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

Michael J. Kingsford

Julian M. Hughes

Reef and Ocean Ecology Laboratory
School of Marine Biology and Aquaculture
James Cook University
James Cook Drive
Townsville, Queensland, Australia 4811
E-mail address (for M. J. Kingsford): Michael.Kingsford@jcu.edu.au

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.

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). Dudgeon et al. (2000) found evidence that high levels of genetic exchange occurred between populations of these fishes on mid- and outer-shelf reefs and concluded that observed differ-

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*.

Distance strata	Reef sampled	Date(s) sampled	Average distance (km) to coast of the three sites ±SE
Inner shelf	Orpheus Island	4 and 5 Sep 2001	15.3 ±0.6
	Pandora Reef	3 Sept 2001	16.4 ±0.3
	Havannah Island	3 and 4 Sep 2001	25.1 ±0.3
Mid-shelf	Bramble Reef	15 Oct 2001	41.1 ±0.5
	Britomart Reef	16 Oct 2001	38.7 ±3.0
	The Slashers	20 Oct 2001	85.3 ±2.4
Outer shelf	Pith Reef	18 Oct 2001	74.4 ±0.9
	Barnett Patches	17 Oct 2001	62.6 ±1.8
	Myrmidon Reef	19 Oct 2001	110.4 ±0.8

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 tetracycline, 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
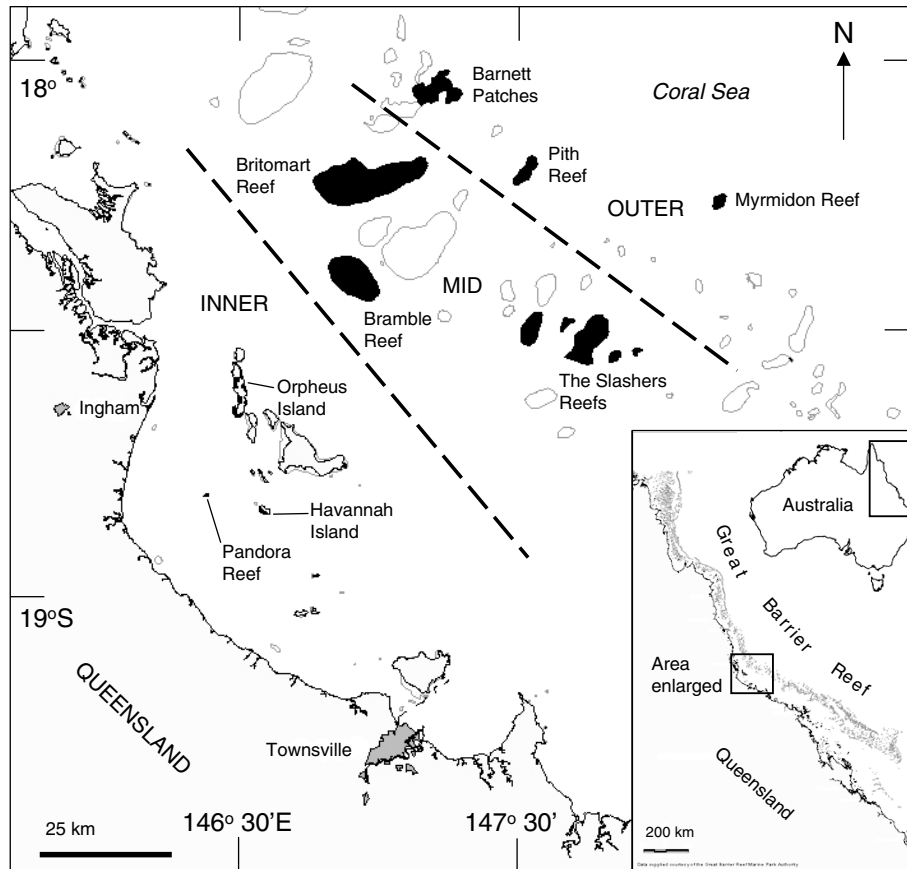
Figure 1

Map of the nine reefs on the central Great Barrier Reef where *Acanthochromis poly-acanthus* were collected. Distance strata from the mainland (i.e. inner-, mid- and outer-shelf distances) are also indicated.

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.

