Growth patterns along environmental gradients of tropical pomacentrid fishes

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Certificate of authorship

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

I also certify that this thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in this thesis.

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Acknowledgements

This thesis is dedicated to my father.

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General abstract

The goal of this thesis is to evaluate latitudinal patterns in the life history traits, standard metabolic rates, and growth potential of two geographically widespread damselfishes, the dispersing *Pomacentrus moluccensis* (Bleeker 1853) and the brood-caring *Acanthochromis polyacanthus* (Bleeker 1855) between Lizard Island, Orpheus Island, and One Tree Island along the Great Barrier Reef, Australia (14° 41' S, 18° 37' S, and 23° 30' S).

P. moluccensis displayed no clear latitudinal maximum age (7-10 years) or asymptotic size (57.3 mmSL +/-3.0) difference, between Lizard, Orpheus, and One Tree Islands. Based on experimental manipulations of water temperature at the three islands the metabolic rate at a given temperature (e.g. 27°C) was significantly lower at the lowest latitude Lizard Island (0.048 mgO_2/g fish/hour) compared to mid- and high-latitude Orpheus and One Tree Islands (0.088 mgO_2/g fish/hour +/-0.004). Regardless of location, the growth of *ad libitum* fed juveniles was consistently higher at higher temperatures (0.0641-0.1190 $\log(g_{(final)}/g_{(initial)})$/day), indicating higher potential growth rates at lower latitudes.

A. polyacanthus displayed a lower asymptotic size at the highest latitude One Tree Island (72.5 mm SL) compared to Orpheus and Lizard Islands (86.9 mmSL +/-2.3) though the maximum age was the same across latitudes (8-10 years). The metabolic rate at a given temperature (e.g. 27°C) was consistently significantly higher at higher latitudes (0.053-0.106 mgO_2/g fish/hour). The growth of *ad libitum* fed juveniles was significantly lower at Lizard Island (0.0575 $\log(g_{(final)}/g_{(initial)})$/day +/-0.0057) than Orpheus and One Tree Islands (0.1303 $\log(g_{(final)}/g_{(initial)})$/day +/-0.0153). These two results in conjunction may indicate that *A. polyacanthus* maintenance costs are low at low latitudes through low metabolism, but has simultaneously reduced its ability to speed up growth rates in periods of abundant food, such as coral spawning (Oct-Nov).

Over the coming century rapid climate change is predicted to increase the average sea-surface temperatures on the GBR, with possible migration of widely distributed species from warmer areas of their distribution to colder. The ensuing changes in reaction norms due to a lateral shift will largely depend on their current geographical and temperature ranges. Based on the results of this study, it appears that *P. moluccensis* might be able to tolerate a transition to warmer habitats, while *A. polyacanthus*, more adapted to its local habitat, would be less able to adjust to a change in temperature regime.

Chapter 1: General introduction

1.1 Life history traits and temperature

One of the primary objectives of ecology research is to understand the individual traits that affect population dynamics, species and communities (e.g. Krebs 1978, McIntosh 1985, Clarke & Johnston 1999, Figueira et al. 2008). These life history traits determine the individual allocations of energy to growth, maintenance, storage and reproduction during the life of an organism (Dunham et al. 1989, Begon et al. 1996). Some of the crucial traits in determining life histories are thus growth, longevity and reproduction (Figueira et al. 2008). These traits are all interconnected, as well as affected by the biotic and abiotic environment (Brett 1979, Rilling & Houde 1998).

As fish are ectotherms, one of the largest abiotic influences on their physiological rates and thereby their life history factors is temperature; lower temperatures would generally be expected to reduce the rate of physiological processes (Johnston & Bennett 1996, Wood & McDonald 1997). Following this reasoning, organisms living in colder, higher latitude environments should, compared with organisms at warmer lower latitudes, display lower growth rates. Since physiological processes would be "slowed down", one would also expect a higher age at maturity, which would lead to a lower reproductive output (Kokita 2003), but one would likewise expect a longer life-span, which may result in larger asymptotic body sizes and a lifetime reproductive output comparable to that of conspecifics living at warmer temperatures (e.g. Atkinson 1994, Mangel & Stamps 2001).

A classic biogeographic test of these hypotheses is across latitudes, where latitude is closely related to environmental temperature. However, studies on a range of temperate organisms have contrarily shown some form of latitudinal compensation in life history traits. Individuals from populations living in high latitude environments may paradoxically maintain physiological rates as high as or even higher than those from low latitudes and thus maintain high growth rates in colder environments (e.g. Levins 1968 on flies; Levin et al. 1969 on mice; Levinton & Monahan 1983 on polychaetes; Rhymer 1992 on birds; Ayrinhac et al. 2004 on insects). The same is true overall for fish, whereby species in colder, high latitude environments display growth rates as high as or even higher than species in warmer, low latitude environments (Conover 1990, Conover 1992, Conover & Schultz 1995, Pörtner et al. 2001). Such latitudinal growth compensation is also found on an intra-specific level between temperate fish populations inhabiting different latitudes. To date information has demonstrated that populations of a given species manifest reduced body size, growth rates and life spans at low relative to high latitudes when raised under common conditions (Conover & Present 1990, Svåsand et al. 1996, Conover et al. 1997, Brown et al. 1998, Billerbeck et al. 2000, Schultz et al. 2002, Yamahira et al. 2007).

Most investigations in this area refer to work on temperate water fishes. However, although the investigation of growth along environmental gradients in tropical fishes is in an early phase, results to date suggest similar patterns to those observed in temperate water species (Choat & Robertson 2002, Choat et al. 2002, Gust et al. 2002b, Choat et al. 2003, Kingsford & Hughes 2005, Robertson et al. 2005, Booth unpubl.).

1.2 Local adaptation

Since life history traits have a huge impact on fitness, they should be expected to evolve in response to local environments (e.g. Stearns 1992, Charlesworth 1994). Many species of reef fish have broad geographical distributions, spanning a wide range of habitats (Gillanders 1995, Meekan et al. 2001, Gust et al. 2002a, Jones et al. 2002), and the large-scale environmental gradients encountered exert major effects on their life history patterns (Mizera & Meszena 2003).

Genetic adaptation to local environment is possible if there is genetic variation in the life history traits, and individuals with different traits vary in fitness (e.g. Sinervo & Adolph 1994, Mousseau 2000). However, for tropical coral reef fishes, the prospect for local adaptation seems to be comparatively low since geographic obstacles to gene flow are usually absent and the early life stage is commonly highly dispersive (Palumbi 1994, Mora & Sale 2002). Selection may however also produce abilities for phenotypic plasticity. This would enable a specific genotype to alter its phenotype to fit the local environment, seasonal change or e.g. climate change (Via & Lande 1985, Stearns 1989). Such an adaptive plasticity could also vary between populations (Stearns & Koella 1986, Scheiner 1993).

1.3 Temperature change consequences

Current climate change predictions indicate an increase in average sea-surface temperatures ongoing and over the coming century (Guinotte et al. 2003, Lough 2007). In the case of rising temperatures, would a species be able to shift habitat to a colder area within its range? Observations have been made of range shifts in marine temperate fishes correlated with above average temperatures (Holbrook et al. 1997, Parker & Dixon 1998, Perry et al. 2005), and we might expect similar responses from tropical coral reef fishes (Munday et al. 2008a). But an individual perfectly suited for its local environment would presumably not perform as well in another environment or if the local environment changes (e.g. Stearns 1992, Schluter 1993). So how the species ranges in temperature and environment will change with global climate change, and the consequences for their continued existence (Visser 2008) largely depend on their current geographical and temperature ranges (Munday et al. 2008a). By studying current differences between the local reactions to temperature changes, we might get an idea of what life history changes to expect with global temperature changes.

1.4 Aims of the thesis

The overall aim of this thesis is to evaluate the existence of latitudinal patterns in the life history of a group of tropical coral reef fishes using both comparative and experimental techniques. In particular, this research tested hypotheses in the area of life history characteristics of damselfishes and their plasticity along the Great Barrier Reef.

Fish populations were sampled from three locations: Lizard Island (14° 41' S, 145° 18' E) a mid-shelf island with surrounding reefs off the coast of Northern Queensland; Orpheus Island (18° 37' S, 146° 30' E) an inner-shelf island with reefs off the Northern Queensland coast approximately 100 km north of Townsville; and One Tree Island (23° 30' S, 152° 05' E) a lagoonal mid-shelf reef in the Capricorn Bunker Group in the southernmost part of the Great Barrier Reef (Fig. 1.1). Ideally, samples should have been taken from a number of cross shelf locations at each latitude, however, limits to scope, time and budget precluded this. To achieve as broad a selection as possible within the scope of the project, specimens were sampled from several sites within each location.

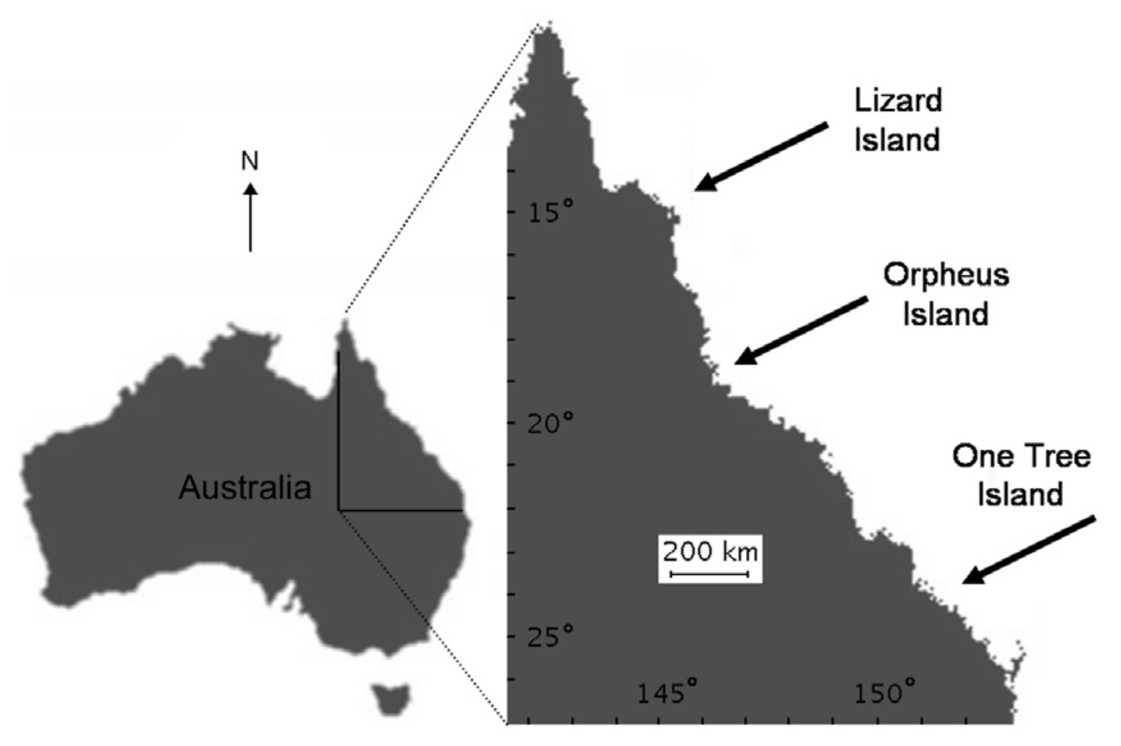

Fig. 1.1: Study sites along the Great Barrier Reef, Australia, at which specimens of *Pomacentrus moluccensis* and *Acanthochromis polyacanthus* were obtained.

Annually, low latitudes have higher, more constant mean temperatures, while higher latitudes are characterized by lower mean temperatures but also a higher variation in temperatures with both higher and lower thermal extremes than at low latitudes. Populations at low latitudes therefore experience warmer and narrower ranges of temperatures than at high latitudes. Summer mean sea surface temperatures differed significantly among all sites (Lizard: 29.1°C; Orpheus: 28.5°C; One Tree: 27.4°C; t-tests, all P<<0.0001; data obtained from www.reeffutures.org, now moved to www.aims.gov.au); data ranges from 2001-2003; temperature proxies for Orpheus and One Tree Islands are Pelorus and Heron, one and 10 km north of their respective proxies).

Two species of damselfishes were the focus of this project: *Pomacentrus moluccensis* (Bleeker 1853) and *Acanthochromis polyacanthus* (Bleeker 1855). These were chosen, since they are common along the Great Barrier Reef, long-lived, and relatively easy to catch in the field. Furthermore, damselfishes are not a target of fisheries on the Great Barrier Reef. Thus patterns in their life histories can be examined without the effects of varying fishing effort among locations. Both species are gonochoristic, site-attached planktivores (Robertson 1973, Allen 1975).

P. moluccensis is closely associating with live coral (Eckert 1984). After the larval phase, which lasts 16-23 days (Brothers et al. 1983, Mapstone 1988), recruits preferentially settle on live corals (Ault & Johnson 1998), and rarely leave their home ranges of 0.1-2 m^2, even as adults (Mapstone 1988). Some *P. moluccensis* larvae may recruit to their natal reef, but considering the East Australia Current, the majority is most likely recruiting to a reef south of their natal reef (see Buechler 2005 on *Amphiprion* spp).

A. polyacanthus nest in small caves or closed-in coral formations (Thresher 1985b, Brolund pers. obs.), defending their young from predators (Allen 1975), which will stay with the parents in a close group until 25-50 mm SL (Robertson 1973, Nakazono 1993, Kavanagh 2000). Sub-adult *A. polyacanthus* roam the reef in large shoals of similar sized individuals associating with the corals (Thresher 1985b, Brolund pers. obs.).

A. polyacanthus displays different colour morphs at different latitudes, partially associated with different genotypes (Planes & Doherty 1997a, Planes & Doherty 1997b, Planes et al. 2001). Van Herwerden & Doherty (2006) established that overall, the species can be divided in a northern-, mid-, and southern- group, which have zones of interbreeding. Lizard and Orpheus Island both belong in the mid-zone, One Tree Island is in the southern zone, however, the specimens observed in this study were all grey, not the black type described by Van Herwerden & Doherty (2006) from Sykes Reef close to One Tree Island. It should be stressed though, that *A. polyacanthus* is a monotypic genus (Van Herwerden & Doherty 2006), there are no other brooding damselfish species (Robertson 1973, Kingsford & Hughes 2005), and the observations of this study are done on interbreeding subtypes within the species (Van Herwerden & Doherty 2006).

1.5 Hypotheses

The main hypotheses of this thesis are that since physiological rates are faster at warmer temperatures (e.g. Wood & McDonald 1997), one should observe lower growth rates and a later onset of maturity at higher latitudes, which in combination should lead to smaller size at maturity at higher latitudes. Since a later onset of maturity would lead to a lessened lifetime reproductive output, a possible adaptation may be to get older at higher latitudes, which should also be an inherent tendency when physiological rates are slower (Ricklefs 2000). The difference in maximum age may lead to similar or higher maximum sizes at higher latitudes.

A further possible adaptation to temperature may lie in the metabolic rate. A lower metabolic rate means less energy spent on maintenance and larger allocation of the ingested energy available for growth and reproduction (Brett 1979, Yamahira & Conover 2002). This will be particularly important for low latitude populations, who experience the highest temperatures. A consequence of a species not able to shift its metabolic rate with warmer temperatures may be higher growth rate at higher latitudes merely because the idling cost is lessened in colder compared to warmer temperatures. Conversely, since food is often a limiting factor (Jones 1986), taking advantage of a period of abundant food, such as coral spawning (Pratchett et al. 2001), may be adversely affected if metabolic rates are set very low to accommodate high temperatures.

Since *A. polyacanthus* does not display a larval stage which might mediate the exchange of genetic material between reefs, it should be better able to adapt to local temperatures than *P. moluccensis*. If temperature adaptation is found, it may manifest in no observable difference between the life history parameters of latitudinally separate populations in spite of significantly different local ambient temperatures. However, this may also mean that *A. polyacanthus* would display a lesser ability than *P. moluccensis* to adapt to changed temperature conditions and to take advantage of periodically higher levels of food.

1.6 Structure of the thesis

While the layout of the thesis is according to the University of Technology Sydney guidelines, the data chapters are written as stand-alone papers intended for publication, with the aim of conciseness and brevity.

