Small cryptic fishes on coral reefs:

A new perspective on reef fish ecology and life histories

Thesis submitted by
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Statement on the Contribution of Others

This James Cook University thesis contains some collaborative work with Dr Christopher Fulton (James Cook University) and Dr Michael Marnane (World Conservation Society). While undertaking these collaborations, I was responsible for the project concept and design, most data collection, all analysis and interpretation, and the synthesis of results into a form suitable for publication. My collaborators provided three additional data sets towards the final data chapter of the thesis and editorial assistance with the publication process.

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Abstract

Small cryptic fishes represent over 50% of fishes on coral reefs. Yet our knowledge of them lags far behind that of larger species and their significance to coral reef ecosystems remains unclear. Vastly different in their ecology due to their small size, this thesis examines their community structure and identifies key life history features that highlight their unique ecological status. These results are combined to model the relative contribution of small cryptic fishes to reef fish assemblages and define their significance to coral reef ecosystems.

Small-scale clove oil samples ($0.4m^2$) were used to quantify the spatial distribution of small (< 10cm) cryptic fishes across reef zones and microhabitats at both exposed and sheltered reefs. Marked variation in abundance, species numbers, size-class distribution and community composition were found among reef zones at exposed sites; in contrast, comparatively little among-zone variation was found at sheltered sites. At exposed sites, there was a strong trend of declining abundance, species numbers and larger body sizes with increasing wave energy; whereas at sheltered sites, microhabitat type played a more important role. There was little taxonomic overlap between sheltered and exposed reefs even of highly abundant species. Overall, wave energy was found to play a pivotal role in the spatial distribution of this community with microhabitat type playing a significant, yet secondary role.

Contrasting the life history (LH) characteristics of the most abundant genus (*Eviota*: 3 species of Gobiidae) at the two study sites with those of existing coral reef fishes in a meta-analysis revealed vastly different LH features. Otolith analysis revealed rapid linear growth trajectories and extremely short maximum life spans of < 100 days (*E. queenslandica* 99 days; *E. melasma* 97 days and *E. sigillata* at 59 days - the shortest recorded lifespan for any vertebrate). Although settlement marks on otoliths disclosed unremarkable pelagic larval durations (PLDs) of 24 - 26 days, this represented 24 - 42% of their total lifespan. The complete lack of response in shortening PLDs to compensate for such short life spans suggests that developmental constraints may be the primary determinant of PLDs in coral reef fishes. Histological examinations indicated that *Eviota* mature at an earlier than expected size and showed a strong female bias in their sex ratios (1 ♂:1.4 - 1.7 ♀) indicating the possibility of protogyny or harem keeping by males. A field tagging study indicated remarkably high daily mortality rates of 7-8% which closely matched otolith-based estimates of 4-7% d^{-1}.

An experimental breeding study using *E. sigillata* revealed a frequent semi-lunar spawning pattern and batch sizes of 108-163 eggs. Although small in comparison to those of larger species, the frequency of spawning events coupled with generational turnover rates of 47 days indicated potential annual offspring production to be orders of magnitude higher than that of much larger reef fish species. Collectively, these LH attributes revealed how the smallest of reef fish size-classes respond to their vastly different ecological environments and highlight the extensive range and versatility of coral reef fish evolutionary strategies.

The relative contribution of the small cryptic group to reef fish assemblages was examined using visual censuses of 14 coral reef fish families. In total, data on 58,944 fish were utilized over five reef zones providing 86g m^{-2} of

biomass. The clear trend among size-class distributions was one of rapidly decreasing densities with increasing size. Small cryptic fishes represented 45-90% of the numbers of individuals across reef zones with a reef average contribution of 67%. Among families, the numerical dominance of the Gobiidae was evident ($11m^{-2} \pm 1.4SE$) with significant contributions made by the Pomacentridae, Apogonidae, Blenniidae, Labridae and Tripterygiidae. For biomass, the Acanthuridae made the largest contribution ($35g\ m^{-2} \pm 11.6SE$) followed by the Pomacentridae, Scaridae and Serranidae. Small cryptic families made up < 3%.

To examine the implications of taxa-specific growth rates in the energy dynamics of coral reef systems, a community growth model was produced. Size-specific growth estimates for all genera censused were calculated over a 7-day period. Overall, small cryptic fishes contributed 79.5% to reef fish assemblage patterns of growth in length and 14% to the period's total weight accumulation in grams. This cryptic contribution stands in marked contrast to the static biomass estimate presented above and highlights the significance of LH's in defining community and ecosystem energetics.

Overall, small cryptic fishes make a substantial contribution to coral reef communities but differ considerably from their larger counterparts in the way they achieve this. Demographic evidence of drastically shortened life spans, rapid linear growth and high turnover rates, coupled with high average abundances and rates of mortality suggests they play a significant role in the energetics of coral reefs. This addition of demographic information on small cryptic reef fishes emphasized this role, uncovered new extremes in vertebrate biology and showcases the rich potential for coral reef fishes to test general life history theory.

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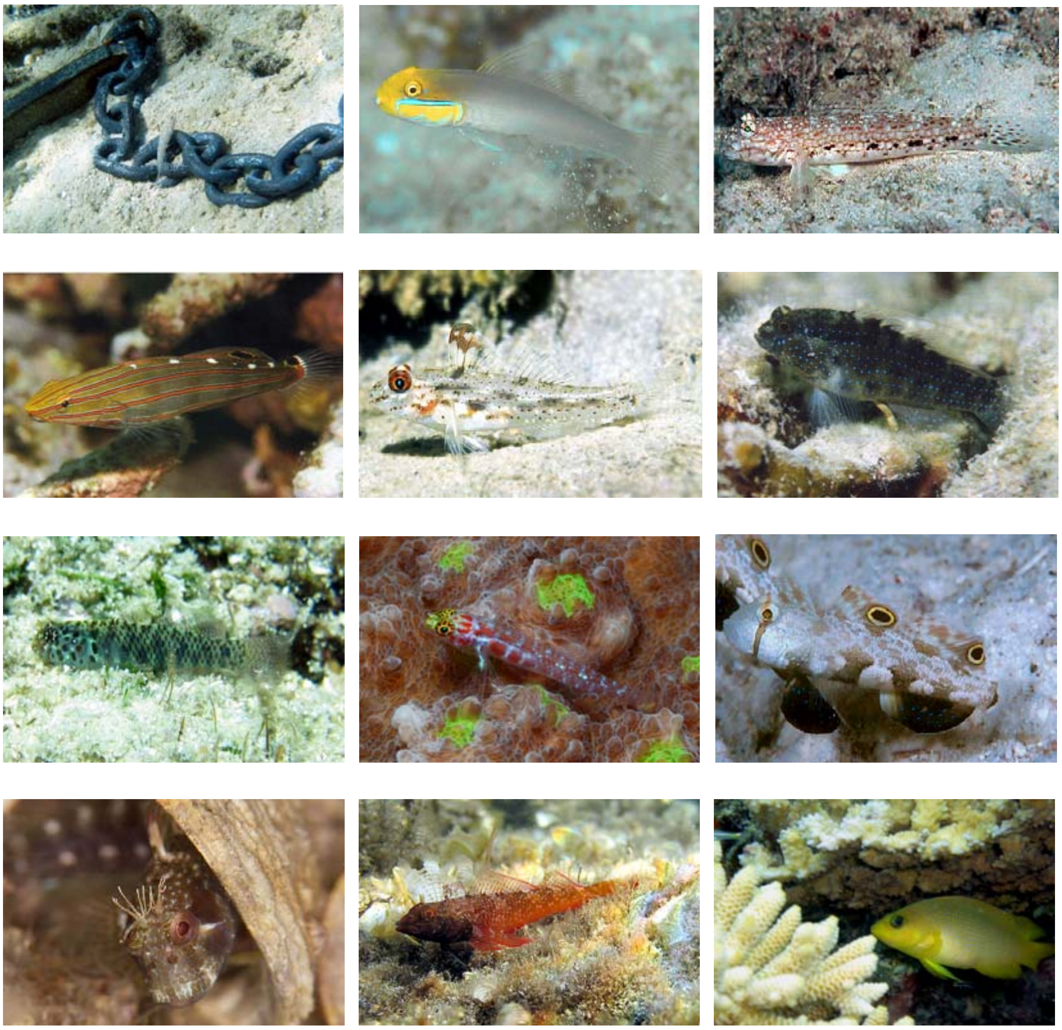
General Introduction

Body size and ecological relationships

Organism abundance, diversity and mass-specific metabolism increase with decreasing size (Brown et al. 2004). As a consequence, smaller organisms are often hypothesised to play the largest roles in ecosystem processes (Makarieva et al. 2004; Nee 2004; Horner-Devine et al. 2004). Within animal taxa, the implications of small body-size in relation to ecology, physiology and behaviour has been intensively studied at an individual organism level (reviewed in Peters 1983; Miller 1996; Munday and Jones 1998). Similarly, the mechanisms responsible for the maintenance of these body-size relationships have also been the focus of much recent (and controversial) attention (e.g. Blackburn and Gaston 1999; Ackerman et al. 2004; Ernest 2005). Although controversial, in the sense that the shape and slope of these relationship plots vary, these studies across a wide range of terrestrial and aquatic ecosystems (e.g. Greenwood et al. 1996; Leaper and Raffaelli 1999; Cohen et al. 2003; Ackerman and Bellwood 2000; Ernest 2005) are unanimous in their acknowledgement that small animals are more numerous, speciose and exhibit vastly different life history characteristics that enhance their dynamic potential in ecosystem processes (e.g. trophics, productivity, energetic consumption). However, despite these general ecological principles, we still know surprisingly little about the smaller animals in ecosystems. Consequently, the relative contributions of small animal taxa to ecosystem processes have been largely overlooked.

Small cryptic fishes on coral reefs

Among animals, fishes encompass the smallest, most speciose and most abundant of all vertebrate taxa (Helfman et al. 1997). With the highest rates of biodiversity found in the tropics (Gaston 2000; Brown et al. 2004), coral reef ecosystems provide a wonderful opportunity to explore the relevance of small fish taxa within the context of ecosystem processes. On coral reefs, small cryptic fishes constitute approximately 50% of individuals and 40% of species (Ackerman and Bellwood 2000) (i.e. fish species of ≤ 100 mm total length that are visually or behaviourally cryptic). Families such as the Gobiidae, Blenniidae, Tripterygiidae and Pseudochromidae feature prominently within this assemblage and constitute some of the most abundant and speciose families found on coral reef systems (Randall et al. 1997) (see panel overleaf). In comparison to larger reef fish species, the ecological knowledge we currently have on this portion of reef fish communities is still in its embryonic stages. The development of sampling methodologies (mostly ichthyocides and anaesthetics) that can accurately (and acceptably) quantify these assemblages has only recently opened up new avenues in the field, and there has lately been a small, but concentrated effort to study the ecology of this fauna at an individual species (e.g. Munday et al 2002; Wilson 2004; Longenecker and Langston 2005), sub-community (Munday et al. 1997; Greenfield and Johnson 1999; Munday 2001; Wilson 2001; Syms and Jones 2004), and community level (Depczynski and Bellwood 2003, 2004; Greenfield 2003; Smith-Vaniz et al. in press). There remains, however, a clear need to quantify an entire small cryptic reef fish community within a single ecosystem in order to move past a purely descriptive or static picture, to a more process-oriented understanding that incorporates the dynamics that characterises coral reef ecosystems. Only in this way can the ecological significance and contribution of small cryptic fish assemblages to ecosystem functioning be critically evaluated.



Panel showing some of the more prominent members of the Lizard Island small cryptic coral reef fish community. From left to right; *Valenciennea muralis* on 10mm anchor chain to indicate scale, *V. strigata, Istigobius goldmanni, Amblygobius rainfordi* – the smallest known herbivore on the Great Barrier Reef (Depczynski and Bellwood 2003), *Fusigobius signipinnis, Asterropteryx semipunctatus, Eviota queenslandica, E. sigillata, Signigobius biocellatus, Salarias patzneri, Enneapterygius* sp. *and Pseudochromis fuscus* (photos R Field, S Hasno, JE Randall, and M Takata).

Linking the ecology of small cryptic fish to coral reef ecosystem processes

To date, the evidence which suggests that small cryptic fish communities play important ecological roles is as circumstantial and fragmented as it is compelling. There is tantalising evidence, for example, that they perform a number of important tasks related to energy-flow within coral reef ecosystems, particularly that of mediating a range of trophic resources at the benthos / predator interface (Norris and Parrish 1988; Ackerman and Bellwood 2000; Depczynski and Bellwood 2003; Greenfield 2003) and the recycling of primary production through detrital pathways (Depczynski and Bellwood 2003; Wilson et al. 2003). In addition, they are able to access habitat and associated trophic resources potentially unavailable to larger fishes (Miller 1996; Munday and Jones 1998), they have much higher basal and sustained metabolic rates (Schmidt-Nielsen 1997; Willmer et al. 2005), and probably have very rapid life cycles, suggesting a capacity to respond rapidly to fluctuations in the status of their local environment (Bellwood et al. in press). Despite these characteristics and their potential role in these processes, their presence, importance and impact is rarely acknowledged. Much of this is due to: (1) problems associated with their correct taxonomic identification (2) past difficulties in accurately censusing these fishes, (3) their cryptic nature – what is not seen may be presumed unimportant, (4) the fact that little hard direct evidence exists to substantiate high rates of predation on these fishes, making claims of their importance as trophic vectors currently intractable, and (5) the presumption that their standing biomass is small, perpetuating the image that their role in ecosystems is similarly a minor one. Collectively, these features have stymied research on this interesting group to a point where we could effectively argue that we do not know what a complete reef fish faunal assemblage is, or what the real significance of reef fish communities to coral reef ecosystem processes are.

Ecosystems operate over temporal as well as spatial scales, marking the importance of life history features and resulting population dynamics of species as an integral part of defining ecosystem function. Currently, there is very little information on the life cycles of small cryptic fish species (Claro and Garcia-Arteaga 2001; Wilson 2004; Longenecker and Langston 2005). Recently, the focus of ageing studies on larger species has so far shown that size and age are decoupled within and among reef fish species, largely as a result of asymptotic growth trajectories and variation among phylogenetic lineages (Choat and Axe 1996; Choat and Robertson 2002). What has become abundantly clear from this work so far is that even small-medium sized species (e.g. pomacentrids, chaetodontids, labrids) tend to live lives of more than 10 years (e.g. Fowler and Doherty 1992; Munday and Jones 1998; Meekan et al. 2001; Berumen 2005). Of the few ageing studies published on small cryptic coral reef fishes, these asymptotic patterns of growth have not held. Instead rapid linear (e.g. Kritzer 2002) or continuous growth trajectories (Wilson 2004; Hernaman and Munday 2005a; Longenecker and Langston 2005) have featured strongly alongside sub-annual life spans. If short life spans leading to rapid generational turnover predominate in small cryptic species, their contribution to ecosystem food-webs, energy flow and budgets may be significantly enhanced beyond that predicted based on their small body-size alone.

Aims and thesis outline

Given the compelling but fragmented nature of our current state of knowledge on these small species, the main objective of this thesis is to investigate the link between small cryptic fishes and coral reef ecosystem processes from a community perspective. A series of observational, experimental and theoretical studies are used to test the general hypothesis that *small cryptic fishes are ecologically important and make a significant contribution to coral reef processes.* With this in mind, the three primary aims are to: (1) describe the spatial distribution of a complete small cryptic coral reef fish assemblage over a gradient of wave exposure and reef zone habitats that encompass an entire reef ecosystem, (2) document the entire life cycle of the most prominent members within this assemblage, to investigate comparative life history features among reef fish species in general, and (3) develop an ecosystem-wide model of individual growth for an entire reef fish assemblage to evaluate the relative contribution of small cryptic fishes to ecosystem energetics.

These aims are addressed in three chapters that encompass five separate studies. **Chapter 1** provides a quantitative basis for the thesis by explicitly describing the spatial community structure of small cryptic coral reef fishes. Abundance, biomass, size-class distribution and species composition across two gradients of wave exposure, two microhabitats and five reef zone profiles are quantified to identify where this group is likely to be most influential in reef processes. **Chapter 2** builds on this foundation by providing a temporal life history component to the thesis. Based on three laboratory and field-based experimental studies, the age and growth, mortality rates and lifetime reproductive output of the three most abundant species from Chapter 1 are quantified. These life cycles are compared with the range of life histories recorded for all coral reef fishes to evaluate the status of life history strategies utilised by small cryptic fish species, and the extent to which their life histories conform to life history theory. **Chapter 3** ties the spatial and temporal components of the previous chapters together at a whole ecosystem level of organization by modelling the theoretical growth of an entire assemblage of cryptic and non-cryptic coral reef fishes. This will quantify and contrast the contributions of 14 reef fish families to reef ecosystem energetics in the form of biomass productivity in order to gauge their relative ecological role and importance to ecosystem function.

These chapters purposely represent stand-alone chapters suitable for publication (see Appendix F) but have been designed to complement each other by providing a coherent sequential narrative that has a clear underlying theme; investigating the importance of small cryptic coral reef fishes through their ecology and life histories.

Chapter 1: Spatial distribution and community structure of small cryptic coral reef fishes

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1.1. Introduction

Of all reef fishes, the community ecology of small cryptic fish assemblages are least well understood. Difficulties associated with accurately censusing these hidden fishes (see Brock 1982, Willis 2001, Edgar et al. 2004) have limited our overall understanding of the dynamics and role of reef fish communities on coral reefs. Recent studies using anaesthetics and ichthyocides have shown that small cryptic fishes (< 10cm) comprise half of the fish numbers on coral reefs (Ackerman and Bellwood 2000, 2002, Greenfield 2003), and constitute a diverse community containing many highly specialised species (e.g. Munday et al. 2002, Depczynski and Bellwood 2004, Hobbs and Munday 2004). Although occupying the lower end of the size spectrum in reef fishes, this group may provide important insights into the role of fishes in ecosystems, as it is often the smallest organisms that are most abundant, diverse and influential in ecosystem processes (May 1978, Begon et al. 1996). However, we currently lack a detailed description of their distribution and abundance at a reef-wide whole ecosystem scale, an essential pre-requisite in unravelling their contribution to reef ecosystem processes.

Published descriptions of small reef fishes have emphasised that species within this group display marked spatial variation at very small spatial scales of centimetres to metres (Luckhurst and Luckhurst 1978, Townsend and Tibbetts 2000, Wilson 2001). Many also exhibit restricted, and often obligate relationships with particular microhabitat types (Munday 2000, Webster and Hixon 2000, Goncalves et al. 2002, Depczynski and Bellwood 2004). At an individual level, limited home and foraging ranges of less than $2m^2$ are consistently reported (Luckhurst and Luckhurst 1978, Reavis 1997, Goncalves and Almada 1998; Depczynski and Bellwood 2004). Despite these studies, nothing is known of the among reef zone variation in small cryptic communities (but see Greenfield and Johnson 1990a and b, 1999 for family-level studies), the level at which most reef fish communities exhibit the greatest variation in composition and abundance (Russ 1984, Williams 1982, 1991). These small-scale observations suggest that the distribution patterns of small cryptic reef fish communities are also likely to display significant variation at larger, among-zone, spatial scales. At these larger among-zone scales, coral reef assemblages are shaped by physical forces acting either directly on individuals, or through indirect influences on habitat or food availability (Fulton et al. 2001, Gust et al. 2001). Given the small size and benthic associations of the small cryptic coral reef fish community, one may hypothesise that these species are highly likely to exhibit marked zonation along these energy gradients. In this study therefore, I describe and quantify the abundance, size composition and community structure of small cryptic coral reef fishes across a gradient of wave exposure to provide a basis for evaluating the role of these fishes in reef processes.

1.2. Materials and methods

Sampling was undertaken in January and February 2003 on reefs around the Lizard Island group (14°40'S, 145° 27'E) in the Cairns section of the Great Barrier Reef (GBR). Lizard Island is a granite island in the mid-shelf region of the GBR. Three sites were censused on the exposed reef front between Bird and South Isles at depths of 1-15 m, and three from the sheltered NW margin of Watsons Bay at depths of 1-6 m (Fig. 1.1). Five reef zones were censused at each site (base, slope, crest, front flat and back flat) at the exposed reef (Fig. 1.2). The lack of a defined slope at the sheltered reef sites meant that only four reef zones could be reliably identified (base, crest, front flat and back flat). Descriptions of reef zones and corresponding wave energy are given (Table 1.1). In each reef zone, four samples were taken in each of two microhabitats, open reef and sand / rubble with a total of 120 censuses at the exposed sites and 96 at the sheltered sites. Open reef microhabitats were flat, open areas of live and / or dead coral fully exposed to the surrounding water column from all sides and above; sand / rubble areas of sand and hard coral rubble where > 50% of sample area contained visible coral rubble pieces of between 20-200mm (Fig. 1.3).

Samples were collected on SCUBA using clove oil and a fine-mesh (2 mm) net covering a basal area of 0.4 m^2 (Fig. 1.4). The weighted net was positioned in a circle on the substratum before approximately 125 ml of a 5:1 - ethanol : clove oil mixture was sprayed into the netted area and left for 1 minute before the search for anaesthetised fish began. Following a 5 min systematic search by two divers, fish were put into labelled, clip-seal plastic bags, and placed

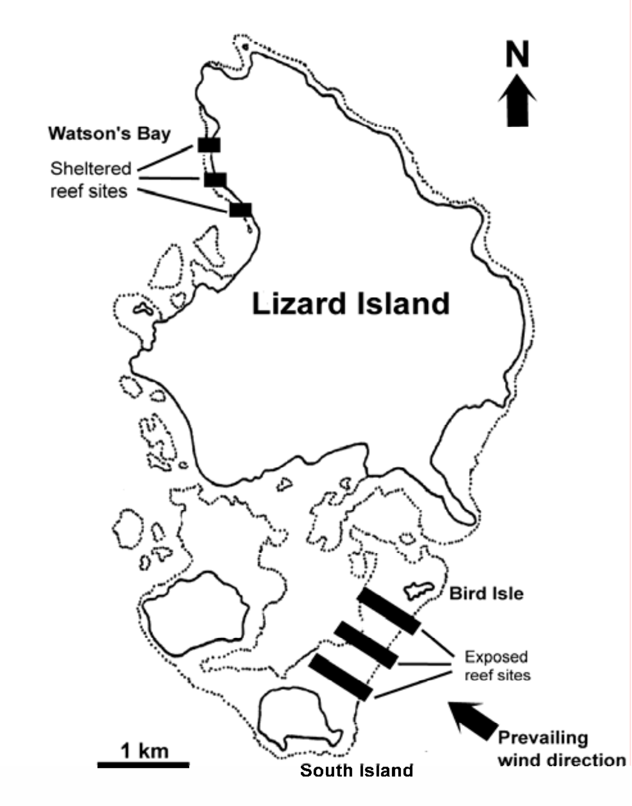

Fig. 1.1: Exposed and sheltered reef sites where the study was conducted at Lizard Island showing spatial scale and prevailing south-easterly wind direction (modified after Fulton and Bellwood 2005).

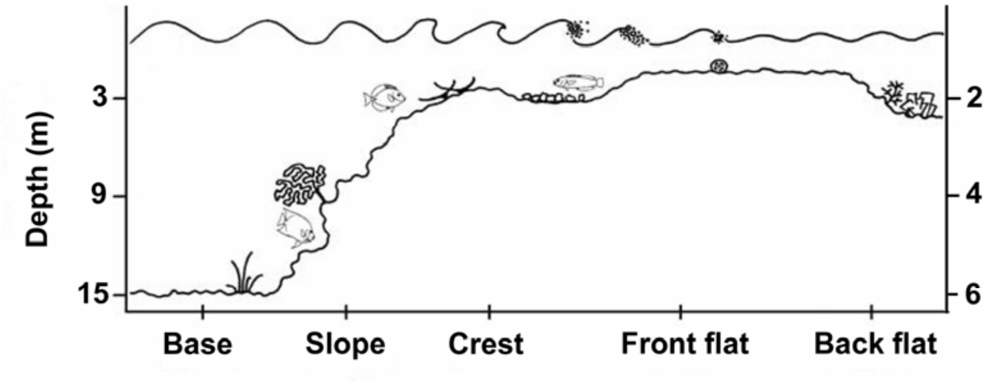

Fig. 1.2: Reef zones and depth along the reef profile (modified after Fulton and Bellwood 2005). Depths on the left-hand *y*-axis are for exposed reef sites; right-hand *y*-axis for sheltered reef sites.

Table 1.1: A description of the environment, depth and wave severity of reef zones at exposed and sheltered reef sites. Wave energy estimates follow Fulton and Bellwood (2005) who recorded values at the same location.

	ENVIRONMENT DESCRIPTION			PHYSICAL PARAMETERS	
Reef Zone	**General Characteristics**	**Heterogeneity**	**Coral Cover**	**Depth (m)**	**Wave energy**
Exposed Reef					
Base	Gently sloping fine sand and rubble environment with isolated coral colonies or outcrops	Moderate	Moderate	10-15	Nil
Slope	Variable incline (10 - 90 degrees) / diverse topography	Highest	High	6-9	Moderate
Crest	High vertical relief	High	Highest	1-3	High
Front Flat	Mostly hard flat substrata covered in algal and coarse sand with occasional coral outcrops	Lowest	Low	2-4	Highest
Back Flat	Flat, varied environment	Moderate	Moderate	2-4	Moderate
Sheltered Reef					
Base	Flat sand and rubble environment with isolated reef outcrops	Lowest	Low	4-6	Nil
Crest	High vertical relief	Highest	High	1-3	Low
Front Flat	Mostly flat, hard substrata environment	Moderate	Moderate	2-4	Low
Back Flat	Flat, varied environment	Moderate	Moderate	1-3	Low

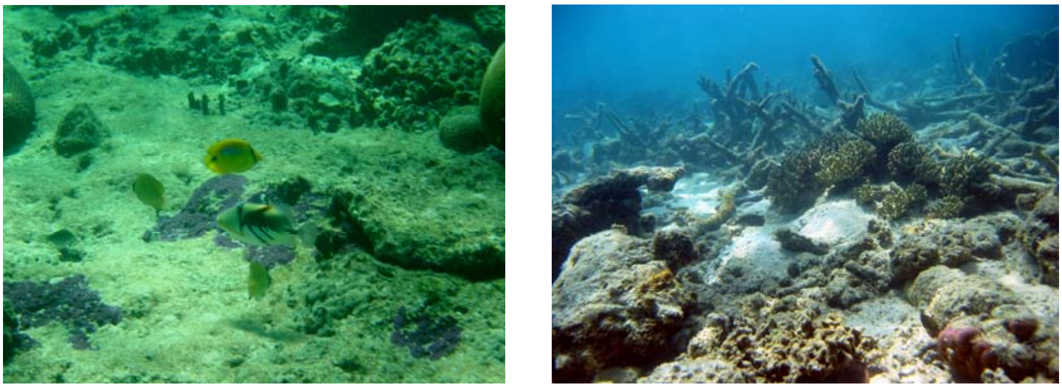

Fig. 1.3: Open reef (left) and sand / rubble microhabitats used in the study.

Fig. 1.4: The small (0.4m^2) weighted sampling net used in this study.

into an ice-water slurry. Specimens were identified, weighed and measured (total length ; TL) at the laboratory, and stored in 70% ethanol. The genus *Eviota* are small and taxonomically challenging to identify (Lachner and Karnella 1980). Thus, positive identifications of highly abundant *Eviota* species were made by HK Larson of the Museum and Art Gallery of the Northern Territory. All other *Eviota* species were provisionally identified as sp. a, sp. b. etc based on a combination of meristics, their cephalic sensory pore system and readily distinguishable body and facial markings; the key recognised traits for the identification of this genus (see Lachner and Karnella 1980). Already numbering some 70 odd-species, the samples probably included several undescribed *Eviota* species.

After initial examination, data were Log_{10} [x + 1] transformed to satisfy requirements for normality and homoscedascity. Differences in the abundances of individuals and number of species among sites, zones and microhabitats were analysed using three-way mixed factorial ANOVAs at exposed and sheltered reef locations separately. Variation in species assemblages among zones were examined using MANOVAs based on the 12 most abundant species (with > 10 individuals across all zones) for exposed and sheltered reef locations separately. Bonferroni-corrected multiple comparisons tests were used to identify differences in species assemblages between zones. Canonical discriminant analyses (CDA) based on structure coefficients graphically identified the characteristics of species assemblages in the four (sheltered) and five (exposed) reef zones. Zone centroids are displayed with 95% confidence clouds. Species abundance is displayed by the relative size of species points on the CDA following square root transformation on raw counts. Differences in size (using weight in grams) of individuals were investigated among zones at exposed and sheltered reef locations separately using one-way ANOVAs followed by Tukey's HSD post-hoc tests to identify where differences lay.

1.3. Results

Patterns of individual and species abundance

A total of 1042 individuals from 44 species in 8 families were sampled over a combined area of 86.4m^2 (216 x 0.4m^2) (Table 1.2). Of these, the top 19 species (> 10 individuals sampled) represented 92.5% of all individuals, with the Gobiidae making up 87.1% of all individuals, and tripterygiids, blenniids and pseudochromids contributing most of the remaining 12.9%. While the Gobiidae dominated all reef zones at sheltered and exposed reef sites, differences in the proportional contribution of non-gobiid families among reef zones varied considerably, particularly at exposed reef sites (Fig. 1.5a-d).

Exposed versus sheltered reefs

Overall, exposed and sheltered reefs were broadly similar and statistically non-significant in both mean individual abundance (exposed 14.6m^{-2} ± 1.4 SE - sheltered 12.5m^{-2} ± 0.9 SE [$t = 0.84$, $df = 214$, $p > 0.05$]) (Fig. 1.6a and b) and mean species numbers (exposed 6.7m^{-2} ± 0.4 SE - sheltered 7.8m^{-2} ± 0.5 SE [$t = -1.83$, $df = 214$, $p > 0.05$]) (Fig. 1.6a and b). Species richness tended to mirror individual abundances among reef zones and habitats. A total of 31 species were recorded on exposed and 36 species on sheltered reefs (Table 1.3). Among reef zones, however, species richness varied considerably at the exposed reef, less so at the sheltered reef. With two exceptions, where abundances were at their lowest (front flat at exposed reef and crest at sheltered reef), the influence of microhabitat on number of individuals and species is consistent (Fig. 1.6 and 1.7[a and b]) (Table 1.4) with the sand / rubble microhabitat samples having more individuals and species than open reef microhabitat samples. A total of 68.5% of all individuals were censused from sand / rubble habitats and 41 of 44 species. In contrast, open reef samples contained only 27 species in total.

Exposed reef

Individual abundance and species richness varied significantly at both the zone and microhabitat level (Table 1.4). The influence of microhabitat on numbers of individuals is apparent for most zones with the exception of the front flat where very low abundances were recorded in both microhabitat types (Fig. 1.6a). Sand / rubble microhabitats contained 70.1% of all sampled individuals on exposed reefs with distinct differences between zones, whereas open reef microhabitats were roughly equal in fish abundance across reef zones.

For reef zones, front flat areas were clearly the most depauperate in terms of individuals and species with base and back flat areas the most populated. A Tukey's post-hoc test identified the front flat as being statistically different from all others for both numbers of individuals and species (Table 1.5); all other reef zones shared varying relationships to one another. In total, 58 individuals and 10 species were found in the front flat zone compared to 176 individuals and 20 different species in back flat zone (Table 1.3).

Sheltered reef

Fish abundance and species richness patterns showed comparatively little among-reef zone variation in sheltered reefs (Fig. 1.6b and 1.7b). A significant site x zone x microhabitat interaction indicates that patterns of abundance at this sheltered reef may be quite complex in comparison to those found at the exposed reef (Table 1.4). A more thorough investigation indicated that statistical differences were primarily driven by the microhabitat and, to a lesser extent, reef zone factors. Inconsistent patterns exist among and within the three factors aside from a trend towards higher abundances in back flat reef zones and sand / rubble microhabitats. A Tukey's post-hoc test identified differences between the back flat and all other reef zones as the major determinant of statistical differences for abundance at the reef zone level (Table 1.6).

