental (e.g., exposure and proximity to coastlines), as well as biotic processes (e.g., availability of food). Strong cross-shelf abiotic and biotic gradients (Wilkinson and Cheshire, 1988) have the potential to influence patterns of abundance and demographic characteristics of fishes associated with coral reefs. Several studies have examined the broad-scale abundance and distribution of a wide variety of organisms across the continental shelf of the GBR, including hard corals (Done, 1982), soft corals (Dinesen, 1983), crustaceans (Preston and Doherty, 1990, 1994), algae (McCook et al., 1997), and reef fishes (Williams, 1982, 1983; Williams and Hatcher, 1983; Russ, 1984a, 1984b; Newman and Williams, 1996; Newman et al., 1997; Gust et al., 2001, 2002). Great cross-shelf differences in abundance are common within and among taxa. Although environmental gradients have often been implicated as causing these patterns and it is also known that environmental features influence demographic characteristics (e.g., growth), there have been few comparisons of demographic characters by geography and spatial scale. Demographic measures are crucial to understanding population dynamics. Population demographics of a number of many fish species have been shown to vary at spatial scales ranging from 100’s of m to 100’s of km (Gillanders, 1995; Meekan et al., 2001; Gust et al., 2002). With the exception of data on a few commercially important taxa (Munro and Williams, 1985; Williams et al., 2003) and some others (e.g., acanthurids and scarids; Choat and Axe, 1996), there are few data on demographic parameters of coral reef fishes and even less on spatial variation within these parameters. Variation in demographics may be common across the shelf. For example, significant differences in the size frequency, growth, mortality, and longevity in populations of three scarids (Scarus frenatus, S. niger, and Chlorurus sordidus) and an acanthurid (Acanthurus lineatus) have been shown between mid- and outer-shelf locations on the northern GBR (Gust et al., 2001, 2002). Du-
ences in the demographic and life history features represented phenotypic plasticity.

*Acanthochromis polyacanthus* (Bleeker) is one of a few species of fish that are found in abundance at all distances across the Great Barrier Reef (Williams, 1982, 1983) and, therefore, was ideal for comparisons of cross-shelf patterns of demographic characteristics. *Acanthochromis polyacanthus* is a polymorphic gonochoristic pomacentrid and site-attached planktivore that inhabits reefs of the Indo-Australian Archipelago and adjacent regions (Allen, 1975). It is extremely wide spread and abundant along (north–south) the GBR (Williams, 1982, 1983). It is unusual among marine reef fishes and unique among damselfishes in that it lacks a dispersive planktonic larval stage (Robertson, 1973). Instead, adult *A. polyacanthus* lay demersal eggs and after hatching, both parents defend a brood of larvae and juveniles for several months (Robertson, 1973; Allen, 1975; Thresher, 1985a, 1995b; Kavanagh, 2000). In contrast to other taxa, therefore, dispersal is likely to be slow within and among reefs. *Acanthochromis polyacanthus* is one of the best studied coral reef fishes on the GBR with respect to predation (Connell, 1996, 1998, 2000), genetics and evolution (Doherty et al., 1994, 1995; Planes and Doherty, 1997a, 1997b), behavior (Robertson, 1973; Allen, 1975; Thresher, 1985a, 1995b; Nakazono, 1993; Kavanagh, 1998), reproductive success (Thresher, 1983), and early life history (Kavanagh, 2000), but no data exist on age, growth, and demographic parameters, such as mortality rates (but see estimates of juvenile mortality while larvae and juveniles are brooded by adults; Connell, 1996).

The objective of this study was to compare the demographic characteristics of *A. polyacanthus* across the continental shelf. Our approach was to sample replicate reefs in the central region of the GBR at multiple distance strata from shore (inner-, mid- and outer-shelf distances). In addition, we chose a section of the GBR where *A. polyacanthus* exhibited the same color pattern (brown anterior and white posterior) and are known to be genetically isolated (Planes and Doherty, 1997b). Any variation in demographic parameters, therefore, could be largely attributed to phenotypic plasticity. The specific objectives of this study were the following: 1) to validate the deposition of annual growth increments for fish of a wide range of sizes and ages by using tetracline, 2) to describe patterns of growth of populations of *A. polyacanthus* within and among distance strata; 3) to describe the age and size structures of populations of *A. polyacanthus* within and among distance strata, and; 4) to calculate the instantaneous mortality and survival rates (Z) of populations of *A. polyacanthus* within and among distance strata.