Chapter 2 examines patterns of variation in life history traits of *A. polyacanthus* and *P. moluccensis* among wild populations from Lizard Island, Orpheus Island and One Tree Island. The goal is to assess whether differences in life histories along a latitudinal gradient conform to predictions based on life history theory. The hypothesis is that populations across latitudes are equal, which should result in lower growth rates at higher latitudes with ensuing smaller sizes and possibly later maturation. If some form of latitudinal compensation is active, results may yield higher growth rates and/or maximum ages at higher latitudes, which may result in larger asymptotic sizes. In preparation for the journal “Environmental Biology of Fishes”.

In chapter 3, oxygen measurements are employed at a range of temperatures to measure the standard metabolism of *A. polyacanthus* and *P. moluccensis* from Lizard Island, Orpheus Island and One Tree Island. The aim is to determine whether 1) the two species have overall different levels of metabolism, 2) for each of the species, the change in temperature elicits a proportionally similar drop or rise in rate of metabolism in specimens from the geographically different populations. Submitted to the journal “Global Change Biology”.

Chapter 4 investigates the growth of juvenile *A. polyacanthus* and *P. moluccensis* from Lizard Island, Orpheus Island and One Tree Island reared at two different temperatures and fed *ad libitum* in common garden experiments. The objective is to establish the growth rate of *ad libitum* fed juvenile damselfish, and how that growth rate changes with temperature, location and species. In preparation for "Journal of the Marine Biological Association".

In chapter 5, the results of the previous chapters are discussed in conjunction and in a more general context, conclusions are drawn from the cross-comparisons of the chapter results and directions for further research are suggested.

1.7 Permits

The necessary permits for this work are listed below. They include permits from Great Barrier Reef Marine Park Authorities, Queensland Department of Primary Industries, a University of Technology ethics permit, and Queensland approved ethics permits from James Cook University. Name of permit holder in parenthesis. Since sampling from the Great Barrier Reef was done over one summer, permit constraints on the yearly sample allowance (section 1.7), affected low sample numbers in some of the studies, which should be noted when assessing the robustness of the results.

Great Barrier Reef Marine Park Authorities: G05/15686.1 (Brolund), G05/12935.1 (Australian Museum), G03/3871.1 (James Cook University), G03/7261.1 (Booth), G05/13485.1 (Figueira & Booth)

Queensland Department of Primary Industries: 55430 (Brolund), PRM38784C (Brolund)

Joint Royal North Shore Hospital / University of Technology Sydney Animal Care and Ethics Committee (not recognized in QLD): 0510_033A (Booth & Brolund)

James Cook University ethics permit: A872_04 (Choat), A873_04 (Choat)

Chapter 2: Comparison of the life histories of two damselfishes with different dispersal patterns from three latitudinally separate populations

Abstract

Many tropical reef fish have broad geographical distributions. Since fish are ectotherms, even small temperature changes can influence growth. In order to investigate a possible difference in the life histories of two widely distributed coral reef fishes, the life history traits of each species were examined at three locations along the Great Barrier Reef, Australia, and compared between locations and between species. The two species differ in their dispersal pattern in that *Acanthochromis polyacanthus* (Bleeker 1855) displays brood-care and thus has a very limited dispersal, which should enable a higher degree of local adaptation. The other, *Pomacentrus moluccensis* (Bleeker 1853), displays the usual pelagic larval stage, enabling it to more effectively disperse between reefs.

The two species displayed different degrees of inter-location differences, in that *P. moluccensis* displayed no significant differences in asymptotic size (L_∞: 57.3 mmSL +/-3.0) and rate of reaching that size (k: 0.433 +/-0.084) and *A. polyacanthus* did with lower asymptotic size and higher rate of reaching that size at One Tree Island (L_∞: 72.5 mmSL; k: 0.508) than at Orpheus and Lizard Islands (L_∞: 86.9 mmSL +/-2.3; k: 0.346 +/-0.036). Both species displayed lower maximum ages at Orpheus Island (7-8 years) compared to the lower latitude Lizard Island and the higher latitude One Tree Island (9-10 years). *A. polyacanthus* matured roughly a year later than *P. moluccensis* (3 and 2 years at Lizard Island; 4 and 2 at Orpheus Island; and 4 and 3 at One Tree Island). Maturity happened approximately at the same percentage of asymptotic size.

2.1 Introduction

Many species of reef fish have broad geographical distributions, spanning a wide range of habitats (Gillanders 1995, Meekan et al. 2001, Gust et al. 2002a, Jones et al. 2002). As fish are ectotherms, even small temperature changes can influence their physiological condition affecting behaviour, growth and reproduction (Wood & McDonald 1997, Munday et al. 2008a). However, except for a few commercially important species (Munro & Williams 1985, Williams et al. 2003) and scarids and acanthurids (e.g. Choat & Axe 1996), there are little data on life history traits of coral reef fishes and even less on their possible intra-specific geographic variation (Kingsford & Hughes 2005). The data we do have suggest that as with temperate species (e.g. Conover & Present 1990), populations of a given tropical reef fish species paradoxically grow to smaller adult sizes and have shorter life spans at lower latitudes than those living at higher latitudes (Choat & Axe 1996, Meekan et al. 2001, Choat & Robertson 2002, Choat et al. 2003, Caldow & Wellington 2003).

Even conservative climate change predictions indicate an increase in average sea-surface temperatures over the coming century (Guinotte et al. 2003, Lough 2007). Since the seasonal changes in temperature ranges experienced by tropical species are narrower than those of temperate species, we can expect tropical fishes to only tolerate a narrower range of temperatures and to faster loose fitness beyond those limits (Munday et al. 2008b). However, the effects of rising sea-surface temperatures on coral reef fish have received little attention (Roessig et al. 2004, Harley et al. 2006).

Under a scenario of rising water temperatures, would a species be able to shift habitat to a colder area within its range, or alternatively adapt to the changed temperature regime? Using strict size selection pressure, Conover & Munch (2002) has shown significant adaptation within three generations in the short-lived silversides (*Menidia*). Observations have been made of range shifts in marine temperate fishes correlated with above average temperatures (Holbrook et al. 1997, Parker & Dixon 1998, Perry et al. 2005), and we might expect similar responses from tropical coral reef fishes (Munday et al. 2008a). But how these ranges will change, and the consequences for their continued existence (Visser 2008) largely depend on their current geographical and temperature ranges (Munday et al. 2008a).

In view of oncoming temperature changes and since life history parameters are vital to understanding population dynamics (Kingsford & Hughes 2005), this study aims to establish and compare the life histories of two coral reef fish species. Critically, I will compare the intra- and inter-specific differences in life history parameters of two widespread damselfishes with dissimilar degrees of dispersal: *Acanthochromis polyacanthus* (Bleeker 1855), which displays parental care for their hatched brood for several months (Robertson 1973, Allen 1975, Thresher 1985a, 1985b, Kavanagh 2000); and *Pomacentrus moluccensis* (Bleeker 1853), which displays a planktonic larval stage (Wellington & Victor 1989, Leis 1991), which allows a degree of drift of genetic material among coral reefs (Sale 1991).

Since physiological rates are faster at warmer temperatures (e.g. Wood & McDonald 1997), for *P. moluccensis*, I expect lower growth rates and a later onset of maturity at higher latitudes, which in combination should lead to smaller size at maturity at higher latitudes. Since a later onset of maturity would lead to a lessened lifetime reproductive output, a possible adaptation may be to get older at higher latitudes, which should also be an inherent tendency when physiological rates are slower (Ricklefs 2000). If the difference in age (or the difference in growth rate) is not large, one may observe similar maximum sizes across latitudes, if the age difference (or the growth rate difference) is larger, one should find higher maximum sizes at higher latitudes.

The inter-generational migration of *A. polyacanthus* is most likely slow between reefs, which should enable a higher degree of local adaptation, increasing the local performance of individuals but also possibly a lowering their ability to adapt to changes in the environment (Kingsford & Hughes 2005, Munday et al. 2008b).

Therefore, I expect a higher degree of adaptation to the local temperatures in *A. polyacanthus* than in *P. moluccensis*, perhaps to the degree that no actual differences are found between locations in the observed life history parameters in spite of between location temperature differences.

2.2 Materials and methods

2.2.1 Study areas and field sampling

Two damselfish species were chosen, which differ in their range of dispersal. *Acanthochromis polyacanthus* (Bleeker 1855) exhibits brood care, and the inter-generational dispersal of the fish is thus limited compared to a fish with a pelagic larval stage, such as most tropical reef fishes including *Pomacentrus moluccensis* (Bleeker 1853) (Doherty et al. 1995). I sampled *P. moluccensis* and *A. polyacanthus* at three localities along the Great Barrier Reef; Lizard Island, Orpheus Island, and One Tree Island (14° 41' S, 18° 37' S, and 23° 30' S) spanning 9° of latitude.

A total of 272 pomacentrids were collected; 52 *A. polyacanthus* and 34 *P. moluccensis* from Lizard Island, 38 and 37 from Orpheus Island, and 65 and 46 from One Tree Island. Collection sites at Lizard Island: the lagoon, out front, coconut beach and turtle beach; Orpheus Island: NE corner and NW corner of the island, and 500m North and directly out front from the research station; One Tree Island: 6 sites inside the lagoon and 2 sites outside on the North side of the lagoon.

A. polyacanthus and *P. moluccensis* collected covered a representative sample of both the juvenile and adult size ranges. Adult size ranges are: 55-83mm standard length (SL) and 50-140mm TL (equals approx. 42-118mm SL (TM Drachen pers. obs.)) for *A. polyacanthus* (Thresher 1983 and Kavanagh 2000, respectively); 35-62mm SL and 25-55mm SL for *P. moluccensis* (Mapstone 1988 and Bray 2001, respectively).

Using SCUBA, I caught fish with barrier nets, hand nets and clove oil. They were put in individual plastic bags with a fresh supply of water and transported under cover in larger water filled tanks by dinghy to the nearby research station. At the research stations they were introduced to flow-through holding tanks in groups of 2-5 specimens for 2-50 hours before euthanization. The holding tanks were kept at ambient temperature of 29-30°C at Lizard, 28-29°C at Orpheus, and 27-28°C at One Tree. Photoperiod was 13L:11D, to roughly follow the natural light pattern. The fish were fed Wardley® Total Marine Flake Food and frozen brine shrimp *ad libitum*. Immediately prior to measurements and dissecting, the fish were killed by clove oil overdose, and standard length (SL) was measured to the nearest 0.5mm.

2.2.2 Age determination

To assess age of the fish both sagittal otoliths were removed, cleaned in distilled water, and stored dry. Fowler (1990) and Fowler & Doherty (1992) validated the forming of annual increments in *P. moluccensis*, and Kingsford & Hughes (2005) their formation in *A. polyacanthus*. One sagitta from each pair was weighed to the nearest 0.1 mg. It was mounted in thermoplastic cement Crystalbond© on a slide edge and ground down to the nucleus using from 16µm to 3µm abrasive paper / lapping film on a flat surface with a little distilled water. The otolith was then set in Crystalbond© on a second slide, and the opposite side was also ground down to the nucleus and polished with 3µm lapping film (Choat et al. 2003). The opaque zones visible in the structure of the otolith were counted along an axis from the primordium to the rim using a compound microscope and white incident light (Fig. 2.1) (Choat & Axe 1996). Each otolith was read three times for annuli. If counts varied more than 10%, the second otolith was processed. If the second otolith was not available the individual was discarded.

2.2.3 Age-based growth modeling

The von Bertalanffy growth function was used to model the growth of the damselfish populations. It is suitable for analyzing and comparing growth rates among latitudinally dispersed species (Schnute 1981, Essington et al. 2001), and is usually a good descriptor for fish growth (Chen et al. 1992), modeling it as: $L_t = L_{\infty}e^{(-k(t-t_{o}))}$, where: L_t is the estimated length at age t, L_{∞} is the theoretical mean asymptotic length, k is a constant describing the rate at which the growth curve approaches the asymptotic length, t is the age of the fish in years, t_0 is the hypothetical age at zero length (can be negative or positive), and e is the base of the natural logarithm. The von Bertalanffy curve was fitted by minimizing the residual sum of squares (Chen et al. 1992, Haddon 2001). Each observed data point is paired with its corresponding data point calculated using the von Bertalanffy growth model. The differences between the observed and the calculated data points are squared (squared residuals), and the sum of squared residuals (SSQ) is minimized by manipulating the von Bertalanffy growth parameters (L_{∞}, k, and t_0).

Two records of longevity were made: one of the actual oldest individuals found (Tmax), and one which was estimated as the mean age of the oldest 10% (mean T_{max}) of each population (Gust et al 2002b, Buechler 2005). When sample sizes are relatively small, longevity estimates based on only the oldest specimen in a population may over-emphasize the age of outliers in local age distributions (Beverton 1992). Therefore when comparing other parameters to longevity, mean T_{max} estimates may provide a more robust result.

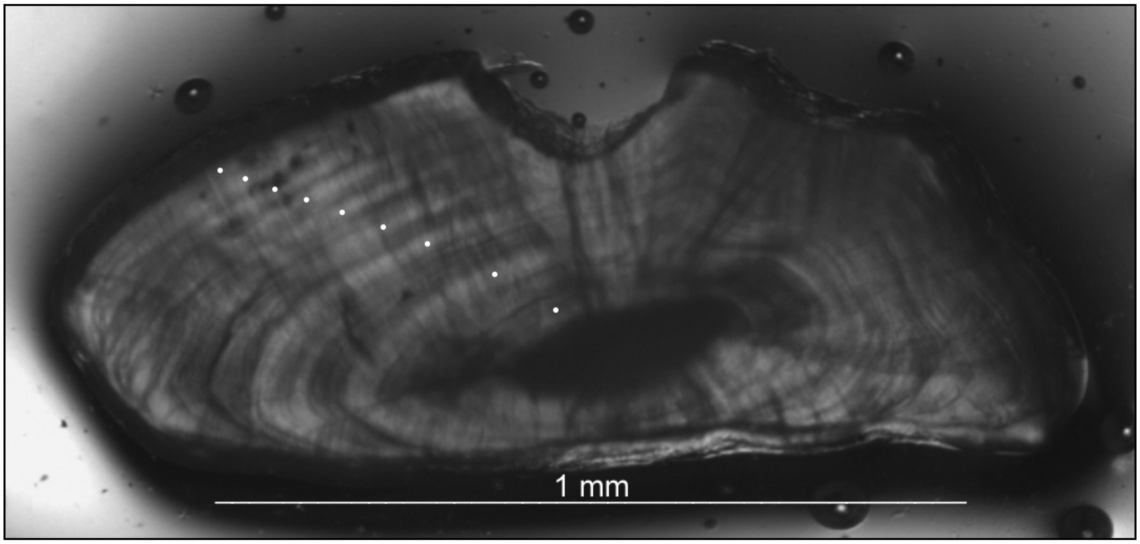

Fig. 2.1: View of the transverse section of a nine year old *P. moluccensis* sagittal otolith with primordium drawn in. White dots indicate yearly increments. Photo by TM Drachen.

2.2.4 Determination of sex and maturity

To determine sex and stage of sexual maturity, gonads were removed and pre-processed by fixing in a formalin acetic acid calcium chloride solution (FAACC: l0 ml 37% formaldehyde, 5 ml glacial acetic acid, 1.3 g calcium chloride (dihydrate), water to 100 ml.) (McCormick & Molony 1992). At a later stage the gonads were de-hydrated in ascending grades of series of ethanol (70%, 80%, 95%, and 100%), cleared in xylol, embedded in paraffin, sectioned at 5 µm, mounted on slides and stained with Harris' haematoxylin and eosin (Asoh 2004). Sectioned and stained tissue was subsequently examined under a light microscope (Leica MZ16 and Olympus BX50).

2.2.5 Comparisons of age at maturity, growth, and longevity

The von Bertalanffy growth curves were compared between species and between locations using a likelihood ratio test (LRT). It tests whether von Bertalanffy growth curves are statistically different, and if so, which of the three parameters (L_∞, k and t_0) are responsible for the difference (Kimura 1980, Cerrato 1990, Haddon 2001). The LRT compares the sum of the two SSQs obtained with each curve individually (see section 2.2.4) with the SSQ obtained if the two curves are coincident. If the two curves are not coincident, the LRT fixes one of the von Bertalanffy growth parameters, e.g. L_∞ to be equal for both growth curves and again minimizes SSQ by manipulating the common L_∞ and the individual k and t_0. Using a χ^2 test, the SSQ thus obtained is compared with the sum of two SSQs from the two individual growth curves. The last section is repeated for the two other von Bertalanffy growth parameters.

To determine significant differences between mean T_{max} of the various populations, F-tests were performed to test for equal variances. Following this either t-tests for unequal or equal variances were performed (Zar 1996).