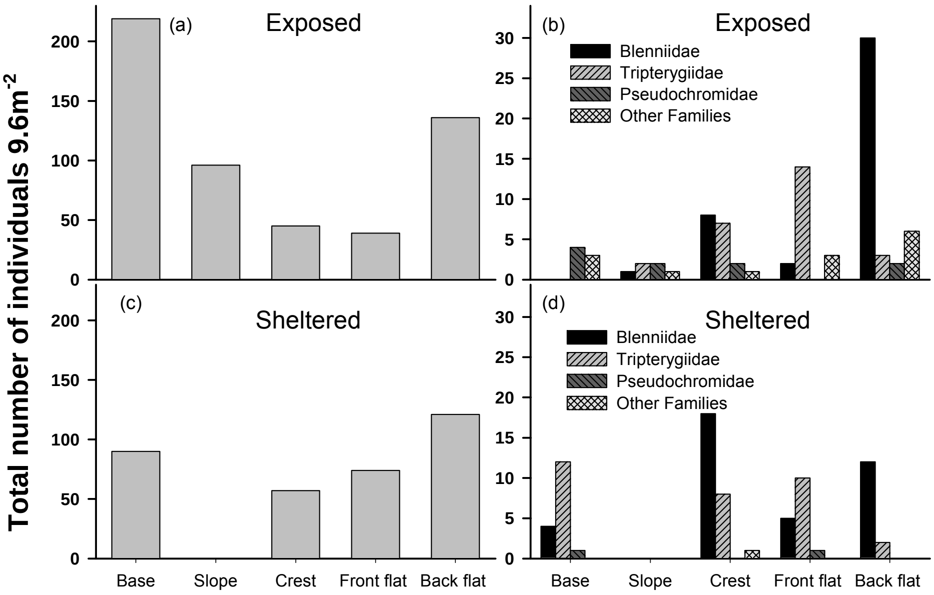

Fig. 1.5. Familial composition of small cryptic reef fishes across reef zones (n=24 with a total area of 9.6m^2 per zone). **a, c** Gobiidae, **b, d** other families. No samples were taken from the slope at sheltered reef sites. Other families are listed in Table 1.2.

Table 1.2: Families (eight total), species, numbers of individuals and numerical and biomass contribution (%) of each species relative to the entire assemblage sampled at exposed (n=120) and sheltered (n=96) reef sites. The 19 most abundant species (**in bold**) represent 92.5% of all individuals sampled and were chosen for further analyses based on their presence (>10 individuals across all reef zones) at either exposed and/or sheltered reef sites.

Family	**Species**	**Abundance**				**Biomass**			
		Ex-posed	**Shel-tered**	**Total (T)**	**% of T**	**Ex-posed**	**Shel-tered**	**T Biomass**	**% of T Biomass**
Gobiidae	***Eviota sigillata***	**192**	**24**	**216**	**20.73**	**6.12**	**0.69**	**6.81**	**4.54**
	Eviota queenslandica	**99**	**41**	**140**	**13.44**	**3.88**	**1.34**	**5.22**	**3.48**
	Eviota melasma	**60**	**21**	**81**	**7.77**	**3.14**	**1.59**	**4.73**	**3.15**
	Asterropteryx semipunctatus	**2**	**72**	**74**	**7.1**	**0.15**	**9.08**	**9.23**	**6.15**
	Istigobius goldmanni	**31**	**33**	**64**	**6.14**	**5**	**5.04**	**10.04**	**6.69**
	***Eviota* sp. Q**	**5**	**34**	**39**	**3.74**	**0.36**	**2.76**	**3.12**	**2.08**
	***Eviota* sp. J**	**32**	**0**	**32**	**3.07**	**0.78**	**0**	**0.78**	**0.52**
	***Eviota* sp. K**	**26**	**6**	**32**	**3.07**	**0.87**	**0.18**	**1.05**	**0.7**
	***Amblyeleotris* sp. A**	**8**	**17**	**25**	**2.4**	**2.7**	**0.39**	**3.09**	**2.06**
	Eviota pellucida	**25**	**0**	**25**	**2.4**	**0.95**	**0**	**0.95**	**0.63**
	***Eviota* sp.O**	**21**	**3**	**24**	**2.3**	**1.45**	**0.29**	**1.74**	**1.16**
	***Callogobius* sp. A**	**0**	**20**	**20**	**1.92**	**0**	**1.48**	**1.48**	**0.99**
	Ctenogobiops feroculus	**0**	**19**	**19**	**1.82**	**0**	**2.22**	**2.22**	**1.48**
	Fusigobius signipinnis	**15**	**2**	**17**	**1.63**	**0**	**1.13**	**0.21**	**0.14**
	Amblygobius phalaena	**4**	**12**	**16**	**1.54**	**2.6**	**4.04**	**6.64**	**4.42**
	Valenciennea muralis	**7**	**9**	**16**	**1.54**	**10.59**	**2.98**	**13.57**	**9.04**
	Callogobius sclateri	3	4	7	0.67	1.7	1.31	3.01	2.01
	Eviota sp. S	1	5	6	0.58	0.01	0.39	0.4	0.27
	Istigobius rigilius	2	3	5	0.48	0.84	0.46	1.3	0.87
	Amblygobius rainfordi	2	1	3	0.29	1.53	0.39	1.92	1.28
	Ctenogobiops pomastictus	0	3	3	0.29	0	0.56	0.56	0.37
	Eviota sp. N	0	3	3	0.29	0	0.16	0.16	0.11
	Eviota sp. P	0	3	3	0.29	0	0.08	0.08	0.05
	Signigobius biocellatus	1	2	3	0.29	0.03	0.34	0.37	0.25
	Trimma striata	3	0	3	0.29	0.29	0	0.29	0.19
	Gobiodon quinquistregatus	0	2	2	0.19	0	1.09	1.09	0.73
	Amblygobius nocturnus	0	2	2	0.19	0	0.59	0.59	0.39
	Fusigobius neophytus	0	2	2	0.19	0	1.75	2.88	1.92
	Eviota sp.F	1	0	1	0.1	0.04	0	0.04	0.03
Blenniidae	***Salarias patzneri***	**30**	**24**	**54**	**5.18**	**13.78**	**16.45**	**30.23**	**20.14**
	Ecsenius stictus	5	3	8	0.77	3.37	2.67	6.04	4.02
	Salarias guttatus	2	3	5	0.48	3.8	2.65	6.45	4.3
	Entomacrodus sp. A	0	4	4	0.38	0	0.92	0.92	0.61
	Ecsenius bicolour	2	2	4	0.38	1.89	4.27	6.16	4.1
	Crossalarias macrospilus	1	1	2	0.19	0.54	1.02	0.54	0.36
	Salarias fasciatus	1	1	2	0.19	0.14	0.41	0.55	0.37
	Istiblennius sp. A	0	1	1	0.1	0	0.31	0.31	0.21
Apogonidae	*Apogon cooki*	3	0	3	0.29	1.82	0	1.82	1.21
	Apogon doederleini	0	1	1	0.1	0	0.16	0.16	0.11
Pseudochromidae	***Pseudochromis fuscus***	**10**	**2**	**12**	**1.15**	**3.74**	**0.91**	**4.65**	**3.1**
Tripterygiidae	***Enneapterygius tutuilae***	**27**	**31**	**58**	**5.57**	**3.27**	**1.84**	**5.11**	**3.4**
Syngnathidae	*Corythoichthys flavofasciatus*	2	0	2	0.19	0.16	0	0.16	0.11
Pinguipedidae	*Parapercis xanthozona*	2	0	2	0.19	3.2	0	3.2	2.13
Muraenidae	sp. A	1	0	1	0.1	0.24	0	0.24	0.16
		626	**416**	**1042**	**100**	**78.98**	**71.94**	**150.11**	**100**

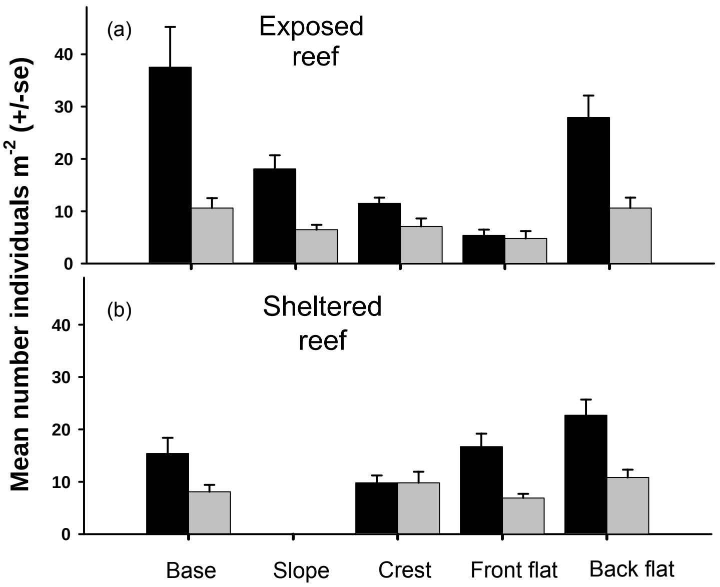

Fig. 1.6: Mean number of individuals m^{-2} (± SE, n = 12 samples) among the reef zones and microhabitats sampled at **a** exposed and **b** sheltered reefs. Black bars: sand / rubble; gray bars: open reef microhabitats. No samples were taken from the slope at sheltered reef sites.

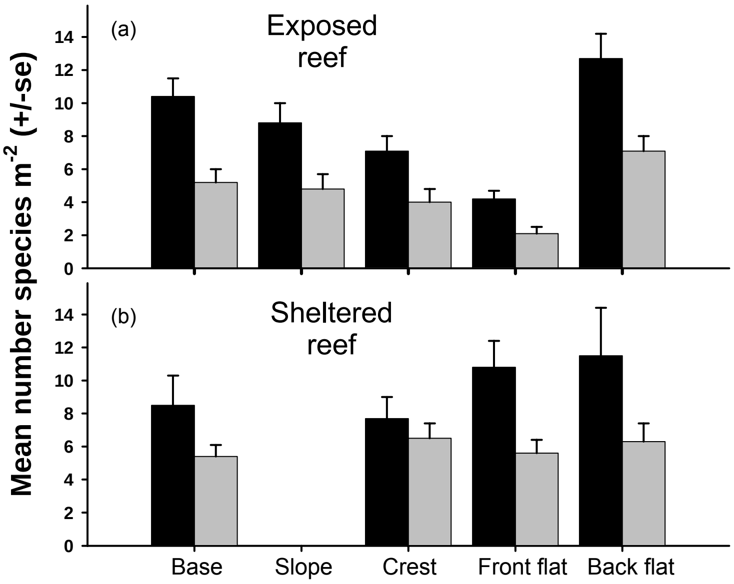

Fig. 1.7: Mean number of species m^{-2} (± SE; n = 12 samples) among the reef zones and microhabitats sampled at **a** exposed and **b** sheltered reefs. Black bars: sand / rubble; gray bars: open reef microhabitats. No samples were taken from the slope at sheltered reef sites.

Table 1.3: Mean fish density, species richness and mean number of individuals per species for exposed and sheltered reefs for each reef zone. Total number of species found at exposed and sheltered reef sites indicated **in bold**.

Zone	Number of individuals	Density (m^{-2})	Number of species / zone	Mean number Individuals / Species
Exposed				
Base	224	23.4	13	16.1 (± 9.6 SE)
Slope	105	10.9	14	7.5 (± 2.9 SE)
Crest	63	6.5	18	3.5 (± 0.9 SE)
Front flat	58	6.0	10	5.8 (± 2.1 SE)
Back flat	176	18.3	20	8.8 (± 4.0 SE)
	Total = 626		**Total = 31**	
Sheltered				
Base	96	10.0	22	4.5 (± 1.0 SE)
Crest	80	8.3	27	3.1 (± 0.7 SE)
Front flat	99	10.3	17	5.4 (± 1.4 SE)
Back flat	141	14.7	17	8.4 (± 2.8 SE)
	Total = 416		**Total = 36**	

Table 1.4: Three-way ANOVA results comparing fish abundance and species richness ($\log_{10}$ [x + 1]) in exposed and sheltered reefs amongst sites, reef zones and microhabitats. Exposed reef location; n=120, 4df: Sheltered; n=96, 3df. **Bold** numbers denote significance at $p < 0.05$.

	Fish abundance			Species richness		
Source	**MS**	**F**	**Sig**	**MS**	**F**	**Sig**
Exposed reef						
Site	0.14	2.51	0.087	0.02	0.07	0.934
Zone	1.15	21.07	**<0.001**	0.40	11.93	**<0.001**
M'habitat	2.73	50.18	**<0.001**	1.12	33.12	**<0.001**
Site x Zone	0.10	1.74	0.099	0.04	1.07	0.389
Site x M'habitat	0.01	0.25	0.776	0.01	0.40	0.672
Zone x M'habitat	0.08	1.39	0.244	0.01	0.21	0.932
Site x Zone x M'habitat	0.05	0.88	0.540	0.02	0.54	0.821
Error	0.05			0.03		
Sheltered reef						
Site	0.09	2.64	0.078	0.05	1.99	0.144
Zone	0.16	4.96	**0.003**	0.04	1.30	0.283
M'habitat	0.85	25.87	**<0.001**	0.44	16.14	**<0.001**
Site x Zone	0.06	1.71	0.130	0.05	1.66	0.143
Site x M'habitat	0.11	3.22	**0.046**	0.09	3.42	**0.038**
Zone x M'habitat	0.10	3.05	**0.034**	0.05	1.64	0.187
Site x Zone x M'habitat	0.10	2.99	**0.012**	0.06	2.20	0.053
Error	0.03			0.03		

Table 1.5: Results of Tukey's post-hoc tests identifying the reef zones that statistically differ from each other in individual and species numbers at the exposed reef location. **Bold** numbers denote significance at $p < 0.05$.

Number of individuals	Base	Slope	Crest	Front flat	**Number of species**	Base	Slope	Crest	Front flat
Base					Base				
Slope	**0.024**				Slope	0.783			
Crest	**0.002**	0.933			Crest	0.270	0.909		
Front flat	**0.000**	**0.000**	**0.001**		Front flat	**0.000**	**0.003**	**0.036**	
Back flat	1.0	**0.021**	**0.002**	**0.000**	Back flat	0.490	0.053	**0.004**	**0.000**

Table 1.6: Results of Tukey's post-hoc tests identifying the reef zones that statistically differ from each other in individual and species numbers at the sheltered reef location. **Bold** numbers denote significance at $p < 0.05$.

Number of individuals	Base	Crest	Front flat	**Number of species**	Base	Crest	Front flat
Base				Base			
Crest	0.833			Crest	0.987		
Front flat	0.998	0.742		Front flat	0.589	0.790	
Back flat	**0.033**	**0.003**	**0.049**	Back flat	0.313	0.504	0.965

Patterns in size

Total lengths of individuals varied from 7.5 – 92.6 mm TL overall, with 91% of all individuals measuring between 7.5 – 29.9 mm (mean 19.1 ± 0.3 SE). Striking differences in the mean weight of individuals were apparent at exposed sites ($F_{4,\ 626} = 13.27$, $p < 0.001$) with the heaviest individuals coming from exposed wave-swept reef zones (crest, front flat and back flat) (Fig. 1.8a). Individuals present at the front flat reef zone had mean weights of 0.34 g (± 0.13 SE); at the crest of 0.18 g (± 0.04 SE); and at the back flat of 0.14 g (± 0.02 SE). These values are in stark contrast to the 0.07 g (± 0.01 SE) in base and slope reef zones. Tukey's post-hoc tests differentiate these two groups. While half of all individuals of < 15 mm at the exposed reef sites were found at the base, the largest individuals (> 45 mm) were predominantly found at crest and back flat reef zones. Of these, approximately half were from the family Blenniidae, with larger gobies (*Amblygobius phalaena, A. rainfordi, Valenciennea muralis* and *Istigobius goldmanni*) making up the remainder. Reef zones at the sheltered sites were less variable, but overall differences were significant ($F_{3,\ 416} = 15.11$, $p < 0.001$). This pattern is due to the crest zone where mean individual weights (0.32 g, ± 0.04 SE) were nearly twice that of the overall mean across all reef zones (0.18 g, ± 0.14 SE) (Fig. 1.8b). For these sites, the crest contained the highest abundance of the > 45 mm size-class, due to the presence of large blenniid species in the crest reef zone. Size-classes were evenly spread across the other three sheltered reef zones.

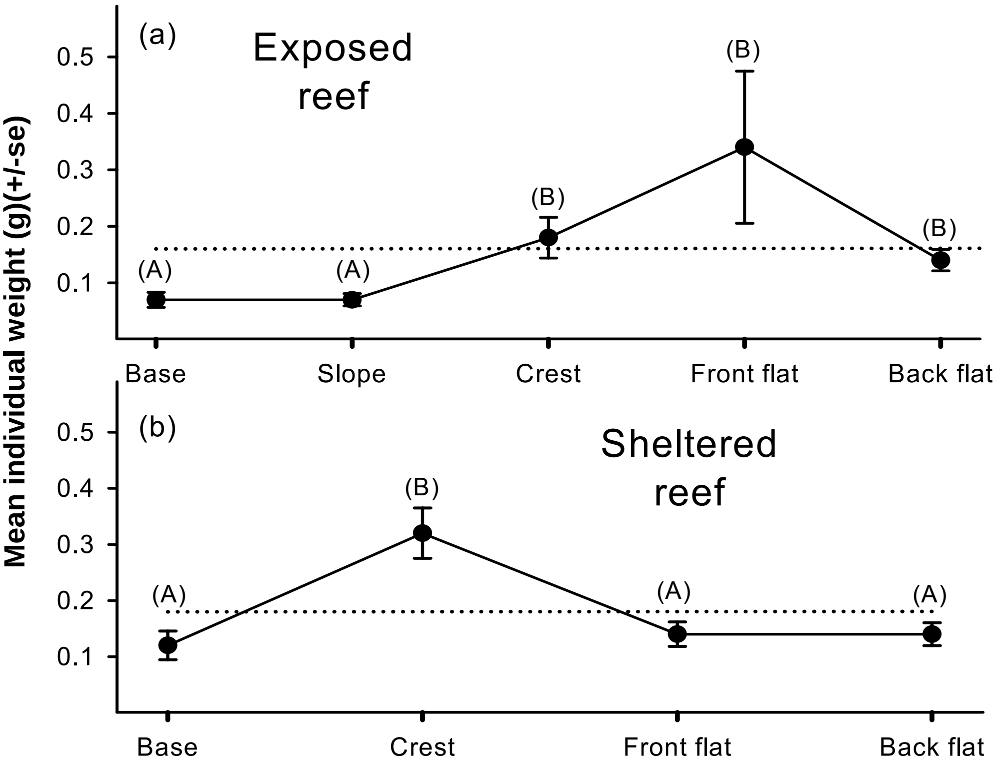

Fig. 1.8: Mean weight in grams (± SE, n = 24 samples) of all individuals censused at **a** exposed and **b** sheltered reef zones. The dotted line represents the average weight (g) across all reef zones for exposed and sheltered reef sites. Letters denote statistically indistinguishable groupings (same letter).

Patterns in Species Assemblages

Only six species (from the 12 selected for analyses) were abundant (with > 10 individuals) at both exposed and sheltered reef sites; *Eviota melasma, E. sigillata, E. queenslandica, I. goldmanni, Enneapterygius tutuilae* and *Salarias patzneri*. *Callogobius* sp. A and *Ctenogobiops feroculus* were found exclusively at sheltered reef sites; *Eviota* sp. J and *E. pellucida* were only found on exposed reef sites. MANOVAs based on the 12 most abundant species at exposed and at sheltered reef sites revealed significant differences in species assemblages among reef zones for both exposed and sheltered reefs (Pillai's trace $p < 0.001$). Post-hoc Bonferroni-corrected multiple comparisons indicated that species abundances varied among reef zones in ten of 12 species at exposed reef sites, and six of 12 at sheltered reef sites (Table 1.7). Canonical discriminant analysis shows the nature of these differences where centroid means and 95% confidence clouds are plotted for each zone at exposed (Fig. 1.9a) and sheltered (Fig. 1.9b) reefs. Except for the front flat and crest, confidence clouds indicate that all other zones have characteristic species assemblages in both exposed and sheltered reef sites. Small, highly abundant species tended to be associated with base and slope zones at exposed reef sites.

Table 1.7: Results of the Bonferroni-corrected multiple comparisons tests identifying the species that differed significantly in abundance among reef zones at exposed and sheltered reef sites. Analyses was based on the 12 most abundant (> 10 individuals across all zones) species censused at (1) exposed and, (2) sheltered reef sites. Letters indicate statistical non-significance (same letter) or significant differences (different letter) of each species among relevant reef zones. No samples were taken from the slope at sheltered reef sites.

Exposed reef	**Base**	**Slope**	**Crest**	**Front flat**	**Back flat**	**Sig**
Eviota melasma	A	A	B	B	B	<0.001
Eviota sp. J	A	B	B	B	B	<0.001
Eviota sigillata	A	A, B	B	B	B	<0.001
Eviota sp. O	A	A	B	A	A	<0.01
Eviota queenslandica	A	A	A	A	B	<0.001
Eviota pellucida	A, C	A	B, C	B, C	B, C	<0.05
Istigobius goldmanni	A	A	A	A	B	<0.001
Enneapterygius tutuilae	B	B	A, B	A	A, B	<0.01
Fusigobius signipinnis	A, B	A	A, B	B	B	<0.05
Salarias patzneri	A	A	A	A	B	<0.001
Sheltered reef						
Eviota melasma	A	-	B	B	B	<0.001
Eviota queenslandica	B	-	B	B	A	<0.001
Asterropteryx semipunctatus	A	-	A, C	A, C	B, C	<0.05
Istigobius goldmanni	B	-	B	A, B	A	<0.001
Salarias patzneri	B	-	A	A	B	<0.01
Ctenogobiops feroculus	B	-	A, B	A, B	A	<0.05

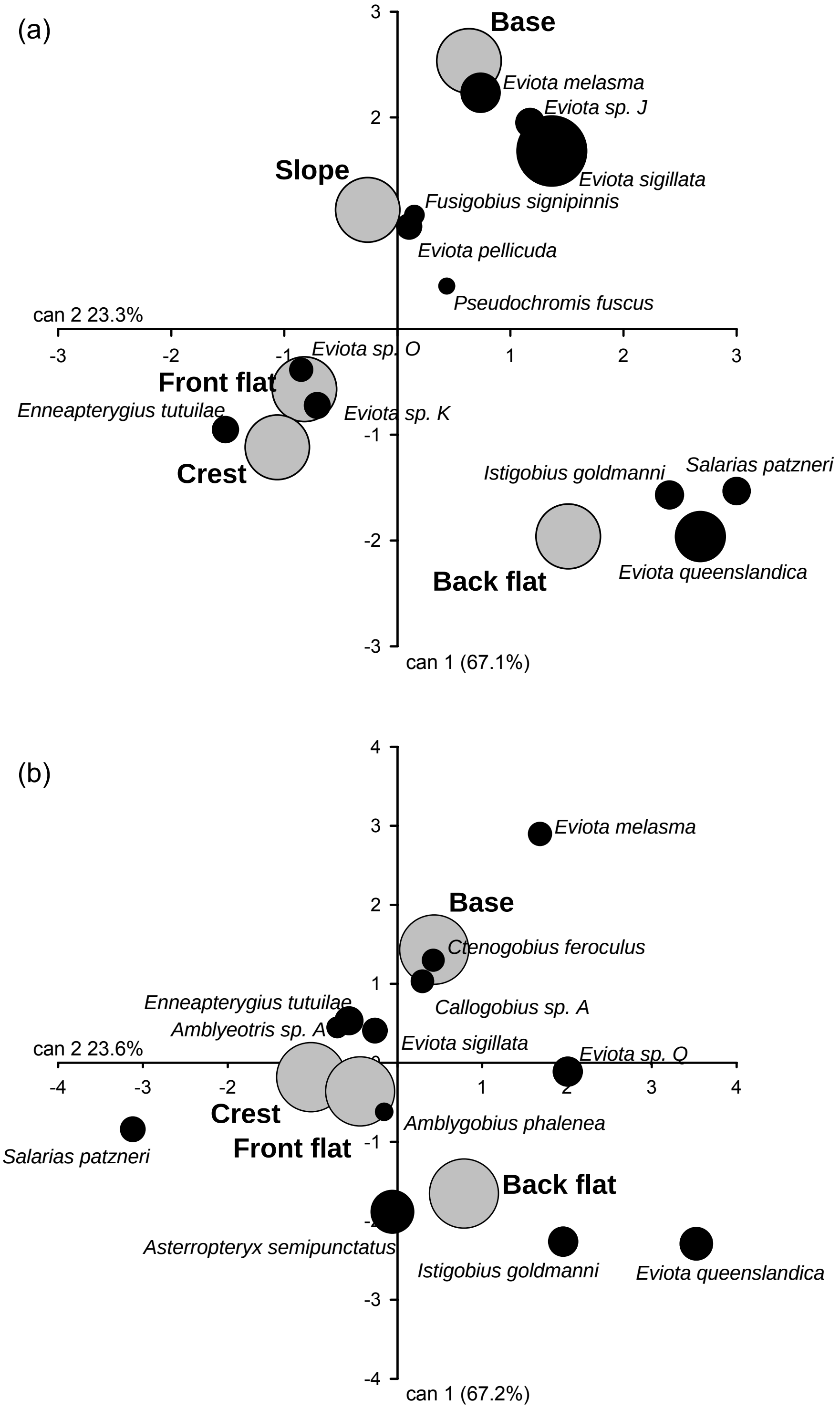

Fig. 1.9: Canonical discriminant analyses (CDA) displaying the relationship between the small cryptic reef fish community (12 most abundant species) and reef zones at **a** exposed and **b** sheltered reef sites. Ninety-five percent confidence clouds surround reef zone centroids (grey circles). Species bubble sizes reflect total abundance of each species (√ transformation from raw counts).

1.4. Discussion

The analysis of the small cryptic reef fish community at Lizard Island revealed three clear trends. Firstly, sand / rubble microhabitats consistently supported more individuals and species than open reef microhabitats, regardless of the location or spatial scale examined. Secondly, although community patterns of abundance, diversity and size/weight-class distribution varied widely among zones at exposed sites, comparatively little variation was exhibited at sheltered sites. Thirdly, species composition of the most abundant taxa varied considerably along wave energy gradients between exposed and sheltered reef sites and among reef zones.

With the exception of depauperate front flat (exposed sites) and crest (sheltered sites) reef zones, the effect of microhabitat type on the distribution patterns of the small reef fish community at Lizard Island was clear; more than two thirds of individuals and 41 out of a possible 44 species were sampled on sand / rubble microhabitats as opposed to 27 species in open reef samples. Intuitively, the relationship between small substratum-bound fishes and their structural environment is likely to be an intimate one, and it has already been well established that microhabitat type plays a pivotal role in the survival, abundance and distribution of these assemblages at small spatial scales (Syms 1995, Prochazka 1998; Munday 2000, Wilson 2001, Willis and Anderson 2003, La Mesa et al. 2004). At this scale, levels of abundance and species richness increases dramatically in more heterogenous environments that offer quality shelter to residents (Caley and St John 1996, Willis and Anderson 2003; Depczynski and Bellwood 2004). Given that microhabit type plays such a key role in structuring small reef fish communities, the question remains, to what extent do larger scale habitat zones influence community distribution structure?

At exposed wave-swept reef zones, I found a dramatic decrease in diversity and abundance, with a corresponding increase in overall fish size. This was most marked in the shallow wave-swept front flat, and to a lesser extent reef crest zones, regardless of microhabitat type. This suggests that microhabitat type plays a minor or secondary role in structuring small reef fish communities under circumstances where incident wave energy is particularly strong. There are two, non-exclusive factors that may account for these patterns. Firstly, wave-induced water motion may directly affect the distribution of many reef fish species through its interaction with swimming performance. Secondly, wave energy influences benthic communities and habitat structure.

The swimming abilities of small cryptic coral reef fishes have yet to be quantified. In larger, more mobile species a direct relationship between wave-induced water motion and swimming mode has been identified for a number of reef fish families (Fulton and Bellwood 2005). It appears that wave-swept habitats may have high energetic costs of occupation which may be a barrier for some species based on their swimming mode and efficiency. Fishes with sustained swimming abilities, usually employing energy-efficient lift-based pectoral locomotion, tend to inhabit wave exposed reef environments while slower thrust-based swimmers occupy more sheltered environments (Bellwood and Wainwright 2001, Fulton and Bellwood 2005). Several lines of evidence suggest that small cryptic fishes are comparatively poor swimmers. Unlike larger, more mobile species, most small cryptic species are substratum-bound (many lacking a swim bladder), spending little or none of their time swimming high in the water column where water movement may be greatest (Shashar et al. 1996, Goncalves and Almada 1998). Furthermore, they lead spatially restrictive lives encompassing home ranges of 0.25 - 2m^2 and tend to exhibit sedentary behaviour (Luckhurst and Luckhurst 1978, Goncalves and Almada 1998; Depczynski and Bellwood 2004). Small cryptic reef fish swimming generally consists of short bursts (1-5 secs) using body and caudal fin propulsion which may be one of the most energetically expensive modes (Wu 1977, Vogel 1994). Furthermore, their predominantly rounded fins suggest they are suited to powerful short-bursts of speed rather than sustained high speed swimming (Sambilay 1990, Vogel 1994). Overall, it would appear that the swimming ability of small cryptic species are generally unsuitable for high energy wave-swept locations.

Despite these limitations, the results indicate that a few species are able to inhabit even severely wave affected reef areas (i.e. families Blenniidae and Tripterygiidae). Size distributions among exposed reef zones provided some interesting insights into the potential role of wave energy and water motion in structuring size-related spatial patterns in these small reef fish communities. The data show that, at exposed reef sites, wave-swept reef zones (i.e. front flat) were inhabited by low numbers of larger, heavier (25-93mm TL) individuals including species with high surface area : volume ratios such as blennies, and calm reef zones (i.e. base) by high numbers of very small, lighter (< 15mm TL) individuals. These results correlate well with previously described patterns in the Caribbean (Greenfield and Johnson 1981; Greenfield 2003) and at Lizard Island (Wilson 2001) where some species of Blenniidae appear to show preferences for shallow, high energy habitats. Differences in size-class distributions across wave exposure gradients have previously been documented in temperate labrids with smilar results to those presented here (Fulton and Bellwood 2004). Shallow, wave-exposed reef zones were not only poorly inhabited by fewer and larger individuals, but smaller individual size-classes were almost entirely absent. In an earlier paper, Fulton and Bellwood (2002) also demonstrated ontogenetic changes in water column use for coral reef wrasses, with smaller individuals remaining close to the substratum, the authors hypothesising that smaller, less competent swimmers were flow-refuging in near-bottom boundary layers or microhabitat scale eddies. Regardless of the underlying mechanisms, the ability to maintain station in these hostile environments is probably very difficult for small individuals and our data suggests that wave-swept environments may provide a serious challenge to their occupation by smaller-sized individuals.

The role of wave energy in shaping marine environments and marine communities has been well documented for many marine ecosystems (Menge 1976, McQuaid and Branch 1985, Denny 1988, Friedlander and Parrish 1998, Denny and Wethey 2001, Bellwood et al. 2002). Because coral reef ecosystems are biogenic in makeup, the presence, absence, type and morphology of reef building organisms are greatly influenced by wave induced water motion (Done 1983, Dineson 1983, Ninio and Meekan 2002), shaping the habitat and living areas of resident biota. Distinct and abrupt changes in reef habitat diversity, complexity and abundance coinciding with changes from one reef zone to another follow depth and corresponding wave energy gradients. The microhabitat at the front flat is essentially level homogenous algal encrusted rock pavement subjected to the highest levels of water motion in our study. Accordingly, open reef microhabitats on exposed wave-swept reef flats theoretically represent the most physically extreme location for small benthic fishes and we found these areas to be poorly inhabited. At sheltered reef sites where more gradual inter-zone changes take place, there was little overall variation in these community parameters. These differences in habitat topography may be a significant influence on small cryptic reef fish communities.

Trophic resource patterns may also be a significant factor in shaping cryptic reef fish distributions. Most small cryptic reef fishes on the Great Barrier Reef are detritivorous (Depczynski and Bellwood 2003). Despite the higher nutritional value of detritus from exposed reef crests (Purcell and Bellwood 2001), loose detrital aggregates settle and concentrate in habitats and reef areas of low water movement such as lagoonal back reefs (Koop and Larkum 1987, Hansen et al. 1992) where they are easily accessed by benthic feeders. For detritivorous species which are physically able to cope with higher water velocities, such as *Ctenochaetus* species (Acanthuridae), reef crests and flats are highly productive and nutritionally-rich reef zones and represent preferred locations. For small cryptic reef fishes, however, these zones are mainly restricted to larger species.

In summary, small cryptic reef fish taxa show a strong level of among-zone variation on coral reefs, but only in locations with high water movement. Microhabitat plays a consistent but secondary role. Regardless of the mechanism, whether direct through water movement impacts on swimming or indirect through habitat or food availability, water movement appears to be a significant factor shaping small cryptic fish communities.