### Materials and methods

#### Study sites and sampling design

Spatial variation in demographics and structures of cross-shelf populations of *A. polyacanthus* was determined by using a partially hierarchical sampling design. Individuals of a wide range of sizes were collected from three replicate reefs within each of three distance strata (inner-, mid- and outer-shelf) spanning the width of the continental shelf of the central Great Barrier Reef near Townsville, Australia (Fig. 1, Table 1). At least 16 fish were collected with hand spears from each of three sites on each reef during September and October 2001. All fish collected were the same brown and white morph (Allen, 1975).

#### Sample processing

All fish were measured (standard length [SL] to the nearest mm) and weighed (to the nearest 0.01 g). Sagittal otoliths were extracted, cleaned in freshwater to remove the sagittal membrane, and allowed to dry.

---

### Table 1

Distance strata and reefs sampled during September and October 2001 over the continental shelf of the central Great Barrier Reef near Townsville, Australia, for analyses of growth patterns, mortality, and size of the tropical damselfish *Acanthochromis polyacanthus*.

<table>
<thead>
<tr>
<th>Distance strata</th>
<th>Reef sampled</th>
<th>Date(s) sampled</th>
<th>Average distance (km) to coast of the three sites ±SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inner shelf</td>
<td>Orpheus Island</td>
<td>4 and 5 Sep 2001</td>
<td>15.3 ±0.6</td>
</tr>
<tr>
<td></td>
<td>Pandora Reef</td>
<td>3 Sept 2001</td>
<td>16.4 ±0.3</td>
</tr>
<tr>
<td></td>
<td>Havannah Island</td>
<td>3 and 4 Sep 2001</td>
<td>25.1 ±0.3</td>
</tr>
<tr>
<td>Mid-shelf</td>
<td>Bramble Reef</td>
<td>15 Oct 2001</td>
<td>41.1 ±0.5</td>
</tr>
<tr>
<td></td>
<td>Britomart Reef</td>
<td>16 Oct 2001</td>
<td>38.7 ±3.0</td>
</tr>
<tr>
<td></td>
<td>The Slashers</td>
<td>20 Oct 2001</td>
<td>85.3 ±2.4</td>
</tr>
<tr>
<td>Outer shelf</td>
<td>Pith Reef</td>
<td>18 Oct 2001</td>
<td>74.4 ±0.9</td>
</tr>
<tr>
<td></td>
<td>Barnett Patches</td>
<td>17 Oct 2001</td>
<td>62.6 ±1.8</td>
</tr>
<tr>
<td></td>
<td>Myrmidon Reef</td>
<td>19 Oct 2001</td>
<td>110.4 ±0.8</td>
</tr>
</tbody>
</table>
overnight. One otolith from each fish was then imbedded in Struers Epofix resin that was allowed to harden overnight in a drying oven at 60°C. A thin (250–300 μm) transverse section perpendicular to the long axis of the otolith was then taken through the core (primordium) of the otolith with a Buehler low-speed saw with two spaced diamond blades. This section was polished by hand with 9-μm lapping film to remove saw blade marks, thereby making the internal structure of the otolith more clearly visible. The polished section was then fixed to a labelled glass microscope slide with Crystal bond thermoplastic glue.

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 with a compound microscope (Leica DMLB) and white incident light source. Alternating translucent and opaque increments were interpreted as annuli. Sections were coded and examined in random order and the opaque increments counted on two occasions by the same observer (JMH) separated by four weeks. 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 by more than two between counting occasions, then the otoliths were re-examined. If, following a third reading, agreement between the third and one of the two other counts was not reached (all matching counts were used in analyses), then the otolith was not included in the analysis; 4.6% of otoliths were rejected on this basis (n=715 fish).

Validation of growth increments

The periodicity of growth increment formation was validated by marking a group of fish (of various sizes) reared in captivity with the antibiotic tetracycline hydrochloride (Sigma-Aldrich, Ballerup, Denmark). Small (known to be 0+ fish) and large fish were chosen to determine if annuli are formed early and late in life. Fish were held at the MARFU Aquarium Facility, James Cook University. For the duration of the experiment, the fish were held in several 70–500 L aquaria at this facility.