Specimens were divided into three stages of maturity: mature (females: standard oocyte staging; males: presence of spermatozoa), developing (females: standard oocyte staging; males: presence of duct material but no spermatozoa), and juvenile (gonads not differentiated) (Hunter et al. 1986, Nakamura et al. 1998, Asoh 2004). The percentage in each maturity stage was plotted against age and size classes. These plots were used to compare the timing of maturation of each species among locations. To compare age and size at maturity between species and locations, the age and size at maturity for each species at each location was estimated as the age and size class at which 50% or more of the individuals were mature. Test for statistical significance was obtained with firstly an F-test for equal variance, and subsequently t-tests (one-tailed, two-sample, equal or un-equal variance as per the F-test) (Zar 1996). The age/size classes were also converted to an age or size class proportional to the calculated mean maximum size (mean T_{max}) or asymptotic size (L_∞).

2.3 Results

2.3.1 Growth curves and parameters

The von Bertalanffy Growth Function (VBGF) implemented on the age and size data of *P. moluccensis*, showed that the three populations of reef fish have very similar VBGF parameters, the probability of coincident curves were 0.1839 to 0.9631 (Fig. 2.3, Tab. 2.1 and 2.2). Implemented on the age and size data of *A. polyacanthus*, the VBGF showed the highest asymptotic adult age (L_∞) and lowest relative speed of reaching L_∞ (k) at Orpheus Island. L_∞ was marginally lower and k marginally higher at Lizard Island, but not significantly so (P=0.9980). But at One Tree Island, L_∞ was significantly lower (P=0.0025) and k significantly higher (P=0.0386) at One Tree compared to Orpheus Island but not Lizard Island (P=0.3234). The t_0 values of *A. polyacanthus* were not significantly different for any of the locations (P=0.4105) (Fig. 2.2, Tab. 2.1 and 2.2).

Comparisons of the VBGF between the two species, revealed significant differences at all three locations (P<0.0001), all due to significantly higher L_∞ for *A. polyacanthus* than for *P. moluccensis* (Lizard Island P=0.0376, Orpheus Island P<0.0001, One Tree Island P=0.0185). Neither the k nor the t_0 values were significantly different between the two species (Tab. 2.1 and 2.2).

2.3.2 Longevity

The mean maximum age (mean T_{max}) calculated for *P. moluccensis* was significantly lower at Orpheus Island (6 years) than at Lizard (8.33) and One Tree (8.6) Islands (P=0.072 and 0.0028 respectively). The mean T_{max} of *A. polyacanthus* was similarly significantly lower at Orpheus Island (6.5 years) than at Lizard (8.8) and One Tree (8.86) Islands (P=0.07 and 0.0012 respectively). Neither compared between the two species overall (P=0.0615), nor compared location by location, did the mean T_{max} differ significantly between the two species (Lizard Island P=0.5281, Orpheus Island P=0.468, One Tree Island P=0.585) (Tab. 2.1 and 2.2). The observed maximum ages (T_{max}) for *P. moluccensis* were 9, 7, and 10 years at Lizard, Orpheus, and One Tree Islands. They were 10, 8, and 10 for *A. polyacanthus* (Tab. 2.1).

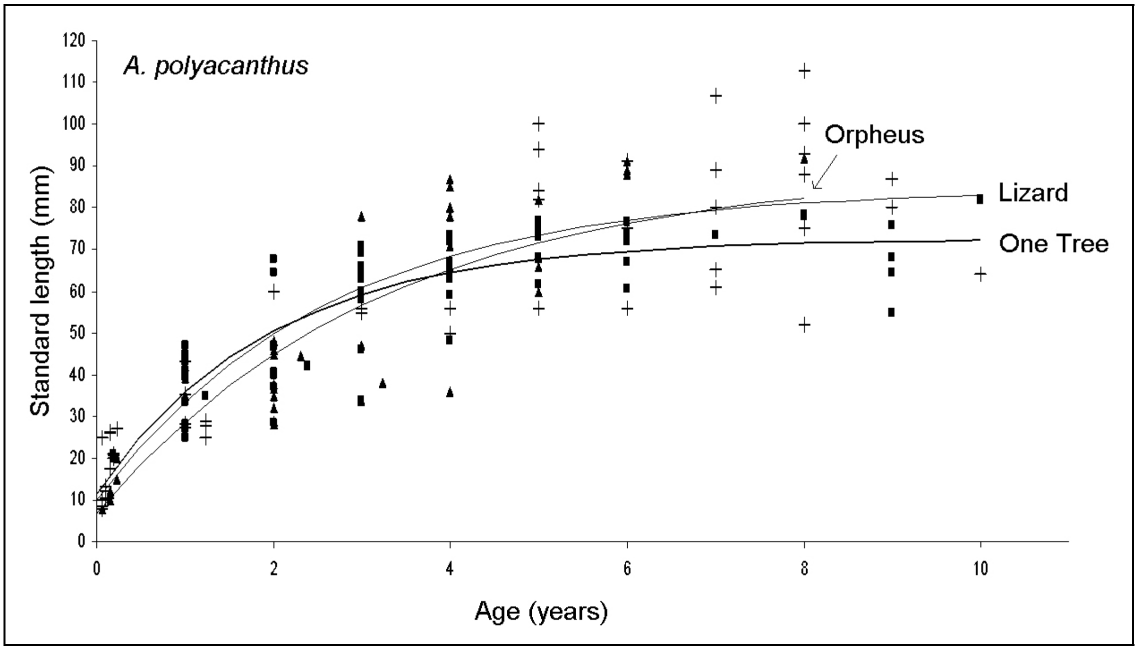

Fig. 2.2: Von Bertalanffy growth functions fitted to size at age data of *A. polyacanthus* at Lizard (+), Orpheus (▲) and One Tree (■) Islands. Von Bertalanffy parameters are listed in table 2.1

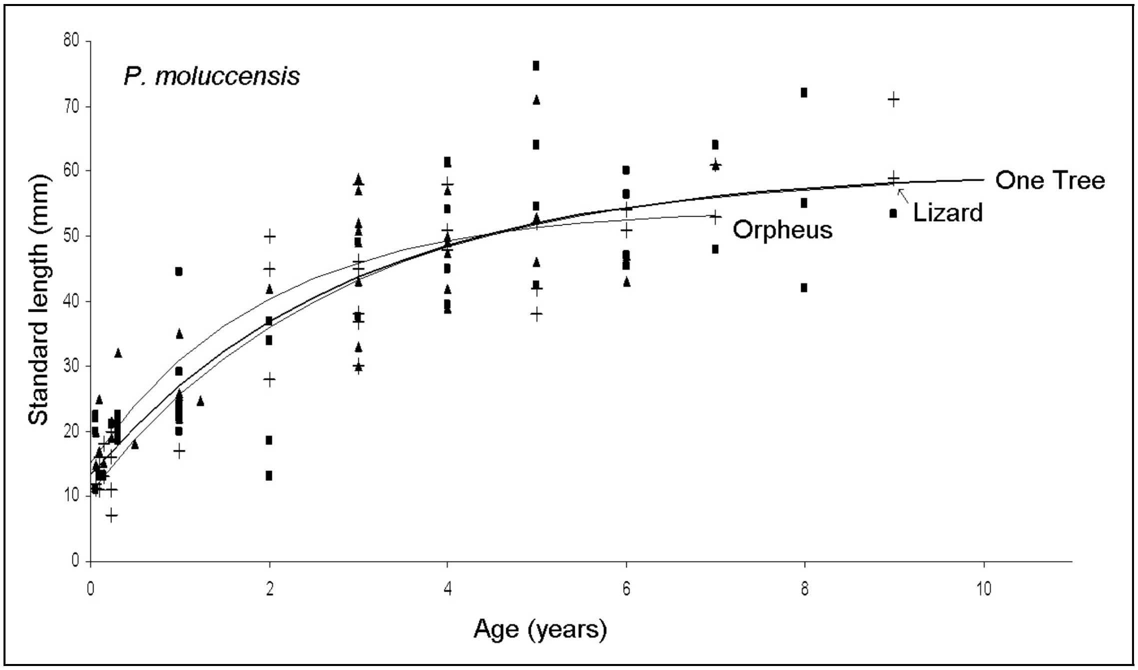

Fig. 2.3: Von Bertalanffy growth functions fitted to size at age data of *P. moluccensis* at Lizard (+), Orpheus (▲) and One Tree (■) Islands. Von Bertalanffy parameters are listed in table 2.1

Tab. 2.1: Von Bertalanffy growth parameters for *A. polyacanthus* (*Ap*) and *P. moluccensis* (*Pm*) from Lizard, Orpheus, and One Tree Islands. L_∞ is the mean asymptotic standard length (mm), k describes the rate at which the growth curve approaches the asymptotic length, t_0 is the theoretical age (years) at length zero. t_{max} is the oldest observed age at each location, while mean t_{max} is the mean age of the oldest 10% of each population.

Species	**Location**	$\mathbf{L_\infty}$	**k**	$\mathbf{t_0}$	$\mathbf{t_{max}}$	**mean** $\mathbf{t_{max}}$
Ap	all	82.1	0.365	-0.4	10	8.67
Ap	Lizard	84.6	0.381	-0.33	10	8.8
Ap	Orpheus	89.1	0.31	-0.25	8	6.5
Ap	One Tree	72.5	0.508	-0.34	10	8.86
Pm	all	58.6	0.393	-0.63	10	8
Pm	Lizard	59.8	0.363	-0.54	9	8.33
Pm	Orpheus	54.3	0.516	-0.63	7	6
Pm	One Tree	60.2	0.349	-0.71	10	8.6

Tab. 2.2: Probabilities that the von Bertalanffy growth function curves (VBGF), VBGF parameters (L_∞, k, and t_0) and mean t_{max} values are equal between populations. VBGF curves and parameters tested with a Likelihood Ratio Test. Mean t_{max} values tested with t-tests. Compared are *A. polyacanthus* (*Ap*) and *P. moluccensis* (*Pm*) from Lizard, Orpheus, and One Tree Islands. Significantly different values are in bold.

Populations compared		**VBGF**	$\mathbf{L_\infty}$	**k**	$\mathbf{t_0}$	**mean** $\mathbf{t_{max}}$
Ap - all	*Pm* - all	**<0.0001**	**0.0087**	0.9208	0.1983	0.0615
Ap - Lizard	*Ap* - Orpheus	0.9980	na	na	na	**0.007**
Ap - Lizard	*Ap* - One Tree	0.3234	na	na	na	0.8993
Ap - Orpheus	*Ap* - One Tree	**0.0198**	**0.0025**	**0.0386**	0.4105	**0.0012**
Pm - Lizard	*Pm* - Orpheus	0.3414	na	na	na	**0.0072**
Pm - Lizard	*Pm* - One Tree	0.9631	na	na	na	0.7246
Pm - Orpheus	*Pm* - One Tree	0.1839	na	na	na	**0.0028**
Ap - Lizard	*Pm* - Lizard	**<0.0001**	**0.0376**	0.9511	0.9672	0.5281
Ap - Orpheus	*Pm* - Orpheus	**<0.0001**	**<0.0001**	0.1150	0.3037	0.468
Ap - One Tree	*Pm* - One Tree	**<0.0001**	**0.0185**	0.1811	0.2588	0.585

2.3.3 Age and size at maturity

The age at maturity for *A. polyacanthus* was three years at Lizard Island, and four at Orpheus and One Tree Island. These ages corresponded to 34.1, 61.5, and 45.2% of the mean t_{max} at Lizard, Orpheus and One Tree Islands respectively. For *P. moluccensis* these ages and percentages were two, two and three and 24, 33.3, and 34.9% respectively at Lizard, Orpheus and One Tree Islands (Tab. 2.3). None of these ages were significantly different between locations, nor between species (P=0.0839 to 0.5) (Tab. 2.4, Fig. 2.4).

The size at maturity was 55.3, 60, and 58 mm SL for *A. polyacanthus* at Lizard, Orpheus and One Tree Island respectively, corresponding to 65.3, 67.3, and 80% of L_∞. For *P. moluccensis*, these sizes were 37.7, 34.8, and 37 mm SL, and 63, 64, and 61.5% respectively (Tab. 2.3). Likewise, theses sizes were not significantly different between locations (P=0.0527 to 0.4008), however inter-specific differences were significantly different (P<0.0001, =0.0003, and <0.0001 for Lizard, Orpheus, and One Tree Island respectively) (Tab. 2.4, Fig. 2.5).

Tab. 2.3: Age and size at sexual maturity of *A. polyacanthus* (*Ap*) and *P. moluccensis* (*Pm*) at Lizard, Orpheus, and One Tree Islands. Age/size at maturation is calculated as the age/size class at which ≥50% are mature, and these age/size classes are also presented as percentages of the mean maximum age/size.

Species	**Location**	**Age (years)**	**% of mean t_{max}**	**Standard length (mm)**	**% of L_∞**
Ap	Lizard	3	34.1	55.3	65.3
Ap	Orpheus	4	61.5	60	67.3
Ap	One Tree	4	45.2	58	80
Pm	Lizard	2	24	37.7	63
Pm	Orpheus	2	33.3	34.8	64
Pm	One Tree	3	34.9	37	61.5

Tab. 2.4: Probabilities that the age and size at sexual maturity are equal between populations. Compared are *A. polyacanthus* (*Ap*) and *P. moluccensis* (*Pm*) from Lizard, Orpheus, and One Tree Islands. Significantly different values are in bold.

Populations compared		**Age (years)**	**Standard length (mm)**
Ap - Lizard	*Ap* - Orpheus	0.1510	0.0770
Ap - Lizard	*Ap* - One Tree	0.0896	0.0527
Ap - Orpheus	*Ap* - One Tree	0.0839	0.4008
Pm - Lizard	*Pm* - Orpheus	0.1358	0.0881
Pm - Lizard	*Pm* - One Tree	0.1737	0.3239
Pm - Orpheus	*Pm* - One Tree	0.4681	0.1429
Ap - Lizard	*Pm* - Lizard	0.5000	**<0.0001**
Ap - Orpheus	*Pm* - Orpheus	0.4412	**0.0003**
Ap - One Tree	*Pm* - One Tree	0.1959	**<0.0001**

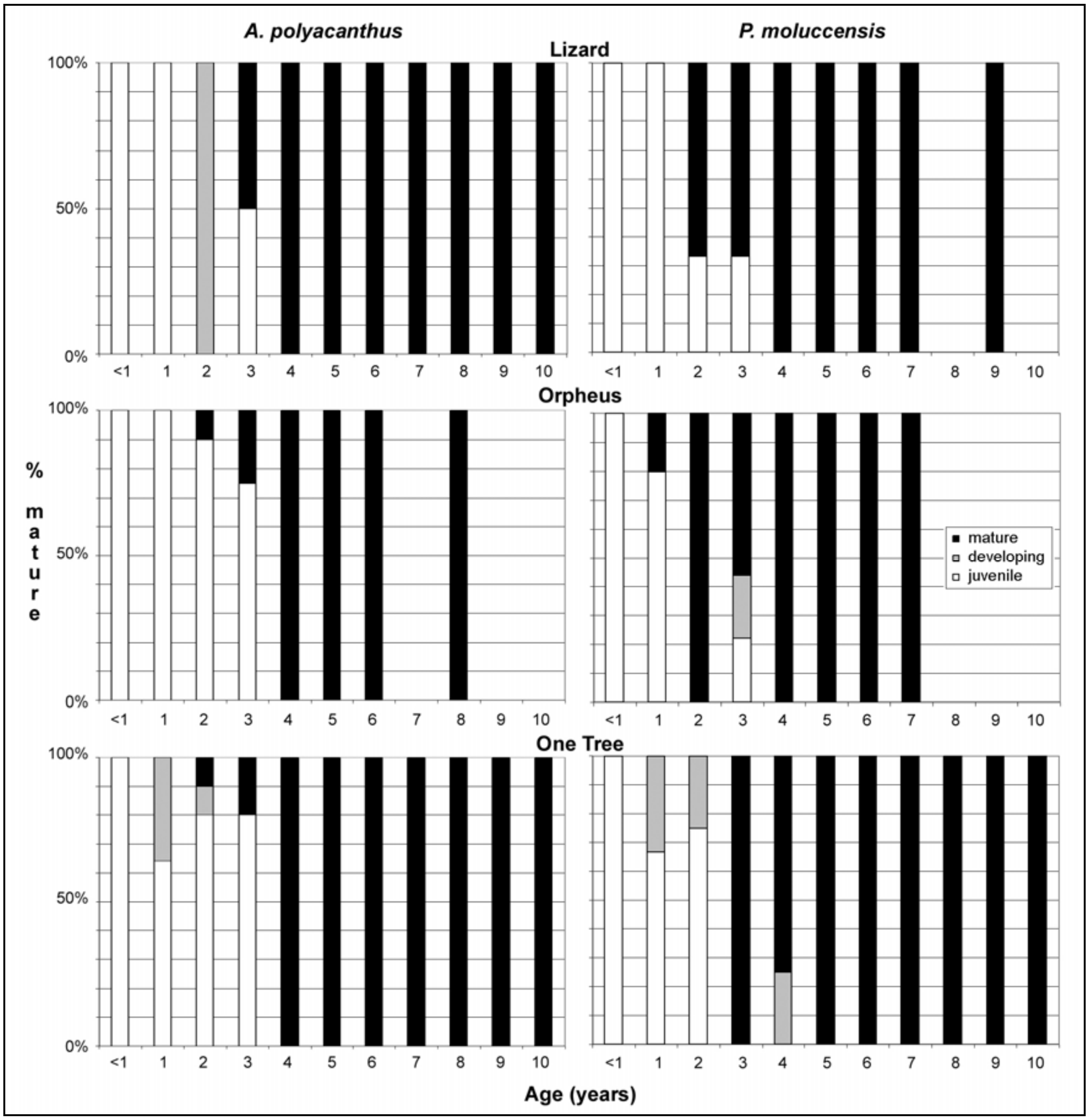

Fig. 2.4: Composition of juvenile, developing and sexually mature *A. polyacanthus* (*Ap*) and *P. moluccensis* (*Pm*) according to age at Lizard, Orpheus, and One Tree Islands.