Chapter 2: Life history strategies in small cryptic coral reef fishes

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2.1. Introduction

Animal life cycles are intimately linked to organism body-size (Calder 1984, Stearns 1992) with variation in body-size initiating generic responses in many life history traits (Ricklefs and Finch 1995). Among the most important of these are the relationships between body-size and growth, mortality and lifespan. Overall, larger bodied organisms tend to exhibit slower, more protracted growth, lower rates of mortality and longer life spans (Calder 1984, Roff 1992). As a group, fishes are the most diverse vertebrate taxa on Earth covering some 25,000 species – half of all the vertebrates (Helfman et al. 1997). Among these, of particular note are the coral reef fishes. Highly diverse and broadly distributed across the tropical and sub-tropical oceans of the world, coral reef fish familial diversity surpasses that of most other vertebrate groups (Sale 1991). Yet despite this tremendous diversity, their life cycles and their characteristics remain poorly documented (Miller 1984; Caley 1998, Choat and Robertson 2002, Kritzer 2002). In spite of this lack of demographic information, the potential for life history diversity and applicability of testing general life history theory in coral reef fishes appears compelling. Exhibiting a host of reproductive modes, growth trajectories, body sizes and life spans amongst enormous diversity (~4000 species), research on coral reef fishes have recently expanded the boundaries of vertebrate biological, evolutionary and life history possibilities (i.e. Kon and Yoshino 2001, Watson and Walker 2004, Depczynski and Bellwood 2005a).

With few exceptions, reef fishes are constrained by evolution to leading complex bi-partite lives that includes a pelagic larval phase before settling onto a coral reef (reviewed by Thresher 1984, Leis 1991, Bonhomme and Planes 2000) where further growth leading to maturation and reproduction takes place. Within our current state of knowledge on reef fish life cycles, there exists two separate groups of roughly similar diversity and abundance, with each group sharing important life cycle characteristics. The first are those of larger (> 100mm total length [TL]), conspicuous species such as the families Scaridae, Labridae, Acanthuridae, Chaetodontidae and Pomacanthidae. In these families, typical comparative life history traits include asymptotic growth, late maturation, low adult mortality, a pelagic seasonal broadcast spawning regime and life spans numbering years leading to high lifetime reproductive output (Thresher 1984, Sponaugle and Cowen 1994, Choat and Axe 1996). In contrast, the second group consists of small (< 100 mm TL), often cryptic species that typically exhibit steep continuous growth throughout their lives, mature at much younger ages but have relatively low lifetime reproductive output due to their small body-size and expected short life spans. This group is expected to suffer from higher rates of size-related adult mortality and exhibit a benthic spawning reproductive strategy that includes parental care of eggs, a feature which has been associated with enhanced offspring survival, predominantly in small-bodied taxa (Roff 1992; Miller 1984; Thresher 1984; Munday and Jones 1998; Hendry et al. 2001; Neff 2003; but see Robertson et al. 1990; Gladstone 1994). This second group includes species in the families Gobiidae, Blenniidae, Tripterygiidae and Pseudochromidae.

Although both groups exhibit highly successful evolutionary strategies, the smaller cryptic reef fishes have received little attention in the literature. This is despite the fact that members of this group are arguably more trophically interlinked within reef systems, by virtue of their short generation times and higher susceptibility to predation, and are often found in higher densities than their larger counterparts (reviewed in Munday and Jones 1998).

To date, demographic studies on this small cryptic component have been particularly lacking and restricted to species in the upper size range (50-120 mm TL) (e.g. Kritzer 2002, Wilson 2004, Hernaman and Munday 2005a, b – but see Longenecker and Langston 2005). However, the modal body-size of small adult cryptic reef fish communities on the Great Barrier Reef (GBR) is 21.0 mm TL at an inner-shelf location (Orpheus Island) and 15.0 mm TL on a mid-shelf location (Lizard Island) (Depczynski and Bellwood 2003, 2005b). Given the numerical dominance of these smaller bodied species and the theoretical relationship between body-size and life history traits, the smaller size classes of coral reef fishes may be a critically important component of coral reef ecosystems. Furthermore, these fishes represent the extremity of the body-size spectrum in vertebrate animals, thereby extending the breadth of life history possibilities and enabling a more complete overview of patterns in life history traits among this diverse assemblage of vertebrates.

Coral reef fishes of the genus *Eviota* are some of the smallest and most abundant fishes on the Great Barrier Reef (GBR), and constitute approximately half of all cryptic individuals on the reefs surrounding Lizard Island (Depczynski and Bellwood 2005b). Numerically ranking 1, 2 and 3 in abundance on these reefs, here we document the complete life cycles of *Eviota sigillata, E. queenslandica* and *E. melasma* in order to quantify the demographic characteristics of this portion of the reef fish community. Specifically, this study aims to quantify the growth and mortality rates of these three species based on laboratory and field experiments. A further aim is to explore the relative proportion of lifespan allocation to pelagic larval durations and juvenile and adult states, across a range of reef fish species based on a meta-analysis of life history data, in order to establish and contrast the full available range of life history strategies exhibited by coral reef fish taxa. Finally, lifetime fecundity is calculated for the three focal species to investigate the costs of extreme small body-size and associated life history traits on lifetime reproductive output and population dynamics. These parameters are then incorporated into an overview of known life history patterns in coral reef fishes in order to assess the contribution of fish assemblages to our understanding of vertebrate life history theory.

2.2. Materials and methods

All collections and field studies were undertaken in January and February 2003 and 2004 on reefs around the Lizard Island group (14°40'S, 145° 27'E) in the Cairns section of the GBR. Individuals for all studies were collected on SCUBA using the anaesthetic clove oil in a 5:1 - ethanol : clove oil mixture and a fine-mesh (2mm) net (following Depczynski and Bellwood 2004). All size and weight measurements throughout are given in total length (TL) and grams (g) respectively.

We used tetracycline validated daily otolith increment analysis (following Schmitt 1984) on a total of 13 *Eviota sigillata* and 6 *E. queenslandica* individuals to ensure accurate age and growth estimation. Daily periodicity of increments was confirmed by comparing the number of increments with the number of post-treatment days (i.e. post-fluorescent band). Mean number of rings for the 17-day trial was 16.61 (± 0.18 SE) for *E. sigillata* and 16.0 (± 0.58 SE) for *E. queenslandica*.

For ageing analyses, a total of 319 *E. sigillata*, 189 *E. queenslandica* and 171 *E. melasma* were collected. Sixty individuals of each species from a full range of available sizes including the 10 largest individuals of each species were used for ageing. Individuals were euthanased within 2 hrs following capture, weighed, measured (mm) and their sagittal otoliths extracted, cleaned, sectioned and rings counted 3 times using a compound microscope (400x) along the longest axis. Any discrepancies of > 10% between counts on a single individual were excluded from the analysis. Growth trajectories from size-at-age plots were fitted to 3 growth models; the von Bertalanffy growth function, a linear and a power curve. Goodness of fit of each model was tested using the residual sums of squares (RSS) and coefficient of determination (r^2) calculated from the residual and explained sums of squares and the best model fitted. Fish trunks were fixed in a 4% formaldehyde, 5% acetic acid and 1.3% calcium chloride (FAACC) solution for later gonad histology.

A meta-analysis of size at age data was generated from a comprehensive search of the coral reef fish literature. All maximum life spans and corresponding sizes of coral reef fish species were recorded to compare *Eviota* to known size at age data in 111 other species (full list described in appendix A). The criteria used to assess the integrity of the data was that it had to have gone through an externally peer review process. One exception was made for the maximum lifespans of seven species. Data from these seven species were genorously donated by a colleague (M Berumen) and verified by me (i.e. otolith rings and specimen sizes recorded).

Like most reef fishes, species of *Eviota* have complex bipartite lives that include a pelagic open-water phase before settling onto a reef to begin the benthic phase of their lives. *Eviota* settlement rings were distinguished by their abrupt transition from widely spaced pre-settlement increments (approximately 5.1µm) to narrower (approximately 2.7µm) increments and correspond to type 1a settlement check marks (Wilson and McCormick 1999). Pre-settlement age was determined by counting the number of rings (days) between hatching (1st ring) and settlement (Fig. 2.1). The life spans and pelagic larval durations (PLDs) of these three *Eviota* species were compared with demographic data for a range of coral reef fish species (life spans and maximum sizes (mm) of 111 species; PLDs of 361 species – as described above and presented in appendices A and B). Cross-referencing size at age data with PLD data identified 27 species (inclusive of 3 *Eviota* spp) in total for which all parameters existed.

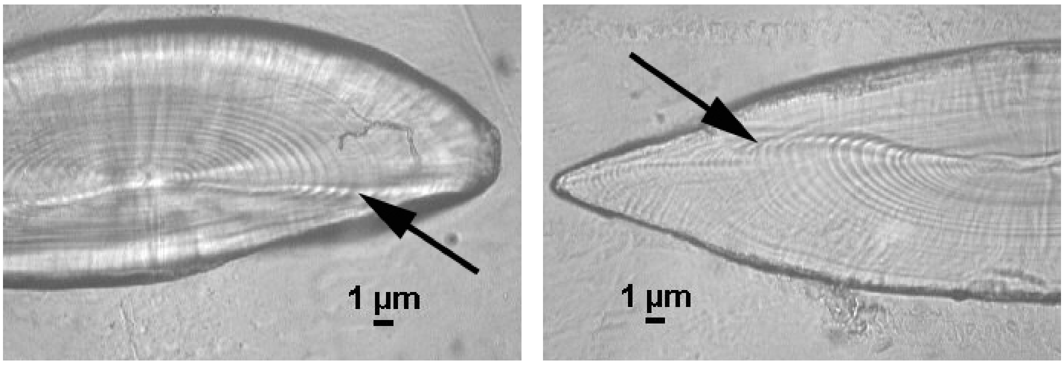


Fig 2.1: Otoliths from a 38 day old 13.9mm TL *Eviota sigillata* (left) and a 57 day old 18.2mm TL *E. melasma*. Arrows indicate settlement check marks at 23 and 27 days post-hatching (*E. sigillata* and *E. melasma* respectively).

Whole fish trunks were sectioned longitudinally in 5µm sections following decalcification and embedding in paraffin wax. Sections were stained using Myer's haematoxylin and Young's eosin-erythrosin. Gonads were sexed and maturity status assessed under a compound microscope (400x). Maturity was defined based on the presence of late vitellogenic and ripe oocytes (stages III-IV) in females (West 1990) and spermatozoa (stages III-IV) in males (Fig 2.2). Histological samples were cross-referenced with ageing data to determine size and age at first maturity.

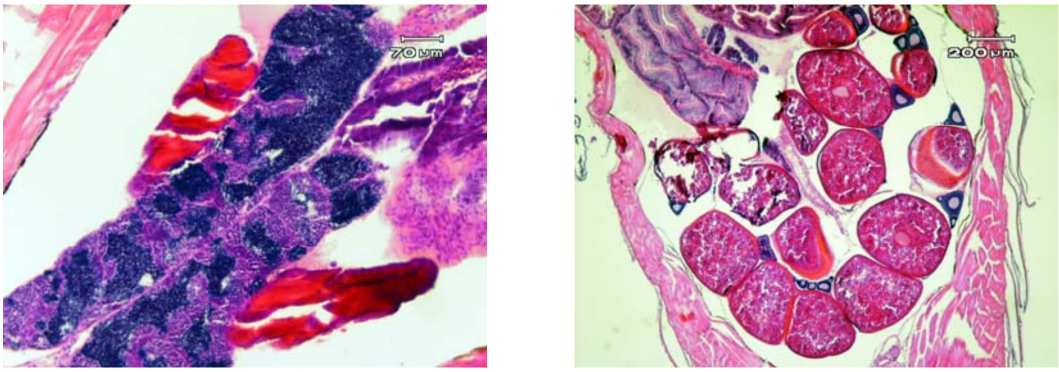


Fig 2.2: Histological sections of the gonads of a mature male (left) and female *Eviota queenslandica*. Male shows accessory gonad structures (in red) and dense sperm crypts of stage II-IV spermatozoa. Female shows mid-late stage II-IV oocytes.

Several *Eviota* species have been successfully bred under artificial conditions and *Eviota queenslandica* and *E. melasma* fecundity data were taken directly from the literature (Sunobe and Nakazono 1987, Sunobe 1998). A similar breeding program was conducted for *E. sigillata.* Four replicates consisting of a single male and 2 females were placed in 15L flow-through aquaria (at 27-28ºC) and fed live food twice daily. In each aquarium, un-lidded 50 x 15mm clear plastic vial "nests" were buried in sand with their opening exposed. *Eviota* lay their eggs on substrate ceilings. Vial ceiling interiors were checked each morning by moving sand away from vial roofs. The swelling abdomen of each female was clearly visible as egg development progressed, and then shrunk following egg-laying, enabling the identity of spawning females to be determined within each replicate aquarium. Vials containing eggs were removed 6 hours later to ensure the completion of the spawning episode (typically 15-45 mins) and all eggs counted (Fig. 2.3). The experiment was continued for 39 days or until the death of the male or females, whichever came first. An estimate of the reproductive efficiency (*RE*) was calculated for each species using the equation:

$$RE = LRO \,/\, M_{max}$$

where lifetime reproductive output (LRO) = $\overline{SE}$ x $\overline{EE}$ and $\overline{SE}$ = mean number of spawning events; $\overline{EE}$ = mean number of eggs per spawning event and M_{max} = maximum number of mature female days. This provides a comparative estimate between species of the rate of reproductive output per unit time (day) by taking the number of adult reproductive days for each species into consideration. It also provides an estimate of the expected lifetime reproductive output from a single female individual. Frequency of spawning events was taken as semi-lunar (14-

day) for *E. queenslandica* and *E. melasma* based on Taru and Sunobe (2000) for *E. abax*, and data presented in this study on *E. sigillata*.

Mean generational turnover ($\overline{GT}$) estimates were calculated using the following:

$$\overline{GT} = AM + [(T_{max} - AM) / 2]$$

where AM = age at female maturation and T_{max} = maximum age. This gives a conservative averaged estimate for the time taken for a new generation to be generated assuming that a stable population exists (i.e. two adults are replaced by two larvae surviving to adulthood) (see Gaillard et al. 2005).

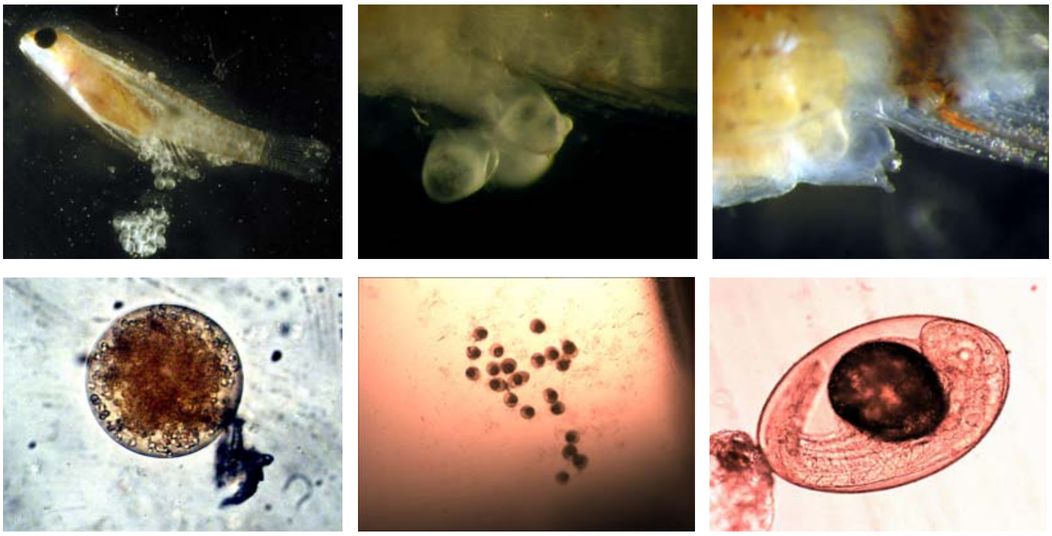


Fig. 2.3: Female *Eviota sigillata* and eggs. From left to right; Female with eggs, eggs exiting the genital papilla, close-up of female genital papilla, recently hydrated egg, eggs attached to the ceiling of the plastic vial nest used in the experiment and late-development embryo. Note the filaments used to attachment eggs to substrate ceiling and provision of the large yolk sac.

Mortality estimates are based on a community-level study that included 36 *E. sigillata*, 20 *E. queenslandica* and 13 *E. melasma* specimens. In total, 146 small, cryptic reef gobies were collected on SCUBA from three 4 x 1m^2 field sites. Field sites were pooled following a non-significant result in a One-Way ANOVA on abundances between sites ($F_{2,\,9} = 0.329$, $p = 0.727$) providing 12 x 1 m^2 replicates. Fish were placed into clip-seal® bags and tagged *in situ* in the dorsal flank using a 29 gauge hypodermic filled with elastomer® (Northwest Marine Technologies Inc., USA). Upon full recovery (approximately 10 mins [*cf.* Munday and Wilson 1998]), tagged individuals were released at their exact site of capture. To control for movement, recaptures 9 days later were conducted using a concentric net arrangement consisting of 1, 2 and 4m^2 nets (Fig. 2.4). Members within this reef fish community have home ranges of 0.25m^2- 2.5m^2 (Luckhurst and Luckhurst 1978, Taru and Sunobe 2000, Depczynski and Bellwood 2004). The position (1, 2 and 4m^2 nets), size, weight, species identification and the presence or absence of tags of each individual was recorded on recapture. An instantaneous mortality estimate based on Hoenig's equation for mortality rates (Hoenig 1983) was also calculated to supplement field mortality estimates for the three *Eviota* species. Hoenig's equation is based on empirical evidence (and not theoretical estimates) over a wide range of marine taxonomic groups ($r^2 = 0.82$) and utilizes maximum species age to calculate mortality rates over time using the equation:

$$\ln Z = 1.46 - 1.01 \ln T_{max}$$

where Z = instantaneous mortality rate and T_{max} is maximum species age. Previous studies to determine 1) mortality from tagging and 2) increased predation risk to tagged individuals were also conducted and found to have no detectable effect (see Depczynski and Bellwood 2005a).

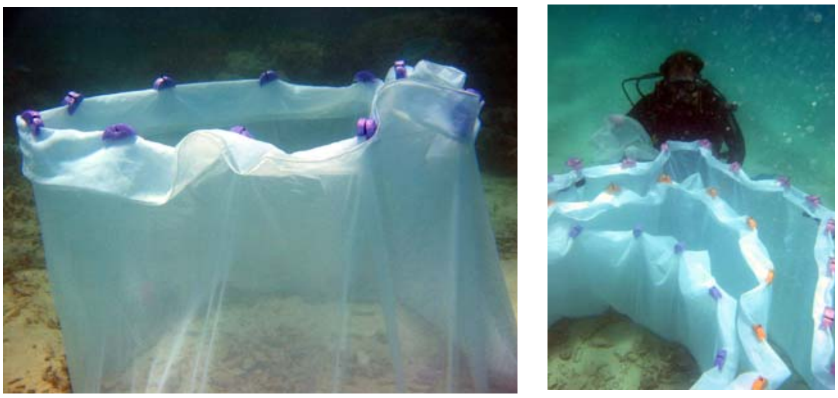


Fig. 2.4: Initial day zero $1m^2$ sampling net (left) and concentric 1, 2 and $4m^2$ net arrangement used for resampling 9 days later.

2.3. Results

Post-settlement growth in all three species was best described by a linear function with maximum sizes of 18mm for *Eviota sigillata*; 25.7mm for *E. queenslandica* and 27.1mm for *E. melasma* (Fig. 2.5a-c). Across all coral reef fish species, the relationship between size and age was highly variable (Fig. 2.6), however, larger species tended to live longer lives (*cf.* Nee et al. 2005). Life spans ranged from 59 days in *Eviota sigillata* to 70 years in the surgeonfish *Prionurus maculatus* (447mm). All three *Eviota* species were located at the extreme bottom end of both the body-size and age spectrum. Without exception, all species with life spans of < 12 months were smaller than 100mm.

Maximum life span in *E. sigillata* was 59 days; *E. melasma* 97 days and *E. queenslandica* 99 days (Fig. 2.5a-c). Projected size at reef settlement in the 3 species was between 7-7.5 mm with mean pelagic larval durations (PLDs) of 24.2 (± 0.33 SE) for *E. queenslandica*, 24.7 (± 0.28 SE) days for *E. sigillata* and 26.2

(± 0.41 SE) for *E. melasma*. This corresponds to maximum “on-the-reef” post-settlement life spans of 34.3 days for *E. sigillata,* 70.8 for *E. melasma* and 73.8 for *E. queenslandica.* The proportion of total lifespan represented by PLDs was 41.8% (*E. sigillata*), 27.0% (*E. melasma*) and 24.4% (*E. queenslandica*). For species where longevity and PLD data are available, proportion of total lifespan equals < 1% of total lifespan (Fig. 2.7). One notable exception to this pattern exists in another small cryptic coral reef fish (*Enneapterygius atriceps*; Longenecker and Langston 2005) where the PLD represents 25.6% of total lifespan.

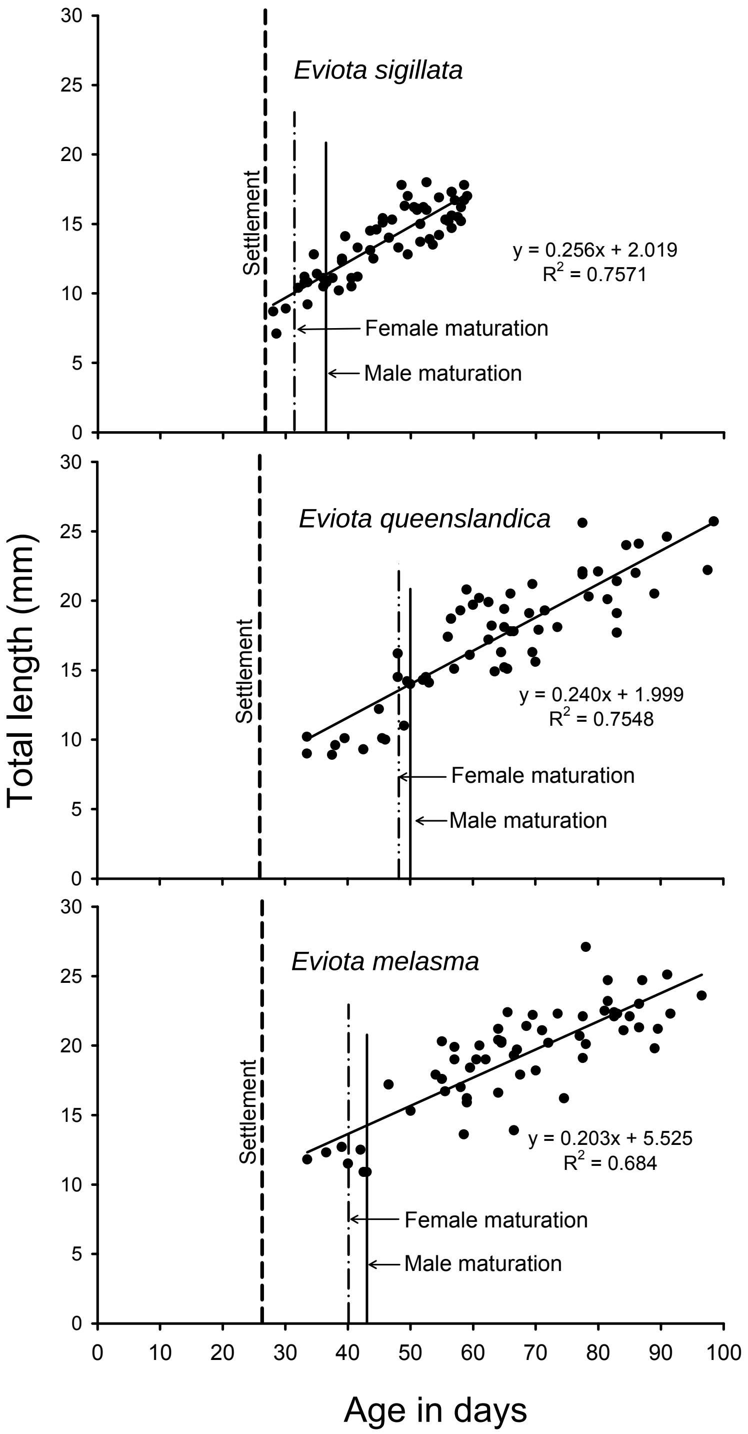


Fig. 2.5: Size (mm total length) at age (d) data summarising the complete life cycles of three coral reef gobies; *Eviota sigillata*, *E. queenslandica* and *E. melasma*. Settlement lines denote the mean age and transition point at which each species moves from its pelagic larval phase to a benthic reef-associated one. Projected rates of growth indicate a linear pattern from post-settlement to death. N = 60 for each species.

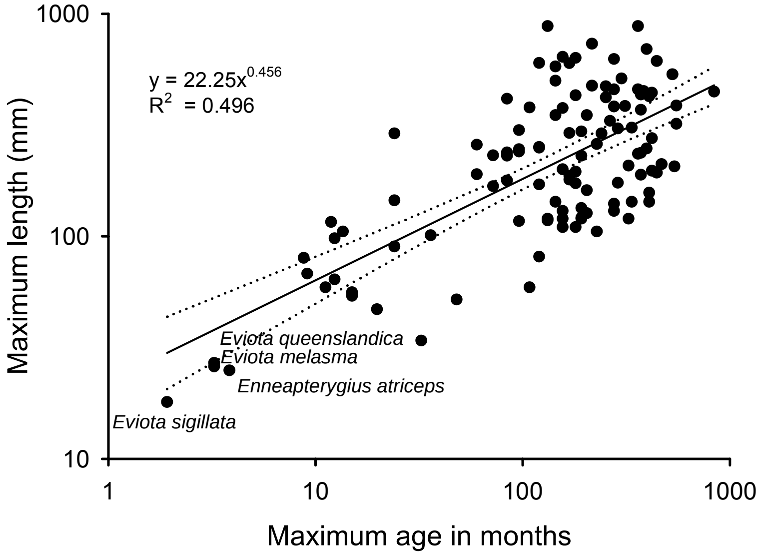


Fig. 2.6: Log-log plot of the relationship between maximum size (mm total length) and maximum age (months) in 114 species of coral reef fishes (as described in appendix A) fitted with 95% confidence intervals (dotted lines). Raw values and corresponding references for each species can be viewed in Appendix A.

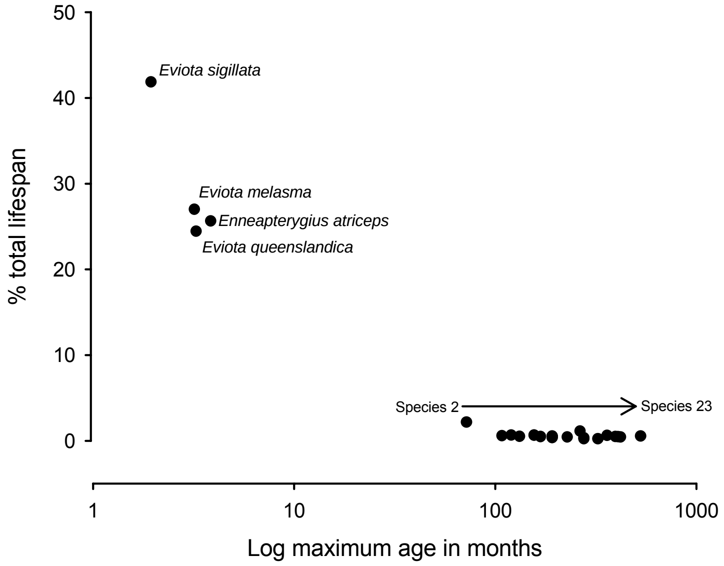


Fig. 2.7: Relationship between pelagic larval duration (PLD) and maximum longevity (logged months) in 27 species of coral reef fishes for which published estimates of both variables are available. Data is presented as % of total lifespan represented by PLD. Except for *Eviota* and *Enneapterygius atriceps*, species names and values are listed in Appendix C and correspond to species data points numbering from left (number 2) to right (number 23). Species 2 - 23 are further plotted in Appendix D to show the degree of variability within these data points.

Sex ratios showed a strong dominance of females (Table 2.1) suggesting the possibility of protogyny or harem keeping by males. Already conspicuous by their unusually extreme life history characteristics, the reproductive features of *E. sigillata* stood out among the *Eviota*. Although size at first maturity in both sexes was similar for *E. sigillata* and *E. melasma*, and only marginally larger in *E. queenslandica*, age at maturation occurred earliest in *E. sigillata.* This corresponded to astonishingly short mean generational turnover rates of 46.5 days for this species (*E. melasma* 68.5 days; *E. queenslandica* 74 days). Among the *Eviota*, *E. sigillata* also exhibited the lowest lifetime reproductive output and efficiency resultant of their shorter life spans and the comparatively smaller numbers of eggs they laid at each spawn. Collectively over a lifetime, this equated to a maximum production of just 243 eggs in comparison to the calculated values for *E. melasma* (781) and *E. queenslandica* (1039).

Of the 69 *Eviota* tagged, 27 were resampled providing a mean mortality rate of 60.9% over the 9 day period. This equates to a daily mortality rate of 6.8% (± 0.65% SE, n=12). The variance reflects variation among sites, not days. Of these 27 individuals, 77.7% were resampled in the 1m^2 net, 14.8% in 2m^2 and 7.5% in 4m^2 supporting existing evidence of the small home ranges of these fishes. Daily field and expected estimates based on Hoenig's mortality equation were similar within each of the three *Eviota* species; *E. sigillata* 8.0 and 7.0%, *E. melasma* 5.1 and 4.2%, *E. queenslandica* 5.6 and 4.2% respectively.

Table 2.1: Demographic and reproductive rates of female *Eviota* species; means are given ± SE.

Species	**♂ : ♀ Sex ratio**	**Size and age at first maturity**	**Mean no. eggs per spawning event ± SE, (range) and [n]**	**Mean frequency of spawning and (interlude range)**	**Lifetime reproductive output (LRO)**	**Reproductive efficiency (RE)**
Eviota sigillata (n = 75)	1: 1.6	♂ 11.1 mm at 36 d ♀ 11.2 mm at 34 d	136.15 ± 4.9 SE (108-163 [n=13])	14 d ± 0.8 SE (11-17 d)	243	9.7
Eviota queenslandica (n = 70)	1: 1.7	♂ 13.1 mm at 50 d ♀ 13.9 mm at 49 d	*291 ± 40.3 SE (160-374 [n=5])	*14 d	1039	20.8
Eviota melasma (n = 79)	1: 1.4	♂ 10.9 mm at 43 d ♀ 11.5 mm at 40 d	*192 ± 26.1 SE (104-270 [n=7])	*14 d	781	13.7

Notes: * denotes data from Sunobe and Nakazono (1995). Mean frequency of spawning events in *E. queenslandica* and *E. melasma* were estimated using Taru and Sunobe (2000) on observed semi-lunar spawning frequencies in *E. abax* and those found in *E. sigillata*. Lifetime reproductive output (*LRO*) is based on mean number of spawning events possible in an adult female lifespan x mean number of eggs per spawning event. Reproductive efficiency (*RE*) is a measure of the comparative efficiency of reproductive output per unit of time (d) when adult female lifespan of each species and lifetime reproductive output is taken into consideration.

2.4. Discussion

Representing some of the shortest-living and earliest-maturing vertebrates known, the three focal species broaden our understanding of the breadth and range of vertebrate life histories and the potential for reef fishes to contribute to this area of research. Consistent with life history theory, these results demonstrate major shifts in patterns of growth, reproductive strategy and the pace and timing of sexual development in coral reef fishes which may help compensate for an exceptionally short lifespan. Accordingly, maximum size and age in short-lived reef fish species have significant implications for the proportion of the total lifespan spent in a pelagic larval environment that probably reflects the minimum size at settlement needed for survival on the reef.

Life spans define the amount of time an organism has to complete all the essential tasks in life and are therefore of primary importance when examining variations among life history traits and strategies within taxonomic groups. Reef fishes display a wide spectrum of life spans from surgeonfishes of > 60 years (Choat and Axe 1996) to *Eviota sigillata* at 59 days, currently the shortest lifespan for a vertebrate animal (Depczynski and Bellwood 2005a). At a gross scale, life spans correlate well with body-size in animals (Ricklefs and Finch 1995, Brown et al. 2004), however, recent evidence has suggested that this life history relationship is not always applicable to coral reef fishes because size and age are decoupled within and between reef fish taxa (Munday and Jones 1998, Choat and Robertson 2002). The addition of demographic size-at-age and longevity data for small (< 100 mm) cryptic reef fish species at the lower end of the body-size spectrum, however, has permitted a re-examination of life history relationships in coral reef fishes.