Figure 1

Map of the nine reefs on the central Great Barrier Reef where Acanthochromis polyacanthus were collected. Distance strata from the mainland (i.e. inner-, mid- and outer-shelf distances) are also indicated.
Adult fish were injected in the coelomic cavity with 0.05 g/mL tetracycline in sterile saline solution at concentrations equivalent to 0.05 g/kg body weight (McFarlane and Beamish, 1987). The approximate weight of each individual was estimated from the relationship between weight and SL. Juveniles were mass marked by immersion in a tetracycline solution (concentration: 0.5g/L) in seawater for 12 hours (overnight). The tetracycline generally forms a very effective time-marker in otoliths; it fluoresces when viewed under ultraviolet light (Geffen, 1992).

The experiment commenced in May 2002 and fish were sacrificed after six months, one year (June 2003), and one-and-a-half years (November 2003). Ten fish had readable otoliths for which validation was attempted. Otolith sections were viewed with a compound microscope and incident ultraviolet light in a darkened room. When a fluorescing tetracycline band was identified, its position in relation to the edge was measured. The section was then examined under reflected white light and measurements of increment widths and marginal increments were recorded. Known time at liberty, expressed as a proportion of one year, was then compared with estimated time at liberty by using the growth of the otoliths. If estimated time at liberty equaled actual time at liberty, it supported the hypothesis that opaque increments were deposited annually. Juveniles and adults were collected on each occasion to determine whether increments were deposited annually, early and late in life.

The length of time for increment formation was also estimated by calculating the number of days after tetracycline treatment. The number of days after treatment was estimated by comparing the position of the tetracycline mark with that of the last (marginal) opaque increment and the width of a full annual increment with the following formula:

\[
\text{Number of days after treatment} = \frac{TE - MI}{IW} \times 365,
\]

where \( TE \) = otolith growth after treatment; \( MI \) = the marginal increment; and \( IW \) = the final full increment width.\(^1\)

Growth

It was hypothesized that patterns of growth would vary with distance from the coast. Growth rates were described by using von Bertalanffy growth functions that provided the best fit to size-at-age data when compared with estimates of the Schnute growth function (Schnute, 1981). The von Bertalanffy expression for length at age \( t \) (\( L_t \)), as a function of time is

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

where \( L_\infty \) = the asymptote of the growth curve (average maximum length); \( L_t \) = length at age \( t \); \( K \) = the rate at which the growth curve approaches the asymptote (\( L_\infty \)); \( t \) = age of fish in years; \( t_0 \) = the theoretical origin of the growth curve (i.e., the hypothetical age of the fish when it has no length); and \( e \) = the base of the natural logarithm.

Differences in growth curves for \( A. \) polyacanthus from each reef sampled were visualized by using the technique of Kimura (1980), where 95% confidence ellipses were generated around the parameter estimates of \( K \) and \( L_\infty \). Confidence ellipses that did not overlap indicated differences in growth parameters and enabled the pooling of data from sites within reefs at each distance stratum. The parameter \( t_0 \) was constrained to minus 0.05 to take into account the approximate size of \( A. \) polyacanthus at hatching (5 mm: Kavanagh, 1998, 2000).

Mortality

The instantaneous rate of mortality (\( Z \)) was calculated by using log-linear regression analyses of age-frequency data sets for \( A. \) polyacanthus populations from each reef (Pauly, 1984). With this method, recruitment was assumed to be 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. The slope of the regression line between year classes estimated the instantaneous mortality rate (\( Z \)):

\[
Z = F + M,
\]

where \( F \) = fishing mortality; and \( M \) = natural mortality (Gust et al., 2002).

Because there is no 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 \( S = e^{-Z} \) (Ricker, 1975). Comparisons of the slopes of age-frequency relationships (for estimates of \( Z \)) were made by using analysis of covariance (ANCOVA) according to the procedures of Zar (1999). 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 us to pool data at the strata level so that comparisons of mortality between shelf positions could be made.

\(^1\) We assumed similar IWs for fish older than 3 years. For fish 3 years or younger the IW was calculated as an average from all experimental fish.
Results

Age validation

All fish treated with tetracycline had clear fluorescent marks in their otoliths (Fig. 2). The positions of the fluorescent tetracycline bands in relation to the otolith margin were consistent with the deposition of opaque zones on an annual basis (Table 2). In general, percent agreement was over 75% (7/10 fish). Differences between actual and estimated time at liberty were probably related to slight variation in the small measurements that were made (i.e., fractions of a mm). The timing of deposition of the opaque increment was estimated to occur in spring because new increments were found at the edge of otoliths of fish that had been marked in May and sacrificed about 200 days later.