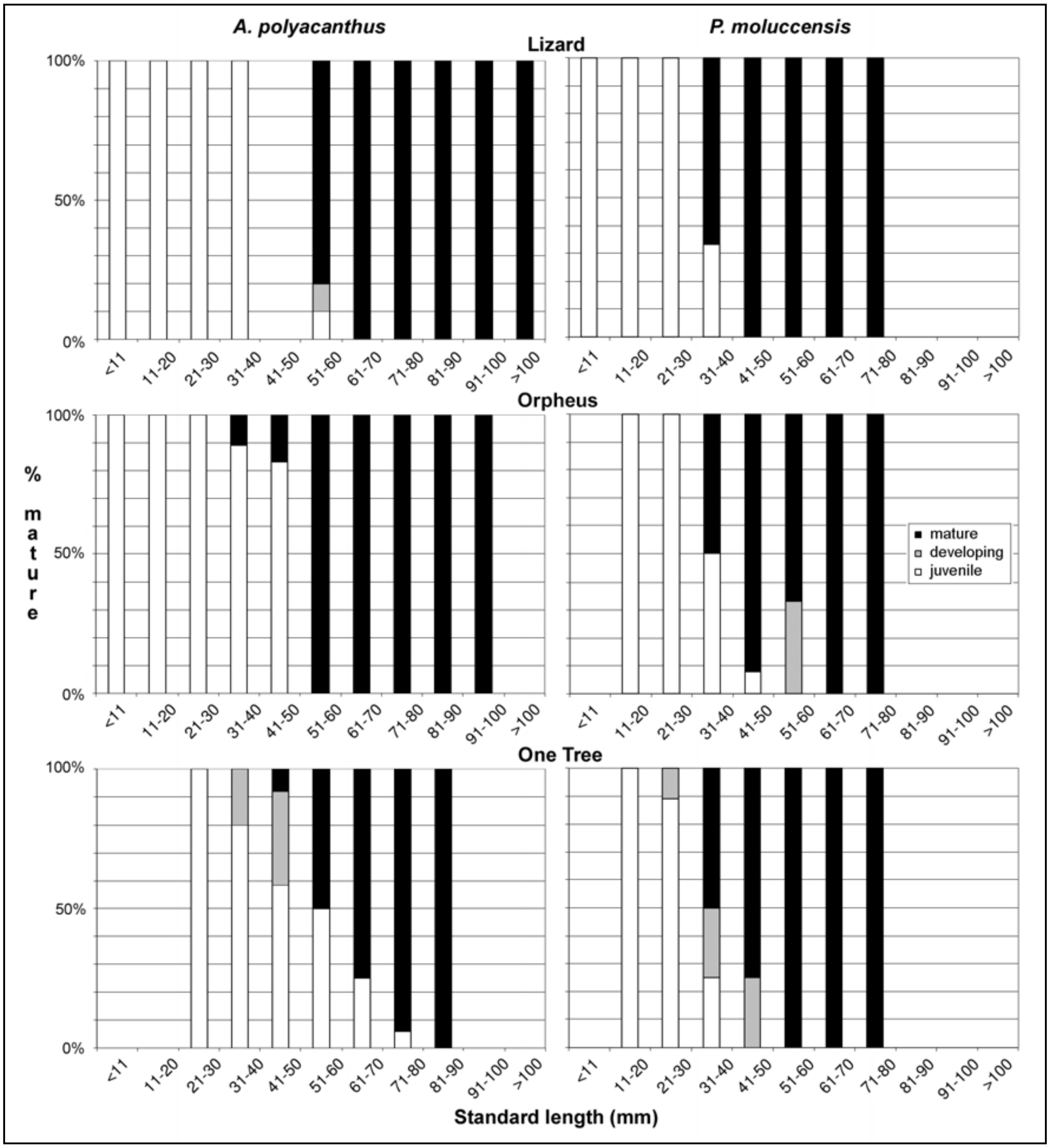

Fig. 2.5: Composition of juvenile, developing and sexually mature *A. polyacanthus* (*Ap*) and *P. moluccensis* (*Pm*) according to size classes at Lizard, Orpheus, and One Tree Islands.

2.4 Discussion

The aim of this study was to establish and compare the life history traits of *A. polyacanthus* and *P. moluccensis* over a latitudinal gradient (Lizard Island, Orpheus Island and One Tree Island along the Great Barrier Reef, Australia). For *P. moluccensis*, I expected to see lower growth rates, similar or possibly larger maximum sizes, higher maximum ages, a later onset of maturity, and smaller size at maturity at higher latitudes. Since most of these differences stem from the expected difference in growth, I expected the observable differences to be lower for *A. polyacanthus*, since I expected the growth of its populations to be more adapted to their local temperature regimes.

2.4.1 Von Bertalanffy growth parameters

There were no significant differences in the asymptotic sizes of *P. moluccensis*, although there was a slight trend for slightly lower asymptotic sizes and slightly faster rate at reaching that asymptotic size (probably as a consequence of the smaller size) at Orpheus Island than at the lower latitude Lizard Island and the higher latitude One Tree Island. The asymptotic size of *P. moluccensis* observed in this study supported that found by Mapstone (1988) at One Tree Island. *A. polyacanthus* displayed a significantly lower asymptotic size and a faster rate of reaching that asymptotic size (again probably as a consequence of the smaller size) at One Tree Island compared to Orpheus Island although not to Lizard Island. The asymptotic sizes observed for *A. polyacanthus* support those found by Kingsford & Hughes (2005) at Orpheus Island.

Thus it seems that there were no clear latitudinal differences in the asymptotic size or the growth rate coefficient of reaching the asymptotic size. However, for both species there was a difference between the inner shelf Orpheus Island and the other two mid-shelf islands. Thus this is probably a cross-shelf effect, confirmed by cross-shelf comparison of *A. polyacanthus* at latitudes around Orpheus Island (18°-18.8° S) by Kingsford & Hughes (2005) who found increased asymptotic size with increasing distance from the coast.

2.4.2 Maximum ages

For both species, the maximum ages recorded were lower at Orpheus than at both Lizard and One Tree Islands. Thus there was no clear latitudinal trend, but neither should the difference be a cross-shelf effect, since Kingsford & Hughes (2005) in their cross-shelf comparison of *A. polyacanthus* found no difference in maximum age with distance from the coast.

However, there are separate studies indicating that maximum ages of *P. moluccensis* increase with increasing latitudes: Beukers (1996) found maximum ages of six years at Lizard Island, which is three years younger than found in this study. Doherty & Fowler found max age of 14 and 18 years at the Capricorn Bunker Group of which One Tree Island is a part (1994a, 1994b), and Worthington et al. (1995) also found a maximum age of 18 years at One Tree Island. These older studies used between 300 and 1200 specimens per study. Thus an explanation for the lack of these very old specimens in the present study may be that the oldest specimens form a very small percentage of the population. Missing the oldest specimens by chance is therefore not unlikely unless exhaustively large samples are procured, which the scope of this study precluded.

2.4.3 Maturity

P. moluccensis displayed a non-significant trend for lower age at maturity at lower (warmer) latitudes. Since the observed maximum age (mean t_{max}, tab. 2.2 and 2.3) at Orpheus was significantly lower than at Lizard and One Tree Islands, the slightly lower age at maturity observed at Lizard Island corresponded to maturity at a slightly lower *percentage of maximum age* at Lizard Island compared to Orpheus Island; and to a similar percentage at One Tree as Orpheus. The maturation ages of two to three years found in this study were similar to those estimated by Mapstone at One Tree Island (1988; 2 years for females, 3 years for males). However, no male / female difference in the timing of sexual maturity (defined by histological examination) was observed in this study.

A. polyacanthus consistently matured at a later age than *P. moluccensis*. Similar to *P. moluccensis*, *A. polyacanthus* also displayed a trend for lower age at maturity at the lowest latitude. The ages corresponded to a slightly higher percentage of maximum age at One Tree Island than at Lizard Island since the maximum ages were similar, and to an appreciably higher percentage of maximum age at Orpheus Island since the maximum age recorded there was significantly lower. The results for age at size found in this study were slightly higher than those estimated by Thresher at One Tree Island (1985b; 2-3 years).

The fact that both species displayed a tendency towards higher age at maturity at higher latitudes raises the question if the lack of significance was due to low sample numbers. With higher sample sizes one might find that the trends for higher age at maturity at higher latitudes are significant. Both species showed very consistent sizes at maturity regardless of latitude. The size at maturity was larger for *A. polyacanthus* than *P. moluccensis*, but compared as a percentage of asymptotic size, they were very similar, except for *A. polyacanthus* at One Tree Island, since the asymptotic size was lower there. The sizes for *A. polyacanthus* match well with the recorded smallest observed size for a brooding female of 65 mm SL by Kavanagh (2000). The observed size at maturity as a percent of asymptotic size, were well within the ranges reported by Choat & Robertson for acanthurids and scarids (2002; 52-87%).

2.4.4 Summary

Although the asymptotic size was larger for *A. polyacanthus* than *P. moluccensis*, none of the other von Bertalanffy growth parameters or the observed maximum age differed significantly between the species. *A. polyacanthus* tended to mature roughly a year later than *P. moluccensis*, but this fact may be coupled to the overall larger size of *A. polyacanthus*. The size at maturity seemed to occur approximately when the same percentage of asymptotic size was reached; however, compared within species, absolute size seemed to be the defining parameter rather than percent asymptotic size.

What is interesting is the difference in how the two species' life history traits change between locations. Basically there were no differences between locations for *P. moluccensis*, while *A. polyacanthus* displayed a higher rate of reaching a lower asymptotic size at One Tree Island compared to Orpheus and Lizard Islands, which contradicts the expected trends of larger sizes and slower growth at higher latitudes. This does probably not mean that *A. polyacanthus* is counter-adapted to One Tree Island, rather that the adaptation could be to more than temperature (e.g. variation in temperature, sunlight intensity). Could the higher growth be coupled with the trend for later maturation at higher latitudes, leaving more resources available for growth for one more year, which should otherwise have been spent on gonad maturation?

The lack of significant latitudinal differences on the life histories of *P. moluccensis* means the different populations manage to upkeep the same levels of growth and size at significantly different temperatures. This implies a good degree of adaptation to the local temperature regimes. This degree of adaptation is what I expected to find for *A. polyacanthus*, and as such presents the reverse of the predicted, namely that *P. moluccensis* seems to be as adapted to its local environment as *A. polyacanthus*. The tendency for higher age at maturity at higher latitudes might again partly explain how *P. moluccensis* can maintain equal life history traits at both low and high temperatures, since fewer resources are diverted to developing the reproductive organs, at least in the early life stages.

Chapter 3: Adaptive metabolic differences across latitudes in coral reef damselfish

Abstract

Small increases in temperature cause large increases in energetic costs of maintenance in ectotherms, because metabolic rate scales exponentially with temperature. On this basis I would expect that fish should fine-tune their metabolic rate according to prevailing ambient temperatures in order to minimize these costs. Although there is evidence for within-species metabolic adaptation across latitudes for a few temperate fish species, it has not been studied in coral reef fish across latitudes. In this study I quantified temperature-specific standard metabolic rates (SMR) of two species of damselfish at three locations along the Great Barrier Reef, Australia spanning 9° of latitude. I chose a species that carries out its entire life cycle at a local scale (*A. polyacanthus*) and therefore is likely to show local adaptation, and a species possessing a broadly dispersive larval stage (*P. moluccensis*) less likely to be locally adapted. As expected, I observed that SMR of *A. polyacanthus* was lowest in the low–latitude population (warmest water temperatures), intermediate at at mid-latititude, and highest at the high-latitude (lowest water temperatures) population. By contrast, SMR of *P. moluccensis* was lowest in low-latitude populations, but mid- and high-latitude populations did not differ from each other. Our results confirm that metabolic adaptation does exist among tropical coral reef fish, but the extent of metabolic adaptation depends upon the species' life-history. I speculate that species without a dispersive life history may be more vulnerable to climate change.

3.1 Introduction

It has long been known that small increases in temperature cause large increases in energetic costs of maintenance in ectotherms, because metabolic rate increases exponentially with temperature (e.g. Fry 1971, Brett 1979, Jobling 1994, Jobling 1996). When energetic costs increase with temperature, this decreases the available energy for allocation to growth and/or reproduction in fish (Brett 1979, Yamahira & Conover 2002), and any decreases in growth rates or reproduction are likely to negatively affect fitness. One way that fish can deal with elevated temperatures to offset the greater energy costs is by eating more, but greater foraging effort in response to temperature increases also increases exposure to predators and substantially reduces survival (Biro et al. 2004b, Biro et al. 2007b). However, there may be many situations in which fish simply cannot sufficiently increase their intake rate, or the costs of doing so are too great. For these reasons, I might predict that the large energetic (e.g. Fry 1971, Brett 1979) and survivorship costs (Biro et al. 2007b) associated with small increases in temperature are strong selective pressures that could favour metabolic adaptation to ambient temperature in fish. Indeed, it would be most energy-efficient to keep standard metabolic rate (SMR: the minimum energy expenditure of an individual at rest) as low as possible, provided this does not adversely affect movement capability for foraging and predator avoidance (Jobling 1996).

There is evidence for metabolic adaptation in a few temperate fish species. For example, southern populations of Atlantic silverside in warmer waters have lower SMR than populations in cooler northern latitudes (Arnott et al. 2006). Similarly, Atlantic salmon (a widely dispersing saltwater species that only reproduces in freshwater) and Nile tilapia (a freshwater species), each acclimated to different temperatures have different capacity (scope) for metabolically adapting to subsequent temperature changes (Peterson & Anderson 1969, Mwangangi & Mutungi 1994). Although there are many studies showing metabolic adaptation to temperatures across different marine species (e.g. Bullock 1955, Evans et al. 1962, Fry & Hochachka 1970, Cano & Nicieza 2006), I know of no study that has investigated within-species metabolic adaptation to local temperature in tropical fish. Metabolic adaptation in tropical fish seems likely given that experimentally elevating water temperature above ambient norms reduces the scope for oxygen uptake and decrease growth rate of coral reef fish (Munday et al. 2008b, Nilsson et al. 2009).

The aim of this study was to quantify temperature-specific metabolic rates in two species of tropical reef fish at three sites that span 9° of latitude the Great Barrier Reef, Australia. I used two damselfish species: 1) *Pomacentrus moluccensis* (Bleeker 1853) with a dispersive pelagic larval stage typical of marine fishes (Wellington & Victor 1989, Leis 1991) that allows drift of genetic material among reefs (Sale 1991), and 2) *Acanthochromis polyacanthus* (Bleeker 1855) that does not have a larval stage and shows clear genetic differentiation among reefs (Robertson 1973, Allen 1975, Thresher 1985a, 1985b, Kavanagh 2000). I predicted that fish from low latitude (warm) populations to display lower temperature-specific rates of metabolism than those from higher latitude (cooler) populations. For the species with a higher degree of local adaptation (*A. polyacanthus*) I predicted greater latitudinal differentiation in metabolic rate than for the widely dispersing species, *P. moluccensis* populations (Fig. 3.1).