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 equalled 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 tetracylcline 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:

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

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

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

where L_∞ = 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_∞);
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_∞. 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):
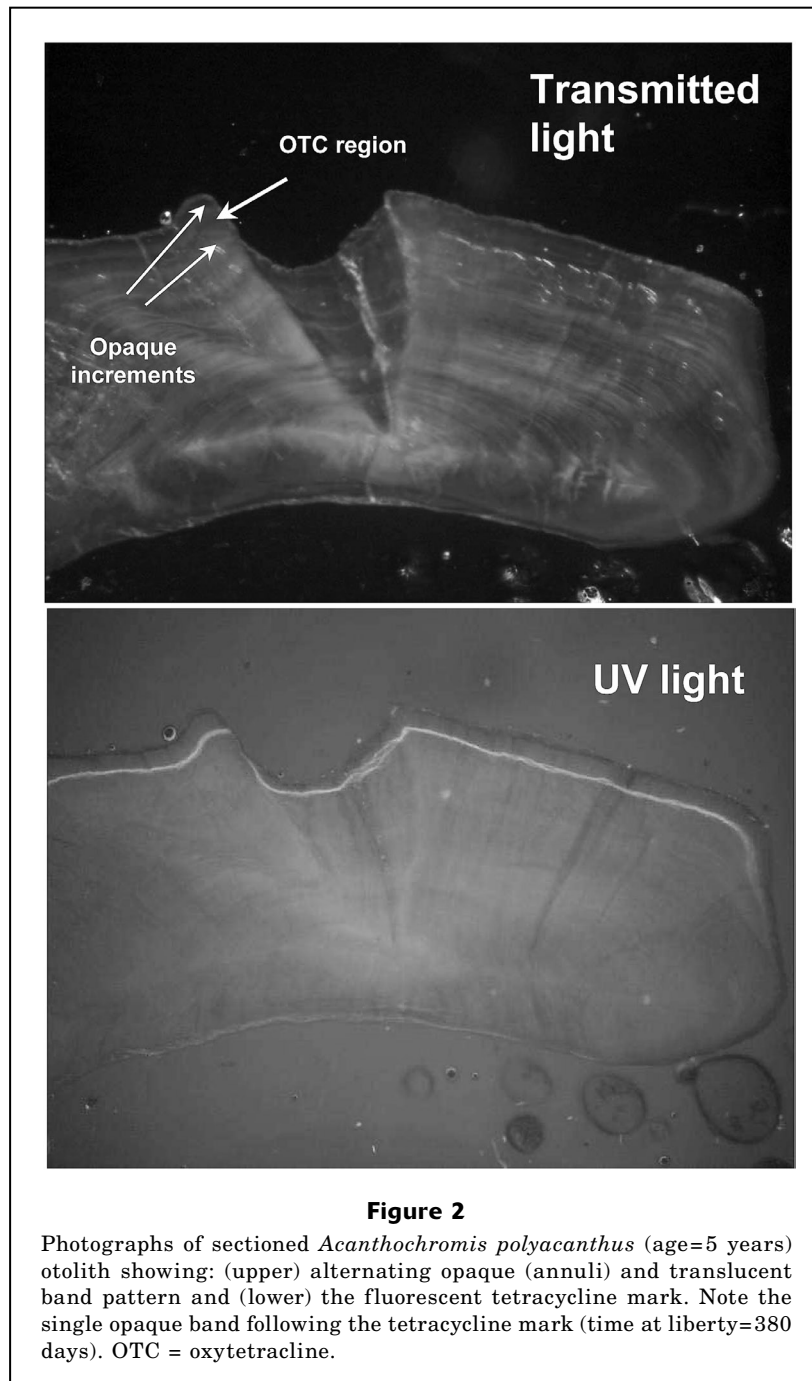
$$Z = F + M,$$

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.

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[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.

Figure 2

Photographs of sectioned *Acanthochromis polyacanthus* (age=5 years) otolith showing: (upper) alternating opaque (annuli) and translucent band pattern and (lower) the fluorescent tetracycline mark. Note the single opaque band following the tetracycline mark (time at liberty=380 days). OTC = oxytetracline.
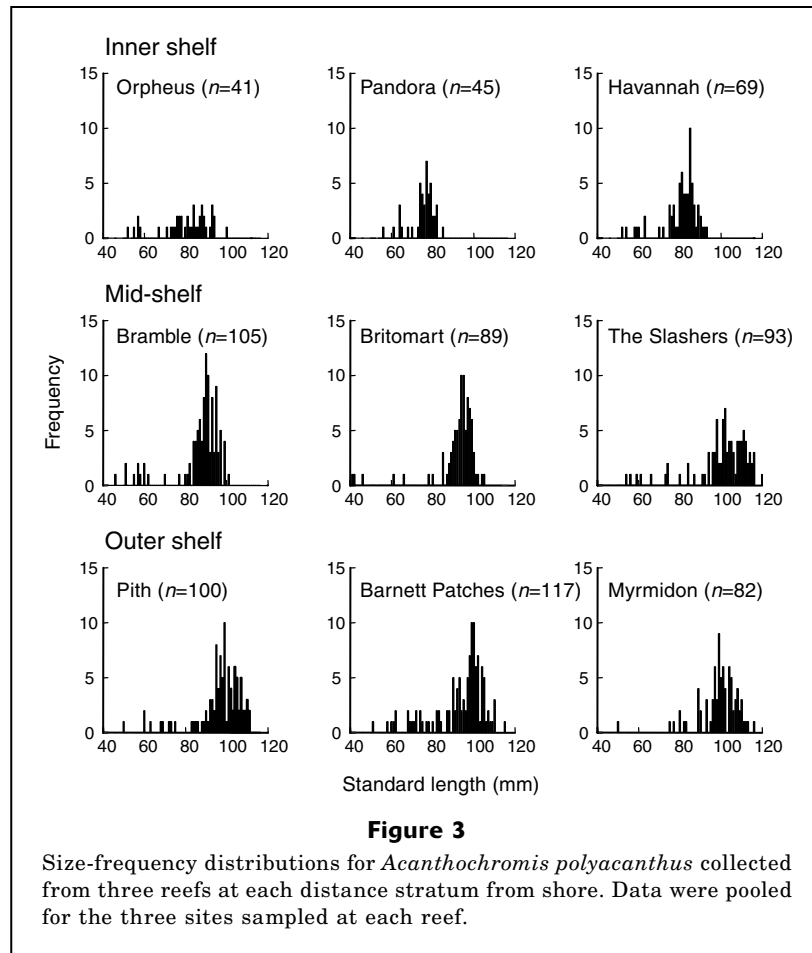
Results