Size and age structures

There were large differences in the size-frequency distributions of fish sampled across the shelf (Fig. 3). At
inner-shelf reefs \( n=155 \), only one fish >100 mm was collected. In contrast, between 38\% and 54\% of fish collected from outer-shelf reefs were >100 mm. A mix of inner- and outer-shelf size-frequency distributions was evident for mid-shelf reefs. Bramble and Britomart reefs had 1\% and 7\% of fish >100 mm, respectively, whereas The Slashers had the highest proportion of fish >100 mm collected of any reef (67\%) including the largest individual fish collected (120 mm); however, this result was more characteristic of outer-shelf reefs. Another conspicuous feature of the cross-shelf size frequencies was the very narrow size range of adult fish collected on inner-shelf reefs in comparison to the size range of fish collected from mid- and outer-shelf locations (Fig. 3). Size selectivity due to the collection technique (hand spear) restricted the numbers of fish <60 mm that could be collected.

Maximum age of \( A. \) polyacanthus was similar at all reefs sampled (Fig. 4; inner shelf: 9–10 yr, mid-shelf: 9–10 yr, outer shelf: 10–11 yr). The largest age class of fish on the inner-and mid-shelf reefs comprised 3–4 year olds, whereas on the outer-shelf reefs, 2-year-old fish made up the largest proportion of the populations. The two oldest fish were both collected from outer-shelf reefs (Myrmidon and Barnett Patches) and were both 11 years old. Strong age-structured cohorts of fish were found at some reefs within the same distance stratum and these cohorts were found only at these reefs and distance stratum. For example, there were strong year classes at Pith and Barnett Patches in years 5 and 6 that were not found at Myrmidon (Fig. 4).

**Growth**

Variation in patterns of growth was greater among distance strata across the shelf than among reefs within a distance strata (Fig. 5). There was variation in growth between individuals from reefs within each shelf position and this resulted in variable size-at-age relationships (Fig. 5). From inner-shelf reefs, fish from Pandora showed small asymptotic sizes and thus had lower average \( L_{\infty} \) (\( L_{\infty}=77.4 \) mm) compared to fish from Orpheus and Havannah (\( L_{\infty}=87.0, 84.2 \) mm, respectively; Table 3). Distinct, non-overlapping ellipses formed in 95\% confidence interval plots of \( L_{\infty} \) in relation to \( K \) confirmed that growth curves for fish from Pandora differed from those at Orpheus and Havannah (Fig. 5). Fish collected from mid-shelf reefs (Bramble, Britomart, and The Slashers) showed differences in growth among all reefs (non-overlapping 95\% confidence ellipses; Fig. 5). Growth of fish

![Figure 3](image-url)

*Figure 3*  
Size-frequency distributions for *Acanthochromis polyacanthus* collected from three reefs at each distance stratum from shore. Data were pooled for the three sites sampled at each reef.
from the outer reefs (Pith, Barnett Patches, and Myrmidon), however, was similar for fish from each of these reefs (overlapping 95% confidence ellipses; Fig. 5). Average maximum length ($L_\infty$) varied across the shelf and differences among strata were generally greater than within-distance strata. The $K$ values for all three
shelf positions were similar and indicated that K values for *A. polyacanthus* converge at asymptotic sizes at approximately the same rate of growth, irrespective of proximity to the coast (Fig. 5 and Table 3). However, an obvious trend for increased $L_\infty$ occurred with increasing distance from the coast (inner shelf: ~83 mm, mid-shelf: ~99 mm, outer shelf: ~102 mm). The growth parameters of fish from The Slashers were more similar to those of fish taken from the outer-shelf reefs than to those we defined *a priori* as mid-shelf (Fig.6). The Slashers are in fact much farther from the coast (85 km), as are Pith Reef (74 km) and Barnett Patches (63 km) on the outer shelf, than the other two mid-shelf reefs (Britomart: 39 km, Bramble: 41 km) (Fig. 1, Table 1).

**Mortality**

Mortality rates for *A. polyacanthus* did not differ significantly between replicate reefs within inner-shelf (test for slopes $df_{(2,19)}$, $F=0.982$, $P=0.39$), mid-shelf (test for slopes $df_{(2,19)}$, $F=1.334$, $P=0.29$) or outer-shelf (test for slopes $df_{(2,19)}$, $F=0.658$, $P=0.53$) locations (Table 4).
Age frequencies, therefore, were pooled at the shelf level (within distance strata; Fig 7).