These additions significantly modify our view of life history patterns in coral reef fishes. First, it establishes that the relationship between size and longevity is maintained at a gross level (*cf.* Nee et al. 2005) much as they are in other taxonomic groups and as predicted by life history theory (Blueweiss et al. 1978, Calder 1984, Brown et al. 2004). Second, the decoupling of size and age may not be applicable to many smaller species due to linear patterns of growth. Third, in spite of the variation in reef fish size at age data, growth trajectories themselves appear to share a strong relationship with species life span. In the vast majority of cases, longer-lived species (years) exhibit curving trajectories appropriately modeled by von Bertalanffy growth curves (e.g. Choat and Axe 1996, Choat and Robertson 2002); medium-lived species (months) may exhibit a paired linear model with a breakpoint (sometimes referred to as the Broken stick model, see Toms and Lesperance 2003) marking a distinct slow-down in growth at or around maturity (e.g. Hernaman and Munday 2005a); while the shortest-lived species (days) exhibit linear patterns of growth (Fig. 2.8). These points highlight the importance of including the entire body-size spectrum when looking at life history relationships within taxonomic groups. This is particularly important in coral reef fishes where > 40% of species are within this < 100 mm body-size threshold (Ackerman and Bellwood 2000).

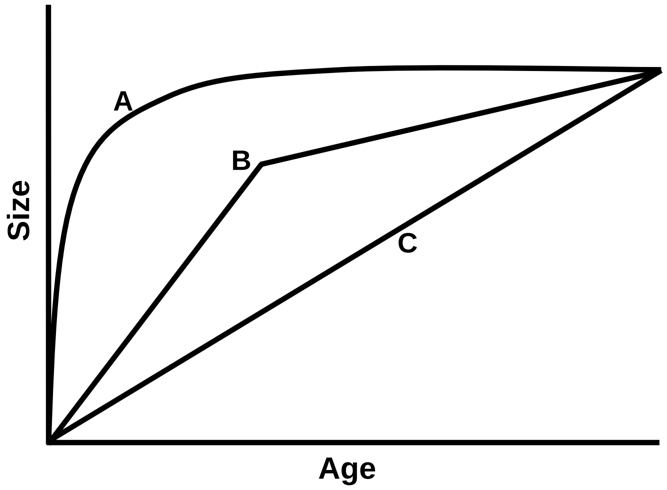


Figure 2.8: Reef fish growth models. **(A)** von Bertalanffy growth, suited to many longer-lived (years) fish species. In this model, initial growth is rapid and linear before (often abruptly) reaching an asymptotic size. Under this growth scenario, size and age become decoupled at, or approaching asymptotic size. **(B)** Breakpoint growth, applicable to many medium-lived (months) fish species. This model consists of two joined linear lines with a "breakpoint" coinciding with, or around, sexual maturation. Further growth slows noticeably at this stage but remains linear. **(C)** Linear growth as seen in *Eviota* and other short-lived (days) fish species. In this model, size and age shares a consistent and ongoing relationship making size a reliable predictor of age.

All three *Eviota* species exhibit linear growth. Linear growth trajectories in reef fishes are becoming increasingly common as the demography of smaller species are revealed (*cf.* Kritzer 2002, Hernaman and Munday 2005a). From a life history perspective, the evolution and maintenance of linear growth is remarkable in that there is no apparent trade-off between somatic growth and reproduction. This is particularly interesting as this is arguably one of the best evidenced of all life history trade-offs in both plant and animal taxa (reviewed in Roff 1992, Stearns 1992, Aday et al. 2003). Supporting reproduction at the same time as maintaining pre-reproductive growth rates requires substantial amounts of additional energy. There are several lines of evidence to suggest that the energy requirements necessary for linear growth and reproduction are available to these small taxa. Studies on a range of small vertebrates provide good evidence of the capacity of these taxa to amass additional surplus or additional energy as required. In small species, the capacity to cost-effectively tap into and utilize potentially abundant and ubiquitous small food items is enhanced due to their ability to exploit microhabitats not available to larger-bodied organisms (Clarke 1996, Miller 1996, Churchfield 1996). Thus, the nutritional needs of small ectothermic vertebrates may be quickly and easily met (Clarke 1996). The probability of ready access to an abundant and nutritionally rich diet has been described for *Eviota queenslandica*. This species is able to procure and utilize a broad range of ubiquitous food items (Depczynski and Bellwood 2003). Furthermore, they do so with minimal foraging effort (< 5% of their daily activities) (Depczynski and Bellwood 2004). Based on these observations, energetic demands supporting both rapid linear growth and reproduction may be easily met in *Eviota*, and other small linear growing coral reef fishes.

Rapid linear growth in the young stages of fishes has traditionally been viewed as a strategy to escape size-related predation; the growth-predation theory (Anderson 1988). However, this concept does little to explain the growth patterns seen in *Eviota* species as their small size ensures that they remain at high risk of predation throughout their lives. The trade-off between female body-size and fecundity provides a more realistic explanation for the rapid growth patterns of *Eviota*. Because the relationship between body-size and clutch size is a volumetric one (Wootton 1990), even small increases in female body-size may equate to proportionally large gains in clutch size. Under these circumstances, batch fecundity in linearly growing species is expected to increase with maternal age. Unfortunately, my breeding program data are inadequate to elucidate these patterns for *Eviota*. However, the female expectation of producing only two (*E. sigillata*) to four (*E. queenslandica* and *E. melasma*) clutches over a lifetime would directly increase the fitness value of maintaining rapid linear growth throughout life. Overall, the lifetime reproductive output of *Eviota* individuals is extremely low by reef fish standards; an inevitable by-product of their short lives and small body-size. In this situation, linear growth to maximize reproductive effort and output via early maturity, a frequent semi-lunar spawning regime (regardless of season – *pers. obs.*) and parental care of eggs is probably critical for the maintenance of local populations and the continued existence of these three species.

In reef fishes with non-linear adult growth, the early (pre-reproductive) portion of life is characterised by steep linear growth, inviting the possibility that small, rapid linear growing species such as *Eviota* may simply never reach an asymptotic size due to premature death on the reef, and have simply readjusted the timing of their life cycle events to compensate for their short lives. Three lines of evidence exist in support of this hypothesis. Firstly, *Eviota* kept in aquaria often live substantially longer lives than they would in the wild, reaching an asymptotic size some time after the maximum life spans recorded in wild individuals (*pers. obs)*. However, after an extended period these captive individuals often show an increasingly wasted appearance, decreased locomotor activity, loss of coordination and a general disinterest or cessation in courting and reproduction with increasing "post-normal" age; all recognized signs of advanced senescence (Ricklefs and Finch 1995, Delbono 2003) and entirely incompatible with survival in the wild. Secondly, all of the oldest *Eviota* individuals from all species had active gonads with germ cells in varying stages of development indicating their ability and willingness to continue reproducing despite approaching their maximum longevities. Thirdly, we recorded extremely high daily mortality rates and short life spans of < 100 days in all three *Eviota* species indicating the severe biological time constraints and selective pressure imposed on these small species.

Among life history traits, mortality is probably the least well documented aspect of an animal's life history (Pauly 1980, Purvis and Harvey 1996). Experimental and theoretical results show that high extrinsic mortality throughout prey life selects for rapid growth (Arendt 1997), earlier size and age at maturity co-occurring with higher early-life reproductive investment (Reznick and Endler

1982) and shorter intrinsic life spans (Williams 1957 - but see Reznick et al. 2004). Unfortunately, few studies document the entire life cycle of coral reef fish species incorporating growth, maturation, reproduction and rates of mortality (but see Hernaman and Munday 2005a, b), making it difficult to assess how mortality rates shape reef fish life history patterns. We documented extremely high daily field mortality rates of 7-8%, which match estimated otolith-based rates, in all three *Eviota* species along with the three key life history traits. Size at female maturity, typically an event that happens at 65% of average asymptotic size in fishes (Charnov 1993), happens at 51% of the mean size of the largest 10% of *Eviota queenslandica* individuals (*sensu* Hernaman and Munday 2005b) and 44% for *E. melasma*, both reductions being consistent with life history theory. Considering that *E. sigillata* is the smallest of the three species, we would expect size at maturity to decrease further still, however, size at maturity takes place at around 11-12 mm representing 63% of the lifespan in the largest 10% of individuals. Perhaps accounting for this deviation from the expected, Miller (1984) points out that there appears to be a functional body-size threshold in gobioid fishes of approximately 10 mm (e.g. the coral reef species *Trimmaton nanus*: Winterbottom and Emery 1981), below which the teleost frame is unable to support reproduction.

For a coral reef fish species, the lengths of *Eviota* pelagic larval durations (PLDs) are unremarkable (24-26 days). However, as a proportion of the total life span, the PLD is striking. While the PLDs of most reef fish species typically make up < 1% of their expected lifespan (see Appendix C), they make up a quarter to nearly half in *Eviota*. *Eviota* do not represent an isolated case among coral reef fish. The PLD of *Enneapterygius atriceps* in the Tripterygiidae is approximately 25% of its total lifespan (Longenecker and Langston 2005). This suggests that there is a lack of response to reduced life spans that crosses taxonomic boundaries. Under these circumstances, the fixed range of PLDs obviously represents a consistent and real constraint among coral reef fishes with a pelagic larval phase that places more pressure on very short-lived species to successfully complete all the necessities of life within a narrow post-settlement time frame.

It is interesting to note that despite their very short life spans, we see no reduction in *Eviota* PLDs. The complete lack of any inter-species correlation between reef fish life spans and PLDs overall (Fig. 2.7), suggests that a minimum functional state (i.e. developmental condition or size) may be necessary before pelagic young are capable of surviving and persisting on the reef (*cf.* Searcy and Sponaugle 2000). It is clear from the short 7-17 day PLDs of the anemone fish genera *Amphiprion* and *Premnas*, that PLDs and corresponding size at settlement can be significantly reduced (i.e. *A. melanopus* 8.1 mm, *P. biaculeatus* 6.8 mm, Job and Bellwood 2000). However, as noted by Job and Bellwood (2000), anemone fish species may be exceptional in that they settle directly into the protective habitats provided by their anemone hosts. For those taxa that do not settle into a protective microhabitat, however, the chances of surviving on a coral reef at such a minute size may be limited. It is noteworthy that very small (maximum 9.1- 30 mm) gobies from the genus *Schindleria* live entirely pelagic lives, despite their close association with coral reefs, and retain juvenile traits rather than undergoing metamorphosis and settlement (Kon and Yoshino 2001, 2002; Watson and Walker 2004). Therefore, the size at which *Eviota* recruit to a coral reef likely represents the approximate minimum at which a “free, open-living” pelagic stage fish is able to settle onto a coral reef.

Overall, our study has shown that the three species of *Eviota* live on the ecological and evolutionary fringe of current life history possibilities for vertebrates. Nevertheless, these miniature species are simply an extension of, rather than a departure from, a life history continuum in vertebrate animals. Life history theory aims to provide evolutionary and ecological explanations for the variability in organism design and trait diversity. Given their extensive range of life history traits, coral reef fishes present us with an ecologically diverse assemblage of vertebrates in which to test basic life history theory.

Chapter 3: The importance of life histories in shaping patterns of energy allocation among fishes on coral reefs

In press in *Oecologia*

3.1. Introduction

Coral reef ecosystems contain very high average vertebrate densities (Sale 1978) and are often described as closed systems where nutrient and energy flow is tightly recycled among residents with limited inputs of energy or nutrients into the system (Sorokin 1990, Arias-Gonzalez et al. 1997; Harris 1999). Within these systems, fishes overwhelmingly dominate vertebrate assemblages and their contribution to trophic energy flow and secondary production in the form of protein biomass is substantial (e.g. Russ 1991; Dalzell 1996; Birkeland 1997; Allison and Ellis 2001). In addition, some reef fish groups are known to play vital functional roles in the maintenance of reef ecosystem function. This dependence extends to a point where their removal may cause catastrophic breakdowns in ecosystem operation (e.g. Hughes 1994; McClanahan and Muthiga 1998; McManus et al. 2000; Bellwood et al. 2003, 2004a). Despite this coherent and well-entrenched knowledge, however, we have yet to quantify the role of each of the components in an entire reef fish assemblage in a way that permits comprehensive estimates of total energy flow and the relative importance of each fish group to the functioning of coral reef ecosystems. Many questions remain, such as: how and what is the allocation of energy among reef fish taxonomic groups, what proportion of energy and biomass production is allocated to growth, and how do different life-history characteristics shape the accumulation, direction and flux of energy in reef ecosystems? The development of this knowledge is crucial in order to understand the forces that shape the organization of these ecosystems and to identify the major contributors to ecosystem function.

A critical (and often forgotten) observation is that ecosystem processes operate at temporal, as well as spatial scales (*cf.* Polis et al. 1996) making the detailing of life histories particularly relevant to understanding the dynamics and energetics of ecosystems. The contribution of different functional groups to ecosystem energy flow are intimately linked to the life history attributes and the abundance of each taxon within the community, their position in ecosystem food-webs, and their role in ecosystem processes (Schulze and Mooney 1994; Mooney et al. 1996). On structurally complex coral reef systems that host a wide range of ecological, behavioural and life history diversity, accurately quantifying all the members of a reef fish community requires the incorporation of both visual census and destructive sampling techniques (Norris and Parrish 1988; Ackerman and Bellwood 2000; Smith-Vaniz et al. in press). Because of the inadequacies of visual census techniques in surveying small cryptic fishes, our past concentration on larger conspicuous reef fish species has biased our perception of a typical reef faunal assemblage. As a result, our understanding of reef processes has been limited and system-wide evaluations are undermined by the failure to account for the missing, cryptic, components.

Due to the paucity of research on small cryptic coral reef fish assemblages, we have yet to progress from descriptive to process-oriented evaluations. However, recent findings have permitted, for the first time, a system-wide evaluation of all reef fish taxa. Although the static biomass of small cryptic fishes may be an order of magnitude lower than their larger counterparts, the productivity of small cryptic fishes through time may be significant. Their "live fast, die young" life histories characterized by high mortality rates, short life spans, rapid linear growth and high reproductive output (Kritzer 2002; Depczynski and Bellwood 2005a, 2006), coupled with high metabolic rates (Miller 1996; Ackerman and Bellwood 2000) argues for a disproportionately important role relative to their sizes. Furthermore, their diverse trophic links reflects their involvement in a number of trophic roles and pathways, in particular carnivory on benthic microfauna and the recycling of primary productivity through detrital pathways (Depczynski and Bellwood 2003; Wilson et al. 2003). Their high rates of mortality also suggest a strong trophic link to primary and secondary consumers in the coral reef food-chain (Kritzer 2002; Wilson 2004; Depczynski and Bellwood 2005a). Collectively, these traits suggest a dynamic role in reef ecosystems considerably beyond that suggested by their small static biomass. However, without placing cryptobenthic assemblages into context relative to the entire reef fish community, their contribution to reef ecosystem energetics remains unclear.

The fate of energy acquired by organisms through the ingestion of food is split into biomass production in the form of growth and reproduction, metabolic activities and waste (Willmer et al. 2005). Although waste and reproduction are difficult to measure in highly mobile aquatic animals, accurately quantifying the rate of growth and metabolism is now possible for many reef fish taxa. New life history information on a rapidly-expanding range of species (e.g. Choat and Robertson 2002; Hernaman and Munday 2005a; Depczynski and Bellwood in press) has recently made it possible to extend this information from the growth of single species to the biomass accumulation of a whole reef fish community. Equations which accurately scale body-size and temperature to metabolic rate have also now been developed for tropical fish species (Clarke and Johnston 1999). Together, these advances have provided the necessary prerequisites for a community-level study which accurately quantifies biomass productivity and energy distribution in a reef fish assemblage at a whole-reef scale.

In this paper, we hypothesise that reef fish taxa contribute widely varying amounts of energy to coral reef ecosystems and that these values are closely aligned to their various life history traits. Particular attention is focussed on the significance of small cryptic fishes as these have been previously overlooked but are likely to differ markedly in their contribution to energetic processes as a result of their vastly different sizes, metabolism and life history strategies. Our system-level quantification of biomass production provides the first quantitative measure of the biomass and energetic characteristics of a complete coral reef fish assemblage based on taxa and size-specific rates of individual growth.

3.2. Materials and methods

In total, 74 genera from 14 of the most abundant cryptic and non-cryptic coral reef fish families were censused in the summer of 2003 at Lizard Island in the northern Great Barrier Reef (14°40'S, 145° 27'E) (Appendix E). Lizard Island is a marine park where no recreational or commercial fishing is allowed. All censuses were conducted between Bird and South Islands and stratified by reef zone (reef base, slope, crest, flat and lagoon; detailed in chapter 1. For the cryptic assemblage (15 genera in 4 families), $0.8m^2$ clove-oil samples were used at 3 sites with 4 replicates in each site x reef zone combination giving a total of 60 samples (methods follow chapter 1). For the non-cryptic assemblage (59 genera in 10 families), underwater visual census (UVC) using 5 x 50m transects were conducted at 2 sites with 3 replicate censuses in each site x reef zone combination providing censuses covering a combined area of 7,500m^2. To complete the assemblage, abundance data acquired earlier for the families Apogonidae and Scaridae were incorporated into the main data set from two separate studies. The Apogonidae were visually censused in spring 1998 using 2 x 200m transects at 3 sites (approx 40 mins / t'sect) providing a total of 9 replicates at the base and slope (although censused, no individuals were recorded on the crest or flat), and 18 in the lagoon; a total area of 14,400m^2. The Scaridae were visually censused in the summer of 2003, using 4 replicate 10-min timed-swims (census area estimated following Bellwood and Wainwright 2001) at the slope, crest, flat and lagoon providing a combined total area of 9,400m^2. The choices of survey techniques reflect the most accurate and logistically feasible ways to census the abundance patterns of the various families (i.e. small cryptic benthic fishes using an anaesthetic [Depczynski and Bellwood 2004]; aggregated and sedentary Apogonidae using unit area UVC [Marnane 2001]; highly mobile or patchy Scaridae using timed swim UVC [Bellwood and Wainwright 2001]). All analyses and comparisons were performed at the genus level and were standardised to a unit area (m^2).

Following transformation of the data (Log_{10} [x + 1]) to satisfy the requirements of normality and homoscedascity, preliminary analyses were performed separately on the clove-oil (cryptic) and visually censused (non-cryptic) assemblages using MANOVAs in order to identify if the abundance and biomass of each genus could be pooled at the site level. To ensure that differences in body shape were accounted for in biomass calculations, length-weight relationships for biomass estimates for all genera were calculated using (in order of preference) direct weights from existing collections, unpublished data from the Great Barrier Reef, and from Kulbicki et al. (2005).

For both cryptic and non-cryptic assemblages, there were no significant differences among genera at the site level (cryptic abundance $F_{32, 84} = 0.831$, $p = 0.717$ and biomass $F_{32, 84} = 0.822$, $p = 0.729$: non-cryptic abundance $F_{28, 2} = 0.354$, $p = 0.896$ and biomass $F_{28, 2} = 8.822$, $p = 0.261$: Apogonidae abundance at base and slope $F_{6, 28} = 1.25$, $p = 0.31$ and in lagoon $F_{4, 30} = 2.01$, $p = 0.11$ and biomass at base and slope $F_{4, 30} = 1.15$, $p = 0.35$ and in lagoon $F_{6, 26} = 1.31$, $p = 0.29$) allowing abundances and biomass data to be pooled.

Statistical analyses comparing abundance (individuals m^{-2}), standing biomass (g), metabolism (O_2 mmol), growth (cm wk^{-1}) and biomass production (g d^{-1}) of cryptic versus non-cryptic patterns were calculated using derived equations (explained on the following pages) and analysed using non-parametric Mann-Whitney U tests as log10 ($x + 1$) transformed data did not meet assumptions for analyses. Seven-day estimates of somatic growth (cm) for each genus x size-class combination was multiplied by abundance counts, converted to mass using length-weight relationships, and presented as total biomass production g m^{-2} among reef fish families, size-classes and reef zones for maximum utility and ease of comparison.

Estimates of somatic growth

Weekly growth estimates were divided among genera using two categories:

1) Long-lived species with asymptotic growth

The projected growth of each individual censused was calculated using a derivation of the von Bertalanffy growth equation: $L_t = L_\infty (1 - e^{-k(t - t_0)})$. The derived equation (1) is presented as follows:

$$L_{t_{field+x}} = L_\infty (1 - e^{-k(T - t_0)}) \tag{1}$$

where $L_{t_{field+x}}$ is the growth (TL in cm) of an individual from time of census + x day(s); L_∞ is the theoretical asymptotic length; k is the growth curvature coefficient; t_0 is the theoretical age in days at length 0; and T is the total age of an individual x day(s) after census, calculated using the following equation:

$$T = t_{field + x} \tag{2}$$

where t_{field} = age at census date and $x = x^1$ / 365 d where x^1 = 7 days following census for this study. The equation to calculate t_{field} is:

$$t_{field} = \frac{1}{k} \ln \{[L_\infty - L_0] / [(1 - L') L_\infty)]\} \tag{3}$$

where L_0 = theoretical length in cm at t_0 and L' = proportion of theoretical asymptotic length that an individual has reached at time of census. The equations to calculate L_0 and L' are:

$$L_0 = L_\infty (1 - e^{kt_0}) \tag{4}$$

$$L' = L_{field} / L_\infty \tag{5}$$

Parameters (L_∞, k and t_0) of the von Bertalanffy growth function (VBGF) for each genus were calculated by taking the parameter means across as many Indo-Pacific species within each genus as possible. Species estimates were taken from (in order of preference) published literature (78%), private data collections (10%) and the FishBase web site (remaining 12%). Where no values of t_0 were found, these were constrained to zero as values of t_0 are invariably close to zero and t_0 holds little information of biological value (Kritzer et al. 2001; Grandcourt 2002). In the few instances where no growth parameters were available within an entire genus, the VBGF parameters of the closest genus-level sister-taxa were used based on published phylogenies (Tang et al. 1999; Craig et al. 2001; Thacker 2003; Bellwood et al. 2004b; Littlewood et al. 2004; Westneat and Alfaro 2005).

2) Short-lived species with linear growth

For taxa with linear growth patterns, weekly growth estimates were simply based on cm d^{-1} x 7 days. These were taken directly from the equation derived from a regression analysis (*y*-intercept constrained to zero) of the size at age data.

Estimates of metabolism

The metabolism of different families and size-classes were calculated to complement dynamic estimates of somatic growth in reef fish assemblages. Resting metabolic rate (RMR) was chosen as the most accurate measurement of metabolic rate (O_2 consumption) for comparisons among families because it is independent of their widely-varying activity levels, and field or actual metabolic rates are widely variable and impractical to measure. Estimated field rates in free-living organisms are commonly cited as being 2-7 times that of RMR (Johnston et al. 1991; Savage et al. 2004). Molar units of oxygen (mmol) were used as they are readily converted to either volumetric (1 mol oxygen gas occupies 22.4L) or energy units (1 mmol oxygen gas equals the use of 434 J). As such, they are useful estimates of metabolic rate for comparison among other taxa from different ecosystems. RMR per unit body weight (g h^{-1}) was estimated among families using the equation; $R_b = aM^b$

where R_b is mmol oxygen gas h^{-1}; a is the constant 0.0072 (recalculated from Clarke and Johnston 1999 for 26ºC [the mean annual sea temperature at Lizard Island), M is wet mass in grams and $b = 0.79$ (scaling exponent from Clarke and Johnston 1999).

3.3. Results

Ecosystem abundance, densities, standing biomass and metabolic rate

The clear trend among size-class distributions of abundance was one of rapidly decreasing densities with increasing size (Fig. 3.1). The 0-2.5cm size-class was by far the most common overall ($11.91 m^{-2}$ ± 3.31 SE and 77% of total assemblage) and dominated modal size-classes at all reef zones (Table 3.1). Although censusing was undertaken at the peak of the recruitment season, a division of individuals into cryptic and non-cryptic fishes indicated that 90% of the fishes in this smallest size-class belonged to cryptic families.

In total, 58,944 individuals were censused over a combined total area of 31.35 km^2 (Appendix E). Mean abundance m^{-2} indicated that small cryptic fishes were more than twice as abundant as their larger, more conspicuous counterparts (14.1 m^2 [± 3.1 SE] to 5.2 m^2 [± 0.4 SE] respectively; Mann-Whitney U test $z = 8.81$, $p < 0.0001$) (Fig. 3.2a) but were responsible for only a small fraction (< 3%; Mann-Whitney U test $z = 13.03$, $p < 0.0001$) of the standing total biomass (Fig. 3.3a).

Patterns of abundance clearly revealed the dominance of the Gobiidae followed by the Pomacentridae, Blenniidae, Labridae and Apogonidae (Fig. 3.2a). Mean abundance among reef zones showed highest densities at the base followed by the lagoon, slope, crest then flat (Table 3.1). Although the reef base supported the highest overall abundance, this zone was heavily populated by gobiids from the genus *Eviota* which constituted 83% of the reef base populations. With fewer *Eviota*, the lagoon, slope and crest are characterised by a diverse range of families. Maximum familial and genera representation was to be found on the slope (all 14 families and 52 of 74 genera) followed by the crest (13 and 51 respectively), lagoon (13 and 47) and base (10 and 33). By far the most taxa-depauperate zone was the reef flat (9 and 25). Unlike abundance, standing biomass patterns among reef zones showed the following trend: lagoon > crest > slope with the base and flat making the smallest contributions (Table 3.1).

With the exception of some small to medium-bodied families (e.g. Pomacentridae, Labridae and Apogonidae), oxygen (O_2) consumption in no way reflected patterns of abundance (Fig. 3.2a and b). Average O_2 consumption across all 14 families was calculated as 0.26 millimoles hr^{-1} m^{-2} with the abundant Pomacentridae utilising more than a third of the total (Fig. 3.2b). Other significant consumers included a number of medium to large-bodied species including the Acanthuridae, Labridae, Scaridae and Serranidae. Interestingly, the Gobiidae and, to a lesser degree, the Blenniidae had estimated oxygen consumption rates similar to many families of medium and large-body size families (e.g. Serranidae, Chaetodontidae, Siganidae and Pomacanthidae) despite their small body mass.

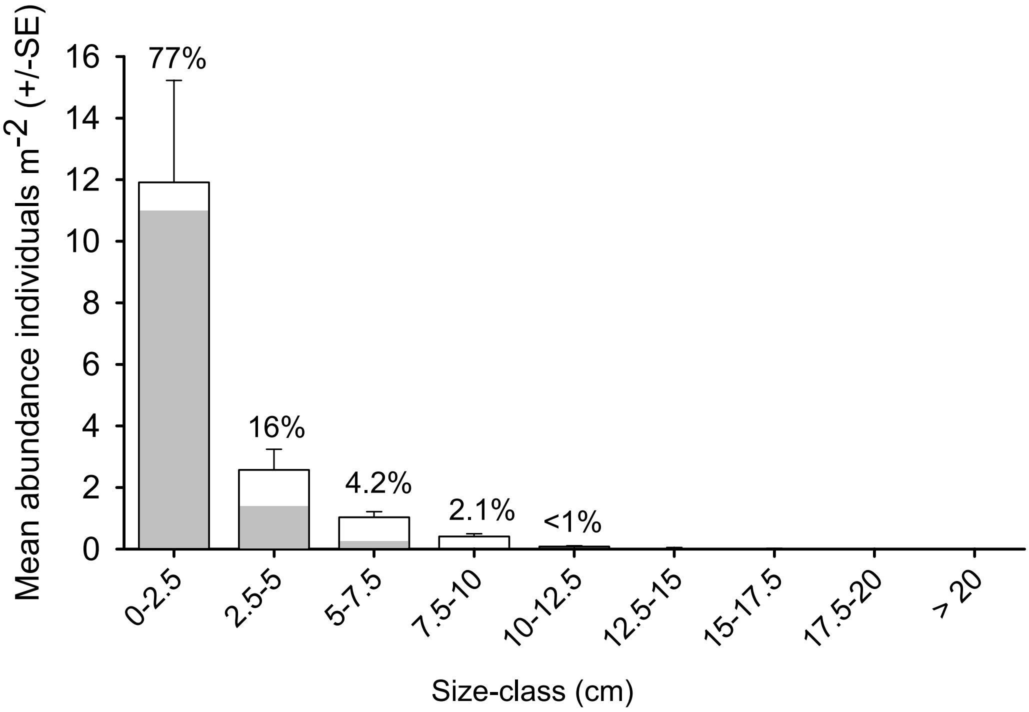


Fig. 3.1: Mean abundance of individuals m-2 (±SE) of different size-classes averaged across the entire reef. Standard errors represent variation among the five reef zones for each size-class. Within bars, cryptic family contributions are shown in grey, non-cryptic families in white. Proportional contribution of each size-class to the entire reef fish assemblage is shown above bars.

Table 3.1: Mean abundance, biomass m^{-2} (±SE) and modal size-class for each reef zone combined across all 14 families. Standard errors represent variation among the 14 family means for each reef zone. Numbers in **bold** denote the maximum among reef zones for each metric; in *italics* the minimum. Percentage relative contribution made by cryptic families for abundance and biomass is also shown. Note that "percentages from cryptic families" for the reef base do not take the family Scaridae into consideration which make up a significant portion of the standing biomass in other reef zones (see Fig. 3.3a).

	Abundance m^{-2} (±SE)	Percentage from cryptic families	Biomass g m^{-2} (±SE)	Percentage from cryptic families	Modal size-class
Base	**42.5 (± 7.2)**	**89.8**	*37.8 (*± 11.2)	**4.2**	0-2.5
Slope	17.7 (± 2.9)	61.9	75.6 (± 10.2)	0.8	0-2.5
Crest	17.1 (± 0.9)	*45.7*	121.0 (± 5.4)	1.1	0-2.5
Flat	*8.1 (± 1.3)*	46.6	38.0 (± 3.3)	*0.6*	0-2.5
Lagoon	19.5 (± 4)	**89.9**	**158.0 (**± 78.2)	1.6	0-2.5
Mean m^{-2}	**21.0 (± 5.7)**	**66.8**	**86.1 (± 23.6)**	**1.5**	**-**

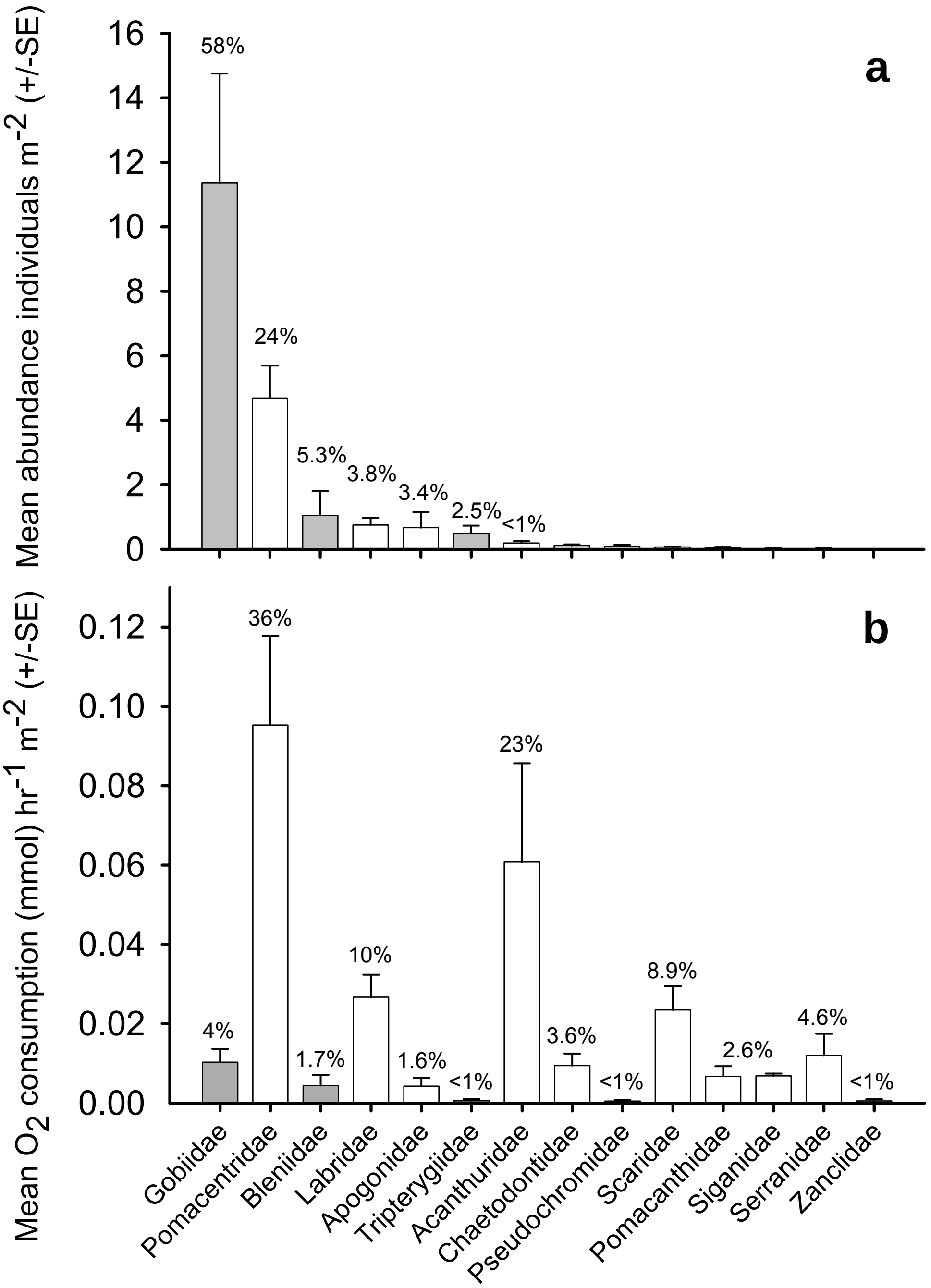


Fig. 3.2: **a** Mean abundance of individuals m^{-2} and **b** oxygen consumption (mmol) hr^{-1} m^{-2} of 14 families of coral reef fishes across all five reef zones (±SE). For conversion of millimoles to joules of energy multiply by 434. For millimoles to litres of oxygen multiply by 0.0224. Standard errors represent variation among the five reef zones for each family. Bars for cryptic families are in grey, non-cryptic families in white. Proportional contribution of each family to the entire reef fish assemblage is shown above bars.