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

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.

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_∞, (L_∞=77.4 mm) compared to fish from Orpheus and Havannah (L_∞=87.0, 84.2 mm, respectively; Table 3). Distinct, non-overlapping ellipses formed in 95% confidence interval plots of L_∞ 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
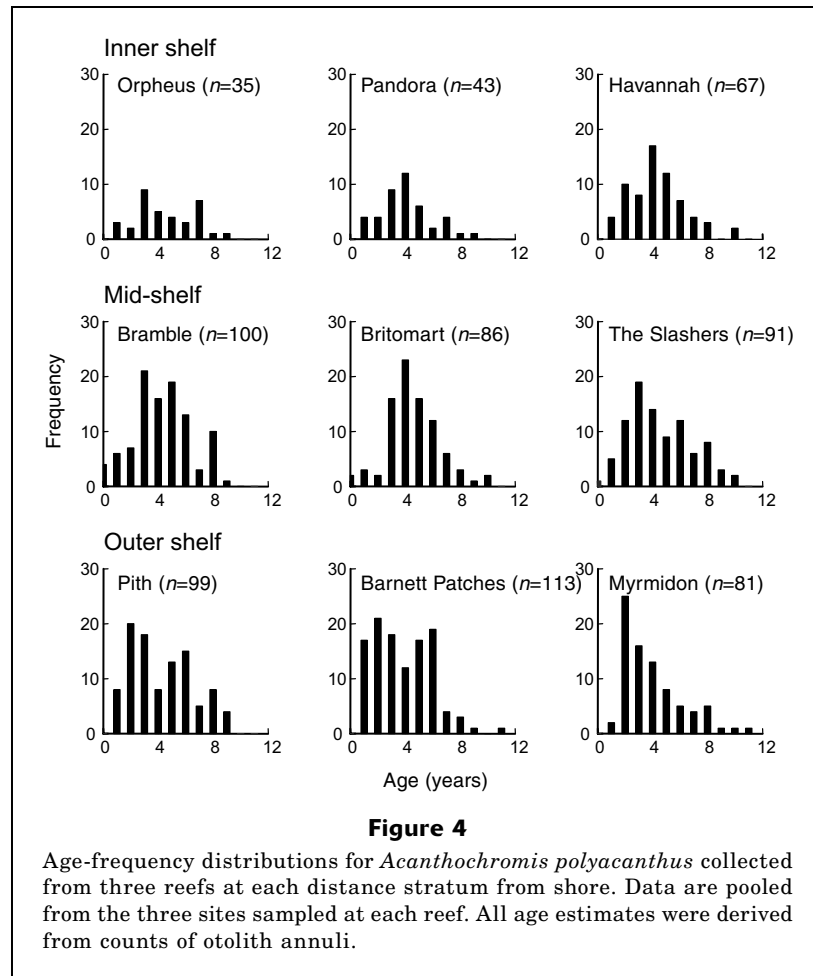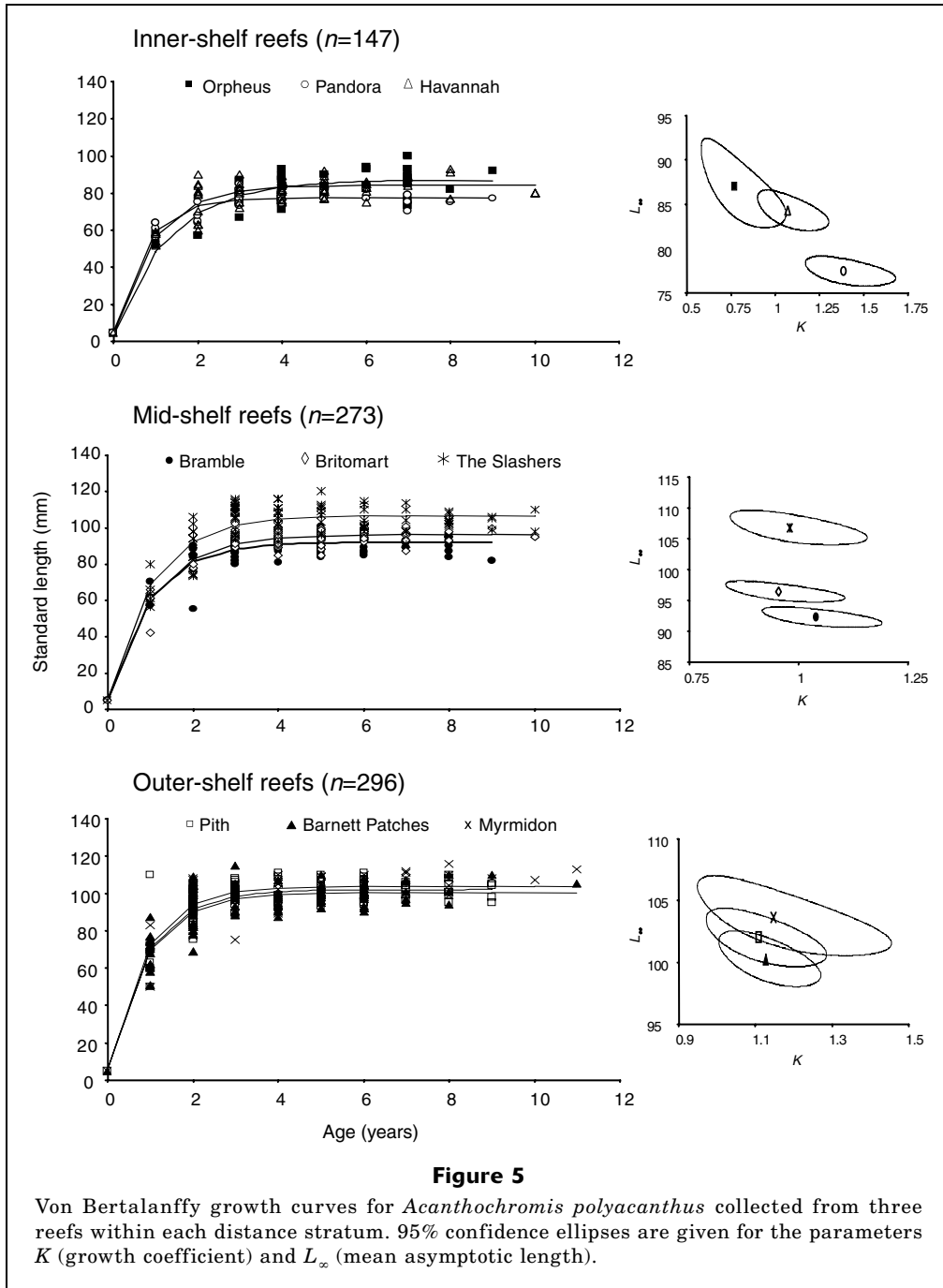
Figure 4