*Acanthochromis polyacanthus* mortality rates did not differ significantly between the inner-, mid- and outer-shelf strata (test for slopes df(8, 63), $F=0.367, P=0.70$) (Fig. 6). Although mortality estimates were progressively lower with increased distance from the coast, this trend was not significant (inner shelf: −0.51, midshelf: −0.48, outer shelf: −0.43; Fig. 6, Table 4). Associated survival rate estimates ($S$) varied between reefs by ~9% per annum at inner- and mid-shelf strata and by ~6% per annum on the outer shelf (Table 3). The mean difference in survival rates for *A. polyacanthus* between the inner and mid-shelf was ~2% and between the mid- and outer shelf was ~3% (Table 4).

**Discussion**

The demographic parameters of $L_\infty$ and patterns of growth for populations of *A. polyacanthus* varied across the shelf on the central GBR. Although there was variation in body size and growth among reefs within a distance stratum, it was minor compared to overall cross-shelf patterns. In this study, mortality estimates and maximum age were similar for populations of fish across the shelf. Thus, in order to explain the cross-shelf trend in body size, fish must have grown faster with increasing distance from shore (Fig. 7, Table 1).

Despite the relative paucity of age-based studies on reef fishes (Choat and Robertson, 2002), variable rates of growth have been previously demonstrated for fish at local scales (hundreds of metres to kilometers: Fowler and Doherty, 1992), medium scales (kilometers to tens of kilometers: Choat and Axe, 1996; Hart and Russ, 1996; Newman et al., 1996; Meekan et al., 2001; Gust et al., 2002), and large scales (thousands of kilometers: Choat and Robertson, 2002). Gust et al. (2002) found that growth patterns of scarids varied between the reef crests of mid- and outer-shelf sampling locations on the northern GBR. In contrast to the results from the current study, however, outer-shelf populations of scarids had smaller asymptotic sizes and slower growth rates than mid-shelf populations. The factors influencing patterns of growth, therefore, vary by group.

Differences in the shape of growth curves between geographic regions or areas may be determined by both genetic and environmental influences (Sebens, 1987). Populations of reef fish are generally considered to be genetically open systems (Sale, 1991) and it is considered unlikely that adaptation of such populations to local conditions through genetic selection can occur (Warner, 1991). *Acanthochromis polyacanthus*, however, possesses a unique life history trait among reef fishes in that it lacks a dispersive larval phase. The major implication of this characteristic is the potential for genetic isolation of populations of these fish. Even reefs that are in relatively close proximity to one another (100's of m) may become “genetic islands” isolated by any barrier that proves impassable to adults (e.g., deep water). Without gene flow, reproductively isolated:

---

### Table 3

<table>
<thead>
<tr>
<th>Shelf location and reef</th>
<th>n</th>
<th>$L_\infty$</th>
<th>$K$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inner shelf</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orpheus Island</td>
<td>36</td>
<td>87.03</td>
<td>0.77</td>
<td>0.83</td>
</tr>
<tr>
<td>Pandora Reef</td>
<td>44</td>
<td>77.43</td>
<td>1.39</td>
<td>0.92</td>
</tr>
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<td>Havannah Island</td>
<td>67</td>
<td>84.23</td>
<td>1.07</td>
<td>0.81</td>
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<tr>
<td>Mid-shelf</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bramble Reef</td>
<td>97</td>
<td>92.24</td>
<td>1.04</td>
<td>0.83</td>
</tr>
<tr>
<td>Britomart Reef</td>
<td>85</td>
<td>96.37</td>
<td>0.95</td>
<td>0.87</td>
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<tr>
<td>The Slashers</td>
<td>91</td>
<td>106.73</td>
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<td>0.75</td>
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<td></td>
</tr>
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<td>Pith Reef</td>
<td>100</td>
<td>101.98</td>
<td>1.11</td>
<td>0.76</td>
</tr>
<tr>
<td>Barnett Patches</td>
<td>114</td>
<td>100.27</td>
<td>1.13</td>
<td>0.78</td>
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<tr>
<td>Myrmidon Reef</td>
<td>82</td>
<td>103.66</td>
<td>1.15</td>
<td>0.70</td>
</tr>
</tbody>
</table>