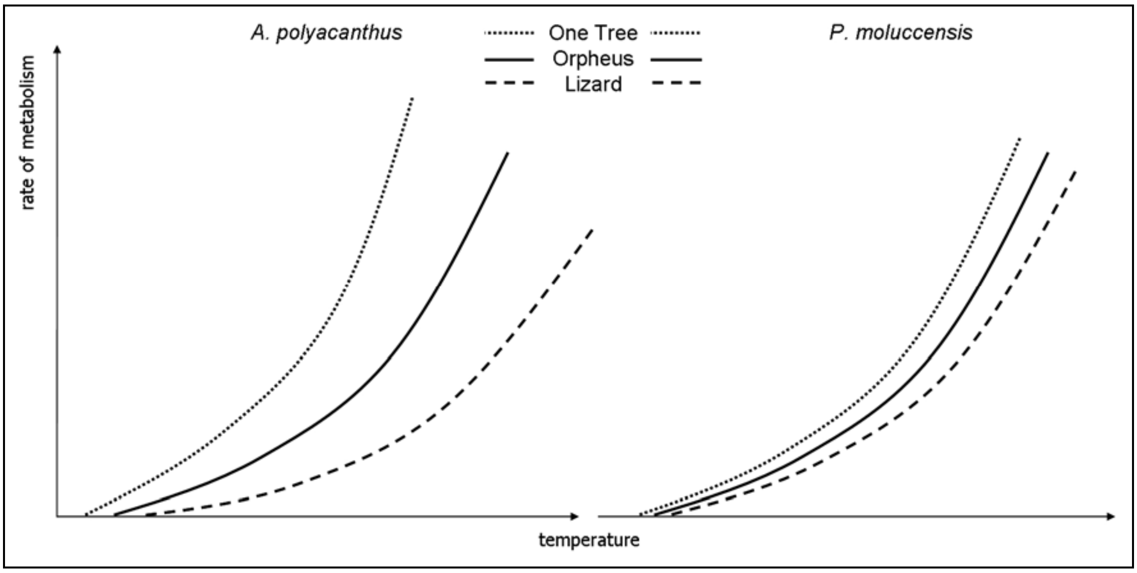

Fig. 3.1: Hypothesized standard metabolic rates for the non-dispersing *A. polyacanthus* and the dispersing *P. moluccensis* damselfish species in relation to temperature and latitudinal locations along the Great Barrier Reef (Lizard Is. = north (warmest), Orpheus Is., and One Tree Island = south (coolest)).

3.2 Materials and methods

3.2.1 Study areas and species

P. moluccensis and *A. polyacanthus* were sampled at three localities along the Great Barrier Reef: Lizard Island (14° 41' S, 145° 18' E), Orpheus Island (18° 37' S, 146° 30' E), and One Tree Island (23° 30' S, 152° 05' E) spanning 9° of latitude. Summer mean sea surface temperatures differed significantly among all sites (Lizard: 29.1°C; Orpheus: 28.5°C; One Tree: 27.4°C; t-tests, all P<<0.0001; data obtained from www.reeffutures.org, now moved to www.aims.gov.au); data ranges from 2001-2003; temperature proxies for Orpheus and One Tree Islands are Pelorus and Heron, one and 10 km north of their respective proxies).

Fish were collected using SCUBA, barrier nets, hand nets, and clove oil solution. Captured fish were placed in individual plastic bags containing water, then transported under cover in larger water-filled tanks to the nearby research station. At the research station they were introduced to flow-through holding tanks at ambient temperature for 24 - 48 hours before on-site experimentation.

A total of 92 damselfish were collected across all species and locations (Tab. 3.1). At each location, fish were collected from four to six different sites and varying in depth from 1½-10m. I captured a representative sample of the adult size range for both species; Thresher (1983) and Kavanagh (2000) reported adult standard lengths of 55-83mm for *A. polyacanthus*, while Mapstone (1988) and Bray (2001) reported adult standard lengths of 25-72mm for *P. moluccensis*. Photoperiod was 13L:11D, to follow the natural light pattern. The fish were fed Wardley® Total Marine Flake Food and frozen brine shrimp *ad libitum*.

3.2.2 Experimental setup

Standard metabolism (Fry 1971, Schurmann & Steffensen 1997) of individual fish was measured as oxygen consumption in fish that had been deprived of food for eight hours prior to experimentation to remove the metabolic cost of digestion (Jobling 1981). For logistical reasons the range of experimental temperatures differed between locations (28.2-31.1°C at Lizard, 25.2-29.3°C at Orpheus, and 24.8-29.4°C at One Tree), representing local ambient temperatures to which they were acclimated, and were kept stable throughout each experiment ±0.1°C.

I estimated oxygen consumption using an oxygen meter connected to a sensor (WTW Oxi 330 / SET) set in a small enclosed chamber (3.1 L) set inside a larger tank. The larger tank was continually supplied with aerated sea water. For fish >55cm SL, a 3.1L chamber was used, for fish <55cm SL a 0.5L chamber was used. The sides of the tank were covered with white cloth so as not to disturb the fish and moreover there was a cover of a piece of 10cm diameter plastic tube (volume 70 ml) for shelter (Fig. 3.2).

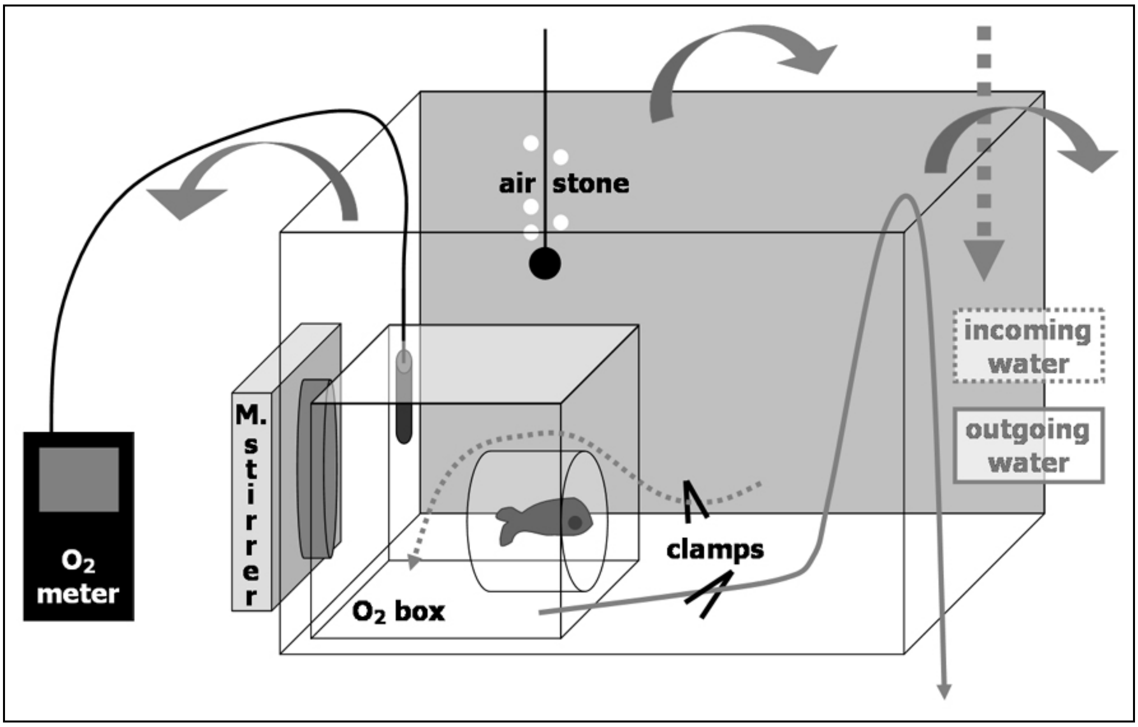

Fig. 3.2: Setup used for measuring the oxygen consumption of damselfish. The fish is in a small enclosed chamber in a larger tank. Fresh sea water is pumped to the larger tank, with overflow over the sides to keep the temperature constant. To ensure ample oxygen in the chamber while the fish acclimates to the new surroundings, the chamber has an outlet, siphoning the water out of the chamber and an inlet letting in fresh aerated water in from the larger tank. At the start of the experiment, the in- and outlets are closed off and the oxygen meter is turned on. A small propeller on the tip of the oxygen sensor ensures that there is even distribution of the oxygen in the water of the chamber. The propeller is driven by the magnetic stirrer outside the larger tank.

The fish was introduced to the chamber one to four hours before the start of the measurements. The period of acclimation time to the chamber was found empirically by comparing the rate of oxygen consumption of individuals that had spent various amounts of time in the setup prior to experiment start. This was implemented via a general linear model analysis in SAS (see the statistics section below), which showed a significant difference (P=0.0022) between individuals that had spent 0 and 1 hour in the setup, but no significant differences between individuals that had spent between 1 and 24 hours in the setup (P=0.5487).

During the acclimation hour preceding each experiment, a small hose siphoned water from the chamber, and another siphoned in fresh sea water from the larger tank to the chamber ensuring sufficient oxygen for the fish. At the start of the experiment, the in- and outlet hoses to the chamber were closed off and measurements commenced. The oxygen concentration (mg/l) and temperature (°C) in the chamber were measured every 30 seconds for one hour. A small magnetically-driven propeller at the tip of the oxygen sensor ensured even distribution of the oxygen in the water of the chamber during measurements. There was a marked reduction in the oxygen consumption when the oxygen concentration levels dropped under 2 mg O_2/L. For a few of the larger specimens, this happened after 25 minutes. Therefore, only the first 20 minutes of each experiment was used for the analyses. A control experiment without any fish showed no detectable rise or fall in the oxygen concentration.

3.2.3 Morphometrics

After experimentation, the fish were euthanized by clove oil overdose. In order to correlate oxygen consumption with size of fish, total wet weight was measured to the nearest 0.5 g. Fish age, maturity and sex ratios were determined through standard otolith processing and histological examinations of gonad tissue, revealing no differences in age distribution or sex ratios among species or sites (Age: F-tests, all P>0.06; Sex ratios: χ^2=0.99, P=0.96; Tab. 3.1).

Tab. 3.1: Ages and sex ratios of the fish used for experimentation. Listed is mean age with minimum and maximum in parenthesis, and sex ratios.

Species	Location	Age (years) mean (min-max)	Sample size	Sex	
				Male	Female
A. polyacanthus	Lizard Island	6.2 (3-10)	12	5	7
	Orpheus Island	4.7 (3-8)	13	7	6
	One Tree Island	4.7 (2-10)	20	10	10
P. moluccensis	Lizard Island	5.3 (2-9)	11	5	6
	Orpheus Island	3.8 (2-7)	17	10	7
	One Tree Island	5.2 (2-10)	19	10	9

3.2.4 Statistical analyses

Analyses were conducted with general linear models, using type III sums of squares tests for the significance of effects using PROC GLM in SAS (Muller & Fetterman 2003). Metabolic rate, body size and temperature were ln-transformed in order to normalize and linearize. Main effects of temperature, fish mass, fish species, location, and interactions involving species, location, and the species*location were tested (there were insufficient data to test for the 3-way species*location*temperature interaction). A significant species*location interaction (after controlling for the main effects of fish mass and temperature) would indicate that differences in SMR among locations varies between the two species. To compare SMR of fish across locations and between species, I used the 'lsmeans' statement to generate the least-squares means and SE's for the location*species interaction, and the 'pdiff' option to determine which populations differed within a species. These means were then plotted in relation to temperature to facilitate comparison with Fig. 3.1.

3.3 Results

After statistically controlling for the expected effects of body mass and temperature on SMR, I observed that metabolic rates differed among locations within species (Fig. 3.3). Larger fish had higher SMR ($F_{1,90}$=214.72, $P<0.0001$) and fish tested at higher temperatures had higher SMR ($F_{1,90}$=26.95, $P<0.0001$). After accounting for these effects, SMR differed among locations within a given species (species*latitude interaction; $F_{2,89}$=4.46, P=0.0144; Fig. 3.3). Least squares means describing this significant interaction effect revealed that the non-dispersing *A. polyacanthus* displayed significantly different metabolic rates between all three locations (Fig. 3.3). At a given temperature, *A. polyacanthus* from the population at low-latitud Lizard Island (warmest site) exhibited lower SMR than fish from the mid-latitude Orpheus Island population ($P<0.02$), and Orpheus Is. fish had lower SMR than fish from the high-latitude One Tree Island (coolest site) population ($P<0.0001$). In contrast, metabolic rates in the dispersive *P. moluccensis* differed only at one latitude, whereby low-latitude (warm) Lizard Island fish had significantly lower metabolism compared to mid- and high-latitude locations (both $P<0.001$), but mid- and high-latitude populations did not differ ($P>0.2$).

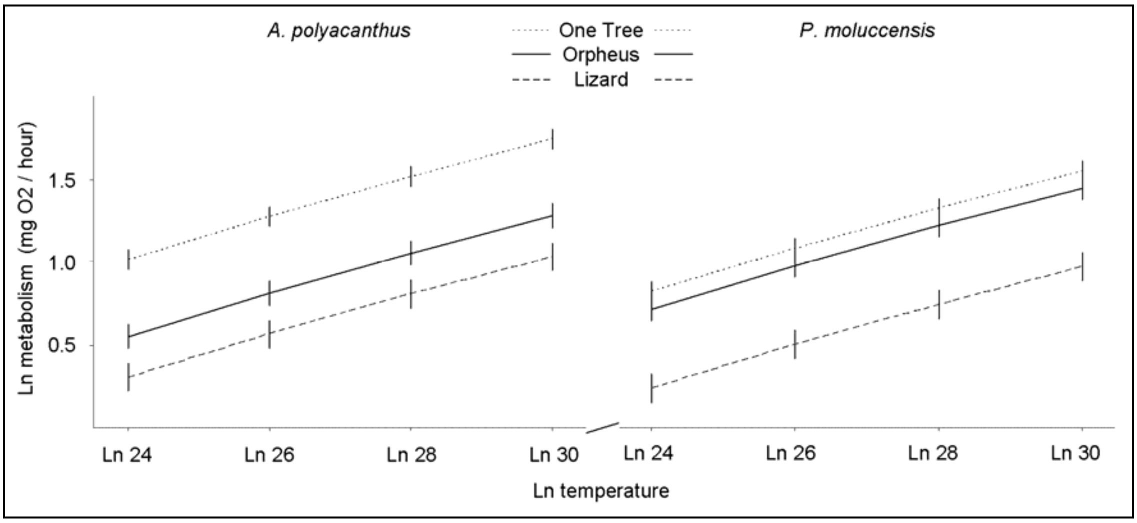

Fig. 3.3: Temperature-specific metabolic rates of two damselfish species at three sites on the Great Barrier Reef. Shown are the model-predicted (least squares) means and standard errors after accounting for body mass effects (standardized to a 13g fish). Ln transformation of SMR and temperature linearizes the exponential relationships shown in Fig. 3.1. Raw data are omitted for clarity because samples come from fish of varying size. See Method section for descriptions of fish sizes and numbers.

3.4 Discussion

As predicted, metabolic adaptation was more pronounced in the non-dispersive *A. polyacanthus*, than in the dispersive *P. moluccensis*. At a given temperature, *A. polyacanthus* displayed significantly different metabolic rates across all three locations, being lowest in the warm low-latitude population, and highest at the cool high-latitude population. In contrast, metabolic rates in the dispersive *P. moluccensis* were significantly lower in the low-latitude (warm) population, but metabolism did not differ between the other two populations. The greater degree of apparent metabolic adaptation in the non-dispersive species suggests potentially more efficient performance at its natal reefs than the widely dispersing species, but at the same time less scope to adapt to temperatures different from that of its native reef. The risk might be short-term, e.g. less ability to survive rapid temperature changes should an oceanographic event happen; or longer term, e.g. less resistance to predicted climate-change warming (Pratchett et al. 2009).