Age-frequency distributions for *Acanthochromis polyacanthus* collected from three reefs at each distance stratum from shore. Data are pooled from the three sites sampled at each reef. All age estimates were derived from counts of otolith annuli.

Table 2

Validation data with the use of tetracycline to determine the periodicity and timing of opaque ring deposition for *Acanthochromis polyacanthus* with the use of tetracycline as a time marker. TAL = time at liberty expressed as a proportion of one year and derived from growth measurements from reared fish treated with tetracycline. TC = tetracycline.

Fish age (yr)	TC to marginal increment (mm)	TAL (mm)	TAL as proportion of year	Estimated days from TC marking	Actual days from TC marking	Percent agreement = (estimated/actual × 100)
1	0.0423	0.30	0.43	110	158	69
1	0.0463	0.33	0.43	120	158	76
1	0.1784	0.94	0.97	344	355	97
5	0.0686	0.80	1.04	291	380	76
5	0.0739	0.83	1.04	304	380	80
5	0.1077	1.00	1.52	365	556	66
5	0.0805	0.81	1.52	295	556	53
6	0.1471	1.46	1.47	532	537	99
7	0.1034	0.90	1.12	327	409	80
7	0.0919	1.30	1.52	474	556	85

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_∞) varied across the shelf and differences among strata were generally greater than within-distance strata. The K values for all three

Figure 5

Von Bertalanffy growth curves for *Acanthochromis polyacanthus* collected from three reefs within each distance stratum. 95% confidence ellipses are given for the parameters K (growth coefficient) and L_∞ (mean asymptotic length).

