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The Trophic Role of Cardinalfishes (Family Apogonidae) on Coral Reefs.

Thesis submitted by

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in November 2001

For the degree of Doctor of Philosophy

in the Department of Marine Biology,

James Cook University, North Queensland.

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ABSTRACT

Cardinalfishes (Family Apogonidae) form the major component of nocturnal fish assemblages on Indo-Pacific reefs, however, they have been largely overlooked in studies of reef tropho-dynamics. This project examined patterns of distribution, abundance and biomass as well as diet, defecation rates and life history parameters of apogonids to determine their importance in reef processes. Patterns of relative abundance and biomass of apogonids were investigated using daytime visual censuses conducted over a range of spatial scales at One Tree Reef and Lizard Island, Great Barrier Reef, Australia. Patterns of apogonid abundance and biomass over reef-wide scales were most strongly related to the degree of wave exposure. The highest abundance and biomass were recorded from lagoonal reef slopes and bases (0.3 to 2.1 fish m^{-2}; 2.2 to 5.1 g m^{-2}), followed by leeward reef slopes and bases. The lowest values (<0.2 fish m^{-2}; <1.3 g m^{-2}) were recorded from exposed locations and reef flats. Patterns were consistent at both One Tree Reef and Lizard Island. This suggests that apogonids are likely to be most important in lagoonal and sheltered systems.

The strength of the relationship between apogonids and their diurnal resting sites was examined in three common species within the One Tree Reef lagoon. Adult *Apogon doederlini, Cheilodipterus artus* and *Cheilodipterus quinquilineatus* were individually tagged using visual fluorescent implants and monitored over 16 months to record their persistence at resting sites. Tagged fish were found within an average of 36 to 79 cm of their initial resting positions during each census throughout an 8 month period in *A. doederlini* and *A. leptacanthus* and throughout a 16 month period in *C. artus* and *C. quinquilineatus*. In addition, 56 to 81% of tagged fish displaced ~1 km, and 33 to 63% of tagged fish displaced ~2 km returned to their point of collection within 3 days. As apogonids are often found densely aggregated at resting sites, their extended use of

specific sites on reefs represents a localised, predictable resource for predators and a significant source of spatial variability in nutrient input to reef systems via faeces.

To assess the trophic role of apogonids on reefs, diet, diel feeding behaviour and nocturnal foraging were examined in seven species in the One Tree Reef lagoon. Between 64 and 93% of fish collected at dawn had identifiable material in the stomach compared with 5 to 36% of fish collected at dusk, suggesting that all seven species were predominantly nocturnal feeders. The movement of apogonids between resting sites and feeding grounds was examined using day and night visual surveys. Apogonids shared restricted resting habitats by day but moved into a range of habitats at night. Species were spatially segregated at night, both horizontally and vertically in the water column. Most species had generalised diets containing primarily emergent plankton and benthic invertebrates, suggesting a role in recycling rather than importation of nutrients and energy on reefs. Dietary differences among species appeared to be driven largely by their feeding positions in the water column at night. Since apogonids feed in a range of habitats then return to restricted resting sites during the day they are likely to play an important role in concentrating nutrients and energy on reefs, providing localised and predictable resources for both predators and detritivore communities.

To investigate the importance of apogonids in the transfer of energy to higher trophic levels, the turnover rates of four common species were examined within the One Tree Reef lagoon. Three independent methods were used: (1) Mortality estimates were calculated from the disappearance of tagged fish over time. Mortality rates were highest in *Apogon cyanosoma* (97.2 % mortality yr $^{-1}$) followed by *Apogon doederlini* (89.6 %), *Cheilodipterus quinquilineatus* (83.7 %) and *Cheilodipterus artus* (78.0 %). (2) Longevity estimates were obtained through otolith analysis of the largest 5 % of individuals of each species collected throughout the course of the study. *A. cyanosoma* and *A. doederlini* appeared to reach a maximum age of around 1 year whilst *C. quinquilineatus* and *C. artus* reached at least 3 years. (3) Populations were surveyed at four-monthly intervals over a period of 2 years. Population dynamics of each species reflected estimates of mortality and longevity. Adult populations of *A. cyanosoma* and *A. doederlini* were found to vary by an order of magnitude throughout a yearly time-frame, primarily driven by variable episodes of recruitment followed by high rates of mortality. *C. quinquilineatus* and *C. artus* populations were more stable, with adult numbers fluctuating by two to three-fold over the course of a year. Additional estimates for 6 species of apogonids from Lizard Island indicate maximum longevities of only one year in most species. Apogonids have much faster turnover rates than most comparatively-sized reef fish taxa and may therefore play a major role in the transfer of energy to higher trophic levels.