Although average temperature differences across our three sites only differed by a few degrees (see Methods), these relatively small differences are actually quite substantial for metabolic costs in light of the fact that metabolism scales exponentially with temperature. Indeed, for the non-dispersing *A. polyacanthus* I observed large and significant SMR differences across latitudes in a manner that is consistent with fish minimizing metabolic costs in warmer (lower) latitudes. In contrast to the non-dispersive species, the SMR of *P. moluccensis* was significantly lower at the warmest (low-latitude) site, but the mid- and high-latitude sites did not differ from each other. These results are consistent with our prediction that I expected less differentiation among populations due to mixing of dispersive larvae over large areas. In particular, the patterns of SMR across latitudes suggest that perhaps the warmest (northernmost) population experiences less mixing than those at mid- to southern portions of the GBR.

It is interesting to point out that, in the case of *A. polyacanthus*, metabolic rates differ much more than would be expected for fish trying to maintain some sort of optimal SMR at the temperatures the fish actually experience at each site. Rather, *A. polyacanthus* at the coolest site had much higher metabolic rates at its average summer temperature than fish at the warmest site at their average summer temperature. It is likely that factors other than just metabolism, such as system productivity (i.e. food abundance), differences in winter water temperatures, or a combination of these or other factors also play a significant role in affecting SMR.

Of course, our experimental design cannot distinguish whether the SMR differences I observed are due to genetic differentiation, acclimation, developmental effects or their combined relative influences. Nonetheless, our results clearly show adaptive reductions in metabolic rates with increases in average temperature across latitudinal populations. Because resting metabolic rate is a repeatable and heritable trait (Nespolo & Franco 2007), I suspect that genes do play a role in the differentiation I observed here (at least for the non-dispersing species). In fact, data from common garden experiments show that large genetic effects on SMR can exist for marine fish populations across temperate latitudes (Arnott et al. 2006). Given that the SMR of *P. moluccensis* did not differ between mid- and high latitude populations indicates that this species is not completely free to modify its metabolism through acclimation or developmental effects. In order to tease out the influence of genetic versus developmental effects would require common garden experiments starting at the egg stage. Such a study would need to employ a controlled breeding experiment and at the same time also manipulate early environment to determine the relative importance of adaptation and acclimation. This has been done for some temperate fish species

(Alvarez et al. 2006, Arnott et al. 2006, Cano & Nicieza 2006), but not yet for tropical taxa, and would constitute a critical next step in the research on metabolism on tropical fish species.

An organism will need to keep its consumption rate correlated to its metabolic rate or lose weight with consequent loss in fitness. Consumption rates plotted over rising temperatures usually describe a skewed bell curve with a more abrupt fall at a crucial high temperature (e.g. Jobling 1996). With global temperature change affecting the Great Barrier Reef (Pratchett et al. 2009), it would be useful to examine the species upper temperature limits for feeding, to test whether individuals at One Tree Island, with the relatively higher metabolism, will be able to maintain their rising metabolism with rising temperatures, with the ensuing need for higher food consumption and resulting predator exposure. One possible future scenario could be that dispersive fish larvae from warmer low latitude habitats will colonize higher latitudes habitats, where they can keep up their rate of feeding to their rate of metabolism. In contrast, local breeders may go extinct when temperatures increase, and in absence of adaptation, a wave of extinction would gradually move from warmer to colder areas. Supporting this idea, Munday et al. (2008b) recently showed diminished growth with increasing temperatures for *A. polyacanthus* in the Orpheus Island area. Similarly, Nilsson et al. (2009) showed decreased ability to maintain oxygen uptake with temperatures above ambient summer temperatures, although *A. polyacanthus* maintained a higher uptake compared with other local fish species.

The results of this study may suggest that *A. polyacanthus* are adapted to the local ambient temperature by virtue of the lack of dispersal and thereby have limited scope for local evolution. *P. moluccensis* on the other hand adapts to the extent the phenotypic plasticity of its genome “allows” it. The often observed countergradient variance in growth (e.g. Conover & Schultz 1995) may therefore simply be the result of less energy being available for growth, since at lower latitudes a larger portion of the acquired energy is going towards maintaining a higher metabolism. By the same reasoning, if fish were to live in a non-food restricted environment, one might see an adaptation towards an increase in the metabolic rate.

Chapter 4: Growth of juvenile damselfishes across a temperature gradient; comparison of a widely dispersing versus a brooding damselfish species from latitudinally separate populations

Abstract

Since fish are ectotherms, ambient temperatures will significantly affect their physiological rates and consequent growth rates. There are many studies on the responses to temperature fluctuations in temperate marine fishes but much less is known about the responses of tropical marine fishes.

To test the variations in growth potential of juvenile tropical fish according to species and location of origin, this study examined the growth potential of juvenile damselfishes of two species, while fed *ad libitum* at different temperatures, from three latitudinally separate locations along the Great Barrier Reef, Australia. After statistically accounting for differences in body size, the dispersing *P. moluccensis* showed no significant difference in growth rate per unit temperature from different latitudes but consistently higher growth rates at higher temperatures (0.0641-0.1190 $\log(g_{(final)}/g_{(initial)})$/day), indicating higher potential growth rates at lower latitudes under normal ambient temperatures. The non-dispersing *A. polyacanthus* had a significantly lower growth rate per unit temperature at the lower latitude Lizard Island (0.0575 $\log(g_{(final)}/g_{(initial)})$/day +/-0.0057) than at the mid- and high latitudes Orpheus and One Tree Islands (0.1303 $\log(g_{(final)}/g_{(initial)})$/day +/-0.0153). This suggests that *A. polyacanthus* at low latitudes may have compromised its ability to achieve very high growth rates, perhaps in trade for an overall higher growth rate under less favourable conditions. It also suggests that *P. moluccensis* individuals may be adapted to a wider range of temperatures than *A. polyacanthus*, allowing specimens to survive at locations far from their natal reef, which indicates higher survival probability in conjunction with thermal climate changes.

4.1 Introduction

One of the primary objectives of ecological research is to understand the factors that affect processes such as growth, mortality and reproduction, thereby influencing population dynamics (Figueira et al. 2008). Since fish are ectotherms, lower ambient temperatures will lower the rate of physiological processes, thereby also the potential growth rate (Wood & McDonald 1997).

Current climate change predictions indicate an increase in average sea-surface temperatures ongoing and over the coming century (Guinotte et al. 2003, Lough 2007). Although there are many studies on the responses to temperature fluctuations in temperate marine fishes (e.g. Jobling 1996, Buckley et al. 2004, Martell et al. 2005), with reports of range shifts in temperate marine species (Holbrook et al. 1997, Parker & Dixon 1998, Perry et al. 2005), much less is known about the responses of tropical marine fishes (Munday et al. 2008a).

In temperate species, mortality during winter of small-sized individuals is higher than that of larger individuals during winter (Biro 2004a). High-latitude populations of temperate widespread species will therefore have a significant selection pressure on them to grow to larger sizes, which combined with a shorter growing season, leads to increased growth rate (Conover 1992, Nicieza et al. 1994, Conover & Schultz 1997). Tropical species may not suffer similar over-winter mortality as the temperate species. Rather, a significant growth constraint may be warm temperatures, which heightens the idling cost of metabolism (see chapter 3) combined with food availability (Jobling 1996, Munday 2008b).

Fish populations might survive temperature changes by either migrating or by adapting to changed temperature conditions. Many tropical reef fish species have broad geographical distributions, spanning a wide range of habitats (e.g. Jones et al. 2002). Populations of such widely distributed reef fish may already be adapted to the local temperatures (e.g. Conover 1992). However, populations adapted to a specific temperature range may be less able to adapt to further temperature changes (Kingsford & Hughes 2005, Munday et al. 2008b). Thus, insights into growth changes that may be expected with global temperature changes may be gained by studying current differences among species in the local reactions to temperature change.

This study examined the effects of temperature on the growth of two common coral-reef fishes, *Pomacentrus moluccensis* (Bleeker 1853) and *Acanthochromis polyacanthus* (Bleeker 1855). They are ideal species to examine the effects of temperature variation on growth because they both have wide distributions, both are abundant, both are very range limited throughout their adult lives (Kavanagh 2000, Harrison & Booth 2007), but differ in their degree of dispersal (e.g. Sale 1991, Kingsford & Hughes 2005). *P. moluccensis* displays the usual pelagic larval stage of reef fishes (Wellington & Victor 1989, Leis 1991). This pelagic stage allows exchange of genetic material among coral reefs (Sale 1991). Contrasting, *A. polyacanthus* lacks this dispersive pelagic larval stage. Instead, *A. polyacanthus* parents defend their brood of larvae and juveniles for several months (Robertson 1973, Allen 1975, Thresher 1985a, 1985b, Kavanagh 2000). For that reason, in contrast to *P. moluccensis*, the inter-generational spreading of *A. polyacanthus* is most likely slow between reefs. This should enable a higher degree of local adaptation, increasing the local performance of individuals but also possibly a lowering their ability to adapt to changes in the environment (Kingsford & Hughes 2005, Munday et al. 2008b).

To investigate the potential local adaptation to temperature, I investigated the potential for intrinsic growth of *P. moluccensis* and *A. polyacanthus* while fed *ad libitum*. Critically, this involved measuring the weight increase in locally-captured juvenile specimens reared at two different temperatures at Lizard Island, Orpheus Island, and One Tree Island along the Great Barrier Reef, Australia. Ideally, since the rate of growth at different temperatures describes a dome-shaped curve (e.g. Jobling 1996), more than two experimental temperatures should have been tested at each location. However, for logistical reasons, only two temperatures were available at each location. One was therefore set to approximately ambient sea surface summer temperature, for the reasoning that due to selection pressure, optimum temperature for growth should be close to ambient temperature of the specific location.

Since *A. polyacanthus* has limited dispersal, I expected it to display a higher degree of adaptation to local temperature than *P. moluccensis*. Since larger and/or faster growing individuals have a higher probability of survival (Anderson 1988, Schultz et al. 1998, Booth & Hixon 1999, Bergenius et al. 2002, Vigliola & Meekan 2002, Wilson

& Meekan 2002, Brunton & Booth 2003, Biro et al. 2004a), such a higher degree of adaptation should translate into higher growth rates for *A. polyacanthus* than *P. moluccensis* at the ambient temperature at each location (Fig. 4.1). However, if higher adaptation to local temperature is coupled with a more limited ability to survive at other than local temperatures, I should find higher growth rates for *P. moluccensis* than *A. polyacanthus* at the manipulated temperature at each location (Fig. 4.1).

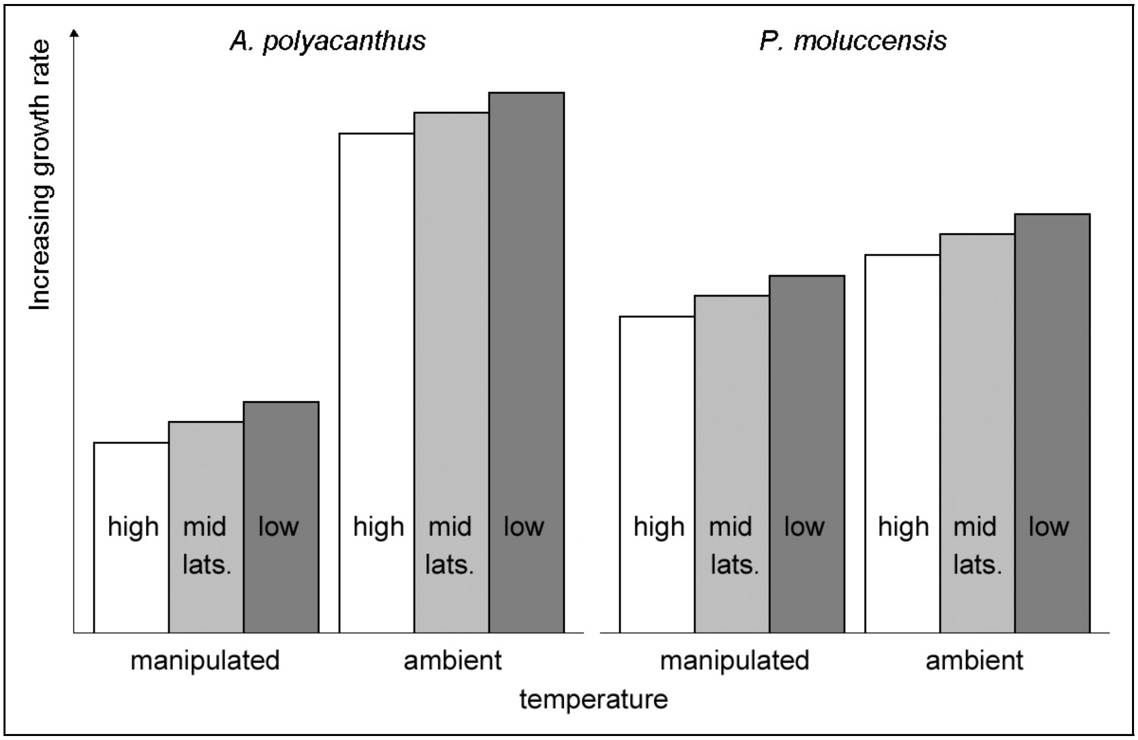

Fig. 4.1: Expected intrinsic growth rates of the non-dispersing *A. polyacanthus* and the dispersing *P. moluccensis* from One Tree Island, Orpheus Island, and Lizard Island (low-, mid-, and high latitude location) at ambient and manipulated temperatures.

4.2 Materials and methods

4.2.1 Study areas and field sampling

I sampled juvenile *Pomacentrus moluccensis* (Bleeker 1853) and *Acanthochromis polyacanthus* (Bleeker 1855) at three localities along the Great Barrier Reef; Lizard Island (14° 41' S, 145° 18' E), Orpheus Island (18° 37' S, 146° 30' E), and One Tree Island (23° 30' S, 152° 05' E) spanning 9° of latitude (Tab. 4.1). The sampled specimens ranged in size; 0.25 to 4.4 g for the *A. polyacanthus* and 0.07 to 1.6 g for the *P. moluccensis*. A total of 300 specimens were sampled, distributed across two species (*A. polyacanthus* and *P. moluccensis*) and three locations (Lizard, Orpheus and One Tree Islands along the Great Barrier Reef, Australia) (Tab. 4.1).

Tab. 4.1: Study sites with latitude, mean sea surface temperatures, sampling dates, and number of fish sampled and in the statistical analyses. *Ap* = *A. polyacanthus*, *Pm* = *P. moluccensis*. Temperature data obtained from Hwww.reeffutures.orgH, now moved to Hwww.aims.gov.auH. Temperatures are from 2001-2003. Pelorus Island serves as temperature proxy for Orpheus Island, Heron Island is proxy for One Tree Island. Pelorus Island is one km north of Orpheus Island, Heron Island is 10 km NW of One Tree Island. Temperatures between the islands are significantly different (one tailed T-test, P<0.0001).

Locality	Latitude	Summer sea surface temperatures (°C) mean (min - max)	Sampling and Experiment dates	Sample # / # in stat. analyses *Ap*	*Pm*
Lizard Island	14° 41' S	29.1 (26.0 – 31.6)	S: 24-26/12 2005 E: 27/12 2005-11/01 2006	50/24	50/29
Orpheus Island	18° 37' S	28.5 (25.6 – 31.9)	S: 29-30/01 2006 E: 31/01-15/02 2006	50/27	50/27
One Tree Island	23° 30' S	27.4 (23.0 – 34.6)	S: 25-26/02 2006 E: 27/02-14/03 2006	50/30	50/28

A. polyacanthus exhibits brood care, and the inter-generational dispersal of the fish is thus limited compared to a fish with a pelagic larval stage, such as most tropical reef fishes including *P. moluccensis* (Robertson 1973, Sale 1991, Kingsford & Hughes 2005). Fish were caught with barrier nets, hand nets and clove oil. They were placed in plastic bags with a fresh supply of seawater and transported under cover in larger seawater-filled tanks by dinghy to the research station.

4.2.2 Husbandry

At the research station the juvenile pomacentrids were let five specimens into 8 – 20 L species specific holding tanks for 1 - 3 days before the initial measurements were taken. The tanks were filled with filtered (McCracken's, FX750RP), aerated sea water and kept at the experiment temperatures of 30°C and 27°C at Lizard, 29°C and 26°C at Orpheus, and 28°C and 25°C at One Tree Island. For logistical reasons only one of the test temperatures at each location could be significantly manipulated. Therefore the warm temperature was set to the ambient setting and the colder temperature set 3°C lower. Photoperiod was 13L:11D. Water characteristics were monitored and maintained at: nitrate <1mg/L, nitrite <0.05mg/L, ammonia <0.25mg/L, phosphate <0.2mg/L, and pH 7.8-8.2. The fish were fed twice daily with finely chopped Wardley® Total Marine Flake Food and frozen, chopped up hatchling Artemia sp. *ad libitum* and tanks were gently siphon cleaned for excess food one to two hours after feeding. The water was aerated and the fish were provided with small pieces of plastic for shelter.