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_∞ 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, mid-shelf: –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_{∞} 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,* how-
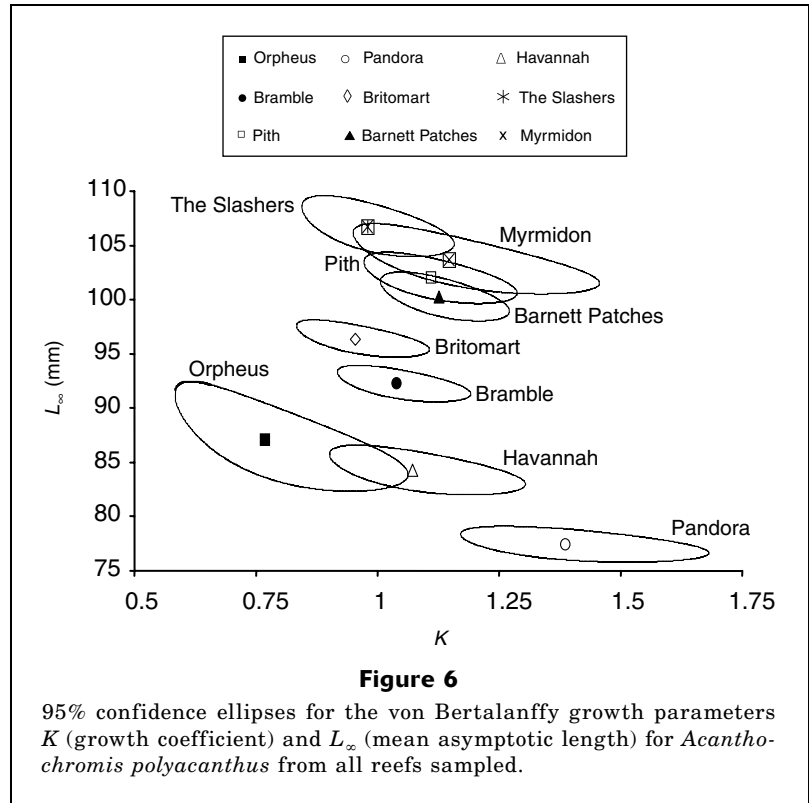

Figure 6

95% confidence ellipses for the von Bertalanffy growth parameters *K* (growth coefficient) and L_{∞} (mean asymptotic length) for *Acanthochromis polyacanthus* from all reefs sampled.

Table 3

Parameters from von Bertalanffy growth models on the fishes collected from different distance strata and reefs.

Shelf location and reef	*n*	L_{∞}	*K*	r^2
Inner shelf				
Orpheus Island	36	87.03	0.77	0.83
Pandora Reef	44	77.43	1.39	0.92
Havannah Island	67	84.23	1.07	0.81
Mid-shelf				
Bramble Reef	97	92.24	1.04	0.83
Britomart Reef	85	96.37	0.95	0.87
The Slashers	91	106.73	0.98	0.75
Outer shelf				
Pith Reef	100	101.98	1.11	0.76
Barnett Patches	114	100.27	1.13	0.78
Myrmidon Reef	82	103.66	1.15	0.70

ever, 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 4

Estimates of mortality (*M*) for fishes collected from different distance strata and reefs. Pooled values are for all reefs within one distance stratum. *n* = number of fish in sample. *S* = animal survival rate.

Reef	*n*	*M*	Pooled *M*	*S* (%)	Pooled *S* (%)
Inner shelf			0.51		60.0
Orpheus Island	30	0.29		74.8	
Pandora Reef	34	0.40		67.0	
Havannah Island	45	0.42		65.7	
Mid-shelf			0.48		61.8
Bramble Reef	83	0.44		64.4	
Britomart Reef	63	0.48		61.9	
The Slashers	73	0.34		71.2	
Outer shelf			0.43		65.1
Pith Reef	91	0.32		72.6	
Barnett Patches	96	0.40		67.0	
Myrmidon Reef	79	0.38		68.4	

Figure 7

Age-based catch curve estimates of *Acanthochromis polyacanthus* mortality rates for reefs pooled by distance strata.