Assemblage Standing Biomass vs. Weekly Biomass Productivity

Biomass estimates indicated that the family Acanthuridae contributed by far the most to standing biomass (39% of total) followed by the highly abundant medium-sized Pomacentridae (15%) and the larger Scaridae (14%) and Serranidae (11%) which all provided more than 10g per m^2 (Fig. 3.3a). Significant contributions were made by most other non-cryptic members of the reef fish assemblage with the exception of the Zanclidae. In comparison, standing biomass estimates for all cryptic families in the assemblage were insignificant.

Weekly growth estimates across all censused individuals was calculated at just over 6.3m and 18.3kg, equating to an average of 2.8cm and 2g among all families for each m^2 of reef area. Differences in mean weekly growth (cm m^{-2} and g m^{-2}) between the cryptic and non-cryptic communities were statistically significant (Mann-Whitney U test $z = -18.99$, $p < 0.0001$ (cm); $z = 17.58$, $p < 0.0001$(g)) and showed interesting patterns. Small cryptic fishes accounted for 87.9% of the total growth in length (cm), yet the corresponding growth in weight (g) was only 14%. Nevertheless, this is markedly higher than the < 3% they contribute to the total standing biomass.

Surprisingly considering their small body-size, some cryptic families contributed as much to weekly biomass productivity as many other seemingly abundant families that contain much larger-sized species. Ranked number one in standing biomass estimates, the Acanthuridae moved down from being the overwhelmingly dominant family (39% of total biomass) to fifth in biomass productivity (9.2%) (Figs 3.3a and b). The Serranidae likewise slipped from fourth (11%) to eighth (2.5%). In comparison, the Gobiidae moved up from tenth

(1.1%) to fourth place (9.7%). Both this family and the Blenniidae (1.7%) made significant and substantial contributions (> 0.02g wk^{-1} m^{-2}) that matched or superseded those of many iconic and abundant non-cryptic families. Thus the Gobiidae contributes more to biomass production than the Acanthuridae while the Blenniidae exceeds the contribution of the Chaetodontidae or Pomacanthidae (Fig. 3.3b). However, it was the medium-bodied and highly abundant Pomacentridae that provided the largest input into biomass production (0.57g m^{-2} ± 0.17 SE).

Reflecting their high densities, the Gobiidae also showed particularly striking patterns of projected weekly growth in length (mean 2.1cm m^{-2} ± 0.26 SE) which was an order of magnitude larger than for any other family (Fig. 3.4). Large-bodied families such as the Acanthuridae, Scaridae and Serranidae spend a large portion of their lives at an asymptotic size, exhibit significantly longer life spans and low overall densities. As a consequence, they contributed very little to growth accrual in length, although they still make substantial contributions to patterns of biomass accumulation.

Weekly growth in length and mass was concentrated at the bottom end in the 0-5 cm size-classes (96% and 34% of total respectively). Of this, small cryptic families accounted for a substantial 66% and 52% respectively. In spite of supporting 34% of all growth production, this less than 5cm size range represents just 0.05% of total standing biomass. The division of growth among reef zones indicated that reef fish growth was primarily concentrated at the base and lagoon (cm), and crest and lagoon (g) (Table 3.2). The contribution of small cryptic fishes to total fish assemblage growth in length averaged 84% among reef zones and was as high as 96% at the reef base. Cryptic families were also calculated to contribute significant amounts of biomass production at the reef base (50% of total biomass contribution) and lagoon (26%) where the highest densities of these small fishes reside. Overall, this cryptic contribution in biomass productivity stands in marked contrast to the static biomass contribution of these taxa.

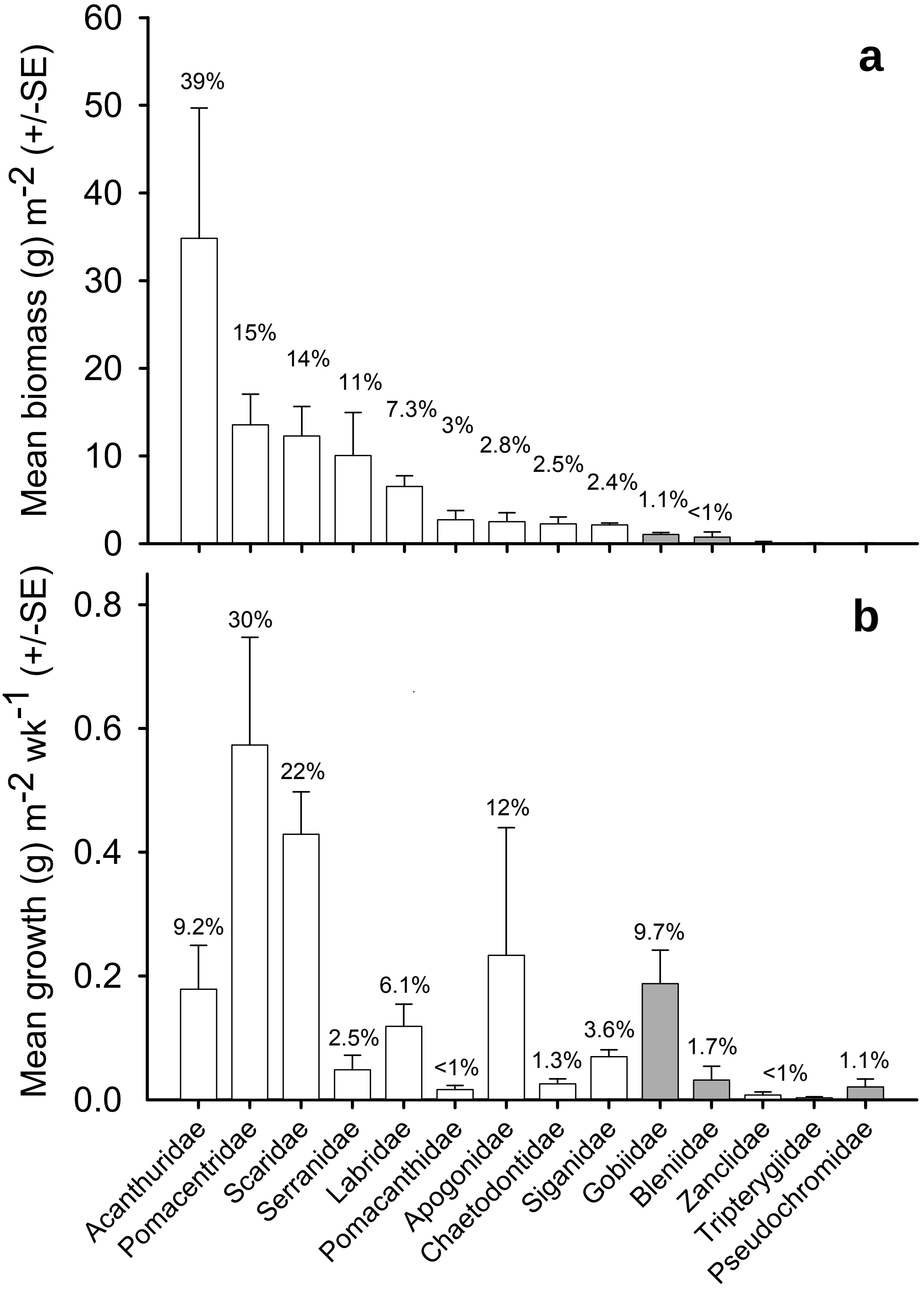


Fig 3.3: **a** Mean biomass (g) m^{-2} and **b** weekly growth (g) m^{-2} of 14 families of coral reef fishes across all five reef zones (±SE). Standard errors represent variation among the five reef zones for each family. Bars for cryptic families are in grey, non-cryptic families in white. Proportional contribution of each family to the entire reef fish assemblage is shown above bars.

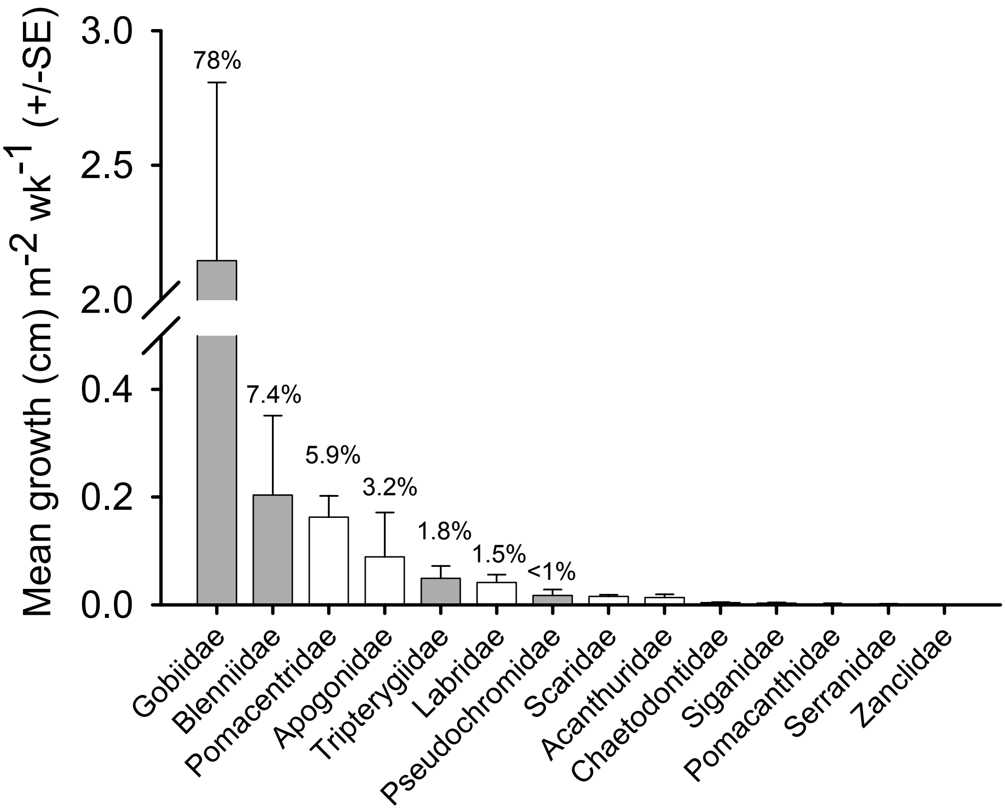


Fig 3.4: Mean weekly growth (cm) m^{-2} (±SE) of 14 families of coral reef fishes across all five reef zones. Standard errors represent variation among the five reef zones for each family. Bars for cryptic families are in grey, non-cryptic families in white. Proportional contribution of each family to the entire reef fish assemblage is shown above bars.

Table 3.2: Mean growth in mass (g) and length (cm) m^{-2} wk^{-1} (±SE) for each reef zone combined across all 14 families. Standard errors represent variation among the 14 family means for each reef zone. Numbers in **bold** denote the maximum among reef zones for each metric; in *italics* the minimum. Note that "percentages from cryptic families" for the reef base do not take the family Scaridae into consideration which make up a large portion of the growth biomass in other reef zones (see Fig. 3.3b).

	Growth (g) m^{-2} wk^{-1} (±SE)	Percentage from cryptic families	Growth (cm) m^{-2} wk^{-1} (±SE)	Percentage from cryptic families
Base	0.08 (± 0.03)	**50.3**	**0.37 (± 0.33)**	**96.1**
Slope	0.07 (± 0.02)	20.6	0.17 (± 0.14)	88.2
Crest	**0.18 (± 0.07)**	7.4	0.14 (± 0.07)	*72.3*
Flat	*0.07 (± 0.02)*	*4.5*	*0.08 (± 0.06)*	75.0
Lagoon	0.14 (± 0.04)	26.2	0.30 (± 0.19)	88.5
Mean m^{-2}	**0.11 (± 0.02)**	**21.8**	**0.21 (± 0.05)**	**84.0**

3.4. Discussion

Currently, there are few links between the life histories of marine organisms and their impact on ecosystem function. Ecosystem ecology, the link between the biological and the physical environment, is tightly centred around ecosystem energetics and nutrient fluxes with groups containing the largest biomass usually assumed to be the most influential (an implicit assumption of most modelling and correlative studies) (Stadler et al. 2004). The wide-spread view that larger-bodied taxonomic groups contribute more to ecosystem processes, especially energetics, is tied to a static picture of how ecosystems operate and is therefore insensitive to the temporal dynamics of individuals within a community. The results clearly reveal marked changes among reef fish families in the relative contributions of taxa to estimated standing biomass versus biomass production. These changes highlight the importance of incorporating taxa-specific life histories when assigning importance to ecosystem processes and offer insights into the mechanisms underlying the energetics and dynamics of coral reef communities. Size and standing biomass alone were not accurate indicators of the potential contribution of taxonomic groups to ecosystem-level processes. Rather, life history features played the biggest role, with exceptional densities and growth in small cryptic fish families providing collective growth potentials equal to or surpassing that of other abundant large-bodied families that are typically represented by individuals 1-3 orders of magnitude heavier.

There is now ample evidence across a range of ecosystems that ecosystem processes such as energy flow and nutrient cycling are heavily influenced by species composition, abundance and diversity (Kinzig et al. 2001; Tilman 2001; Loreau et al. 2002). If this is the case then the attributes of species are a very important component of how ecosystems function. Species differ in many ways, not least of which are their life cycle characteristics, trophic affiliations and inter-species relationships. For small fishes on coral reefs, predation is a constant and inescapable part of their entire life cycle and probably represents the difference between projected and realised growth within this study. For vertebrates, these small fishes may occupy a unique position in coral reef ecosystem food-webs. A study by Arias-Gonzalez and co-workers (1997) identified two primary and independent trophic cycles operating within coral reef food webs: a long detrital-based cycle, mainly through microbial chains, and a shorter, more direct route via predation which passes through the middle and top layers of food webs. The small cryptic reef fish community's dependence on detritus and its constituents as a major food source is well documented on the Great Barrier Reef (GBR) (Wilson et al. 2003; Depczynski and Bellwood 2003) and rates of predation on this group from larger fishes are projected to be high (Reavis 1997; Munday and Jones 1998; Kritzer 2002; Wilson 2004; Depczynski and Bellwood 2005a, in press). Given the high densities of small cryptic fishes, this community sits at the apex of the detrital chain and at the base of the predatory chain providing a potentially important trophic interface between the two disparate trophic pathways.

The degree of trophic inter-linkage is an important and integral factor in defining the energetic contribution of species to ecosystems (McCann et al. 1998; Pauly et al. 2000). Species with low or distant connections to other parts of ecosystem food chains are expected to contribute less to ecosystem energetics (Leveque 2003). Evidence suggesting strong trophic connections between small cryptic fish species and other coral reef organisms is compelling. We know that small cryptic fishes feed on a wide variety of food items encompassing all the major trophic modes (Depczynski and Bellwood 2003). Secondly, both otolith and field-based studies on these fishes have consistently indicated that its members suffer from very high rates of mortality (e.g. Kritzer 2002; Depczynski and Bellwood 2005a; Longnecker and Langston 2005), with most suggesting that predation is the primary mechanism (e.g. Reavis 1997; Wilson 2004; Hernaman and Munday 2005b). These species may thus be subject to exceptionally severe predation throughout life. To date, our best documented examples of the impact of predation on small coral reef fishes have come from quantifying its effects on juvenile fishes that have recently settled onto coral reefs from a former pelagic existence (e.g. Schmitt and Holbrook 1999; Webster 2002; Almany and Webster 2006). Although the mechanistic details remain controversial, these studies have found that post-settlement predatory processes are likely to play an important role in regulating community structure and prey populations (Holbrook and Schmitt 2002, 2003; Webster 2002; McCormick and Hoey 2004; Almany and Webster 2006). Predation also appears to be size-selective for smaller individuals (Sogard 1997; Brunton and Booth 2003; Hawn et al. 2005) and may make a significant contribution to ecosystem trophodynamics over the course of the breeding season (see Jones and McCormick 2002). Interestingly, our study over the summer recruitment season showed that 90% of the 0-2.5 cm size-class at Lizard Island was composed of small adult cryptic fishes rather than new recruits from non-cryptic families.

Currently, there is little direct evidence for predation on small cryptic fishes (but see Hiatt and Strasburg 1960; Sano et al. 1984; Norris and Parrish

1988). Rapid through-put rates leading to empty digestive tracts and advanced digestion of prey limit the ability of predator gut-content analyses to accurately identify prey species (Norris and Parrish 1988; Connell and Kingsford 1997; Beukers-Stewart and Jones 2004). Of those studies that have overcome these problems, most have concentrated on larger reef fish predators (almost exclusively Serranids) and found their diets to be dominated by fishes from the families Clupeidae, Apogonidae, Pomacentridae and Labridae with only minor contributions from cryptic families (Kingsford 1992: St John et al. 2001; Beukers-Stewart and Jones 2004). This opens up the possibility that either their susceptibility to fish predation is exceptionally low or that there is an important intermediate trophic level of small piscivores to account for their high rates of mortality. Currently, all lines of evidence support their status as readily utilised and ubiquitous prey items (e.g. their size, life history designs, the community composition and distribution, trophic organization and the predatory characteristics of coral reefs). Small to medium piscivorous predatory fishes are a prominent feature of the coral reef landscape at Lizard Island (*cf.* Stewart and Jones 2001; McCormick and Hoey 2004; Almany and Webster 2006). The family Pseudochromidae and many species belonging to the nocturnally-foraging Apogonidae for example, are well known piscivores on small fishes (Vivien 1975; Sano et al. 1984; Stewart and Jones 2001; Marnane and Bellwood 2002; McCormick and Holmes 2006). Ranging in body-size from 1.5-15cm, their reliance on new recruits as a food source is at best seasonal, as most of these juvenile prey species quickly grow larger than these predators themselves. Seasonal and ontogenetic prey switching are common-place in marine ecosystems

(Trenkel et al. 2005) and have also previously been recorded in Lizard Island piscivores (St John 1999; Stewart and Jones 2001; Beukers-Stewart and Jones 2004). So it seems realistic to propose that small cryptic species may be essential prey items for piscivorous predators, particularly over the six-month period where there is little apparent recruitment input on the GBR (Russell et al. 1977; Doherty 1991; *cf.* Robertson 1998), and that these piscivores are themselves tightly inter-linked to higher trophic levels through predation, thus providing a continuum of energy flow along coral reef food-webs.

Additional sources of life history-related energy input into reef ecosystems comes from the rapid turnover and sub-annual life cycles of many abundant small cryptic species (Kritzer 2002; Depczynski and Bellwood 2005a, in press; Wilson 2004; Longnecker and Langston 2005). All available evidence suggests that cryptic species are exclusively benthic egg-layers on reef substrata with egg production and recruitment throughout the year being essential in these species to avoid extinction. Rich in protein, occurrences of reef fish egg predation on coral reefs from con-specifics (Itzkowitz 1990), small predatory fish (Hiatt and Strasburg 1960; Sano et al. 1984; Haley and Muller 2002) and invertebrate species (Itzkowitz and Koch 1991) have all been recorded and cryptobenthic fish eggs may provide an additional winter food source for many coral reef species.

It has been long suspected that small cryptic reef fishes play an important role in reef processes although the context of this speculation has always been qualitative in nature (e.g. Hiatt and Strasburg 1960; Allen et al. 1992; Randall et al. 1997; Greenfield 2003; but see Ackerman and Bellwood 2000). Quantification of relative biomass production within a complete reef fish assemblage has now revealed the highly productive nature of many reef fish families, particularly small cryptic taxa, helping identify the key underlying mechanisms and the pathways along which their contribution towards the energy flux of coral reef ecosystems flows. There is little doubt that life histories can leave a strong imprint on how ecosystems operate through time. Looking at the community structure and growth within each component species, we reveal for the first time the dynamic nature of energy flow within reef fish communities and questioned previously long-held assumptions. This includes the impression that: (1) the highest abundances of fishes are to be found in habitat-complex reef slopes, crests and lagoons rather than reef bases; (2) smaller size-classes during recruitment seasons are primarily composed of the recently recruited young; and (3) body-size and static biomass reflects relative ecosystem importance. All three now appear in doubt and need re-evaluation.

Reef fishes play important functional roles in coral reef ecosystem processes but the magnitude and relative importance of different groups to these processes has remained largely unexplored. Our challenge now is to understand what, how much, and under what conditions various groups contribute to key ecosystem processes and energy budgets. Narrowing the gap from projected to realised growth is an integral part of this endeavour.

Concluding Discussion

The sheer diversity, ubiquity and abundance of small cryptic fish faunas make defining their significance and contribution to reef ecosystems a fundamental prerequisite to understanding the importance of reef fishes in coral reef ecosystem function. This study contrasts the ecology and life histories of small cryptic fishes with that of the larger, conspicuous reef fish species. The results provided a firm quantitative basis for a long-held assumption, that small cryptic fishes are an integral, important, yet qualitatively different component of coral reef ecosystems (e.g. Hiatt and Strasburg 1960; Allen et al. 1992; Randall et al. 1997; Greenfield 2003).

Previously, the only work that defined the significance of an entire small cryptic fish assemblage was undertaken in one habitat at a single reef location with the primary aim of quantifying the abundance, diversity and biomass of this local fauna (Ackerman and Bellwood 2000). The first objective of the present study, therefore, was to extend this preliminary work to incorporate the physical environment so that the intensity and location of energy flow within small cryptic fish assemblages could be determined at a reef-wide scale (Chapter 1). Using measurements of abundance, diversity, species composition and size-structure among gradients of wave energy, reef depth and microhabitat type, small cryptic fishes showed remarkably strong levels of community structure for all features examined. The overriding influence of wave energy suggested that any potential role of small reef fishes in ecosystem processes would be exerted most strongly in calmer reef areas.

The community level approach employed in the present study has highlighted an important inconsistency in the role of microhabitats in defining the spatial structure of small cryptic assemblages. Traditionally, microhabitats have featured strongly as a key determinant of the spatial distributions of small cryptic species (e.g. Luckhurst and Luckhurst 1978; Clarke 1989; Kuwamura et al. 1994; Munday et al. 1997; Munday 2000, 2002; Hobbs and Munday 2004). However, this may not be the general pattern exhibited by small cryptic species. It appears that a focus on highly specialised species may have inadvertently fostered a misconception that microhabitats play the leading role in shaping the distribution of small cryptic fish communities. In the present study, many abundant species displayed no strong requirement for a particular microhabitat type or reef zone. These two appear to mark the ends of a spectrum of habitat variation from coral-dwelling specialists to broad-ranging habitat generalists, with both shaped by wave activity and microhabitat availability. Ultimately, what has become clear from this work is that the community structures of small cryptic coral reef fishes are equally as complex as those recorded for larger coral reef fishes.

The life history characteristics of coral reef fishes are currently ill-defined (Caley 1998; Choat and Robertson 2002), particularly for small cryptic species (Wilson 2004; Hernaman and Munday 2005a; Longnecker and Langston 2005). Given that body-size is such an important life history correlate, the in-depth investigation of the complete life cycles of some of the smallest (and most abundant) species has brought to light the extraordinarily broad range and evolutionary versatility of coral reef fish life history strategies (Chapter 2). Comparative analyses among taxa illustrated the extreme plasticity of some life history traits (i.e. growth, timing of maturation, frequency of reproduction and longevity), while emphasising the inflexible nature of others (i.e. pelagic larval durations and the timing of maturation in *Eviota sigillata*), regardless of the severe time constraints imposed on these small species.

The diversity of species, ecological niches and body-sizes in coral reef fishes, coupled with the sensitive chronological schedule of life cycle events recorded in otoliths, presents us with a model system in which to test the importance of ecological relationships in the evolution of vertebrates. Small cryptic fishes have revealed the latest in a string of recent exceptional biological records that extend beyond fish taxa to vertebrates in general. Various small coral reef fish species now provide the earliest maturing (Kon and Yoshino 2001), smallest (Watson and Walker 2004) and shortest-living (Chapter 2) of all vertebrates. Given that we have barely scratched the surface of coral reef fish demographics, to have uncovered such an interesting array of life history features suggests that testing prevailing evolutionary and ecological theory within these fishes offers a promising new research area.

Of all the features of small cryptic reef fish communities recorded in the present study, the quantification of biomass productivity probably best exemplifies the significance of small cryptic fishes in coral reef processes (Chapter 3). Small cryptic fishes underpin a significant proportion of the energy flowing through the Lizard Island coral reef fish community. The ecology and life history features of these fishes directly shape the nature of this contribution with high average densities, rapid growth and turnover rates, and close trophic linkages within food-webs. In close concordance with these findings, two recent single-species studies on small cryptic fishes (the goby *Istigobius decoratus* and the blenny *Salarias patzneri*) have also argued strongly for the inclusion of life history features when quantifying the energetic contribution of fishes on coral reefs (Kritzer 2002; Wilson 2004). Clearly, the life histories of small cryptic species are markedly different to those recorded in larger species. How we quantify and rank the significance of taxonomic groups in ecosystem energetics is fundamental to our understanding of their role in these processes. By taking taxon-specific life histories into consideration, this study has explicitly demonstrated the need to incorporate life history features when evaluating the contribution of taxa to ecosystem energetics.

The study of small cryptic coral reef fishes offers novel opportunities to many different areas of scientific research. Population ecologists and geneticists are likely to find the rapid turnover of new generations within such short time frames very appealing. Also, given that we share the same vertebrate heritage as fishes, and that *Eviota* life spans are comparable to those of wild *Drosophila*, human ageing researchers have recently shown a great deal of interest in *Eviota* physiology and genetics. So far, the main focus of this new area of research has been on the extension of life spans through the identification and manipulation of recessive mutations in ageing-related genes that are thought to be responsible for the very short life spans of some animals (Cohen et al. 2004; Wood et al. 2004). It is interesting to think of coral reef fishes contributing to such distant and diverse scientific disciplines.

Concluding remarks

In order to understand how our ecosystems function, a necessary first step is to develop an adequate understanding of the relative contribution of the various species and communities that underlie ecosystem processes. It is clear that small cryptic coral reef fish communities have traditionally been overlooked and under-valued within this context. As a whole, this study has emphasised the significance of this small cryptic community and the fact that any evaluation cannot be made without considering their ecology and life history. Hidden within the ecological and life history details of each component species lies the real source of the community's diversity and unique contribution to the flux and fate of energy on coral reef ecosystems.

The information presented herein extends our knowledge of patterns and processes on coral reefs and underlines the rich ecological and life history diversity of coral reef fishes. It is hoped that this study will help to provide a foundation from which to address more process-oriented questions in coral reef ecology and open up new lines of investigation aimed at evaluating the significance of smaller coral reef taxa in ecosystem processes. There is still a lot to learn from these small fishes but, we can now say with some confidence, that small cryptic coral reef fishes are ecologically important and do indeed make a significant contribution to coral reef ecosystem processes. Overall, it is clear that although these fishes may be small and hard to see, they are not to be overlooked.

References

Ackerman JL, Bellwood DR (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. Mar Ecol Prog Ser 206: 227-237

Ackerman JL, Bellwood DR (2002) Comparative efficiency of clove oil vs rotenone for sampling tropical reef fish assemblages. J Fish Biol 60: 893-901

Ackerman JL, Bellwood DR, Brown JH (2004) The contribution of small individuals to density body-size relationships: examination of energetic equivalence in reef fishes. Oecologia 139: 568-571

Aday DD, Wahl DH, Philipp DP (2003) Assessing population-specific and environmental influences on bluegill life histories: a common garden approach. Ecology 84: 3370- 3375

Allen LG, Bouvier LS, Jensen RE (1992) Abundance, diversity, and seasonality of cryptic fishes and their contribution to a temperate fish assemblage off Santa Catalina Island, California. Bull Southern Calif Acad Sci 91: 55-69

Allison EH, Ellis F (2001) The livelihoods approach and management of small scale fisheries. Mar Policy 25: 377-388

Almany GR, Webster MS (2006) The predation gauntlet: early post-settlement mortality in reef fishes. Coral Reefs 25: 19-22

Anderson JT (1988) A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J Northwest Atl Fish Sci 8: 55-66

Arendt JD (1997) Adaptive intrinsic growth rates: an integration across taxa. Q Rev Biol 72: 149-177

Arias-Gonzalez JE, Delesalle B, Salvat B, Galzin R (1997) Trophic functioning of the Tiahura sector, Moorea Island, French Polynesia. Coral reefs 16: 231-246

Begon M, Harper JL, Townsend CR (1996) *Ecology; individuals, populations and communities*, 3rd edn. Blackwell Science Ltd, Carlton

Bellwood DR, Wainwright PC (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. Coral Reefs 20: 139-150

Bellwood DR, Wainwright PC, Fulton CJ, Hoey A (2002) Assembly rules and functional groups at global biogeographical scales. Funct Ecol 16: 557-562

Bellwood DR, Hoey A, Choat H (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol Lett 6: 281-285

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004a) Confronting the coral reef crisis. Nature 429: 827-833

Bellwood DR, van Herwerden L, Konow N (2004b) Evolution and biogeography of marine angelfishes (Pisces: Pomacanthidae). Mol Phylogenet Evol 33: 140-155

Bellwood DR, Hoey AS, Ackerman JL, Depczynski M (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Glob Change Biol 12: 1587-1594

Berumen ML (2005) The importance of juveniles in modelling growth: butterfly fish at Lizard Island. Environ Biol Fishes 72: 409-413

Beukers-Stewart BD, Jones GP (2004) The influence of prey abundance on the feeding of two piscivorous species of coral reef fish. J Exp Mar Biol Ecol 299: 155-184

Birkeland C (1997) Symbiosis, fisheries and economic development on coral reefs. Trends Ecol Evol 12: 364-367

Blackburn TM, Gaston KJ (1999) The relation between animal abundance and body size: a review of the mechanisms. Adv Ecol Res 28: 181-210

Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationships between body size and some life history parameters. Oecologia 37: 257-272

Bonhomme F, Planes S (2000) Some evolutionary arguments about what maintains the pelagic interval in reef fishes. Environ Biol Fish 59: 365-383

Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. Bull Mar Sci 32: 269-276

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85: 1771-1789

Brunton BJ, Booth DJ (2003) Density- and size-dependent mortality of a settling coral-reef damselfish (*Pomacentrus moluccensis* Bleeker). Oecologia 137: 377-384

Calder WA (1984) *Size, function, and life history*. Harvard University Press, Cambridge

Caley MJ (1998) Age-specific mortality rates in reef fishes: Evidence and implications. Aust J Ecol 23: 241-245.