4.2.3 Morphometrics

Fish were measured on day one and day 15 of the experiment period, the length of which was chosen for logistical reasons. I measured standard length (SL) to the nearest 0.1 mm and total wet weight (WW) to the nearest 0.001g. On day 15 of the experiment period, the fish were killed by clove oil overdose, and SL and WW were taken again.

In some tanks one or two of the two largest fish would occasionally antagonize one or two of the smallest. In a natural setting, the smallest individuals would be able to avoid being antagonized by swimming away or into smaller crevices in the corals where the larger aggressor cannot follow (Brolund, pers. obs.). In the current setup, they did not have this option. Therefore only the data from the three largest individuals of each tank was used in the analyses to avoid artefactual aggression effects. This left between 24 and 30 specimens from each location for the statistical analyses.

4.2.4 Statistical analyses

Growth rate was calculated as: (log (final mass) – log (initial mass)) / days in experiment (Björnsson et al. 2007). Growth rates were arcsin and square-root transformed to linearize.

To initially test for the best model composition for analysis of growth, interactions were tested (individual and synergistic interactions by the factors: species (*A. polyacanthus* and *P. moluccensis*), initial mass, temperature, location (Lizard, Orpheus, and One Tree Islands), and tank allocation). Main effects of initial mass, fish species, and interactions involving location, temperature and species were found significant via MANOVA in SAS.

Analyses were then conducted with general linear models, using type III sums of squares tests for the relative significance of effects using PROC GLM in SAS (Muller & Fetterman 2003). A significant species*location*temperature interaction (after controlling for the main effects of fish initial mass and temperature) would indicate that differences in growth among locations varies between the two species. To compare growth of fish across locations and between species, we used the 'lsmeans' statement to generate the least-squares means and SE's for the species*location*temperature interaction, and the 'pdiff' option to determine which populations differed within a species.

4.3 Results

Significant effects on growth rate were found between species (*A. polyacanthus* and *P. moluccensis*) ($F_{1,163}$=7.18; P=0.0082), from initial body mass ($F_{1,163}$=30.6; P<0.0001), from location by temperature (Lizard Island 30 and 27°C; Orpheus Island 29 and 26°C; One Tree Island 28 and 25°C) ($F_{5,160}$=5.62; P<0.0001), and from an interaction of location, temperature and species ($F_{5,160}$=16.07; P<0.0001).

After statistically correcting for fish initial mass, the least squares means values of growth rate (Tab. 4.2 and Fig. 4.2) revealed significant differences (Tab. 4.3) in the temperature effects on growth rate of the two species (t=2.68, P=0.0082). *P. moluccensis* displayed a gradually increasing rate of growth according to temperature. At each island *A. polyacanthus* displayed no significant differences between the growth rates at the two test temperatures (Tab. 4.3; t=0.50-1.70; P=0.0917-0.6149).

The highest growth rate of *P. moluccensis*, that of the 30°C regime at Lizard Island, was not significantly different from the highest growth rates of *A. polyacanthus* (all temperatures at Orpheus and One Tree Islands; t=0.31-1.56; P=0.1212-0.7604). Likewise, the low growth rates of *A. polyacanthus* at Lizard Island at the low and high temperatures were not significantly different from the two and four lowest growth rates of *P. moluccensis*, respectively (Fig. 4.2; Tab. 4.3; t=0.09-1.84; P=0.0677-0.9304).

Tab. 4.2: Least squares means of the growth ((log(final mass/initial mass))/day) of *A. polyacanthus* and *P. moluccensis* from Lizard Island, Orpheus Island and One Tree Island.

Species	Location	Temperature °C	Least Squares Means of growth	Standard Error
A. polyacanthus	One Tree	25	0.1150	0.0081
		28	0.1333	0.0090
	Orpheus	26	0.1399	0.0109
		29	0.1456	0.0118
	Lizard	27	0.0631	0.0081
		30	0.0518	0.0093
P. moluccensis	One Tree	25	0.0718	0.0083
		28	0.0833	0.0083
	Orpheus	26	0.0641	0.0087
		29	0.0974	0.0082
	Lizard	27	0.0819	0.0089
		30	0.1190	0.0087

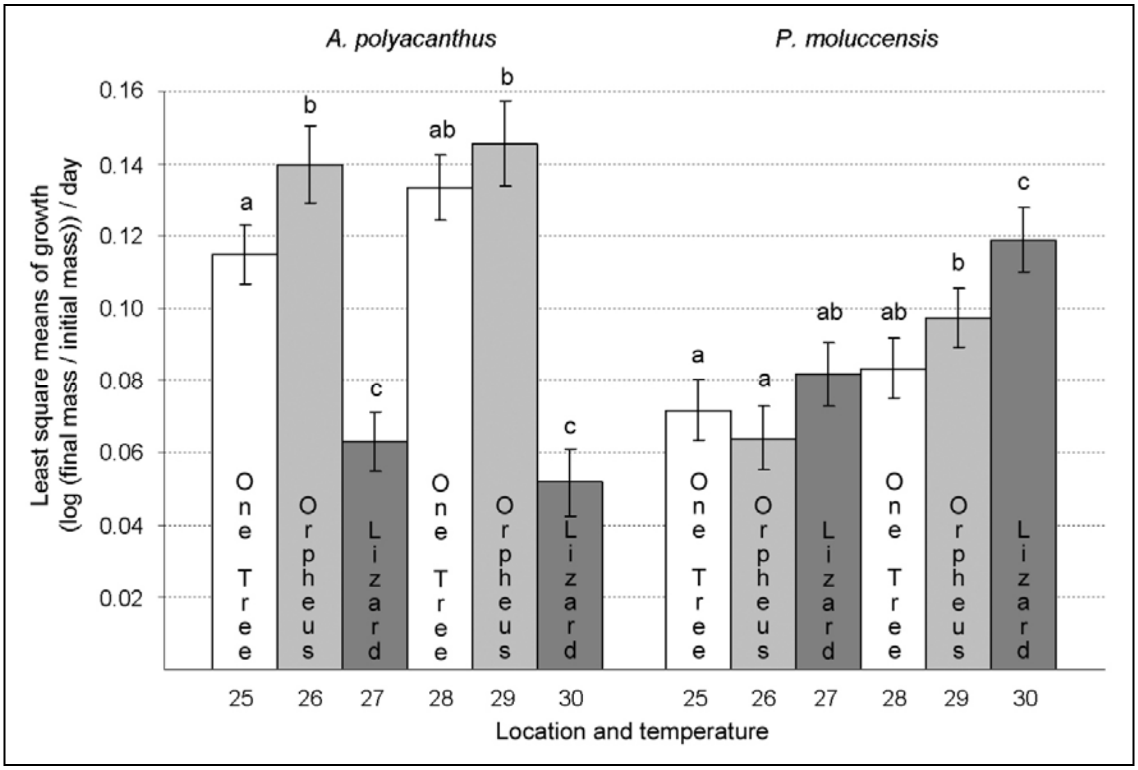

Fig. 4.2: The calculated least squares means of growth rate of *A. polyacanthus* and *P. moluccensis* at Lizard, Orpheus, and One Tree Islands at two temperatures at each location. Letters above bars indicate statistically similar means for each species. The global r^2 of the model is 0.41.

Tab. 4.3: Comparisons of Least Squares Means, listed are results of t-test (3 digits) and probabilities (5 digits) of equal growth rates between *A. polyacanthus* (*Ap*) and *P. moluccensis* (*Pm*) from Lizard Island, Orpheus Island and One Tree Island at the two temperatures tested at each location.

		Lizard 30°C		**Lizard 27°C**		**Orpheus 29°C**		**Orpheus 26°C**		**OneTree 28°C**		**OneTree 25°C**	
		Ap	***Pm***	***Ap***	***Pm***	***Ap***	***Pm***	***Ap***	***Pm***	***Ap***	***Pm***	***Ap***	***Pm***
Lizard 30°C	***Ap***	-	-5.54 <0.0001	-0.94 0.3486	-2.45 0.0154	-5.88 <0.0001	-3.83 0.0002	-5.83 <0.0001	-0.99 0.3238	-6.03 <0.0001	-2.61 0.0101	-4.98 <0.0001	-1.65 0.1002
	Pm	5.54 <0.0001	-	5.11 <0.0001	3.45 0.0007	-1.56 0.1212	2.03 0.0445	-1.30 0.1955	4.82 <0.0001	-1.01 0.3121	3.30 0.0012	0.31 0.7604	4.36 <0.0001
Lizard 27°C	***Ap***	0.94 0.3486	-5.11 <0.0001	-	-1.69 0.0922	-5.23 <0.0001	-3.18 0.0018	-5.17 <0.0001	-0.09 0.9304	-5.38 <0.0001	-1.84 0.0677	-4.30 <0.0001	-0.79 0.4298
	Pm	2.45 0.0154	-3.45 0.0007	1.69 0.0922	-	-3.72 0.0003	-1.44 0.1521	-3.59 0.0004	1.54 0.1252	-3.62 0.0004	-0.12 0.9009	-2.55 0.0118	0.92 0.3591
Orpheus 29°C	***Ap***	5.88 <0.0001	1.56 0.1212	5.23 <0.0001	3.72 0.0003	-	2.97 0.0035	0.50 0.6149	5.08 <0.0001	1.06 0.2910	3.84 0.0002	2.47 0.0145	4.54 <0.0001
	Pm	3.83 0.0002	-2.03 0.0445	3.18 0.0018	1.44 0.1521	-2.97 0.0035	-	-2.78 0.0061	2.97 0.0035	-2.68 0.0082	1.32 0.1894	-1.43 0.1546	2.39 0.0182
Orpheus 26°C	***Ap***	5.83 <0.0001	1.30 0.1955	5.17 <0.0001	3.59 0.0004	-0.50 0.6149	2.78 0.0061	-	5.01 <0.0001	0.60 0.5503	3,70 0.0003	2.13 0.0350	4.45 <0.0001
	Pm	0.99 0.3238	-4.82 <0.0001	0.09 0.9304	-1.54 0.1252	-5.08 <0.0001	-2.97 0.0035	-5.01 <0.0001	-	-5.17 <0.0001	-1.68 0.0950	-4.09 <0.0001	-0.67 0.5019
OneTree 28°C	***Ap***	6.03 <0.0001	1.01 0.3121	5.38 <0.0001	3.62 0.0004	-1.06 0.2910	2.68 0.0082	-0.60 0.5503	5.17 <0.0001	-	3.72 0.0003	1.70 0.0917	4.57 <0.0001
	Pm	2.61 0.0101	-3.30 0.0012	1.84 0.0677	0.12 0.9009	-3.84 0.0002	-1.32 0.1894	-3.70 0.0003	1.68 0.0950	-3.72 0.0003	-	-2.56 0.0113	1.05 0.2952
OneTree 25°C	***Ap***	4.98 <0.0001	-0.31 0.7604	4.30 <0.0001	2.55 0.0118	-2.47 0.0145	1.43 0.1546	-2.13 0.0350	4.09 <0.0001	-1.70 0.0917	2.56 0.0113	-	3.49 0.0006
	Pm	1.65 0.1002	-4.36 <0.0001	0.79 0.4298	-0.92 0.3591	-4.54 <0.0001	-2.39 0.0182	-4.45 <0.0001	0.67 0.5019	-4.57 <0.0001	-1.05 0.2952	-3.49 0.0006	-

4.4 Discussion

The aim of this study was to examine possible differences in the growth rate of two species of damselfish from three locations along the Great Barrier Reef. Significant effects on growth rates were found between species, from initial body mass, from location by temperature, and from an interaction of location, temperature and species. After statistically accounting for differences in size, the results showed that 1) the range of growth rates was not significantly different between the two species, since the highest growth rates of the dispersing *P. moluccensis* were not significantly different from the highest growth rates of the non-dispersing *A. polyacanthus*, and the lowest growth rates of *P. moluccensis* were not significantly different from the lowest growth rates of *A. polyacanthus*. However, the rate of growth according to temperature was differently distributed for the two species, namely in that: 2) *P. moluccensis* showed significant differences in growth rate per unit temperature, 3) *A. polyacanthus* displayed no clear temperature effect on growth rate (but see below), and 4) *A. polyacanthus* displayed lower growth rates at the low latitude than at the mid- and high latitudes.

I predicted that *A. polyacanthus* would be better adapted to the local temperature. Thus the first result of this study, that the range of the rate of growth was not significantly different between the two species, contrasts the predictions. However this higher degree of adaptation or acclimation to the local temperature could mean an overall higher growth rate, but also a lower capacity for rapid growth in periods of sufficient food (Pratchett et al. 2001, Kavanagh 2005) at Lizard Island compared to Orpheus and One Tree Islands. It could also very tentatively mean that *P. moluccensis* is more plastic than *A. polyacanthus* in its phenotype with regards to growth rate sensitivity to temperature. The plasticity may lie e.g. in an ability to alter its behaviour to fit the temperature regime encountered (Biro, pers. comm.). *A. polyacanthus* is presumably adapted to other factors in its local habitat than temperature, and a tradeoff for the adaptations might have decreased its ability to adapt to changes in temperature (e.g. Angilletta et al. 2003, Booth & Biro 2008).

The location by temperature effect on the growth rate of *P. moluccensis* seemed to be more due to temperature than location, since the species displays a gradually increasing rate of growth according to temperature. However, I did not have a sufficiently large data set to test this difference statistically. Furthermore, the maximum tolerable temperature for growth of *P. moluccensis* seems to be higher than 30°C. Through individual tagging Booth (unpublished) has shown growth and mortality of *P. moluccensis* in the wild to be higher at Lizard Island than One Tree Island. Given the ambient temperature differences of these two locations, this confirms the second observation in this study: as predicted in the introduction, seemingly regardless of location *P. moluccensis* displays differences in growth rate according to temperature.

The results for the growth rate of *P. moluccensis* partially contrast those found by Bray (2001). She investigated the growth rate of juvenile *P. moluccensis* from Lizard Island, John Brewer Reef and One Tree Island, reared for approximately 65 days at 23 and 28°C and found no significant influence of temperature on the growth rate. However, she also found no significant influence of location on the growth rate, which supports the impression from this study that the differences in *P. moluccensis* growth rate were due to temperature differences rather than location.

The third observation, that *A. polyacanthus* displayed no clear temperature effect on growth rate, contrasts the expectations, since I expected *A. polyacanthus* to perform well at the normal local ambient temperature and less well at an altered temperature. It is possible that with higher specimen numbers, the difference observed in *A. polyacanthus* growth rate at the two temperatures at Lizard Island would have been significantly different. However, the reality may be that the temperature optimum for growth is not at either of the two test temperatures but in-between. Since growth rate according to temperature is not linear, but rather a dome-shaped curve (e.g. Jobling 1996), the two test temperatures might in fact “straddle” the optimum of the growth/temperature curve. Thus this part of the conclusion is uncertain at best.

However, Munday et al. (2008b) investigated the growth rate of juvenile *A. polyacanthus* from Orpheus Island, reared at 26, 28, and 31°C. They found significantly lower growth at 31°C compared to 26 and 28°C for juvenile specimens fed a high quality diet. But they found no significant differences between 26 and 28°C. The results of that study correspond well with this, in that there was no significant difference between growth rates of *A. polyacanthus* at Orpheus Island at 26 and 29°C. From

Munday et al. (2008b) it seems that 31°C is near the thermal tolerance of juvenile *A. polyacanthus*.

I predicted that we should see evidence of latitudinal growth compensation in *A. polyacanthus* so that in spite of lower temperatures, individuals at high latitudes should be able to uphold a growth rate as high as those observed at lower latitudes. The fourth observation of this study seems to fulfill this prediction in that *A. polyacanthus* displayed lower growth rates at both temperatures at the low latitude location compared to all temperatures at the mid- and high latitude locations. However, *A. polyacanthus* seems much hampered in growth at Lizard Island compared to the other two latitudes. For the growth rate in the 30°C regime, the explanation might be that the species is nearing its temperature tolerance limits for growth (Munday et al. 2008b showed a temperature tolerance limit close to 31°C at Orpheus Island). However, this does not explain the observed growth rate at 27°C. A better explanation might be that the rate of metabolism is overall lower at Lizard Island than at both Orpheus and One Tree Island, thereby limiting the ability for burst growth when conditions allow (see chapter 3).