Defecation rates in apogonids were examined in four species from the One Tree Reef lagoon through the collection of faeces from individuals between dawn and dusk. Fish were collected between 0430 and 0515 hrs and transferred to individual containers from which faeces were collected over the following 12 hrs, then filtered onto pre-weighed filter papers and dried at 60^0C. The dry weight of faeces produced by each fish was regressed against wet body weight to obtain defecation rates for each species. These defecation rates were then multiplied by apogonid biomass estimates to obtain defecation rates per m^2 of reef. The estimated defecation rate for all combined apogonids at resting sites was 693 ± 260 mg dry faeces m^{-2} day^{-1}. This rate was comparable to defecation rates for resting schools of haemulids from the Caribbean which were found to enhance local coral growth.

In summary, apogonids play a role which is functionally very different to that of diurnal planktivores. Apogonids are major predators of emergent plankton, a trophic pathway that has received little attention on reefs. This material is consumed in a range of reef and non-reef habitats, then concentrated in the form of fish biomass and faeces at restricted resting sites on the reef. Energy is rapidly transferred to higher trophic levels through fast biomass turnover rates, and to detritivores through a significant input of faeces at the resting sites. Since apogonids return to the same resting sites on a daily basis for extended periods of time, resting schools of apogonids are likely to represent a significant predictable resource for both predators and detritivore communities. Apogonids are generally missed or underestimated in visual censuses of reef fish assemblages, however, this thesis suggests that apogonids form an important component in reef processes. A failure to incorporate apogonids in studies of the role of fishes on reefs is likely to result in an incomplete model of reef system function.

CHAPTER 1: PREFACE

Fishes play an integral part in the tropho-dynamics of coral reefs (Parrish 1989). Visual census techniques are the stock-standard methods employed in assessing reef fish communities, however, these methods are inherently biased towards the larger and more visually apparent taxa (Brock 1982). As a result, what we know of the role of fishes in reef processes is generally limited to the most conspicuous reef fish taxa. A range of studies have examined the role of grazing in large herbivorous taxa in cycling primary productivity on reefs (Hatcher 1983). Similarly, diurnal planktivores are a conspicuous part of any reef system and a number of studies have examined the role of planktivores in transferring energy between open water communities and reef systems (Hamner et al. 1982). However, a number of highly abundant reef fish families are generally missed, or at best underestimated, using standard visual census techniques. This is largely due to their small size and/or cryptic habits (Brock 1982, Munday & Jones 1998).

We know virtually nothing of the role of small, cryptic fishes in reef processes, however, quantitative estimates suggest that these fishes may be far more important than is currently recognised (Ackerman & Bellwood 2000). Small fishes have higher mass-specific metabolic demands than larger fishes (Clarke & Johnston 1999), suggesting that these taxa may have a disproportionately high contribution to reef energy budgets. Ackerman and Bellwood (2000) suggest that more than 50% of the energy consumed by reef fishes may be attributed to taxa smaller than 10 cm in length. In addition, small fishes are likely to be shorter-lived than larger fishes (Miller 1979). Hence, whilst small fishes may constitute a slightly lower standing biomass on reefs than larger reef fish taxa (Goldman & Talbot 1976, Ackerman & Bellwood 2000), the turnover rate of this biomass may be significant in reef processes.

With an increasing popularity of modelling reef energetics in order to predict fisheries yields (eg. Pauly & Christensen 1992, Van Rooij et al. 1998), there is an urgent need for empirical data on the trophic biology, ecology and life-histories of small, cryptic reef fishes in order to understand the ramifications of neglecting them from these models. The most abundant taxa of small, cryptic fishes on Indo-Pacific reefs are from the families Gobiidae, Blenniidae and Apogonidae (Brock 1982, Munday & Jones 1998, Ackerman & Bellwood 2000). However, virtually nothing is known of the life histories, trophic biology and ecology of these taxa (Munday & Jones 1998).