Caley JM, St John J (1996) Refuge availability structures assemblages of tropical reef fishes. J Anim Ecol 65: 414-428

Charnov EL (1993) *Life history invariants: some explorations of symmetryin evolutionary ecology*. Oxford University Press, Oxford

Choat JH, Axe LM (1996) Growth and longevity in acanthurid fishes; and analysis of otolith increments. Mar Ecol Prog Ser 134: 15-26

Choat JH, Robertson DR (2002) Age-based studies. In: Sale PF (ed) *Coral reef fishes - dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, pp 57-80

Churchfield S (1996) Ecology of very small terrestrial mammals. Symp Zool Soc Lond 69: 259-276

Clarke RD (1989) Population fluctuation, competition and microhabitat distribution of two species of tube blennies, *Acanthemblemaria* (Teleostei: Chaenopsidae). Bull Mar Sci 44: 1174-1185

Clarke BT (1996) Small size in amphibians – its ecological and evolutionary implications. Symp Zool Soci Lond 69: 201-224

Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 68: 893-905

Claro R, Garcia-Arteaga JP (2001) Growth patterns of fishes of the Cuban shelf. In: Claro R, Lindeman KC, Parenti LR (eds.) *Ecology of the marine fishes of Cuba.* Smithsonian Institution Press, Washington, pp 149-178

Cohen HY, Miller C, Bitterman KJ, Wall NR, Hekking B, Kessler B, Howitz KT, Gorospe M, de Cabo R, Sinclair DA (2004) Calorie restriction promotes mammalian cell survival by inducing the SITR1 deacetylase. Science 305: 390-392

Cohen JE, Jonsson T, Carpenter SR (2003) Ecological community description using the food web, species abundance and body size. Proc Nat Acad Sci 100: 1781-1786

Connell SD, Kingsford MJ (1997) The utility of descriptive information for assessing the impact of coral reef piscivores on their prey. Proc 8th Int. Coral Reef Symp. 1: 999-1004

Craig MT, Pondella DJ, Franck JPC, Hafner JC (2001) On the Status of the Serranid Fish Genus *Epinephelus*: Evidence for Paraphyly Based upon 16S rDNA Sequence. Mol Phylogenet Evol 19: 121-130

Dalzell P (1996) Catch rates, selectivity and yields of reef fishing. In: Polunin NVC, Roberts CM (eds) *Reef Fisheries*. Chapman and Hall, London pp 161-192

Delbono O (2003) Neutral control of ageing skeletal muscle. Ageing Cell 2: 21-29

Denny MW (1988) *Biology and the mechanics of the wave-swept environment*. Princeton University Press, Princeton

Denny M, Wethey D (2001) Physical processes that generate patterns in marine communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine Community Ecology*. Sinauer Assoc Inc, Sunderland, pp 3-37

Depczynski M, Bellwood DR (2003) The role of cryptobenthic reef fishes in coral reef trophodynamics. Mar Ecol Prog Ser 256: 183-191

Depczynski M, Bellwood DR (2004) Microhabitat utilization patterns in cryptobenthic coral reef fish communities. Mar Biol 145: 455-463

Depczynski M, Bellwood DR (2005a) Shortest recorded vertebrate lifespan found in a coral reef fish. Current Biol 15 (8): R288-R289

Depczynski M, Bellwood DR (2005b) Spatial variability in community structure of small cryptic coral reef fishes. Mar Ecol Prog Ser 303: 283-293

Depczynski M, Bellwood DR (in press) Extremes, plasticity and invariance in vertebrate life histories: insights from coral reef fishes. Ecology 87: 3119-3127

Dineson ZD (1983) Patterns in the distribution of soft corals across the central Great Barrier Reef. Coral Reefs 1: 229-236

Doherty PJ (1991) Spatial and temporal patterns in recruitment. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, Sydney pp 261-293

Done TJ (1983) Coral zonation: its nature and significance. In: Barnes DJ (ed) *Perspectives on coral reefs*. Aust Instit Mar Sci, Townsville, pp 107-147

Edgar GJ, Barrett NS, Morton AJ (2004) Biases associated with the use of underwater visual census techniques to quantify the density and size structure of fish populations. J Exp Mar Bio Ecol: 308: 269-290

Ernest MSK (2005) Body size, energy use, and community structure of small mammals. Ecology 86: 1407-1413

Fowler AJ, Doherty PJ (1992) Validation of annual growth increments in the otoliths of two species of damselfishes from the Southern Great Barrier Reef. Mar Freshw Res 43: 1057-1068

Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian reef. J Exp Mar Biol Ecol 224: 1-30

Fulton CJ, Bellwood DR, Wainwright PC (2001) The relationship between swimming ability and habitat use in wrasses (Labridae). Mar Biol 139: 25-33

Fulton CJ, Bellwood DR (2002) Ontogenetic habitat use in labrid fishes: an ecomorphological perspective. Mar Ecol Prog Ser 236: 255-262

Fulton CJ, Bellwood DR (2004) Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. Mar Biol 144: 429-437

Fulton CJ, Bellwood DR (2005) Wave-induced water motion and the functional implications for coral reef fish assemblages. Limnol Oceanogr 50: 255 264

Gaillard J-M, Yoccoz NG, Lebreton J-D, Bonenfont C, Devillard S, Loison A, Pontier D, Allaine D (2005) Generation time: A reliable metric to measure life-history variation among mammalian populations. Am Nat 166: 119-123

Gaston KJ (2000) Global patterns in biodiversity. Nature 405: 220-227

Gladstone W (1994) Lek-like spawning, parental care and mating periodicity of the triggerfish *Pseudobalistes flavimarginatus* (Balistidae). Environ Biol Fishes 39: 249-257

Goncalves EJ, Almada VC (1998) A comparative study of territoriality in intertidal and subtidal blennioids (Teleostei, Blennioidei). Environ Biol Fish 51: 257-264

Goncalves EJ, Barbosa M, Cabral HN, Henriques M (2002) Ontogenetic shifts in patterns of microhabitat utilization in the small-headed clingfish, *Apletodon dentatus* (Gobiesocidae). Environ Biol Fish 63: 333-339

Grandcourt EM (2002) Demographic characteristics of exploited reef fish from the Seychelles: a preliminary study. Mar Freshw Res 53: 123-130

Greenfield DW (2003) A survey of the small reef fishes of Kane'ohe Bay O'ahu, Hawaiian Islands. Pac Sci 57: 45-76

Greenfield DW, Johnson RK (1981) The blennioid fishes of Belize and Honduras, central America, with comments on their systematics, ecology, and distribution (Blenniidae, Chaenopsidae, Labrisomidae, Tripterygiidae). Fieldiana Zool, New Series 8: 1-106

Greenfield DW, Johnson RK (1990a) Community structure of western Caribbean blennioid fishes. Copeia 1990: 433-448

Greenfield DW, Johnson RK (1990b) Assemblage structure and habitat associations of western Caribbean gobies (Teleostei: Gobiidae). Copeia 1999: 251-266

Greenfield DW, Johnson RK (1999) Assemblage structure and habitat associations of western Caribbean gobies (Teleostei: Gobiidae). Copeia 1999: 251-261

Greenwood JJD, Gregory RD, Harris RD, Morris PA, Yalden DW (1996) Relations between abundance, body size and species number in British birds and mammals. Phil Trans Roy Soc Lond B 351: 265-278

Gust N, Choat JH, McCormick MI (2001) Spatial variability in reef fish distribution, abundance, size and biomass: a multi-scale analysis. Mar Ecol Prog Ser 214: 237-251

Haley MP, Muller CR (2002) Territorial behaviour of beaugregory damselfish (*Stegastes leucogaster*) in response to egg predators. J Exp Mar Biol Ecol 273: 151-159

Hansen JA, Klumpp DW, Alongi DM, Dayton PK, Riddle MJ (1992) Detrital pathways in a coral reef lagoon. Mar Biol 113: 363-372

Harris GP (1999) This is not the end of limnology (or of science): the world may well be a lot simpler than we think. Freshw Biol 42: 689-706

Hawn AT, Martin GB, Sandin SA, Hare JA (2005) Early juvenile mortality in the coral reef fish *Chromis cyanea* (Pomacentridae): the growth-mortality revisited. Bull Mar Sci 77: 309-318

Helfman, GS, Collette BB, Facey DE (1997) *The diversity of fishes*. Blackwell Science Inc, Massachusetts, USA

Hendry AP, Day T, Cooper AB (2001) Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. Am Nat 157: 387-407

Hernaman V, Munday PL (2005a) Life history characteristics of coral reef gobies: I. Growth and lifespan. Mar Ecol Prog Ser 290: 207-221

Hernaman V, Munday PL (2005b) Life history characteristics of coral reef gobies: II. Mortality rate, mating system and timing of maturation. Mar Ecol Prog Ser 290: 223-237

Hiatt RW, Strasburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol Monogr 30: 65-127

Hobbs JPA, Munday PL (2004) Intraspecific competition controls spatial distribution and social organization of the coral-dwelling goby *Gobiobon histrio* Mar Ecol Prog Ser 278: 253-259

Hoenig JM (1983) Empirical use of longevity data to estimate mortality rates. Fish Bull (US) 82: 898-903

Holbrook, SJ, Schmitt RJ (2002) Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecology 83: 2855-2868

Holbrook, SJ, Schmitt RJ (2003) Spatial and temporal mortality in of newly settled damselfish: patterns, causes and co-variation with settlement. Oecologia 135: 532-541

Horner-Devine CM, Carney KM, Brendan J, Bohannan M (2004) An ecological perspective on bacterial biodiversity. Proc Roy Soc B 271: 113-122

Hughes T (1994) Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. Science 265: 1547-1551

Itzkowitz M (1990) Heterospecific intruders, territorial defence and reproductive successin the beaugregory damselfish. J Exp Mar Biol Ecol 140: 49-59

Itzkowitz M, Koch T (1991) Relationship between damselfish egg loss and brittlestars. Bull Mar Sci 48: 164-166

Job SD, Bellwood DR (2000) Light sensitivity in larval fishes: Implications for vertical zonation in the pelagic zone. Limnol and Oceanogr 45: 362-371

Johnston IA, Clarke A, Ward P (1991) Temperature and metabolic rate in sedentary fish from the Antarctic, North Sea and Indo-West Pacific Ocean. Mar Biol 109: 191-195

Jones GP, McCormick MI (2002) Numerical and energetic processes in the ecology of coral reef fishes. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem.* Academic Press, San Diego pp 221-238

Kingsford MJ (1992) Spatial and temporal variation in predation on reef fishes by the coral trout (*Plectropomus leopardus*, Serranidae). Coral Reefs 11: 193-198

Kinzig AP, Pacala SW, Tilman D (eds) (2001) *The functional consequences of biodiversity*. Princeton University Press, Princeton

Kon T, Yoshino T (2001) Extremely early maturity found in Okinawan goiioid fishes. Ichthyol Res 49: 224-228

Kon T, Yoshino T (2002) Diversity and evolution of life histories of gobioid fishes from the viewpoint of heterochrony. Mar Freshw Res 53: 377-402

Koop K, Larkum AWD (1987) Deposition of organic material in a coral reef lagoon, One Tree Island, Great Barrier Reef. Est Coast Shelf Sci 25: 1-9

Kritzer JP (2002) Stock structure, mortality and growth of the decorated goby, *Istigobius decoratus* (Gobiidae), at Lizard Island, Great Barrier Reef. Environ Biol Fish 63: 211-216

Kritzer JP, Davies CR, Mapstone BD (2001) Characterizing fish populations: effects of sample size and population structure on the precision of demographic parameter estimates. Can J Fish Aquat Sci 58: 1557-1568

Kulbicki M, Guillemot N, Amand M (2005) A general approach to length-weight relationships for New Caledonian lagoon fishes. Cybium 29: 235-252

Kuwamura T, Yogo Y, Nakashima Y (1994) Population dynamics of goby *Paragobiodon echinocephalus* and host coral *Stylophora pistillata.* Mar Ecol Prog Ser 103: 17-23

Lachner EA, Karnella SJ (1980) Fishes of the Indo-Pacific genus Eviota with descriptions of eight new species (Teleostei: Gobiidae). Smithson Contrib Zool 315: 1-127

La Mesa G, Micalizzi M, Giaccone G, Vacchi M (2004) Cryptobenthic fishes of the Ciclopi Islands marine reserve (central Mediterranean Sea): assemblage composition, structure and relations with habitat features. Mar Biol 145: 233-242

Leaper R, Raffaelli D (1999) Defining the abundance body-size constraint space: data from a real food web. Ecol Lett 2: 191-199

Leis JM (1991) The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp 183-230

Leveque C (2003) *Ecology, from ecosystem to biosphere*. Science Publishers Inc, Plymouth

Littlewood TJ, McDonald SM, Gill AC, Cribb TH (2004) Molecular phylogenetics of *Chaetodon* and the Chaetodontidae (Teleostei: Perciformes) with reference to morphology. Zootaxa 779: 1-20

Longenecker K, Langston R (2005) Life history of the Hawaiian blackhead triplefin, *Enneapterygius atriceps* (Blennioidei, Tripterygiidae). Environ Biol Fish 73: 243-251

Loreau M, Naeem S, Inchausti P (eds) (2002) *Biodiversity and ecosystem functioning*. Oxford University Press, Oxford

Luckhurst BE, Luckhurst K (1978) Diurnal space utilisation in coral reef fish communities. Mar Biol 49: 325-332

Makarieva AM, Gorshkov VG, Li BL (2004) Body size, energy consumption and allometric scaling: a new dimension in the diversity-stability debate. Ecol Complexity 1: 139-175

Marnane MJ (2001) The trophic role of Cardinalfishes (Family Apogonidae) on coral reefs. PhD thesis, James Cook University, Townsville, Australia

Marnane MJ, Bellwood DR (2002) Diet and nocturnal foraging in Cardinalfishes (Apogonidae) at One Tree Reef, Great Barrier Reef, Australia. Mar Ecol Prog Ser 231: 261-268

May RM (1978) The dynamics and diversity of insect faunas. In: Mound LA, Walcoff N (eds) *Diversity of insect faunas, Symposia of the Royal Entomological Society of London*. Blackwell Scientific Publications, Oxford, pp 188-294

McCann K, Hastings A, Huxel GR (1998) Weak trophic interactions and the balance of nature. Nature 395: 794-798

McClanahan TR, Muthiga NA (1998) An ecological shift in a remote coral atoll of Belize over 25 years. Environ Conserv 25: 122-130

McCormick MI, Hoey AS (2004) Larval growth history determines juvenile growth and survival in a tropical marine fish. Oikos 106: 22-242

McCormick MI, Holmes TH (2006) Prey experience of predation influences mortality rates at settlement in a coral reef fish, *Pomacentrus amboinensis*. J Fish Biol 68: 969-974

McManus JW, Menez LAB, Kesner-Reyes KN, Vergara SG, Ablan MC (2000) Coral reef fishing and coral-algal phase-shifts: implications for global reef status. ICES J Mar Sci 57: 572-578

McQuaid CD, Branch GM (1985) Trophic structure of rocky intertidal communities: Response to wave action and implications for energy flow. Mar Ecol Prog Ser 22: 153-161

Meekan MG, Ackerman Jl, Wellington GM (2001) Demography and age structure of coral reef damselfishes in the tropical eastern Pacific Ocean. Mar Ecol Prog Ser 212: 223-232

Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol Monogr 46: 355-393

Miller PJ (1984) The tokology of gobioid fishes. In: Potts GW, Wootton RJ (eds) *Fish reproduction: Strategies and tactics*. Academic Press, London, pp 119-153

Miller PJ (1996) The functional ecology of small fish: some opportunities and consequences. Symposium Zoological Society London 69: 175-199

Mooney HA, Cushman J, Medina E, Sala OE, Schulze ED (eds) (1996) Functional roles of biodiversity: a global perspective. John Wiley and Sons Ltd, Brisbane

Munday PL (2000) Interactions between habitat use and patterns of abundance in coral-dwelling fishes of the genus *Gobiodon*. Environ Biol Fishes 58: 355-369

Munday Pl (2001) Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology 82 (8): 2177-2189

Munday PL (2002) Does habitat availability determine geographical-scale abundances of coral-dwelling fishes? Coral Reefs 21: 105-116

Munday PL, Jones GP, Caley MJ (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. Mar Ecol Prog Ser 152: 227-239

Munday PL, Jones GP (1998) The ecological implications of small body size among coral-reef fishes. Oceanogr Mar Biol Ann Rev 36: 373-411

Munday PL, Wilson SK (1998) Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. J Fish Biol 51: 931-938

Munday PL, Pierce SJ, Jones GP, Larson HK (2002) Habitat use, social organization and reproductive biology of the seawhip goby, *Bryaninops yongei*. Mar Freshw Res 53: 757-768

Nee S (2004) More than meets the eye. Nature 429: 804-805

Nee S, Celograve N, West SA, Grafen A (2005) The illusion of invariant quantities in life histories. Science 309: 1236-1239

Neff BD (2003) Decisions about parental care in response to perceived paternity. Nature 422: 716-719

Ninio R, Meekan MG (2002) Spatial patterns in benthic communities and the dynamics of a mosaic ecosystem on the Great Barrier Reef, Australia. Coral Reefs 21: 95-103

Norris JE, Parrish JD (1988) Predator-prey relationships among fishes in pristine coral reef communities. Proc 6th Int Coral Reef Symp 2: 107-113

Pauly D (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperatures in 175 fish stocks. J Cons Int Explor Mer 39: 175-192

Pauly D, Christensen V, Walters C (2000) Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J Mar Sci 57: 697-706

Peters RH (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge, UK

Polis GA, Holt RD, Menge BA, Winemiller KO (1996) Time, space, and life history: influences on food webs. In: Polis GA, Winemiller KO (eds) *Food webs; integration of patterns and dynamics.* Chapman and Hall, New York pp 435-460

Prochazka K (1998) Spatial and trophic partitioning in cryptic fish communities of shallow subtidal reefs in False Bay, South Africa. Environ Biol Fish 51: 201-220

Purcell SW, Bellwood DR (2001) Spatial patterns of epilithic algal and detrital resources on a windward coral reef. Coral Reefs 20: 117-125

Purvis A, Harvey PH (1996) Miniature mammals: life-history strategies and macroevolution. Symp Zool Soc Lond 69: 159-174

Randall JE, Allen GR, Steene RC (eds) (1997) *Fishes of the Great Barrier Reef and Coral Sea*. Crawford House Publishing Pty Ltd, Bathurst

Reavis RH (1997) The natural history of a monogamous coral-reef fish, *Valenciennea strigata* (Gobiidae):1. Abundance, growth, survival and predation. Environ Biol Fish 49: 239-246

Reznick D (1983) The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology 64: 862-873

Reznick D, Endler JA (1982) The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution 36: 160-177

Reznick D, Bryant MJ, Roff D, Ghalambor CK, Ghalambor DE (2004) Effect of extrinsic mortality on the evolution of senescence in guppies. Nature 431: 1095-1099

Ricklefs RE, Finch CE (1995) *Ageing: a natural history*. WH Freeman and Co, Oxford

Robertson DR (1998) Implications of body size for interspecific interactions and assemblage structure organization among coral-reef fishes. Aust J Ecol 23: 252-257

Robertson DR, Peterson CW, Brawn JD (1990) Lunar reproductive cycles of benthic-brooding reef fishes: Reflections of larval biology or adult biology. Ecol Monogr 60: 311-329

Roff DA (1983) An allocation model of growth and reproduction in fish. Can J Fish Aquat Sci 40: 1395-1404

Roff DA (1992) *The evolution of life histories*. Chapman and Hall, London

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

Russ GR (1991) Coral reef fisheries: Effects and yields. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego pp 601-635

Russell BC, Anderson GRV, Talbot FH (1977) Seasonality and recruitment in coral reef fishes. Aust J Mar Freshw Res 28: 521-528

Sale PF (1978) Reef fishes and other vertebrates: a comparison of social structures. In: Lighter FJ (ed) *Contrasts in behaviour*. John Wiley, New York pp 314-346

Sale PF (1991) The ecology of fishes on coral reefs. Academic Press, San Diego

Sambilay VCJ (1990) Interrelationships between swimming speed, caudal fin aspect ratio and body length of fishes. Fishbyte 8: 16-20

Sano M, Shimizu M, Nose Y (1984) Food habits of teleostean reef fishes in Okinawa Island, southern Japan. Univ Mus Univ Tokyo, Bull No 25: 1-128

Savage VM, Gillooly JF, Woodruff WH, West GB, Allen AP, Enquist BJ, Brown JH (2004) The predominance of quarter-power scaling in biology. Funct Ecol 18: 257-282

Schmidt PD (1984) Marking growth increments in otoliths of larval and juvenile fish by immersion in tetracycline to examine the rate of increment formation. Fish Bull (US) 82: 237-242.

Schmitt RJ, Holbrook SJ (1999) Mortality of juvenile damselfish: implications for assessing processes that determine abundance. Ecology 80: 35-50

Schmidt-Nielsen (1997) *Animal physiology: adaptation and environment*, 5th edn. Cambridge University Press, Cambridge

Schulze ED, Mooney HA (eds) (1994) Biodiversity and ecosystem function. Springer-Verlag, Berlin

Searcy SP, Sponaugle S (2000) Variable larval growth in a coral reef fish. Mar Ecol Prog Ser 206: 213-226

Shashar N, Kinane S, Jokiel PL, Patterson MR (1996) Hydromechanical boundary layers over a coral reef. J Exp Mar Biol Ecol 199: 17-28

Smith-Vaniz WF, Jelks HL, Rocha LA (in press) Relevance of cryptic fishes in biodiversity assessments: a case study at Buck Island Reef National Monument, St Croix. Bull Mar Sci

Sogard S (1997) Size-selective mortality in the juvenile stage of teleost fishes: A review. Bull Mar Sci 60: 1129-1157

Sorokin IY (1990) Aspects of trophic relations, productivity and energy balance on coral-reef ecosystems. In: Dubinski Z (ed) *Ecosystems of the world: Coral reefs*, vol 25, Elsevier, Amsterdam pp 101-409

Sponaugle S, Cowen RK (1994) Larval durations and recruitment patterns of two Caribbean gobies (Gobiidae): contrasting early life histories in demersal spawners. Mar Biol 120: 133-143

Stadler B, Muhlenberg E, Michalzik B (2004) The ecology driving nutrient fluxes in forests. In: Weisser WW, Siemann E (eds) Insects and ecosystem function. Springer-Verlag, Berlin pp 213-239

Stearns SC (1992) *The evolution of life histories*. Oxford University Press, New York

Stewart BD, Jones GP (2001) Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. Mar Biol 138: 383-397

St John J (1999) Ontogenetic changes in the diet of a large coral reef grouper *Plectropomus leopardus* (Serranidae): patterns in taxa, size and habitat of prey. Mar Ecol Prog Ser 180: 233-246

St John J, Russ GR, Brown IW (2001) The diet of the large coral reef serranid *Plectropomus leopardus* in two fishing zones on the Great Barrier Reef, Australia. Fish Bull 99: 180-192

Sunobe T, Nakazono A (1987) Embryonic development and larvae of genus *Eviota* (Pisces: Gobiidae) I. *Eviota abax* and *E. storthynx*. J Fac Agric Kyushu Univ 31: 287-295

Sunobe T, Nakazono A (1995) Embryonic development and larvae of genus *Eviota* (Pisces: Gobiidae) II. Description of seven species. Nat Hist Res 3: 153-159

Sunobe T (1998) Reproductive behavior in six species of *Eviota* (Gobiidae) in aquaria. Ichthyol Res 45: 409-412

Syms C (1995) Multi-scale analysis of habitat association in a guild of blennioid fishes. Mar Ecol Prog Ser 125:31-43

Syms C, Jones GP (2004) Habitat structure, disturbance and the composition of sand- dwelling goby assemblages in a coral reef lagoon. Mar Ecol Prog Ser 268: 221-230

Tang KL, Berendzen PB, Wiley EO, Morrissey JF, Winterbottom R, Johnson DG (1999) The phylogenetic relationships of the suborder Acanthuroidei (Teleostei: Perciformes). Based on molecular and morphological evidence. Mol Phylogenet Evol 11: 415-425

Taru M, Sunobe T (2000) Notes on reproductive ecology of the gobiid fish *Eviota abax* at Kominato, Jpn Bull Mar Sci 66: 507-512

Thacker CE (2003) Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidei). Mol Phylogenet Evol 26: 354-368

Thresher RE (1984) *Reproduction in reef fishes*. TFH Publications, Neptune City

Tilman D (2001) Functional diversity. In: Levin SA (ed) *Encyclopedia of biodiversity*, vol 2. Academic Press, San Diego pp 109-120

Toms JD, Lesperance ML (2003) Piecewise regression: a tool for identifying ecological thresholds. Ecology 84: 2034-2041

Townsend KA, Tibbetts IR (2000) Biomass and distribution of herbivorous blennies in the southern Great Barrier Reef. J Fish Biol 56: 774-791

Trenkel VM, Pinnegar JK, Dawson WA, du Buit MH, Tidd AN (2005) Spatial and temporal structure of predator-prey relationships in the Celtic Sea fish community. Mar Ecol Prog Ser 299: 257-268

Vivien ML (1975) Place of apogonid fish in the food webs of a Malagasy coral reef. Micronesica 11: 185-196

Vogel S (1994) *Life in moving fluids: the physical biology of flow*, 2nd edn. Princeton University Press, Princeton

Watson W, Walker HJ Jr (2004) The world’s smallest vertebrate, *Schindleria brevipinguis*, a new paedomorphic species in the family Schindleriidae (Perciformes: Gobioidei). Rec Aust Mus 56: 139-142

Webster MS (2002) Role of predators in the early post-settlement demography of coral-reef fishes. Oecologia 131: 52-60

Webster MS, Hixon MA (2000) Mechanisms and individual consequences of intraspecific competition in a coral-reef fish. Mar Ecol Prog Ser 196: 187-194

West G (1990) Methods of assessing ovarian development in fishes: a review. Aust J Mar Freshw Res 41: 199-222

Westneat MW, Alfaro ME (2005) Phylogenetic relationships and evolutionary history of the reef fish family Labridae. Mol Phylogenet Evol 36: 370-390

Williams D McB (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs 1: 35-43

Williams GC (1957) Pleiotropy, natural selection and the evolution of senescence. Evolution 11: 398-411

Williams D McB (1991) Patterns and processes in the distribution of coral reef fishes. In: *The ecology of fishes on coral reefs*. Sale PF (ed). Academic Press, San Diego, pp. 437-474

Willis TJ (2001) Visual census methods underestimate density and diversity of cryptic reef fishes. J Fish Biol 59: 1408-1411

Willis TJ, Anderson MJ (2003) Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. Mar Ecol Prog Ser 257: 209-221

Willmer P, Stone G, Johnston I (eds) (2005) *Environmental physiology of animals*. 2nd edition Blackwell Publishing, Carlton

Wilson S (2001) Multiscale habitat associations of detrivorous blennies (Blenniidae: Salariini). Coral Reefs 20: 245-251

Wilson SK (2004) Growth, mortality and turnover rates of a small detritivorous fish. Mar Ecol Progr Ser 284: 253-259

Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanogr Mar Biol Ann Rev 41: 279-309

Wilson DT, McCormick MI (1999) Microstructure of settlement-marks in the otoliths of tropical reef fishes. Mar Biol 134: 29-41

Wood JG, Rogina B, Lavu S, Howitz K, Helfand SL, Tatar M, Sinclair D (2004) Sirtuin activators mimic calorie restriction and delay ageing in metazoans. Nature 430: 686-689

Wootton RJ (1990) *Ecology of teleost fishes*. Chapman and Hall, London

Winterbottom R, Emery AR (1981) A new genus and two new species of gobiid fishes (Perciformes) from the Chagos Archipelago, Central Indian Ocean. Environ Biol Fish 6: 139-149

Wu TY (1977) Introduction to the scaling of aquatic locomotion. In: Pedley TJ (ed) *Scale effects in animal locomotion*. Academic Press, London, pp 203-232

Appendix A

List of the 111 species plus 3 *Eviota* species included in Fig. 3.3, their maximum age (in years and months), maximum recorded lengths (mm) and source.

No.	Family	Species	Tmax in years	Tmax in months	Max length (mm)	Reference
1	Acanthuriidae	*Acanthurus auranticavus*	30	360	235	Choat, J. H., and D. R. Robertson. 2002
2	Acanthuriidae	*Acanthurus bahianus*	31	372	189	Choat, J. H., and D. R. Robertson. 2002
3	Acanthuriidae	*Acanthurus blochii*	35	420	276	Choat, J. H., and D. R. Robertson. 2002
4	Acanthuriidae	*Acanthurus chirugus*	13	156	200	Choat, J. H., and D. R. Robertson. 2002
5	Acanthuriidae	*Acanthurus coeruleus*	37	444	193	Choat, J. H., and D. R. Robertson. 2002
6	Acanthuriidae	*Acanthurus dussumieri*	28	336	308	Choat, J. H., and D. R. Robertson. 2002
7	Acanthuriidae	*Acanthurus lineatus*	45	540	206	Choat, J. H., and L. M. Axe. 1996
8	Acanthuriidae	*Acanthurus mata*	23	276	383	Choat, J. H., and D. R. Robertson. 2002
9	Acanthuriidae	*Acanthurus nigricans*	34	408	143	Choat, J. H., and D. R. Robertson. 2002
10	Acanthuriidae	*Acanthurus nigrofuscus*	16	192	120	Choat, J. H., and D. R. Robertson. 2002
11	Acanthuriidae	*Acanthurus olivaceus*	33	396	248	Choat, J. H., and L. M. Axe. 1996
12	Acanthuriidae	*Acanthurus pyroferus*	28	336	143	Choat, J. H., and D. R. Robertson. 2002
13	Acanthuriidae	*Acanthurus xanthopterus*	34	408	426	Choat, J. H., and D. R. Robertson. 2002
14	Acanthuriidae	*Ctenochaetus striatus*	35	420	197	Choat, J. H., and L. M. Axe. 1996
15	Acanthuriidae	*Naso annulatus*	23	276	626	Choat, J. H., and D. R. Robertson. 2002
16	Acanthuriidae	*Naso brachycentron*	31	372	434	Choat, J. H., and D. R. Robertson. 2002
17	Acanthuriidae	*Naso brevirostris*	22	264	330	Choat, J. H., and L. M. Axe. 1996
18	Acanthuriidae	*Naso hexacanthus*	44	528	534	Choat, J. H., and L. M. Axe. 1996
19	Acanthuriidae	*Naso lituratus*	39	468	211	Choat, J. H., and D. R. Robertson. 2002
20	Acanthuriidae	*Naso tuberosus*	23	276	457	Choat, J. H., and L. M. Axe. 1996
21	Acanthuriidae	*Naso unicornis*	30	360	457	Choat, J. H., and L. M. Axe. 1996
22	Acanthuriidae	*Naso vlamingii*	46	552	387	Choat, J. H., and L. M. Axe. 1996
23	Acanthuriidae	*Prionurus maculatus*	70	840	447	Choat, J. H., and L. M. Axe. 1996
24	Acanthuriidae	*Zebrasoma scopas*	34	408	157	Choat, J. H., and L. M. Axe. 1996
25	Acanthuriidae	*Zebrasoma veliferum*	27	324	208	Choat, J. H., and D. R. Robertson. 2002
26	Blenniidae	*Salarias patzneri*	340	4080	59	Wilson, S. K. 2004.
27	Chaetodontidae	*Chaetodon auriga*	6	72	168	Berumen, M. L. unpublished data
28	Chaetodontidae	*Chaetodon baronessa*	16	192	121	Berumen, M. L. 2005.
29	Chaetodontidae	*Chaetodon citrinellus*	11	132	118	Berumen, M. L. 2005.
30	Chaetodontidae	*Chaetodon lineolatus*	8	96	246	Berumen, M. L. unpublished data
31	Chaetodontidae	*Chaetodon lunulatus*	17	204	127	Berumen, M. L. unpublished data
32	Chaetodontidae	*Chaetodon melannotus*	24	288	174	Berumen, M. L. unpublished data
33	Chaetodontidae	*Chaetodon ornatissimus*	15	180	173	Berumen, M. L. unpublished data
34	Chaetodontidae	*Chaetodon trifascialis*	12	144	143	Berumen, M. L. 2005.
35	Chaetodontidae	*Chaetodon vagabundus*	17	204	161	Berumen, M. L. unpublished data
36	Chaetodontidae	*Chelmon rostratus*	14	168	180	Berumen, M. L. unpublished data
37	Gobiidae	*Amblygobius bynoensis*	1.03	12.36	98	Hernaman, V. and P. L. Munday. 2005.
38	Gobiidae	*Amblygobius phalaena*	1.13	13.56	105	Hernaman, V. and P. L. Munday. 2005.
39	Gobiidae	*Asterropteryx semipunctatus*	1.25	15	56	Hernaman, V. and P. L. Munday. 2005.
40	Gobiidae	*Bathygobius coalitus*	0.76	9.12	68	Shafer, D. J. 2000.
41	Gobiidae	*Eviota melasma*	0.27	3.24	27	Present study
42	Gobiidae	*Eviota queenslandica*	0.27	3.24	26	Present study
43	Gobiidae	*Eviota sigillata*	0.16	1.92	18	Present study
44	Gobiidae	*Gobiodon histrio*	>4	48	52	Munday, P. L. 2001.
45	Gobiidae	*Istigobius decoratus*	0.73	8.76	80	Kritzer, J. P. 2002a.
46	Gobiidae	*Istigobius goldmanni*	1.03	12.36	64	Hernaman, V. and P. L. Munday. 2005.
47	Gobiidae	*Valenciennea muralis*	0.99	11.88	116	Hernaman, V. and P. L. Munday. 2005.
48	Gobiidae	*Valenciennea strigata*	2	24	145	Reavis, R. H. 1997.
49	Haemulidae	*Haemulon plumieri*	13	156	640	Manooch, C. S., and C. A. Barans. 1982.
50	Holocentridae	*Myripristis amaena*	14	168	187	Dee, A. J., and R. L. Radtke. 1989.
51	Labridae	*Choerodon venustus*	10	120	601	Platten, J. R., et al. 2002.
52	Labridae	*Pseudocheilinops ataenia*	2.7	32.4	34	Hubble, M. 2003.
53	Labridae	*Pseudocheilinus hexataenia*	1.65	19.8	47	Hubble, M. 2003.
54	Labridae	*Pseudocheilinus evanidus*	1.25	15	54	Hubble, M. 2003.
55	Labridae	*Halichoeres melanurus*	2	24	90	Hubble, M. 2003.
56	Labridae	*Bodianus mesothorax*	23	276	130	Hubble, M. 2003.
57	Labridae	*Bodianus axillaris*	16	192	134	Hubble, M. 2003.
58	Labridae	*Choerodon fasciatus*	10	120	171	Hubble, M. 2003.
59	Labridae	*Cheilinus fasciatus*	15	180	195	Hubble, M. 2003.
60	Labridae	*Epibulus insidiator*	16	192	230	Hubble, M. 2003.
61	Labridae	*Hemigymnus melapterus*	7	84	230	Hubble, M. 2003.
62	Lethrinidae	*Lethrinus miniatus*	21	252	472	Williams, D. McB., et al. 2003.
63	Lutjanidae	*Lutjanus carponotatus*	17	204	350	Kritzer, J. P. 2002b.
64	Lutjanidae	*Lutjanus adetti*	24	288	305	Newman, S. J., et al. 1996.