---

### Figure 6

95% confidence ellipses for the von Bertalanffy growth parameters $K$ (growth coefficient) and $L_\infty$ (mean asymptotic length) for *Acanthochromis polyacanthus* from all reefs sampled.
populations are expected to diverge over time with respect to their genetic composition (Doherty et al., 1994). Numerous studies have examined the genetic relationships between populations of *A. polyacanthus* on the GBR (Doherty et al., 1994, 1995; Planes and Doherty, 1997a, 1997b). Isozyme analyses of populations of different color morphs at various spatial scales have shown significant genetic variation at both the regional (1000's of km) and local (100's of m) level, which under normal circumstances would suggest separate species for each color morph (Doherty et al., 1994; Planes and Doherty, 1997a). However, differences in the growth rates of *A. polyacanthus* across the continental shelf in this study are unlikely to reflect genetic differences between the populations sampled because all individuals collected were of the same color morph and were from a relatively small area (about 400 km², cf. 450,000 km² for the entire GBR).

Environmental influences that can affect patterns of growth include predation pressure, temperature, and related effects on metabolism, variations in resources (e.g., abundance of planktonic food), and variation in water condition (e.g., turbidity).

High rates of predation may “drive” faster growth (Werner, 1984), or conversely, select for early maturation and smaller adult size (Reznick et al., 1990; Hutchings, 1997). It is unlikely that the cross-shelf patterns in growth that we found were determined by differences in mortality rates. Some data on serranid abundance (Williams, 1982) and anecdotal accounts have indicated that predator abundance is greatest on mid- and outer reefs of the GBR (Gust et al., 2001). Our measures of instantaneous mortality (Z) and age maximum, however, did not vary with distance from the mainland. Furthermore, in contrast to the patterns that Gust et al. (2001) found for scarids, $L_a$ increased with distance from the coast. Mortality rates have been shown to vary among locations within reefs for several species of coral reef fish (Alden, 1986; Eckert, 1987; Sale and Ferrell, 1988; Beukers and Jones, 1997) including *A. polyacanthus* juveniles (Connell, 1996), as well as over larger spatial scales (Meekan et al., 2001; Gust et al., 2002). In contrast to these last two studies, particularly that of Gust et al. (2002), mortality rates for *A. polyacanthus* were similar at all three cross-shelf strata. We acknowledge, however, that no data were available on mortality rates of fish from zero to two years of age. It is possible that mortality rates do vary with distance from shore over this age range.

An increase in adult size may occur when individuals experience a decline in average temperature during development (Atkinson, 1994). It is also well established that metabolism and growth are increased at higher ambient temperatures in ectotherms (Schmidt-Nielsen, 1990). Differences in temperature between the water bodies spanning inner-, mid- and outer-shelf positions in the central GBR do occur; relatively shallow near-

---

**Table 4**

<table>
<thead>
<tr>
<th>Reef</th>
<th>Pooled M</th>
<th>S (%)</th>
<th>Pooled S (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inner shelf</td>
<td>0.51</td>
<td>60.0</td>
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</tr>
<tr>
<td>Orpheus Island</td>
<td>0.29</td>
<td>74.8</td>
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<tr>
<td>Pandora Reef</td>
<td>0.40</td>
<td>67.0</td>
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<td>Havannah Island</td>
<td>0.42</td>
<td>65.7</td>
<td></td>
</tr>
<tr>
<td>Mid-shelf</td>
<td>0.48</td>
<td>61.8</td>
<td></td>
</tr>
<tr>
<td>Bramble Reef</td>
<td>0.44</td>
<td>64.4</td>
<td></td>
</tr>
<tr>
<td>Britomart Reef</td>
<td>0.48</td>
<td>61.9</td>
<td></td>
</tr>
<tr>
<td>The Slashers</td>
<td>0.34</td>
<td>71.2</td>
<td></td>
</tr>
<tr>
<td>Outer shelf</td>
<td>0.43</td>
<td>65.1</td>
<td></td>
</tr>
<tr>
<td>Pith Reef</td>
<td>0.32</td>
<td>72.6</td>
<td></td>
</tr>
<tr>
<td>Barnett Patches</td>
<td>0.40</td>
<td>67.0</td>
<td></td>
</tr>
<tr>
<td>Myrmidon Reef</td>
<td>0.38</td>
<td>68.4</td>
<td></td>
</tr>
</tbody>
</table>

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**Figure 7**

Age-based catch curve estimates of *Acanthochromis polyacanthus* mortality rates for reefs pooled by distance strata.
shore waters are the warmest and outer-shelf waters are the coolest (Wolanski, 2001). The opposite pattern of growth to the one observed in this study would be predicted by a cross-shelf gradient in water temperature. It is also considered unlikely that local upwelling events on outer-shelf reefs could produce the observed differences, but they could influence primary productivity and abundance of food (zooplankton) through nutrient-rich waters. An increase in average annual temperature correlates with maximum age in some fishes (review Choat and Robertson, 2002), but we found no differences in age maximum across the shelf. We conclude that any differences in temperature across the shelf are not persistent enough to affect cross-shelf patterns of growth of *A. polyacanthus*.