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 indicted 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
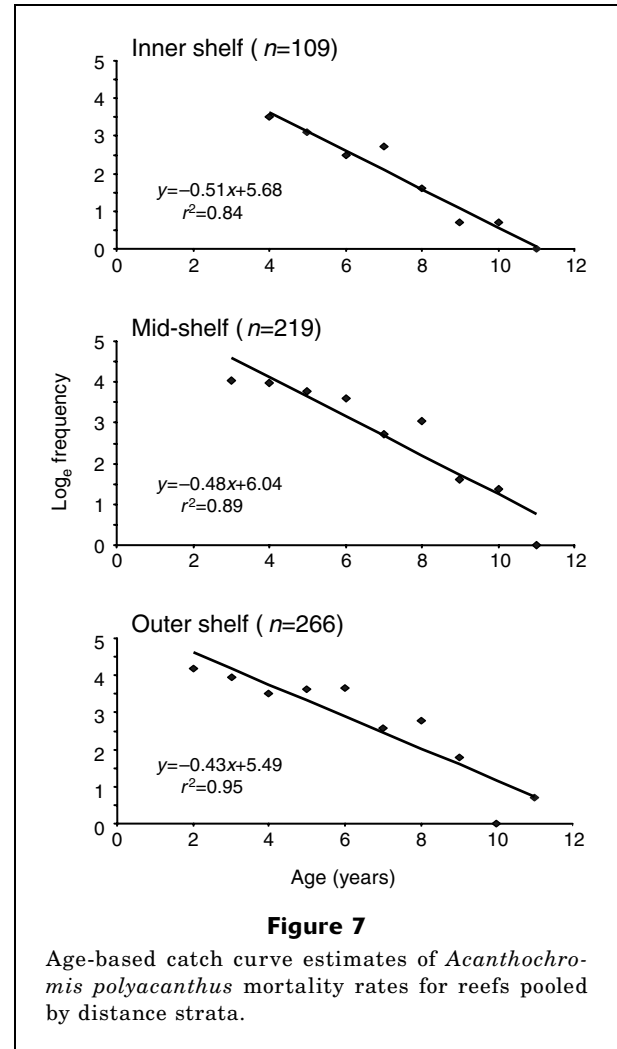
al. (2001) found for scarids, L_∞ increased with distance from the coast. Mortality rates have been shown to vary among locations within reefs for several species of coral reef fish (Aldenhoven, 1986; Eckert, 1987; Sale and Ferrell, 1988; Beukers and Jones, 1997) including *A. polyacanthus* juveniles (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-

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 this 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.

Acknowledgments

Literature cited

Aldenhoven, J. M.
    1986. Local variation in mortality rates and life history estimates of the coral reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). Mar. Biol. 92:237–244.

Allen, G. R.
   1975.   Damselfishes of the South Seas, 240 p.   Tropical
       Fish Hobbyist Publications, Neptune City, NJ.
Andrews J. C., and P. Gentien.
   1982.   Upwelling as a source of nutrients for the Great
       Barrier Reef ecosystems: a solution to Darwin's ques-
       tion?   Mar. Ecol. Prog. Ser. 8:257–269.
Atkinson, D.
   1994.   Temperature and organism size—a biological law
       for ectotherms?   Adv. Ecol. Res. 25:1–58.
Beukers, J. J., and G. P. Jones.
   1997.   Habitat complexity modifies the impact of pisci-
       vores on a coral reef fish population.   Oecologia 114:
       50–69.
Choat, J.
   1991.   The biology of herbivorous fishes on coral reefs.
       In The ecology of fishes on coral reefs (P. F. Sale, ed.),
       p. 120–155.   Academic Press, San Diego, CA.
Choat, J., and L. Axe.
   1996.   Growth and longevity in acanthurid fishes: an
       analysis of otolith increments.   Mar. Ecol. Prog. Ser.
       134:15–26.
Choat, J., and D. R. Robertson.
   2002.   Age-based studies.   *In* Coral reef fishes (P. F.
       Sale, ed.), p. 57–80.   Academic Press, Amsterdam, The
       Netherlands.
Connell, S. D.
   1996.   Variations in mortality of a coral reef fish: links
       with predator abundance.   Mar. Biol. 126:347–352.
   1998.   Effects of predators on growth, mortality and abun-
       dance of a juvenile reef fish: evidence from manipula-
       tions of predator and prey abundance.   Mar. Ecol. Prog.
       Ser. 169:251–261.
   2000.   Is there safety-in-numbers for prey?   Oikos
       88(3):527–532.
Dinesen, Z. D.
   1983.   Patterns in the distribution of soft corals across the
       central Great Barrier Reef.   Coral Reefs 1:229–236.
Doherty, P. J., S. Planes, and P. Mather.
   1994.   *Acanthochromis polyacanthus*, a fish lacking
       larval dispersal, has genetically differentiated popula-
       tions at local and regional scales on the Great Barrier
       Reef.   Mar. Biol. 121(1):11–21.
   1995.   Gene flow and larval duration in seven spe-
       cies of fish from the Great Barrier Reef.   Ecology
       76(8):2373–2391.
Done, T. J.
   1982.   Patterns in the distribution of coral communities
       across the central Great Barrier Reef.   Coral Reefs
       1:95–107.
Dudgeon, C. L., N. Gust, and D. Blair.
   2000.   No apparent genetic basis to demographic differ-
       ences in scarid fishes across the continental shelf of the
       Great Barrier Reef.   Mar. Biol. 137:1059–1066.
Eckert, G. J.
   1987.   Estimates of adult and juvenile mortality for labrid
       fishes at One Tree Reef, Great Barrier Reef.   Mar.
       Biol. 95:167–171.
Fowler, A. J., and P. J. Doherty.
   1992.   Validation of annual growth increments in the
       otoliths of two species of damselfish from the south-
       ern Great Barrier Reef.   Aust. J. Mar. Freshw. Res.
       43:1057–1068.
Geffen, A. J.
   1992.   Validation of otolith increment deposition rate.   *In*
       Otolith microstructure examination and analysis (D. K.