There is a caveat to these conclusions since growth rate over temperature describes a dome-shaped curve (e.g. Jobling 1996). The conclusions of this study are limited by this fact since it is uncertain if one of the test temperatures at each location is at the apex of each species' growth curve. The largest intra-location differences observed are for *P. moluccensis* at Lizard and Orpheus Islands. If I hypothetically assume that for *A. polyacanthus* at Lizard Island one would find higher growth rates at 29°C, the growth rate difference would probably be within that same order of magnitude higher than the currently observed growth rates as the differences observed for *P. moluccensis* at Lizard and Orpheus Islands. That would still leave the results for *A. polyacanthus* at Lizard Island significantly lower than *A. polyacanthus* at Orpheus and One Tree Islands, especially considering one should presumably do the same hypothetical heightening of the growth rate for e.g. 27 or 28°C at Orpheus Island and at 26 or 27°C at One Tree Island.

It is possible that a higher degree of acclimation to the test temperature would have been possible, had the experiment run for longer. This would hypothetically have "smoothed" the results so that the growth at both temperatures at each location would have been more similar. If, contrastingly the fish exhibited no acclimation, the differences between the test temperatures should hypothetically have been higher.

Yamahira et al. (2007) demonstrated substantial genetically-based variation in thermal reaction norms for growth rates among latitudinal populations of *Oryzias latipes*. High latitude individuals grew faster and accelerated their growth more rapidly with temperature than low latitude individuals. However, high latitude individuals did not compensate their annual growth rates by shifting thermal reaction norms toward lower temperature ranges to thereby extend the growing season. Yamahira et al. (2007) suggested that the reason for this could be that food is only available during shorter periods of a year in higher latitude environments. This should mean that conditions allowing, high latitude populations should display a higher growth rate potential than low latitude populations, which is what this study has shown for *A. polyacanthus* although not for *P. moluccensis*.

Even though the statistical significance of the parameters calculated with the general linear model were all highly significant, the r^2 of the model is only 0.41. This is most likely due to a combination of small number of test subjects per treatment and a high inter-individual variation. Nevertheless, the statistical differences in the growth rates of *A. polyacanthus* are at highly significant levels (α=0.01%, Tab. 4.3), and though the statistical differences in *P. moluccensis* are not as high (α=5%, Tab. 4.3), the growth rates are consistently statistically significantly increasing with temperature. Another explanation may lie in animal "personalities", which has been shown to influence the use of risky habitats (Biro et al. 2007) and the resting metabolic rate (Careau et al. 2008), both of which should affect individual growth as well. Inter-individual variation would presumably not affect the significance of the various parameters tested on growth, but might affect their specific input on growth and thus account for the relatively low r^2 of the model.

At One Tree Island, juvenile *P. moluccensis* become more active with higher temperatures (Biro, pers. comm.). One explanation for the growth differences observed in *P. moluccensis* in this study and by Booth (unpublished) could be the presumably higher winter activity of *P. moluccensis* at Lizard Island than One Tree Island inferred from Biro's observations. Thus, due to activity level, individuals at Lizard should presumably forage more for food, and thus also be more exposed to predators, thereby accounting for the higher mortality. This would also validate the findings of this study, namely that the populations of *P. moluccensis* are similar at least with regards to juvenile growth rate, that the observed differences are environmental rather than differences in the populations, since given enough food, the populations react in the same manner and to the same degree to temperature.

Chapter 5: General discussion

5.1 Results summary and interpretations

The aim of this thesis was to evaluate the existence of latitudinal patterns in the life history and metabolism of two damselfishes, the dispersing *P. moluccensis* and the brood-caring *A. polyacanthus* between Lizard Island, Orpheus Island and One Tree Island (14° 41' S, 18° 37' S, and 23° 30' S respectively) along the Great Barrier Reef, Australia.

Specifically, the patterns of variation in life history traits, standard metabolic rate and growth potential were investigated. This was done to assess whether possible differences along a latitudinal gradient would expose some sort of latitudinal compensation mechanism; and if this compensation would differ between the two species.

The two species displayed different degrees of inter-location differences; *P. moluccensis* displayed no significant differences in asymptotic size (L_∞: 57.3 mm SL +/-3.0) and rate of reaching that size (k: 0.433 +/-0.084) whereas *A. polyacanthus* did, displaying lower asymptotic size and higher rate of reaching that size at One Tree Island (L_∞: 72.5 mm SL; k: 0.508) than at Orpheus Island and Lizard Island (L_∞: 86.9 mm SL +/-2.3; k: 0.346 +/-0.036). Both species displayed lower maximum ages at Orpheus Island compared to the lower latitude Lizard Island and the higher latitude One Tree Island (*A. polyacanthus*: 10, 8, and 10; *P. moluccensis*: 9, 7, and 10 years at Lizard, Orpheus and One Tree Islands, respectively). *A. polyacanthus* matured one year later than *P. moluccensis*. Both species matured one year later at the high latitude location compared to the low latitude location (*A. polyacanthus*: 3, 4, and 4; *P. moluccensis*: 2, 2, and 3 years at Lizard, Orpheus and One Tree Islands, respectively). Maturity happened approximately at the same percentage of asymptotic size (approximately at 65%).

There were thus no strong latitudinal effects on the life history traits such as maximum size and age, but there was a tendency for later age at maturity at higher latitudes. Overall though, the lack of significant latitudinal differences on the life histories of both fishes implies a not in-significant degree of adaptation to the local temperature regimes, since both manage to upkeep the same levels of growth and size at significantly different temperatures, with the exception of *A. polyacanthus* which at One Tree Island displays lower asymptotic size.

There were evident latitudinal differences in the temperature response of standard metabolic rate in both species. After statistically accounting for differences in temperature and body mass, *P. moluccensis* showed a significantly lower metabolic rate at Lizard Island compared to Orpheus Island and One Tree Island, whereas *A. polyacanthus* displayed significantly different metabolic rates at all three locations, with higher metabolic rates at higher latitudes. Only at Lizard Island was an inter-specific difference evident, with *A. polyacanthus* displaying higher metabolic rates than *P. moluccensis*.

The two species exhibited significantly different growth potentials. Furthermore, the growth potential was significantly influenced by body mass, location and temperature. However, the results for *P. moluccensis* showed an overall rise in growth rate with temperature regardless of location, indicating less locational influence (i.e. less inter-population difference) on its growth potential. The contrary was observed for *A. polyacanthus*; growth rate was very much higher at Orpheus and One Tree Islands than at Lizard Island. The magnitude of the inter-location differences in growth rate may indicate that for *A. polyacanthus*, location had a larger impact on growth potential than the 3 degree temperature range tested; albeit with the caveat that in each location only two temperatures were tested in a dome-shaped relationship between growth and temperature. In summary, the results of this part of the study indicate larger inter-population differences in *A. polyacanthus* than in *P. moluccensis* with regards to growth potential.

Overall, *P. moluccensis* displayed no latitudinal age or size difference, but the metabolic rate at a given temperature was lower at the lowest latitude, indicating some thermal adaptation between locations. This might explain *P. moluccensis*' ability to display similar growth curves at three locations with significantly different temperature regimes. The growth potential was the same at each location, but was temperature-dependent, resulting in higher potential growth rate at lower latitudes. *A. polyacanthus* displayed a tendency for greater size at the highest latitude, although the maximum age was the same across latitudes. The metabolic rate at a given temperature was higher at higher latitudes but the growth potential lower at only the lowest latitude.

5.2 Comparison of results of this study with previous research

The maximum ages of *A. polyacanthus* observed in this study (10, 8, and 10 at Lizard, Orpheus, and One Tree Islands, respectively) were comparable to those found at Orpheus by Kingsford & Hughes (2005: 9 years). Bray (2001) found a latitudinal effect on maximum ages of *P. moluccensis* with higher ages at higher latitudes. However, no such latitudinal relationship was found in this study. The observed maximum age of *P. moluccensis* in this study at Lizard Island (9 years) was higher than the 6 and 7 years reported by Beukers (1996) and Bray (2001) respectively. The 7 years found at Orpheus Island was two years younger than the 9 years reported by Fowler (1990) on John Brewer Reef, and the 10 years found in this study at One Tree Island was lower than the maximum ages found at One Tree Island or from the neighbouring reefs by Mapstone (1988: 13 years), Doherty & Fowler (1994a: 14 years; 1994b: 18 years) and Worthington et al. (1995: 18 years). The oldest of these are far older than the observations in this study, and older than any observations at Lizard Island.

One explanation for the discrepancies in observed maximum ages is that the percentage of very old individuals in a population is low (e.g. Doherty & Fowler 1994a, Kingsford & Hughes 2005). Since old individuals will therefore be rare, they would also be more elusive and thus harder to sample. Thus in a study with a smaller dataset, the chance of sampling the oldest individuals in a population is lower.

Booth (unpublished) observed faster growth for individually tagged *P. moluccensis* at Lizard compared to One Tree Island, which corresponds with the findings of the juvenile growth potential results but not with the results from the age at size data, which revealed no significant differences in *P. moluccensis* growth from any of the three locations. This discrepancy may be due to yearly fluctuations in condition of fish resulting in some year classes displaying faster growth than others. The considerable individual spread from the Von Bertalanffy Growth curves (chapter 2, fig. 2.2 and 2.3) supports this theory. To elucidate this possible fluctuation, tracking the growth of different year classes would be necessary, e.g. via individual tagging.

The large differences found in the juvenile growth rate potential of *A. polyacanthus* at Lizard Island compared to Orpheus and One Tree Islands is probably connected to the significantly lower metabolism, which could be an adaptive mechanism to lower maintenance costs at higher temperatures. This could potentially limit the growth potential in a situation where food was not a limiting source, as it usually is in the wild (e.g. Jones 1986, Booth 2004). However, this would not explain why *P. moluccensis* displays a significantly higher growth rate potential and lower metabolism at Lizard Island, unless the temperature tolerance for growth rate is nearly reached at 30°C for *A. polyacanthus* but not for *P. moluccensis*. Theoretically, *P. moluccensis* should be able to withstand higher temperatures if the recruits of a specific reef have been transported from further north by the East Australian Current such as found for clownfish by Buechler (2005). *P. moluccensis* is distributed further north than Lizard Island and should thus experience higher temperatures than at Lizard Island. *A. polyacanthus* is also distributed further north than Lizard Island, but a closer adaptation to the local temperature regime might explain a lower thermal range of tolerance than that displayed by *P. moluccensis*.

There are large differences in the ability to tolerate hypoxia in coral reef fish (Nilsson et al. 2008). Long-term metabolic rate depends on the oxygen intake, while the immediate rate of metabolism in ectotherms is highly dependent on the temperature (Jobling 1996). Thus a high upper thermal limit should be coupled to a higher tolerance for low-oxygen conditions (Nilsson et al. 2008). To rule out a possible alternate effect on the metabolic rate in this study (chapter 3) caused by low oxygen conditions, the water in the experimental setup was well aerated, regardless of water temperature. Hence low oxygen condition was never a part of the test for metabolic rate, only temperature.

The significantly lower growth rate of juvenile *A. polyacanthus* at Lizard Island observed in chapter 4 could be caused by a metabolic rate set to a low level due to the higher ambient temperatures, and not being able to shift it up at the low test temperature during the duration of the growth experiments? This would imply that the ability to rapidly shift metabolic rate observed in chapter 3 only occurs later in life.

Over the coming century rapid climate change is predicted increase the average sea-surface temperatures, with possible migration of widely distributed species from warmer areas of its distribution to colder. The ensuing changes in reaction norms due to a lateral shift will largely depend on their current geographical and temperature ranges. Based on the temperature manipulations of this study, it seems as though *P. moluccensis* might be able to tolerate a transition, while *A. polyacanthus*, while more adapted to its local habitat, would also be less able to adjust to a change in temperature regime.

5.3 Caveats

Some points of possible concern should be noted: The high- and low- latitude locations One Tree and Lizard Island are mid-shelf reefs, whereas the mid-latitude location Orpheus Island is an inner shelf reef. Furthermore, One Tree Island is an enclosed lagoonal reef with bi-daily water exchange with the outside ocean, the waters at Orpheus Island are eutrophied, especially the leeward eastern side facing the mainland (Eddie, pers. comm., Brolund, pers. obs.), while Lizard Island is a fairly clear water reef. Thus some of the adaptations observed may not be to temperature differences alone. However, this does not change the differences, or lack of same, observed between Lizard Island and One Tree Island, and with regards to the metabolic results, cross shelf location seems to matter less than latitude. Furthermore, in their cross shelf study of *A. polyacanthus* life history traits Kingsford & Hughes (2005) found no cross shelf differences in maximum age or growth rate but increased asymptotic size with increasing distance from the coast.

Unfortunately, primarily due to budget restrictions location replications at each of the three latitudes were precluded (e.g. sampling from other Capricorn Bunker Group reefs than One Tree Island). Furthermore, in the time allotted at One Tree Island, the weather only permitted one sampling trip to just outside the lagoon. To alleviate the potential problem of special circumstances at specific sites, several sites within each location were sampled: at One Tree Island several sites within the first and third lagoon and from the more exposed sites outside the lagoon on the northern side; at Orpheus Island, both from the leeward western side of the island and across the northern channel to Pelorus Island and from the more exposed reefs off the north eastern side of Orpheus Island; at Lizard Island from the leeward eastern Turtle Bay, from the sheltered lagoon front south west of the island, and from the more exposed Coconut Beach to the south.

Furthermore, the number of test specimens used was in some cases on the low side. This was due to permit related limits to the number of specimens allowed to be taken from each location, coupled with budget restrictions, which meant all collection was done over one summer. However, the majority of results were either a clear statistically significant or non-significant, which should mean very few if any type II errors in the thesis.

The instances of possible type II errors are: 1) The inter- and intra-specific differences in age at maturity in chapter 2 might have been significantly different had higher number of specimens been used. Nevertheless, clear trends are still obvious, but I cannot confirm them as statistically significant; 2) The growth of juvenile *A. polyacanthus* at the two test temperatures at each location in chapter 4 might have been statistically different had more specimens been tested and/or more temperatures employed; and 3) Large inter-individual variation was found in the von Bertalanffy growth figures (chapter 2, fig. 2.2 and 2.3). It should be pointed out, that these differences are still smaller than the between-location differences e.g. observed in *A. polyacanthus*. However, more differences might have been significant had a higher number of specimens from each site and each location been included in these analyses. As with the results of the cross-shelf study of Kingsford & Hughes (2005), significant differences might have been found in the von Bertalanffy growth curves of individuals from different locations but on approximately the same latitude. Other than the above three possibilities, the data should not hide type II errors, since non-significant differences were on the level of α >20%.

Finally, reaction norms were observed for only two damselfish species. Since *A. polyacanthus* is the only damselfish displaying brood-care, it is not a very typical damselfish. However, reaction norms for *P. moluccensis* might not be typical of its family.

5.4 Further research

It would be desirable to include many directions of related research in this study: seasonal differences in patterns, inter-location differences in food availability, the speed of possible adaptation of an individual to changes in temperature (months?), latitudinal differences in yearly and lifetime reproductive effort. However, limits to scope, time and budget precluded their study in this PhD.

To test the possible explanations brought up in these studies, one would need to replicate onshore – offshore to elucidate if cross-shelf and other intra-latitudinal differences may outweigh the latitudinal differences found in these studies. This is only partly done for *A. polyacanthus* by Kingford & Hughes (2005) and Munday et al. (2008b).

In order to further compare possible latitudinal difference in the interaction between metabolism, growth potential and lifetime growth, data on the food availability at the different locations would be needed (e.g. by gut content and lipid analysis). It would also be informative to experimentally manipulate other environmental factors.

Common garden rearing of first generation offspring of parents wild caught from different latitudes would constitute a cumbersome but also informative project to establish the genotypic contribution to the growth responses to different temperature regimes.

The unique lack of pelagic larval stage of *A. polyacanthus* makes it useful to compare responses to other reef damselfishes. Further studies on the geographical differences in its reaction norms should prove useful as a base case for comparisons with reaction norms of dispersing reef fish species.

This would also elucidate possible intra-specific effects, since there are genetically proven differences in the populations of *A. polyacanthus* (Planes & Doherty 1997b, Planes et al. 2001, Van Herwerden et al. 2006). It would be interesting to see if growth rates were similar in genetically-divergent populations of *A. polyacanthus* at the same field temperatures.

In view of oncoming climate changes one of the most pressing issues is gathering latitudinally widespread life history data from more tropical reef fish families to try to assess some of the impacts of global climate change.

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