Differences in growth profiles can be more realistically attributed to cross-shelf variation in some limiting resource(s). This variation in resources may influence the quality and quantity of food, suitable nest sites, refuges from predators and (or) wave exposure, and density of conspecifics and (or) other species that compete with *A. polyacanthus* for resources. Correlative studies have concluded that the distribution and abundance of coral reef fishes is strongly influenced (directly and indirectly) by physical factors such as wave exposure, sediment loads, water depth, and topographical complexity, as well as by biological factors (Williams, 1982). These factors also have the potential to affect growth rates.

A combination of reduced resource levels and high population densities on outer-shelf reefs strongly indicated that growth profiles represent density dependence in scarids (Gust et al., 2001, 2002). Density of con- and hetero-specifics was not recorded for our study, but densities of *A. polyacanthus* were clearly greatest on the mid- and outer-shelf reefs. This observation is contrary to the pattern noted by Williams (1982) who found greatest abundances of *A. polyacanthus* on inner- and mid-shelf reefs. Thresher (1983) suggested that food abundance is a limiting resource for *A. polyacanthus* and interspecific competition for food does occur. Thus, it is plausible that variation in abundance of and competition for food across the shelf may have influenced the growth rates observed in the present study. The large differences in cross-shelf densities and *L*~∞~'s of *A. polyacanthus* indicate that competition may be less important than variation in quantity and quality of food across the shelf.

Biomass of planktivores is generally highest at mid-shelf reefs on the central GBR (Williams and Hatcher, 1983). Although data on cross-shelf abundance and distribution of plankton are limited, Williams and Hatcher attributed this pattern to the increased availability of food (zooplankton) in mid-shelf waters. Upwelling of cold, nutrient-rich water from the edge of the continental shelf results in high biomasses of phytoplankton. Aging of the water (time since upwelling) is accompanied by a shift in dominant planktonic biomass to herbivorous and then carnivorous zooplankton. This shift in biomass composition occurs simultaneously with the prevailing wind-driven passage of water across the shelf and ultimately leads to the greatest biomass of zooplankton occurring in mid-shelf waters (Andrews and Gentien, 1982; Sammarco and Crenshaw, 1984; Williams et al., 1988). Food quality has also been previously shown to limit growth and reproduction in herbivorous coral reef fishes (Horn, 1989; Choat, 1991).

Despite a high abundance of zooplankton near shore, these waters also have higher turbidity than mid- and outer-shelf reefs. Visual impairment caused by very turbid waters may hinder the ability of fish to feed on planktonic organisms and this hypothesis has been suggested as a factor contributing to the low relative abundances of planktivorous fish on inner-shelf reefs (Williams et al., 1986). It is possible that this factor may retard the growth and influence the maximum size of planktivores like *A. polyacanthus* by effectively reducing food availability. Interestingly, lowest *L*~∞~ values were found at the most turbid inshore reef, Pandora. Lower visibility near shore, however, did not appear to affect the mortality rates of *A. polyacanthus* at inner-shelf reefs.

There were clear differences in growth, size maxima, and age structures for populations of *A. polyacanthus* across the continental shelf of the central GBR. Although *Acanthochromis polyacanthus* grew faster and to a larger size with increasing distance from the mainland, cross-shelf mortality rates and maximum ages were similar. Because these populations of fish are unlikely to be genetically distinct, we suggest that biotic and physical processes are the most plausible cause of these cross-shelf patterns. Increased abundance of zooplankton in mid- and outer-shelf waters, coupled with potential visual impairment associated with high turbidity levels on the inner shelf, are likely mechanisms that explain the observed patterns, but multifactorial manipulative experiments are required to determine the relative contribution of these factors to variation in demographic parameters. Our study therefore cautions against pooling demographic parameters over broad spatial scales without considering cross-shelf variation.

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