Stevenson, and S. E. Campana, eds.), p. 101–113.   Can.
       Spec. Publ. Fish. Aquat. Sci. 117.
Gillanders, B. M.
   1995.   Feeding ecology of the temperate marine fish *Acho-
       erodus viridis* (Labridae): size, seasonal and site-specific
       differences.   Mar. Freshw. Res. 46(7):1009–1020.
Gust, N., J. H. Choat, and J. L. Ackerman.
   2001.   Demographic plasticity in tropical reef fishes.   Mar.
       Biol. 140:1039–1051.
Gust, N., J. H. Choat, and M. McCormick.
   2002.   Spatial variability in reef fish distribution, abun-
       dance, size and biomass: a multi-scale analysis.   Mar.
       Ecol. Prog. Ser. 214:237–251.
Hart, A. M., and G. R. Russ.
   1996.   Response of herbivorous fishes to crown of
       thorns starfish *Acanthaster planci* outbreaks III. Age,
       growth, mortality and maturity indices of *Acanthurus
       nigrofuscus*.   Mar. Ecol. Prog. Ser. 136:25–35.
Horn, M. H.
   1989.   Biology of marine herbivorous fishes.   Oceanogr.
       Mar. Biol. Annu. Rev. 27:167–272.
Hutchings, J. A.
   1997.   Life history responses to environmental variability
       in early life.   *In* Early life history and recruitment in
       fish populations (R. C. Chambers, and E. A. Trippel,
       eds.), p. 139–168.   Chapman & Hall, London, UK.
Kavanagh, K.
   1998.   Notes on the frequency and function of glanc-
       ing behavior in juvenile *Acanthochromis* (Poma-
       centridae).   Copeia 1998(2):493–496.
   2000.   Larval brooding in the marine damselfish *Acan-
       thochromis polyacanthus* (Pomacentridae) is correlated
       with highly divergent morphology, ontogeny and life-
       history traits.   Bull. Mar. Sci. 66(2):321–37.
Kimura, D. K.
   1980.   Likelihood methods for comparison of von Berta-
       lanffy growth curves.   Fish. Bull. 77:765–776.
McCook, L. J., I. R. Price, and D. W. Klumpp.
   1997.   Macro algae on the Great Barrier Reef: causes or con-
       sequences, indicators or models of reef degradation?   Proc.
       8th Int. Coral Reef Symp. 2:1851–1856.
McFarlane, G. A., and R. J. Beamish.
   1987.   Selection of dosages of oxytetracycline for age valida-
       tion studies.   Can. J. Fish. Aquat. Sci. 44:905–909.
Meekan, M. G., J. L. Ackerman, and G. M. Wellington.
   2001.   Demography and age structures of coral reef dam-
       selfishes in the tropical eastern Pacific Ocean.   Mar.
       Ecol. Prog. Ser. 212:223–232.
Munro, J. L., and D. M. Williams.
   1985.   Assessment and management of coral reef fisheries:
       biological, environmental and sociological aspects.   Proc.
       5th Int. Coral Reef Congr. 4:545–581.
Nakazono, A.
   1993.   One-parent removal experiment in the brood-caring
       damselfish, *Acanthochromis polyacanthus*, with pre-
       liminary data on reproductive biology.   Aust. J. Mar.
       Freshw. Res. 44(5):699–707.
Newman, S. J., and D. M. Williams.
   1996.   Variation in reef associated assemblages of the
       Lutjanidae and Lethrinidae at different distances off-
       shore in the central Great Barrier Reef.   Environ. Biol.
       Fish. 46:123–138.
Newman, S. J., D. M. Williams, and G. R. Russ.
   1996.   Age validation, growth and mortality rates of the
       tropical snappers (Pisces: Lutjanidae) *Lutjanus adetii*
       (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790)

from the central Great Barrier Reef, Australia. Mar. Freshw. Res. 47:575–584.

    1997. Patterns of zonation of assemblages of the Lutjanidae, Lethrinidae and Serranidae (Epinephelinae) within and among mid shelf and outer shelf reefs in the central Great Barrier Reef. Mar. Freshw. Res. 48:119–128.

Pauly, D.
    1984. Fish population dynamics in tropical waters. ICLARM Stud. Rev. 8:1–325.

Planes, S., and P. J. Doherty.
    1997a. Genetic and color interactions at a contact zone of *Acanthochromis polyacanthus*: a marine fish lacking pelagic larvae. Evolution 51(4):1232–1243.