65	Lutjanidae	*Lutjanus quinquelineatus*	31	372	237	Newman, S. J., et al. 1996.
66	Pomacanthidae	*Centropyge bicolor*	13	156	130	Aldenhoven, J. M. 1986.
67	Pomacanthidae	*Pomacanthus imperator*	16	192	296	Chung, K. N., and Y. S. Woo. 1999.
68	Pomacentridae	*Pomacentrus moluccensis*	9	108	59	Fowler, A. J., and P. J. Doherty. 1992.
69	Pomacentridae	*Pomacentrus wardi*	10	120	81	Fowler, A. J., and P. J. Doherty. 1992.
70	Pomacentridae	*Stegastes acapulcoensis*	23	276	140	Meekan, M. G., et al. 2001.
71	Pomacentridae	*Stegastes altus*	13	156	120	Kohda, M. A. 1996.
72	Pomacentridae	*Stegastes arcifrons*	27	324	120	Meekan, M. G., et al. 2001.
73	Pomacentridae	*Stegastes flavilatus*	13	156	110	Meekan, M. G., et al. 2001.
74	Pomacentridae	*Stegastes fuscus*	15	180	110	Schwanborn, S. H. L., and B. P. Ferreira. 2002.
75	Pomacentridae	*Stegastes leucorus beebei*	19	228	105	Meekan, M. G., et al. 2001.
76	Pomacentridae	*Stegastes rectifraenum*	11	132	120	Meekan, M. G., et al. 2001.
77	Priacanthidae	*Priacanthus tayenus*	2	24	290	Ingles, J., and D. Pauly. 1984.
78	Scaridae	*Bolbometopon muricatum*	33	396	694	Choat, J. H., and D. R. Robertson. 2002
79	Scaridae	*Cetoscarus bicolor*	21	252	421	Choat, J. H., and D. R. Robertson. 2002
80	Scaridae	*Chlorurus gibbus*	12	144	500	Choat, J. H., et al. 1996
81	Scaridae	*Chlorurus microrhinos*	15	180	430	Choat, J. H., and D. R. Robertson. 2002
82	Scaridae	*Chlorurus sordidus*	10	120	250	Choat, J. H., et al. 1996
83	Scaridae	*Hipposcarus longiceps*	12	144	350	Choat, J. H., and D. R. Robertson. 2002
84	Scaridae	*Scarus altipinnis*	13	156	377	Choat, J. H., and D. R. Robertson. 2002
85	Scaridae	*Scarus chameleon*	6	72	231	Choat, J. H., and D. R. Robertson. 2002
86	Scaridae	*Scarus frenatus*	20	240	290	Choat, J. H., et al. 1996
87	Scaridae	*Scarus iserti*	8	96	117	Choat, J. H., and D. R. Robertson. 2002
88	Scaridae	*Scarus niger*	19	228	260	Choat, J. H., et al. 1996
89	Scaridae	*Scarus pscittacus*	5	60	190	Choat, J. H., et al. 1996
90	Scaridae	*Scarus rivulatus*	8	96	300	Choat, J. H., et al. 1996
91	Scaridae	*Scarus schlegeli*	8	96	240	Choat, J. H., et al. 1996
92	Scaridae	*Sparisoma atomarium*	3	36	101	Choat, J. H., and D. R. Robertson. 2002
93	Scaridae	*Sparisoma aurofrenatum*	7	84	178	Choat, J. H., and D. R. Robertson. 2002
94	Scaridae	*Sparisoma chrysopterum*	5	60	258	Choat, J. H., and D. R. Robertson. 2002
95	Scaridae	*Sparisoma rubripinne*	7	84	238	Choat, J. H., and D. R. Robertson. 2002
96	Scaridae	*Sparisoma strigatum*	10	120	252	Choat, J. H., and D. R. Robertson. 2002
97	Scaridae	*Sparisoma viride*	9	108	379	Choat, J. H. et al. 2003.
98	Serranidae	*Aethaloperca rogaa*	32	384	449	Mosse, J. W. 2001.
99	Serranidae	*Anyperodon leucogramicus*	25	300	512	Mosse, J. W. 2001.
100	Serranidae	*Cephalopholis argus*	26	312	385	Mosse, J. W. 2001.
101	Serranidae	*Cephalopholis cyanostigma*	46	552	320	Mosse, J. W. 2001.
102	Serranidae	*Cephalopholis miniatus*	35	420	442	Mosse, J. W. 2001.
103	Serranidae	*Cephalopholis panamensis*	14	168	291	Craig, M. T., et al. 1999.
104	Serranidae	*Epinephelus fuscoguttatus*	30	360	880	Mosse, J. W. 2001.
105	Serranidae	*Epinephelus guttatus*	18	216	475	Sadovy, Y., et al. 1992.
106	Serranidae	*Epinephelus labriformis*	31	372	370	Craig, M. T., et al. 1999.
107	Serranidae	*Epinephelus polyphekadion*	37	444	613	Mosse, J. W. 2001.
108	Serranidae	*Plectropomus aerolatus*	15	180	633	Mosse, J. W. 2001.
109	Serranidae	*Plectropomus laevis*	11	132	880	Mosse, J. W. 2001.
110	Serranidae	*Plectropomus leopardus*	14	168	600	Ferreira, B. P., and G. R. Russ. 1994.
111	Serranidae	*Plectropomus maculatus*	12	144	580	Ferreira, B. P., and G. R. Russ. 1994.
112	Serranidae	*Variola louti*	7	84	415	Mosse, J. W. 2001.
113	Sparidae	*Pagrus pagrus*	18	216	733	Potts, J. C., and C. S. Manooch. 2002.
114	Tripterygiidae	*Enneapterygius longiceps*	0.32	3.84	26	Longenecker, K., and R. Langston. 2005.

Appendix B

List of the pelagic larval durations (PLDs) of 361 coral reef fish species and their sources.

No.	Family	Genus	Mean PLD	Reference
1	Acanthuridae	*Acanthurus nigrofuscus*	31	Wilson, D. T., and M. I. McCormick. 1999.
2	Acanthuridae	*Acanthurus olivaceus*	60.8	Wilson, D. T., and M. I. McCormick. 1999.
3	Acanthuridae	*Acanthurus sp. 1*	60	Wilson, D. T., and M. I. McCormick. 1999.
4	Acanthuridae	*Acanthurus sp. 2*	62	Wilson, D. T., and M. I. McCormick. 1999.
5	Acanthuridae	*Acanthurus sp. 3*	46	Wilson, D. T., and M. I. McCormick. 1999.
6	Acanthuridae	*Ctenochaetus binotatus*	57	Wilson, D. T., and M. I. McCormick. 1999.
7	Acanthuridae	*Ctenochaetus striatus*	57	Wilson, D. T., and M. I. McCormick. 1999.
8	Acanthuridae	*Naso brevirostris*	90.8	Wilson, D. T., and M. I. McCormick. 1999.
9	Acanthuridae	*Naso hexacanthus*	91.2	Wilson, D. T., and M. I. McCormick. 1999.
10	Acanthuridae	*Naso sp.*	84	Brothers, E. B., et al. 1983.
11	Acanthuridae	*Naso unicornis*	71	Wilson, D. T., and M. I. McCormick. 1999.
12	Acanthuridae	*Zebrasoma scopas*	59.8	Wilson, D. T., and M. I. McCormick. 1999.
13	Apogonidae	*Apogon cyanosoma*	18.2	Brothers, E. B., et al. 1983.
14	Apogonidae	*Apogon doederlieni*	22.6	Brothers, E. B., et al. 1983.
15	Apogonidae	*Cheilodipterus quinquelineata*	23.1	Brothers, E. B., et al. 1983.
16	Blenniidae	*Petroscrites fallax*	21	Brothers, E. B., et al. 1983.
17	Blenniidae	*Petroscrites mitratus*	24.5	Brothers, E. B., et al. 1983.
18	Chaetodontidae	*Chaetodon auriga*	48	Wilson, D. T., and M. I. McCormick. 1999.
19	Chaetodontidae	*Chaetodon baronessa*	33	Wilson, D. T., and M. I. McCormick. 1999.
20	Chaetodontidae	*Chaetodon plebius*	39	Brothers, E. B., et al. 1983.
21	Chaetodontidae	*Chaetodon plebius*	45.2	Fowler, A. J. 1989.
22	Chaetodontidae	*Chaetodon rainfordi*	35	Brothers, E. B., et al. 1983.
23	Chaetodontidae	*Chaetodon rainfordi*	27.8	Fowler, A. J. 1989.
24	Chaetodontidae	*Chelmon rostratus*	25.5	Brothers, E. B., et al. 1983.
25	Gobiidae	*Amblygobius phalaena*	19	Bay, L. K., et al. in press
26	Gobiidae	*Amblygobius rainfordi*	40.3	Brothers, E. B., et al. 1983.
27	Gobiidae	*Fusigobius glaucofraenum*	26.8	Sponaugle, S., and R. K. Cowen. 1994.
28	Gobiidae	*Eviota melasma*	26.2	Present study
29	Gobiidae	*Eviota sigillata*	24.7	Present study
30	Gobiidae	*Eviota queenslandica*	24.2	Present study
31	Gobiidae	*Gnatholepis thompsoni*	70	Sponaugle, S., and R. K. Cowen. 1994.
32	Gobiidae	*Gobiodon sp. A*	22	Brothers, E. B., et al. 1983.
33	Gobiidae	*Gobiodon sp. B*	29.8	Brothers, E. B., et al. 1983.
34	Gobiidae	*Gobiodon sp. C*	40	Brothers, E. B., et al. 1983.
35	Gobiidae	*Paragobiodon echinocephalus*	36	Brothers, E. B., et al. 1983.
36	Gobiidae	*Paragobiodon lacunicola*	31	Brothers, E. B., et al. 1983.
37	Gobiidae	*Paragobiodon melanosoma*	42.3	Brothers, E. B., et al. 1983.
38	Labridae	*Anampses chrysocephalus*	29.5	Victor, B. C. 1986.
39	Labridae	*Anampses cuvier*	44.5	Victor, B. C. 1986.
40	Labridae	*Anampses twistii*	28.8	Victor, B. C. 1986.
41	Labridae	*Bodianus axillaris*	23.5	Victor, B. C. 1986.
42	Labridae	*Bodianus bilunatus*	66.8	Victor, B. C. 1986.
43	Labridae	*Bodianus diplotaenia*	39.5	Victor, B. C. 1986.
44	Labridae	*Bodianus eclancheri*	32.3	Victor, B. C., and G. M. Wellington. 2000.
45	Labridae	*Bodianus mesothorax*	30.3	Victor, B. C. 1986.
46	Labridae	*Bodianus rufus*	41.6	Victor, B. C. 1986.
47	Labridae	*Cheilinus bimaculatus*	46.7	Victor, B. C. 1986.
48	Labridae	*Cheilinus chlorourus*	27.1	Victor, B. C. 1986.
49	Labridae	*Cheilinus diagrammus*	26.1	Victor, B. C. 1986.
50	Labridae	*Cheilinus fasciatus*	25.7	Victor, B. C. 1986.
51	Labridae	*Cheilinus undulatus*	34.3	Victor, B. C. 1986.
52	Labridae	*Cheilinus unifasciatus*	36.2	Victor, B. C. 1986.
53	Labridae	*Cheilinus trilobatus*	29.6	Victor, B. C. 1986.
54	Labridae	*Cheilio inermis*	56.1	Victor, B. C. 1986.

55	Labridae	*Choerodon anchorago*	19.3	Victor, B. C. 1986.
56	Labridae	*Cirrhilabrus cyanopleura*	21.1	Victor, B. C. 1986.
57	Labridae	*Cirrhilabrus temninki*	28	Brothers, E. B., et al. 1983.
58	Labridae	*Clepticus parrae*	38.5	Victor, B. C. 1986.
59	Labridae	*Coris flavovittata*	53	Victor, B. C. 1986.
60	Labridae	*Coris gaimard*	44.9	Victor, B. C. 1986.
61	Labridae	*Coris variegata*	30.5	Brothers, E. B., et al. 1983.
62	Labridae	*Coris variegata*	22	Victor, B. C. 1986.
63	Labridae	*Coris venusta*	46.1	Victor, B. C. 1986.
64	Labridae	*Cymolutes lecluse*	75.9	Victor, B. C. 1986.
65	Labridae	*Cymolutes praetextatus*	71	Victor, B. C. 1986.
66	Labridae	*Diproctacanthus xanthurus*	17.3	Victor, B. C. 1986.
67	Labridae	*Doratonotus megalepis*	21.9	Victor, B. C. 1986.
68	Labridae	*Epibulus insidiator*	30.4	Victor, B. C. 1986.
69	Labridae	*Gomphosus varius*	51.8	Victor, B. C. 1986.
70	Labridae	*Halichoeres adustus*	33	Victor, B. C., and G. M. Wellington. 2000.
71	Labridae	*Halichoeres argus*	25	Victor, B. C. 1986.
72	Labridae	*Halichoeres biocellatus*	24.8	Victor, B. C. 1986.
73	Labridae	*Halichoeres bivattus*	24.1	Victor, B. C. 1986.
74	Labridae	*Halichoeres chierchiae*	31.3	Victor, B. C. 1986.
75	Labridae	*Halichoeres chloropterus*	21.1	Victor, B. C. 1986.
76	Labridae	*Halichoeres chrysus*	26.1	Victor, B. C. 1986.
77	Labridae	*Halichoeres discolor*	32	Victor, B. C., and G. M. Wellington. 2000.
78	Labridae	*Halichoeres dispilus*	41.1	Victor, B. C. 1986.
79	Labridae	*Halichoeres garnoti*	25.9	Victor, B. C. 1986.
80	Labridae	*Halichoeres hoeveni*	27.5	Brothers, E. B., et al. 1983.
81	Labridae	*Halichoeres hortulanus*	32.5	Victor, B. C. 1986.
82	Labridae	*Halichoeres insularis*	35.5	Victor, B. C., and G. M. Wellington. 2000.
83	Labridae	*Halichoeres maculipinna*	25.8	Victor, B. C. 1986.
84	Labridae	*Halichoeres margaritaceus*	21.7	Victor, B. C. 1986.
85	Labridae	*Halichoeres marginatus*	22.2	Victor, B. C. 1986.
86	Labridae	*Halichoeres melanotis*	35.7	Victor, B. C., and G. M. Wellington. 2000.
87	Labridae	*Halichoeres melanurus*	22.1	Victor, B. C. 1986.
88	Labridae	*Halichoeres nebulosus*	23.9	Victor, B. C. 1986.
89	Labridae	*Halichoeres nicholsi*	32.4	Victor, B. C. 1986.
90	Labridae	*Halichoeres notospilus*	37.9	Victor, B. C., and G. M. Wellington. 2000.
91	Labridae	*Halichoeres ornatissimus*	39.5	Victor, B. C. 1986.
92	Labridae	*Halichoeres pictus*	24.9	Victor, B. C. 1986.
93	Labridae	*Halichoeres poeyi*	24.1	Victor, B. C. 1986.
94	Labridae	*Halichoeres prosopeion*	21.2	Victor, B. C. 1986.
95	Labridae	*Halichoeres radiatus*	24.9	Victor, B. C. 1986.
96	Labridae	*Halichoeres richmondi*	20.8	Victor, B. C. 1986.
97	Labridae	*Halichoeres scapularis*	24.4	Victor, B. C. 1986.
98	Labridae	*Halichoeres semicinctus*	29.9	Victor, B. C. 1986.
99	Labridae	*Halichoeres sp. nov*	37	Victor, B. C., and G. M. Wellington. 2000.
100	Labridae	*Halichoeres trimaculatus*	26.8	Victor, B. C. 1986.
101	Labridae	*Hemigymnus fasciatus*	25.8	Victor, B. C. 1986.
102	Labridae	*Hemigymnus melapterus*	23.9	Victor, B. C. 1986.
103	Labridae	*Labrichthys unilineatus*	19.2	Victor, B. C. 1986.
104	Labridae	*Labroides bicolor*	24.5	Victor, B. C. 1986.
105	Labridae	*Labroides dimidiatus*	26	Brothers, E. B., et al. 1983.
106	Labridae	*Labroides pectoralis*	26.8	Victor, B. C. 1986.
107	Labridae	*Labroides phthirophagus*	32.1	Victor, B. C. 1986.
108	Labridae	*Labropsis micronesia*	22	Victor, B. C. 1986.
109	Labridae	*Labropsis xanthonota*	30.5	Victor, B. C. 1986.
110	Labridae	*Lachnolaimus maximus*	25.8	Victor, B. C. 1986.
111	Labridae	*Macropharyngodon geoffroy*	32.3	Victor, B. C. 1986.
112	Labridae	*Macropharyngodon meleagris*	25	Victor, B. C. 1986.
113	Labridae	*Macropharyngodon negrosensis*	25	Victor, B. C. 1986.

114	Labridae	*Novaculichthys macrolepidotus*	70.5	Victor, B. C. 1986.
115	Labridae	*Novaculichthys taeniourus*	55	Victor, B. C. 1986.
116	Labridae	*Oxyjulis californica*	39.4	Victor, B. C. 1986.
117	Labridae	*Pseudocheilinus evanidus*	35.6	Victor, B. C. 1986.
118	Labridae	*Pseudocheilinus hexataenia*	35	Victor, B. C. 1986.
119	Labridae	*Pseudocheilinus octaenia*	35.5	Victor, B. C. 1986.
120	Labridae	*Pseudocheilinus octotaenia*	47.7	Victor, B. C. 1986.
121	Labridae	*Pseudocheilinus tetrataenia*	49.3	Victor, B. C. 1986.
122	Labridae	*Pseudojuloides cerasinus*	42.4	Victor, B. C. 1986.
123	Labridae	*Pseudojulus melanotis*	35.7	Victor, B. C. 1986.
124	Labridae	*Pseudojulus notospilus*	37.6	Victor, B. C. 1986.
125	Labridae	*Pteragogus cryptus*	20.6	Victor, B. C. 1986.
126	Labridae	*Pteragogus flagellifera*	23	Victor, B. C. 1986.
127	Labridae	*Pteragogus guttatus*	20.5	Victor, B. C. 1986.
128	Labridae	*Semicossyphus darwini*	37	Victor, B. C., and G. M. Wellington. 2000.
129	Labridae	*Semicossyphus pulcher*	37.4	Victor, B. C. 1986.
130	Labridae	*Stethojulis balteata*	42.1	Victor, B. C. 1986.
131	Labridae	*Stethojulis bandenensis*	26.4	Victor, B. C. 1986.
132	Labridae	*Stethojulis sp. A*	26	Brothers, E. B., et al. 1983.
133	Labridae	*Stethojulis strigiventer*	23.4	Victor, B. C. 1986.
134	Labridae	*Tautoga onitis*	25.4	Victor, B. C. 1986.
135	Labridae	*Tautogolabrus adspersus*	28.4	Victor, B. C. 1986.
136	Labridae	*Thalassoma amblycephalum*	72.4	Victor, B. C. 1986.
137	Labridae	*Thalassoma ballieui*	84	Victor, B. C. 1986.
138	Labridae	*Thalassoma bifsciatum*	49.3	Victor, B. C. 1986.
139	Labridae	*Thalassoma duperrey*	89.2	Victor, B. C. 1986.
140	Labridae	*Thalassoma grammaticum*	61.8	Victor, B. C., and G. M. Wellington. 2000.
141	Labridae	*Thalassoma hardwicke*	47	Victor, B. C. 1986.
142	Labridae	*Thalassoma janseni*	63.3	Victor, B. C. 1986.
143	Labridae	*Thalassoma lucasanum*	74.3	Victor, B. C. 1986.
144	Labridae	*Thalassoma lunare*	54.7	Brothers, E. B., et al. 1983.
145	Labridae	*Thalassoma lutescens*	78	Victor, B. C. 1986.
146	Labridae	*Thalassoma purpureum*	57.7	Victor, B. C., and G. M. Wellington. 2000.
147	Labridae	*Thalassoma quinquevittatum*	56.4	Victor, B. C. 1986.
148	Labridae	*Thalassoma robertsoni*	58.6	Victor, B. C., and G. M. Wellington. 2000.
149	Labridae	*Thalassoma trilobatum*	78.3	Victor, B. C. 1986.
150	Labridae	*Thalassoma virens*	68.8	Victor, B. C., and G. M. Wellington. 2000.
151	Labridae	*Xyrichtys martinicencis*	78.3	Victor, B. C. 1986.
152	Labridae	*Xyrichtys mundiceps*	59.2	Victor, B. C., and G. M. Wellington. 2000.
153	Labridae	*Xyrichtys novacula*	50.5	Victor, B. C. 1986.
154	Labridae	*Xyrichtys pavo*	51	Victor, B. C., and G. M. Wellington. 2000.
155	Labridae	*Xyrichtys pavoninus*	57	Victor, B. C. 1986.
156	Labridae	*Xyrichtys sp. nov*	70.7	Victor, B. C., and G. M. Wellington. 2000.
157	Labridae	*Xyrichtys splendens*	103.9	Victor, B. C. 1986.
158	Labridae	*Xyrichtys victori*	73.7	Victor, B. C., and G. M. Wellington. 2000.
159	Labridae	*Xyrichtys wellingtoni*	68	Victor, B. C., and G. M. Wellington. 2000.
160	Lethrinidae	*Lethrinus nebulosus*	37	Brothers, E. B., et al. 1983.
161	Lutjanidae	*Hoplopagrus guntheri*	21.9	Zapata, F. A., and P. A. Herron. 2002.
162	Lutjanidae	*Lutjanus argentiventris*	21.3	Zapata, F. A., and P. A. Herron. 2002.
163	Lutjanidae	*Lutjanus guttatus*	24.1	Zapata, F. A., and P. A. Herron. 2002.
164	Lutjanidae	*Lutjanus viridis*	36.2	Zapata, F. A., and P. A. Herron. 2002.
165	Lutjanidae	*Pterocaesio chrysozona*	42	Doherty, P. J., et al. 1995.
166	Monacanthidae	*Monacanthus chinensis*	20	Brothers, E. B., et al. 1983.
167	Monacanthidae	*Paraluteres prionurus*	28	Brothers, E. B., et al. 1983.
168	Mullidae	*Upeneus tragula*	31.1	McCormick, M. I. 1994.
169	Nemipteridae	*Scolopsis dubiosus*	19	Brothers, E. B., et al. 1983.
170	Pomicanthidae	*Apolemichthys trimaculatus*	24.2	Thresher, R. E., and E. B. Brothers. 1985.
171	Pomicanthidae	*Centropyge acanthops*	34	Thresher, R. E., and E. B. Brothers. 1985.
172	Pomicanthidae	*Centropyge argi*	36.8	Thresher, R. E., and E. B. Brothers. 1989.

173	Pomicanthidae	*Centropyge bicolor*	32	Thresher, R. E., and E. B. Brothers. 1985.
174	Pomicanthidae	*Centropyge bispinosus*	32	Thresher, R. E., and E. B. Brothers. 1985.
175	Pomicanthidae	*Centropyge eibli*	25.3	Thresher, R. E., and E. B. Brothers. 1985.
176	Pomicanthidae	*Centropyge ferrugatus*	38	Thresher, R. E., and E. B. Brothers. 1985.
177	Pomicanthidae	*Centropyge fisheri*	38.3	Thresher, R. E., and E. B. Brothers. 1985.
178	Pomicanthidae	*Centropyge flavissimus*	30.3	Thresher, R. E., and E. B. Brothers. 1985.
179	Pomicanthidae	*Centropyge heraldi*	32	Thresher, R. E., and E. B. Brothers. 1985.
180	Pomicanthidae	*Centropyge interruptus*	31.5	Thresher, R. E., and E. B. Brothers. 1985.
181	Pomicanthidae	*Centropyge loriculus*	38	Thresher, R. E., and E. B. Brothers. 1985.
182	Pomicanthidae	*Centropyge multifasciatus*	26.2	Thresher, R. E., and E. B. Brothers. 1985.
183	Pomicanthidae	*Centropyge nox*	31.5	Thresher, R. E., and E. B. Brothers. 1985.
184	Pomicanthidae	*Centropyge potteri*	35.5	Thresher, R. E., and E. B. Brothers. 1985.
185	Pomicanthidae	*Centropyge tibicen*	30	Thresher, R. E., and E. B. Brothers. 1985.
186	Pomicanthidae	*Centropyge vroliki*	29	Thresher, R. E., and E. B. Brothers. 1985.
187	Pomicanthidae	*Chaetodontoplus duboulayi*	21.6	Thresher, R. E., and E. B. Brothers. 1985.
188	Pomicanthidae	*Chaetodontoplus melansoma*	22.2	Thresher, R. E., and E. B. Brothers. 1985.
189	Pomicanthidae	*Chaetodontoplus mesoleucus*	19.9	Thresher, R. E., and E. B. Brothers. 1985.
190	Pomicanthidae	*Chaetodontoplus personifer*	23.3	Thresher, R. E., and E. B. Brothers. 1985.
191	Pomicanthidae	*Chaetodontoplus septentrionalis*	23	Thresher, R. E., and E. B. Brothers. 1985.
192	Pomicanthidae	*Genicanthus bellus*	25	Thresher, R. E., and E. B. Brothers. 1985.
193	Pomicanthidae	*Genicanthus melanospilos*	25	Thresher, R. E., and E. B. Brothers. 1985.
194	Pomicanthidae	*Holocanthus bermudensis*	22.7	Thresher, R. E., and E. B. Brothers. 1989.
195	Pomicanthidae	*Holocanthus cliliaris*	22.4	Thresher, R. E., and E. B. Brothers. 1989.
196	Pomicanthidae	*Holocanthus tricolor*	29.7	Thresher, R. E., and E. B. Brothers. 1989.
197	Pomicanthidae	*Holocanthus venustus*	25	Thresher, R. E., and E. B. Brothers. 1985.
198	Pomicanthidae	*Pomacanthus annularis*	21	Thresher, R. E., and E. B. Brothers. 1985.
199	Pomicanthidae	*Pomacanthus arcuatus*	21.3	Thresher, R. E., and E. B. Brothers. 1989.
200	Pomicanthidae	*Pomacanthus imperator*	22	Thresher, R. E., and E. B. Brothers. 1985.
201	Pomicanthidae	*Pomacanthus navarchus*	22.8	Thresher, R. E., and E. B. Brothers. 1985.
202	Pomicanthidae	*Pomacanthus paru*	17.7	Thresher, R. E., and E. B. Brothers. 1989.
203	Pomicanthidae	*Pomacanthus semicirculatus*	19.5	Thresher, R. E., and E. B. Brothers. 1985.
204	Pomicanthidae	*Pomacanthus sextriatus*	18	Thresher, R. E., and E. B. Brothers. 1985.
205	Pomicanthidae	*Pomacanthus xanthometapon*	20.4	Thresher, R. E., and E. B. Brothers. 1985.
206	Pomicanthidae	*Pygoplites diacanthus*	24.5	Thresher, R. E., and E. B. Brothers. 1985.
207	Pomacentridae	*Abudefduf abdominalis*	17.5	Wellington, G. M., and B. C. Victor. 1989.
208	Pomacentridae	*Abudefduf bengalensis*	22.8	Thresher, R. E., and E. B. Brothers. 1989.
209	Pomacentridae	*Abudefduf coelestinus*	21.4	Thresher, R. E., and E. B. Brothers. 1989.
210	Pomacentridae	*Abudefduf concolor*	22	Wellington, G. M., and B. C. Victor. 1989.
211	Pomacentridae	*Abudefduf declivifrons*	21.9	Victor, B. C., and G. M. Wellington. 2000.
212	Pomacentridae	*Abudefduf lorentzi*	23	Thresher, R. E., et al. 1989.
213	Pomacentridae	*Abudefduf saxatilis*	27.2	Thresher, R. E., and E. B. Brothers. 1989.
214	Pomacentridae	*Abudefduf sexfasciatus*	17.3	Wellington, G. M., and B. C. Victor. 1989.
215	Pomacentridae	*Abudefduf sordidus*	26.1	Wellington, G. M., and B. C. Victor. 1989.
216	Pomacentridae	*Abudefduf taurus*	27.7	Thresher, R. E., and E. B. Brothers. 1989.
217	Pomacentridae	*Abudefduf taurus*	18.1	Wellington, G. M., and B. C. Victor. 1989.
218	Pomacentridae	*Abudefduf troschelii*	18.1	Victor, B. C., and G. M. Wellington. 2000.
219	Pomacentridae	*Abudefduf vaigiensis*	22.1	Thresher, R. E., and E. B. Brothers. 1989.
220	Pomacentridae	*Abudefduf vaigiensis*	18.3	Wellington, G. M., and B. C. Victor. 1989.
221	Pomacentridae	*Abudefduf whitleyi*	18.3	Thresher, R. E., et al. 1989.
222	Pomacentridae	*Acanthochromis polyacanthus*	0	Thresher, R. E., et al. 1989.
223	Pomacentridae	*Amblyglyphidodon aureus*	16	Wellington, G. M., and B. C. Victor. 1989.
224	Pomacentridae	*Amblyglyphidodon curacao*	13.1	Wellington, G. M., and B. C. Victor. 1989.
225	Pomacentridae	*Amblyglyphidodon leucogaster*	15	Wellington, G. M., and B. C. Victor. 1989.
226	Pomacentridae	*Amblyglyphidodon ternatensis*	20	Wellington, G. M., and B. C. Victor. 1989.
227	Pomacentridae	*Amphiprion akindynos*	11.8	Thresher, R. E., et al. 1989.
228	Pomacentridae	*Amphiprion chysopterus*	17	Thresher, R. E., and E. B. Brothers. 1989.
229	Pomacentridae	*Amphiprion clarkii*	15.5	Wellington, G. M., and B. C. Victor. 1989.
230	Pomacentridae	*Amphiprion melanopus*	18.6	Wellington, G. M., and B. C. Victor. 1989.
231	Pomacentridae	*Amphiprion percula*	10.7	Thresher, R. E., and E. B. Brothers. 1989.