Apogonids form the major component of nocturnal planktivore assemblages on Indo-Pacific reefs (Hobson 1991). Whilst diurnal planktivores have received much attention on coral reefs (Nagelkerken et al. 2000), little is known of the role of nocturnal planktivores in reef processes. The majority of our knowledge of the role of nocturnal planktivores in reef processes stems form work in the Caribbean (Hobson 1991), particularly from studies of the family Haemulidae (e.g. Meyer & Schultz 1985, Helfman 1993, Nagelkerken et al. 2000). Data suggests that nocturnal planktivores are likely to be functionally distinct from diurnal planktivores in two major aspects: firstly, most nocturnal planktivores consume relatively large prey of reef origin. This prey consists mostly of plankton that emerges from the substrate into the water column at night. By contrast, diurnal planktivores consume relatively small prey of oceanic origin (Hobson 1991). Secondly, whilst the majority of diurnal planktivores feed in the water column directly above their resting sites, nocturnal planktivores generally move into other habitats to feed (Hobson 1991), often migrating large distances on nocturnal forays (Helfman 1993, Burke 1995). However, the role of nocturnal planktivores on

Indo-Pacific reefs may be quite different to that observed in the Caribbean. Indo-Pacific nocturnal planktivore assemblages are dominated by apogonids rather than haemulids and the process of transferring material between seagrass communities and the reef may not be applicable to most Indo-Pacific coral reefs. Since apogonids form the major component of nocturnal planktivore assemblages on Indo-Pacific reefs, data on their role in reef processes will greatly improve our understanding of this trophic pathway.

Apogonids are highly abundant on Indo-Pacific reefs, commonly ranking second to third highest of all reef fish families (Bellwood 1996). They are also one of the most speciose reef fish families, with more than 100 species from 18 genera recorded form the Great Barrier Reef alone (Randall et al. 1997). Apogonids are ubiquitous in tropical, sub-tropical and temperate marine environments, occurring in a range of habitats from estuaries to ocean depths of up to several hundred metres (Allen 1993). However, the greatest diversity and abundance of apogonids is encountered on tropical Indo-Pacific reefs (Allen 1993).

Preliminary aging data suggests that apogonids may be relatively short-lived compared to other reef fish families, with maximum longevities of only 4 months reported in *Rhabdamia gracilis* from the Solomon Islands (Milton & Blaber 1995) and only 4 to 6 months in *Foa brachygramma* from Green Island, Great Barrier Reef (Fisher 1991). Longevity estimates for other, similar-sized taxa, such as pomacentrids, suggest maximum lifespans of generally greater than 10 years (e.g. Doherty & Fowler 1994, Kohda 1996). If apogonid populations are turning over at higher rates than other reef fish taxa, their contribution to reef energy budgets may be far greater than their standing biomass would suggest.

Whilst little dietary information is available for Indo-Pacific apogonids, available data suggests that prey is consumed from both reef and non-reef sources, including open water, sand and seagrass habitats (Chave 1978, Fisher 1991, Vivien 1975). It is possible, therefore, that apogonids are responsible for a net flux of material between habitats. Apogonids may also be significant predators of demersal plankton (Vivien 1975), a trophic pathway which has received little attention on coral reefs (Parrish 1989).

Much of the research on apogonids to date has examined their breeding behaviour (e.g. Kuwamura 1985, Okuda 1997). Apogonids are mouth-brooders, with males holding egg clutches for periods of approximately 3 to 5 days before eggs hatch and are released into the plankton. Since males hold numerous clutches of eggs throughout the spawning season, and do not usually feed during brooding, their condition rapidly deteriorates as the spawning season progresses (Okuda 1996). Female apogonids have been reported to exhibit similar rates of deterioration during the spawning season due to a high output of gametes (Okuda 2001). The high output of gametes is evident in apogonids having possibly one of the highest recruitment rates of all reef fish families (Doherty 1991). This suggests the possibility that apogonids may have life-histories that involve rapid turnover rates of populations.

Only one study has attempted to examine the role of apogonids in reef processes. Vivien (1975) examined the distribution and feeding ecology of apogonids from Tulear, Madagascar, in an attempt to infer their role in reef tropho-dynamics. Vivien (1975) reported that most species of apogonids were nocturnal, with the possibility of diurnal or crepuscular feeding in at least two species. Apogonids were found to be significant predators of emergent plankton and benthic invertebrates and may have been involved in the transport of material between habitats. Whilst this study was mainly concerned with diet, it provides a baseline of information regarding possible roles of apogonids in reef processes.