    1997b. Genetic relationships of the color morphs of *Acanthochromis polyacanthus* (Pomacentridae) on the northern Great Barrier Reef. Mar. Biol. 130(1):109–117.

Preston, N. P., and P. J. Doherty.
    1990. Cross-shelf patterns in the community structure of coral dwelling Crustacea in the central region of the Great Barrier Reef. 1. Agile shrimps. Mar. Ecol. Prog. Ser. 66:47–61.

    1994. Cross-shelf patterns in the community structure of coral dwelling Crustacea in the central region of the Great Barrier Reef. 2. Cryptofauna. Mar. Ecol. Prog. Ser. 104:27–38.

Reznick, D. N., H. Bryga, and J. A. Endler.
    1990. Experimentally-induced life history evolution in a natural population. Nature 346:357–359.

Ricker, W. E.
    1975. Computation and interpretation of biological statistics of fish populations, 392. Bull. Fish. Res. Board Canada 191, Ottawa, Canada.

Robertson, D. R.
    1973. Field observations on the reproductive behavior of a pomacentrid fish, *Acanthochromis polyacanthus*. Zeitschrift für Tierpsychologie 32:319–324.

Russ, G.
    1984a. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef I. Levels of variability across the entire continental shelf. Mar. Ecol. Prog. Ser. 20:23–34.

    1984b. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef II. Patterns of zonation of mid-shelf and outer-shelf reefs. Mar. Ecol. Prog. Ser. 20:35–44.

Sale, P. F.
    1991. Reef fish communities: open non equilibrial systems. *In* The ecology of fishes on coral reefs (P. F. Sale, ed.), p. 564–598. Academic Press, San Diego, CA.

Sale, P. F., and D. J. Ferrell.
    1988. Early survivorship of juvenile coral reef fishes. Coral Reefs 7:117–124.

Sammarco, P. W., and H. Crenshaw.
    1984. Plankton community dynamics of the central Great Barrier Reef lagoon: analysis of data from Ikeda et al. Mar. Biol. 82:167–180.

Schmidt-Nielsen, K.
    1990. Animal physiology: adaptation to environment, 4th ed., 602 p. Cambridge Univ. Press, Cambridge, UK.

Schnute, J.
    1981. Versatile growth model with stable parameters. Can. J. Fish. Aquat. Sci. 38:1128–1140.

Sebens, K. P.
    1987. The ecology of indeterminate growth in animals. Annu. Rev. Ecol. Syst. 18:371–407.

Thresher, R. E.
    1983. Habitat effects on reproductive successes in the coral reef fish, *Acanthochromis polyacanthus*. Ecology 64:1184–1199.

    1985a. Distribution, abundance and reproductive success in the coral reef fish *Acanthochromis polyacanthus*. Ecology 66:1139–1150.

    1985b. Brood-directed parental aggression and early brood loss in the coral reef fish *Acanthochromis polyacanthus*. Anim. Behav. 33:897–907.

Warner, R. R.
    1991. The use of phenotypic plasticity in coral reef fishes as tests of theory in evolutionary ecology. *In* The ecology of fishes on coral reefs (P. F. Sale, ed.), p. 387–398. Academic Press, San Diego, CA.

Werner, E. E.
    1985. The mechanisms of species interactions and community organization in fish. *In* Ecological communities (D. R. Strong, ed.), p. 360–382. Princeton Univ. Press, Princeton, NJ.

Wilkinson, C. R., and A. C. Cheshire.
    1988. Cross shelf variations in coral reef structure and function- influences of land and ocean. Proc. 6th Int. Coral Reef Symp. 1:227–233.

Williams, D. M.
    1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs 1:35–43.

    1983. Longitudinal and latitudinal variation in the structure of reef fish communities. *In* The inaugural Great Barrier Reef conference (J. T. Baker, R. M. Carter, P. W. Sammarco, and K. P. Stark, eds.), p. 265–270. James Cook Univ. Press, Townsville, Queensland, Australia.

Williams, D. M., and A. I. Hatcher.
    1983. Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. Mar. Ecol. Prog. Ser. 10:239–250.

Williams, D. M., P. Dixon, and S. English.
    1988. Cross-shelf distribution of copepods and fish larvae across the central Great Barrier Reef. Mar. Biol. 99:577–589.

Williams, D. M., G. Russ, and P. J. Doherty.
    1986. Reef fish: large-scale distribution and recruitment. Oceanus 29(2):76–82.

Williams, D. M., C. R. Davies, B. D. Mapstone, and G. R. Russ.
    2003. Scales of spatial variation in demography of a large coral reef fish: an exception to the typical model? Fish. Bull. 101: 673–683.

Wolanski, E.
    2001. Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef, 356 p. CRC Press, Boca Raton, FL

Zar, J. H.
    1999. Biostatistical analysis, 4th ed., 663 p. Prentice Hall, Upper Saddle River, NJ.