232	Pomacentridae	*Amphiprion perideraion*	10.6	Thresher, R. E., and E. B. Brothers. 1989.
233	Pomacentridae	*Amphiprion perideraion*	18	Wellington, G. M., and B. C. Victor. 1989.
234	Pomacentridae	*Amphiprion polymus*	11	Thresher, R. E., and E. B. Brothers. 1989.
235	Pomacentridae	*Amphiprion tricinctus*	10.1	Thresher, R. E., and E. B. Brothers. 1989.
236	Pomacentridae	*Cheiloprion labiatus*	16.5	Wellington, G. M., and B. C. Victor. 1989.
237	Pomacentridae	*Chromis agilis*	32.7	Wellington, G. M., and B. C. Victor. 1989.
238	Pomacentridae	*Chromis alpha*	30	Wellington, G. M., and B. C. Victor. 1989.
239	Pomacentridae	*Chromis alta*	18.7	Wellington, G. M., and B. C. Victor. 1989.
240	Pomacentridae	*Chromis ambionensis*	22.1	Thresher, R. E., et al. 1989.
241	Pomacentridae	*Chromis atrilobata*	28.9	Victor, B. C., and G. M. Wellington. 2000.
242	Pomacentridae	*Chromis atrilobata*	33	Wellington, G. M., and B. C. Victor. 1989.
243	Pomacentridae	*Chromis atripectoralis*	20.3	Thresher, R. E., and E. B. Brothers. 1989.
244	Pomacentridae	*Chromis atripes*	31.4	Wellington, G. M., and B. C. Victor. 1989.
245	Pomacentridae	*Chromis caudalis*	27	Wellington, G. M., and B. C. Victor. 1989.
246	Pomacentridae	*Chromis chysura*	23.2	Thresher, R. E., et al. 1989.
247	Pomacentridae	*Chromis cyanea*	30.5	Wellington, G. M., and B. C. Victor. 1989.
248	Pomacentridae	*Chromis cyaneus*	35.1	Thresher, R. E., and E. B. Brothers. 1989.
249	Pomacentridae	*Chromis delta*	24	Wellington, G. M., and B. C. Victor. 1989.
250	Pomacentridae	*Chromis hanui*	27	Wellington, G. M., and B. C. Victor. 1989.
251	Pomacentridae	*Chromis insolata*	19.8	Wellington, G. M., and B. C. Victor. 1989.
252	Pomacentridae	*Chromis insolatas*	31.7	Thresher, R. E., and E. B. Brothers. 1989.
253	Pomacentridae	*Chromis iomelas*	24.4	Thresher, R. E., et al. 1989.
254	Pomacentridae	*Chromis lepidolepis*	30.6	Wellington, G. M., and B. C. Victor. 1989.
255	Pomacentridae	*Chromis limbaughi*	22.8	Victor, B. C., and G. M. Wellington. 2000.
256	Pomacentridae	*Chromis lineata*	37	Wellington, G. M., and B. C. Victor. 1989.
257	Pomacentridae	*Chromis margaritifer*	33.2	Wellington, G. M., and B. C. Victor. 1989.
258	Pomacentridae	*Chromis multilineata*	25.8	Wellington, G. M., and B. C. Victor. 1989.
259	Pomacentridae	*Chromis punctipinnis*	35.2	Wellington, G. M., and B. C. Victor. 1989.
260	Pomacentridae	*Chromis retrofasciata*	18.7	Wellington, G. M., and B. C. Victor. 1989.
261	Pomacentridae	*Chromis ternatensis*	28.3	Wellington, G. M., and B. C. Victor. 1989.
262	Pomacentridae	*Chromis vanderbilti*	31	Wellington, G. M., and B. C. Victor. 1989.
263	Pomacentridae	*Chromis viridis*	20.7	Wellington, G. M., and B. C. Victor. 1989.
264	Pomacentridae	*Chromis weberi*	31.2	Wellington, G. M., and B. C. Victor. 1989.
265	Pomacentridae	*Chromis xanthura*	28.2	Wellington, G. M., and B. C. Victor. 1989.
266	Pomacentridae	*Chrysiptera biocellatus*	18.2	Wellington, G. M., and B. C. Victor. 1989.
267	Pomacentridae	*Chrysiptera cyanea*	15.4	Wellington, G. M., and B. C. Victor. 1989.
268	Pomacentridae	*Chrysiptera cyanea*	17.4	Thresher, R. E., and E. B. Brothers. 1989.
269	Pomacentridae	*Chrysiptera flavipinnis*	19	Thresher, R. E., and E. B. Brothers. 1989.
270	Pomacentridae	*Chrysiptera glauca*	17.5	Wellington, G. M., and B. C. Victor. 1989.
271	Pomacentridae	*Chrysiptera leucopomus*	20.9	Wellington, G. M., and B. C. Victor. 1989.
272	Pomacentridae	*Chrysiptera oxycephala*	21.5	Wellington, G. M., and B. C. Victor. 1989.
273	Pomacentridae	*Chrysiptera rex*	19.3	Wellington, G. M., and B. C. Victor. 1989.
274	Pomacentridae	*Chrysiptera rollandi*	18.5	Thresher, R. E., and E. B. Brothers. 1989.
275	Pomacentridae	*Chrysiptera talboti*	22	Thresher, R. E., and E. B. Brothers. 1989.
276	Pomacentridae	*Chrysiptera traceyi*	23	Wellington, G. M., and B. C. Victor. 1989.
277	Pomacentridae	*Dascyllus albisella*	26.8	Wellington, G. M., and B. C. Victor. 1989.
278	Pomacentridae	*Dascyllus aruanus*	20	Wellington, G. M., and B. C. Victor. 1989.
279	Pomacentridae	*Dascyllus melanurus*	21.2	Wellington, G. M., and B. C. Victor. 1989.
280	Pomacentridae	*Dascyllus reticulatus*	20.6	Wellington, G. M., and B. C. Victor. 1989.
281	Pomacentridae	*Dascyllus trimaculatus*	26	Wellington, G. M., and B. C. Victor. 1989.
282	Pomacentridae	*Dischistodus chrysopoecilus*	19.5	Wellington, G. M., and B. C. Victor. 1989.
283	Pomacentridae	*Dischistodus melanotus*	13.7	Wellington, G. M., and B. C. Victor. 1989.
284	Pomacentridae	*Dischistodus notophtalmus*	16	Thresher, R. E., and E. B. Brothers. 1989.
285	Pomacentridae	*Dischistodus perpicillatus*	13.8	Wellington, G. M., and B. C. Victor. 1989.
286	Pomacentridae	*Dischistodus pseudochrysopoecilus*	14.3	Wellington, G. M., and B. C. Victor. 1989.
287	Pomacentridae	*Glyphidodontops hemicyaneus*	19.3	Thresher, R. E., et al. 1989.
288	Pomacentridae	*Glyphidodontops rollandi*	23.3	Brothers, E. B., et al. 1983.
289	Pomacentridae	*Glyphidodontops talboti*	22	Brothers, E. B., et al. 1983.
290	Pomacentridae	*Hemiglyphidodon plagiometapon*	18	Wellington, G. M., and B. C. Victor. 1989.

291	Pomacentridae	*Hypsypops rubicundua*	20	Wellington, G. M., and B. C. Victor. 1989.
292	Pomacentridae	*Lepidozygus tapeinosoma*	15.7	Thresher, R. E., et al. 1989.
293	Pomacentridae	*Microspathodon bairdii*	28.9	Victor, B. C., and G. M. Wellington. 2000.
294	Pomacentridae	*Microspathodon chrysurus*	23	Wellington, G. M., and B. C. Victor. 1989.
295	Pomacentridae	*Microspathodon dorsalis*	34	Wellington, G. M., and B. C. Victor. 1989.
296	Pomacentridae	*Neoglyphidodon nigroris*	17	Thresher, R. E., et al. 1989.
297	Pomacentridae	*Neopomacentrus azysron*	24	Brothers, E. B., et al. 1983.
298	Pomacentridae	*Neopomacentrus cyanomos*	18.2	Thresher, R. E., et al. 1989.
299	Pomacentridae	*Neopomacentrus nemurus*	19.2	Wellington, G. M., and B. C. Victor. 1989.
300	Pomacentridae	*Nexilosus latifrons*	29.2	Victor, B. C., and G. M. Wellington. 2000.
301	Pomacentridae	*Paraglyphidodon melas*	16.1	Wellington, G. M., and B. C. Victor. 1989.
302	Pomacentridae	*Paraglyphidodon nigroris*	21.7	Wellington, G. M., and B. C. Victor. 1989.
303	Pomacentridae	*Plectroglyphidodon dickii*	26.6	Wellington, G. M., and B. C. Victor. 1989.
304	Pomacentridae	*Plectroglyphidodon imparipennis*	17.5	Wellington, G. M., and B. C. Victor. 1989.
305	Pomacentridae	*Plectroglyphidodon johnstinianus*	31.7	Thresher, R. E., et al. 1989.
306	Pomacentridae	*Plectroglyphidodon lacrymatus*	20.4	Wellington, G. M., and B. C. Victor. 1989.
307	Pomacentridae	*Plectroglyphidodon sindonis*	30	Wellington, G. M., and B. C. Victor. 1989.
308	Pomacentridae	*Pomacentrus alexanderae*	17.7	Wellington, G. M., and B. C. Victor. 1989.
309	Pomacentridae	*Pomacentrus amboinensis*	23.4	Brothers, E. B., et al. 1983.
310	Pomacentridae	*Pomacentrus arenarius*	22.9	Thresher, R. E., and E. B. Brothers. 1989.
311	Pomacentridae	*Pomacentrus australis*	75	Brothers, E. B., et al. 1983.
312	Pomacentridae	*Pomacentrus australis*	25	Thresher, R. E., and E. B. Brothers. 1989.
313	Pomacentridae	*Pomacentrus bankenensis*	18.8	Wellington, G. M., and B. C. Victor. 1989.
314	Pomacentridae	*Pomacentrus brachialis*	18	Thresher, R. E., et al. 1989.
315	Pomacentridae	*Pomacentrus burroughi*	16.8	Wellington, G. M., and B. C. Victor. 1989.
316	Pomacentridae	*Pomacentrus chrysurus*	19.5	Thresher, R. E., et al. 1989.
317	Pomacentridae	*Pomacentrus coelestris*	19.1	Thresher, R. E., and E. B. Brothers. 1989.
318	Pomacentridae	*Pomacentrus emarginatus*	18.4	Wellington, G. M., and B. C. Victor. 1989.
319	Pomacentridae	*Pomacentrus grammorhynchus*	14.8	Wellington, G. M., and B. C. Victor. 1989.
320	Pomacentridae	*Pomacentrus lepidogenys*	20	Wellington, G. M., and B. C. Victor. 1989.
321	Pomacentridae	*Pomacentrus moluccensis*	19.6	Wellington, G. M., and B. C. Victor. 1989.
322	Pomacentridae	*Pomacentrus nagasakiensis*	24.5	Wilson, D. T., and M. I. McCormick. 1997.
323	Pomacentridae	*Pomacentrus pavo*	22.4	Wellington, G. M., and B. C. Victor. 1989.
324	Pomacentridae	*Pomacentrus philippinus*	16	Wellington, G. M., and B. C. Victor. 1989.
325	Pomacentridae	*Pomacentrus popei*	23.5	Brothers, E. B., et al. 1983.
326	Pomacentridae	*Pomacentrus reidi*	18	Wellington, G. M., and B. C. Victor. 1989.
327	Pomacentridae	*Pomacentrus rhodonotus*	15.8	Wellington, G. M., and B. C. Victor. 1989.
328	Pomacentridae	*Pomacentrus simsiang*	15.8	Wellington, G. M., and B. C. Victor. 1989.
329	Pomacentridae	*Pomacentrus sp. A*	23	Brothers, E. B., et al. 1983.
330	Pomacentridae	*Pomacentrus sp. B*	22.9	Brothers, E. B., et al. 1983.
331	Pomacentridae	*Pomacentrus taeniometopon*	15.7	Wellington, G. M., and B. C. Victor. 1989.
332	Pomacentridae	*Pomacentrus vaiuli*	16.8	Wellington, G. M., and B. C. Victor. 1989.
333	Pomacentridae	*Pomacentrus wardi*	24.3	Brothers, E. B., et al. 1983.
334	Pomacentridae	*Premnas biaculeatus*	8.4	Thresher, R. E., et al. 1989.
335	Pomacentridae	*Pristotis jerdoni*	25.3	Thresher, R. E., et al. 1989.
336	Pomacentridae	*Stegastes acapulcoensis*	21.3	Wellington, G. M., and B. C. Victor. 1989.
337	Pomacentridae	*Stegastes apicalis*	29.7	Thresher, R. E., et al. 1989.
338	Pomacentridae	*Stegastes arcrifrons*	25.3	Wellington, G. M., and B. C. Victor. 1989.
339	Pomacentridae	*Stegastes baldwini*	26	Victor, B. C., and G. M. Wellington. 2000.
340	Pomacentridae	*Stegastes diaencaeus*	21.3	Wellington, G. M., and B. C. Victor. 1989.
341	Pomacentridae	*Stegastes dorsopunicans*	21.2	Wellington, G. M., and B. C. Victor. 1989.
342	Pomacentridae	*Stegastes fasciolatus*	25	Wellington, G. M., and B. C. Victor. 1989.
343	Pomacentridae	*Stegastes flavilatus*	31.2	Wellington, G. M., and B. C. Victor. 1989.
344	Pomacentridae	*Stegastes leucorus beebei*	31.2	Wellington, G. M., and B. C. Victor. 1989.
345	Pomacentridae	*Stegastes leucorus leucorus*	34	Victor, B. C., and G. M. Wellington. 2000.
346	Pomacentridae	*Stegastes leucostictus*	28.5	Thresher, R. E., and E. B. Brothers. 1989.
347	Pomacentridae	*Stegastes leucostictus*	20.1	Wellington, G. M., and B. C. Victor. 1989.
348	Pomacentridae	*Stegastes lividus*	25	Wellington, G. M., and B. C. Victor. 1989.
349	Pomacentridae	*Stegastes nigricans*	24	Wellington, G. M., and B. C. Victor. 1989.

350	Pomacentridae	*Stegastes partitus*	28.8	Wellington, G. M., and B. C. Victor. 1989.
351	Pomacentridae	*Stegastes planifrons*	26.8	Thresher, R. E., and E. B. Brothers. 1989.
352	Pomacentridae	*Stegastes planifrons*	21.4	Wellington, G. M., and B. C. Victor. 1989.
353	Pomacentridae	*Stegastes rectifraenum*	21.5	Victor, B. C., and G. M. Wellington. 2000.
354	Pomacentridae	*Stegastes redemptus*	23	Wellington, G. M., and B. C. Victor. 1989.
355	Pomacentridae	*Stegastes sp. 1*	21	Wellington, G. M., and B. C. Victor. 1989.
356	Pomacentridae	*Stegastes sp. 2*	22.5	Wellington, G. M., and B. C. Victor. 1989.
357	Pomacentridae	*Stegastes variabilis*	26.6	Thresher, R. E., and E. B. Brothers. 1989.
358	Pomacentridae	*Stegastes variabilis*	23.3	Wellington, G. M., and B. C. Victor. 1989.
359	Scaridae	*Unidentified*	41.3	Brothers, E. B., et al. 1983.
360	Scaridae	*Unidentified*	48	Brothers, E. B., et al. 1983.
361	Tripterygiidae	*Enneapterygius atriceps*	30	Longenecker, K., and R. Langston. 2005.

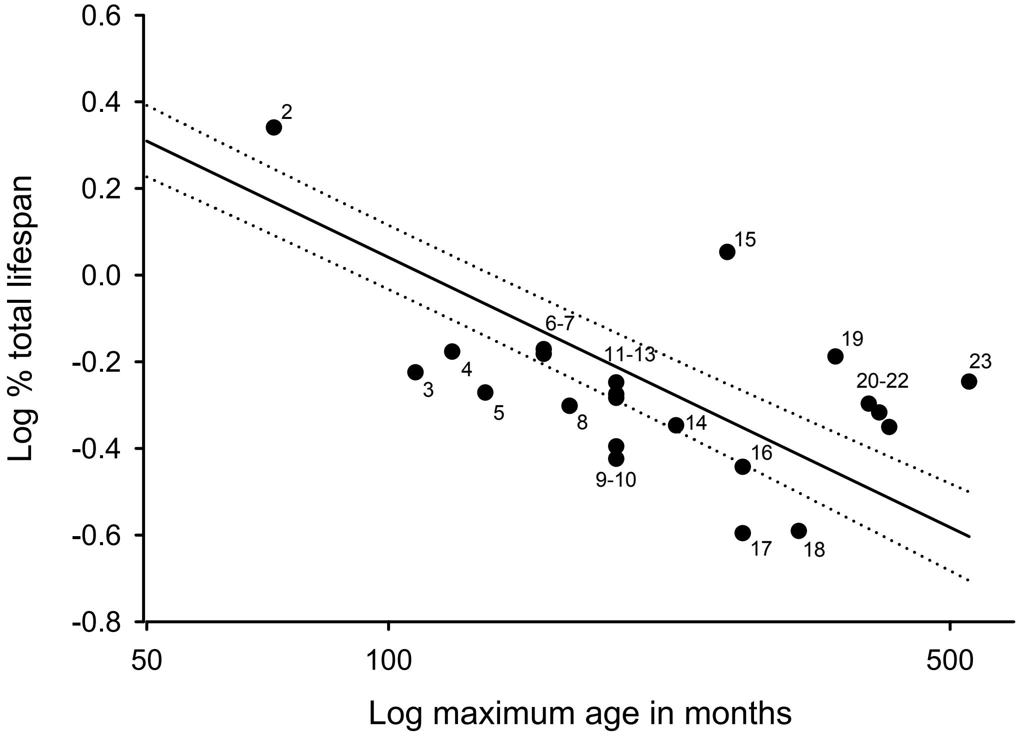
Appendix C

List of species for which published estimates of both maximum age and pelagic larval duration are available. Sequence follows data points from left to right shown in Fig. 3. References follow those in Appendices A and B.

No.	Family	Species	Tmax in years	Tmax in months	Reference	Mean PLD	Reference
1	Tripterygiidae	*Enneapterygius atriceps*	0.32	3.84	Longenecker, K., and R. Langston. 2005.	30	Longenecker, K., and R. Langston. 2005.
2	Chaetodontidae	*Chaetodon auriga*	6	72	Berumen, M. L. unpublished data	48	Wilson, D. T., and M. I. McCormick. 1999.
3	Pomacentridae	*Pomacentrus moluccensis*	9	108	Fowler, A. J., and P. J. Doherty. 1992.	19.6	Wellington, G. M., and B. C. Victor. 1989.
4	Pomacentridae	*Pomacentrus wardi*	10	120	Fowler, A. J., and P. J. Doherty. 1992.	24.3	Brothers, E. B., et al. 1983.
5	Pomacentridae	*Stegastes rectifraenum*	11	132	Meekan, M. G., et al. 2001.	21.5	Victor, B. C., and G. M. Wellington. 2000.
6	Pomacentridae	*Stegastes flavilatus*	13	156	Meekan, M. G., et al. 2001.	31.2	Wellington, G. M., and B. C. Victor. 1989.
7	Pomicanthidae	*Centropyge bicolor*	13	156	Aldenhoven, J. M. 1986.	32	Thresher, R. E., and E. B. Brothers. 1985.
8	Chaetodontidae	*Chelmon rostratus*	14	168	Berumen, M. L. unpublished data	25.5	Brothers, E. B., et al. 1983.
9	Pomicanthidae	*Pomacanthus imperator*	16	192	Chung, K. N., and Y. S. Woo. 1999.	22	Thresher, R. E., and E. B. Brothers. 1985.
10	Labridae	*Bodianus axillaris*	16	192	Hubble, M. 2003.	23.5	Victor, B. C. 1986.
11	Labridae	*Epibulus insidiator*	16	192	Hubble, M. 2003.	30.4	Victor, B. C. 1986.
12	Acanthuridae	*Acanthurus nigrofuscus*	16	192	Choat, J. H., and D. R. Robertson. 2002	31	Wilson, D. T., and M. I. McCormick. 1999.
13	Chaetodontidae	*Chaetodon baronessa*	16	192	Berumen, M. L. 2005.	33	Wilson, D. T., and M. I. McCormick. 1999.
14	Pomacentridae	*Stegastes leucorus beebei*	19	228	Meekan, M. G., et al. 2001.	31.2	Wellington, G. M., and B. C. Victor. 1989.
15	Acanthuridae	*Naso brevirostris*	22	264	Choat, J. H., and L. M. Axe. 1996	90.8	Wilson, D. T., and M. I. McCormick. 1999.
16	Pomacentridae	*Stegastes acapulcoensis*	23	276	Meekan, M. G., et al. 2001.	21.3	Wellington, G. M., and B. C. Victor. 1989.
17	Labridae	*Bodianus mesothorax*	23	276	Hubble, M. 2003.	30.3	Victor, B. C. 1986.
18	Pomacentridae	*Stegastes arcrifrons*	27	324	Meekan, M. G., et al. 2001.	25.3	Wellington, G. M., and B. C. Victor. 1989.
19	Acanthuridae	*Naso unicornis*	30	360	Choat, J. H., and L. M. Axe. 1996	71	Wilson, D. T., and M. I. McCormick. 1999.
20	Acanthuridae	*Acanthurus olivaceus*	33	396	Choat, J. H., and L. M. Axe. 1996	60.8	Wilson, D. T., and M. I. McCormick. 1999.
21	Acanthuridae	*Zebrasoma scopas*	34	408	Choat, J. H., and L. M. Axe. 1996	59.8	Wilson, D. T., and M. I. McCormick. 1999.
22	Acanthuridae	*Ctenochaetus striatus*	35	420	Choat, J. H., and L. M. Axe. 1996	57	Wilson, D. T., and M. I. McCormick. 1999.
23	Acanthuridae	*Naso hexacanthus*	44	528	Choat, J. H., and L. M. Axe. 1996	91.2	Wilson, D. T., and M. I. McCormick. 1999.

Appendix D

Log-log plot of the % of total lifespan and maximum ages in months of the 23 larger species in figure 2.7. Numbers on the plot correspond to species listed in appendix C.



Appendices references

Aldenhoven JM (1986) Local variation in mortality rates and life expectancy estimates of the coral-reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). Mar Biol 92: 237-244

Bay LK, Buechler K, Gagliano M, Caley JM (in press) Intraspecific variation in the pelagic larval duration of tropical reef fishes. J Fish Biol

Berumen ML (2005) The importance of juveniles in modelling growth: butterfly fish at Lizard Island. Environ Biol Fishes 72: 409-413

Brothers EB, Williams D McB, Sale PF (1983) Length of larval life in twelve families of fishes at "One Tree Lagoon", Great Barrier Reef, Australia. Mar Biol 76: 319-324

Choat JH, Axe LM (1996) Growth and longevity in acanthurid fishes; and analysis of otolith increments. Mar Ecol Prog Ser 134: 15-26

Choat JH, Robertson DR (2002) Age-based studies. Pages 57-80 *in* P. F. Sale, editor. Coral Reef Fishes – Dynamics and Diversity in a Complex Ecosystem. Academic, San Diego, USA

Choat JH, Axe LM Lou DC (1996) Growth and longevity in fishes of the family Scaridae. Mar Ecol Prog Ser 145: 33-41

Chung KN, Woo YS (1999) Age and growth by scale analysis of *Pomacanthus imperator* (Teleostei: Pomacanthidae) from Dongsha Islands, Southern China. Environ Biol Fishes. 55: 399-412

Craig MT, Pondella DJ, Hafner JC (1999) Analysis of age and growth in two Eastern Pacific groupers (Serranidae: Epinephelinae). Bull Mar Sci 65: 807-815

Dee AJ, Radtke RL (1989) Age and growth of the brick soldierfish, *Mypristis amaena* Coral Reefs 8: 79-85

Doherty PJ, Planes S, Mather P (1995) Gene flow and larval duration in seven species of fish from the Great Barrier Reef. Ecology 76: 2373-2391

Ferreira BP, Russ GR (1994) Age validation and estimation of growth rate of the oral trout *Plectropomus leopardus* (Lacepede 1802) from Lizard Island, Northern Great Barrier Reef. Fish Bull 92: 46-57

Fowler AJ (1989) Description, interpretation and use of the microstructure of otoliths from juvenile butterflyfishes (family Chaetodontidae). Mar Biol 102: 167-181

Fowler AJ, Doherty PJ (1992) Validation of annual growth increments in the otoliths of two species of Damselfishes from the Southern Great Barrier Reef. Mar Freshw Res 43: 1057-1068

Hernaman V, Munday PL (2005) Life history characteristics of coral reef gobies: I. Growth and lifespan. Mar Ecol Prog Ser 290: 207-221

Hubble M (2003) The ecological significance of body size in tropical wrasses (Pisces: Labridae). PhD Thesis. James Cook University, Australia

Ingles J, Pauly D (1984) An atlas of the growth, mortality and recruitment of Philippines fishes. ICLARM Tech. Rep. 13. 127 p. International Center for Living Aquatic Resources Management, Manila, Philippines

Kohda MA (1996) A damselfish living for more than 15 years: a longevity record for small reef fishes. Ichthyol Res 43: 459-462

Kritzer JP (2002a) Stock structure, mortality and growth of the decorated goby, *Istigobius decoratus* (Gobiidae), at Lizard Island, Great Barrier Reef. Environ Biol Fishes 63: 211-216

Kritzer JP (2002b) Variation in the population biology of the stripey bass *Lutjanus carponotatus* within and between two island groups on the Great Barrier Reef. Mar Ecol Prog Ser 243: 191-207

Longenecker K, Langston R (2005) Life history of the Hawaiian blackhead triplefin, *Enneapterygius atriceps* (Blennioidei, Tripterygiidae). Environ Biol Fishes 73: 243-251

Manooch, CS, Barans CA (1982) Distribution, abundance, and age and growth of the tomtate, *Haemulon aurolineatum*, along the southeastern United States coast. Fish Bull 80: 1-19

McCormick MI (1994) Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the Northern Great Barrier Reef lagoon. Mar Ecol Prog Ser 103: 1-15.

Meekan MG, Ackerman JL, Wellington GM (2001) Demography and age structure of coral reef damselfishes in the tropical eastern Pacific Ocean. Mar Ecol Prog Ser 212: 223-232

Mosse JW (2001) Population biology of *Cephalopholis cyanostigma* (Serranidae) of the Great Barrier Reef, Australia. PhD Thesis. James Cook University, Australia

Munday PL (2001) Fitness consequences of habitat use and competition among coral-dwelling fishes. Oecologia 128: 585-593

Newman SJ, Williams DMcB, Russ GR (1996) Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae), *Lutjanus adetti* (Castelnau, 1873) and *Lutjanus quinquelineatus* (Bloch, 1790) from the Central Great Barrier Reef, Australia. Mar Freshw Res 47: 575-584

Platten JR, Tibbetts IR, Sheaves MJ (2002) The influence of increased line-fishing mortality on the sex ratio and age of sex reversal of the venus tusk fish. J Fish Biol 60: 301-318

Potts JC, Manooch CS (2002) Estimated ages of red porgy (*Pagrus pagrus*) from fishery-dependent and fishery-independent data and a comparison of growth parameters. Fish Bull 100: 81-89

Reavis RH (1997) The natural history of a monogamous coral-reef fish, *Valenciennea strigata* (Gobiidae): 1. abundance, growth, survival and predation. Environ Biol Fishes 49: 239-246

Sadovy Y, Figuerda M, Roman A (1992) Age and growth of red hind *Epinephelus guttatus* in Puerto Rico and St James. Fish Bull 90: 516-528

Schwamborn SHL, Ferreira BP (2002) Age structure and growth of the dusky damselfish, *Stegastes fuscus*, from Tamandare reefs, Pernambuco, Brazil. Environ Biol Fishes 63: 79-88

Shafer DJ (2000) Evaluation of periodic and aperiodic otolith structure and somatic-otolith scaling for use in retrospective life history analysis of a tropical marine goby, *Bathygobius coalitus*. Mar Ecol Prog Ser 199: 217-229

Sponaugle S, Cowen RK (1994) Larval durations and recruitment patterns of two Caribbean gobies (Gobiidae): contrasting early life histories in demersal spawners. Mar Biol 120: 133-143

Thresher RE, Brothers EB (1985) Reproductive ecology and biogeography of Indo-West Pacific angelfishes (Pisces: Pomacanthidae). Evolution 39: 878-887

Thresher RE, Brothers EB (1989) Evidence of intra- and inter-oceanic regional differences in the early life history of reef-associated fishes. Mar Ecol Prog Ser 57: 187-205

Thresher RE, Colin PL, Bell LJ (1989) Planktonic duration, distribution and population structure of western and central Pacific damselfishes (Pomacentridae). Copeia 1989: 420-434

Victor BC (1986) Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (Labridae). Mar Biol 90: 317-326

Victor BC, Wellington GM (2000) Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. Mar Ecol Prog Ser 205: 241-248

Wellington GM, Victor BC (1989) Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Mar Biol 101: 557-567

Williams AJ, Davies CR, Mapstone BD, Russ GR (2003) Scales of spatial variation in demography of a large coral-reef fish - an exception to the typical model? Fish Bull 101: 673-683

Wilson DT, McCormick MI (1997) Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. Mar Ecol Prog Ser 153: 259-271

Wilson DT, McCormick MI (1999) Microstructure of settlement-marks in the otoliths of tropical reef fishes. Mar Biol 134: 29-41

Wilson SK (2004) Growth, mortality and turnover rates of a small detritivorous fish. Mar Ecol Prog Ser 284: 253-259

Zapata FA, Herron PA (2002) Pelagic larval duration and geographic distribution of tropical eastern Pacific snappers (Pisces: Lutjanidae). Mar Ecol Prog Ser 230: 295-300

Appendix E

List of the 74 genera and 14 families of the most abundant non-cryptic and cryptic coral reef fish taxa censused at Lizard Island in the northern Great Barrier Reef.

Non-cryptic taxa		**Cryptic taxa**	
Family	**Genus**	**Family**	**Genus**
Acanthuridae	*Acanthurus*	Blenniidae	*Crossalarias*
	Ctenochaetus		*Ecsenius*
	Naso		*Salarias*
	Zebrasoma	*Gobiidae*	*Amblyeleotris*
Apogonidae	*Apogon*		*Amblygobius*
	Cheilodipterus		*Asterropteryx*
	Rhabdamia		*Callogobius*
Chaetodontidae	*Chaetodon*		*Fusigobius*
	Chelmon		*Ctenogobiops*
	Heniochus		*Eviota*
Labridae	*Anampses*		*Istigobius*
	Bodianus		*Trimma*
	Cheilinus		*Valenciennea*
	Cheilio	Pseudochromidae	*Pseudochromis*
	Choerodon	Tripterygiidae	*Enneapterygius*
	Cirrhilabrus		
	Coris		
	Epibulus		
	Gomphosus		
	Halichoeres		
	Hemigymnus		
	Hologymnosus		
	Labrichthys		
	Labroides		
	Macropharyngodon		
	Novaculichthys		
	Oxycheilinus		
	Pseudocheilinus		
	Stethojulis		
	Thalassoma		
Pomacanthidae	*Centropyge*		
	Pomacanthus		
	Pygoplites		
Pomacentridae	*Abudefduf*		
	Acanthochromis		
	Amblyglyphidodon		
	Amphiprion		
	Chromis		
	Chrysiptera		
	Dascyllus		
	Dischistodus		
	Hemiglyphidodon		
	Neoglyphidodon		
	Neopomacentrus		
	Plectroglyphidodon		
	Stegastes		
Scaridae	*Calotomus*		
	Chlorurus		
	Hipposcarus		
	Scarus		
Serranidae	*Cephalopholis*		
	Cromileptes		
	Epinephelus		
	Plectropomus		
	Variola		
Siganidae	*Lo*		
	Siganus		
Zanclidae	*Zanclus*		

Appendix F
PhD publications list

Depczynski M, Bellwood DR (2005) Shortest recorded vertebrate lifespan found in a coral reef fish. Current Biol 15 (8): R288-R289

Depczynski M, Bellwood DR (2005) Spatial variability in community structure of small cryptic coral reef fishes. Mar Ecol Prog Ser 303: 283-293

Depczynski M, Bellwood DR (2006) Extremes, plasticity and invariance in vertebrate life histories: insights from coral reef fishes. Ecology 87: 3119-3127

Depczynski M, Fulton CJ, Marnane MJ, Bellwood DR (in press) Life history patterns shape energy allocation among fishes on coral reefs. Oecologia