Given the potential importance of apogonids in reef processes, the specific aims of this thesis are to:

i) Quantify the spatial patterns of abundance and biomass of apogonids on reefs.

ii) Examine the strength of resting site fidelity.

iii) Investigate patterns of nocturnal foraging and diet.

iv) Quantify rates of faeces deposition at resting sites.

v) Quantify the turnover rates of apogonid populations.

Chapter 2 investigates the spatial patterns of abundance and biomass of apogonids on reefs to understand where they are likely to have the greatest influence in reef processes. This is achieved through daytime visual censuses over a reef-wide scale at two different reef systems. This study will also provide minimum estimates of apogonid abundance and biomass on reefs for incorporation into later models of energy transfer.

Chapter 3 investigates the strength of resting site fidelity in apogonids. If apogonids return to the same resting sites on a daily basis they may be responsible for providing a predictable, localised resource for detritivore communities and diurnal predators. The strength of resting site fidelity is examined through large-scale tagging and monitoring studies in three common species.

Chapter 4 evaluates nocturnal foraging patterns and diet. If apogonids move between diurnal resting sites and nocturnal foraging grounds in other habitats they are likely to play an active role in nutrient and energy transfer on reefs. A direct comparison of day and night distribution patterns is used to examine foraging movements. The relative importance of apogonids in transferring material between open water communities and the reef versus recycling material within reef systems will depend largely upon the origin of prey types. Therefore diet is also assessed in a range of species to determine whether prey taxa are primarily of reef or non-reef origin.

Chapter 5 investigates the transfer of resources from apogonids to other trophic levels. If apogonids are using the same resting sites on a daily basis they may provide localised, spatially predictable resources for detritivore communities and diurnal piscivores through: a) defecation, and b) predation. The transfer of resources to detritivore communities is examined through quantifying defecation rates in a range of species. The transfer of resources to higher trophic levels is assessed through an examination of turnover rates and population dynamics in apogonids.

Chapter 6 synthesises the results of each chapter and compares the importance of apogonids in each identified role with other reef fish taxa and with whole reef processes. This synthesis will produce an overall estimate of the role and importance of apogonids on coral reefs.

CHAPTER 2: PATTERNS OF DISTRIBUTION, ABUNDANCE AND BIOMASS OF APOGONIDS ON REEFS.

2.1 INTRODUCTION

Patterns of distribution and abundance of fishes on coral reefs vary widely over many spatial and temporal scales (Williams 1991). In order to understand the role of any group on coral reefs, therefore, it is first necessary to identify the spatial scales at which they are likely to influence reef processes (Connell and Kingsford 1998). The first step in understanding the role of apogonids in reef processes is a quantitative description of their patterns of distribution and abundance. Currently, little information is available on the within-reef abundance patterns of apogonids. Published accounts of apogonid distributions to date have been largely qualitative (Vivien 1975, Chave 1978, Allen 1993) or have focused on only one habitat within a reef system (Luckhurst & Luckhurst 1978, Greenfield and Johnston 1990, Stewart & Jones 2001). Additionally, there is no published information on patterns of biomass of apogonids on reefs.

Apogonids often form dense, multispecific schools at daytime resting sites on the reef (Greenfield and Johnson 1990, Allen 1993). If apogonids feed in a range of habitats, then return to familiar shelter sites, they may play a significant role in the concentration of energy and nutrients at localised, predictable sites on the reef. This may have important implications for both detritivore communities (cf. Bray et al. 1981) and diurnal predators (Stewart & Jones 2001). This study, therefore, aims to describe diurnal patterns of abundance and biomass of apogonids over a range of spatial scales. Data obtained will identify locations on reefs where resting schools of apogonids are likely to have the greatest influence on diurnal predators and detritivore communities.

2.2 MATERIALS AND METHODS

Pilot studies to determine optimal transect dimensions were conducted at Orpheus Island ($18^{0}38$'S, $146^{0}29$'E), central Great Barrier Reef (GBR), during July 1997. During pilot studies, the numerical abundances of apogonids were estimated over a range of transect lengths: 30m, 50m, 100m and 200m. A two metre transect width was preselected since this was the widest transect dimension that still allowed adequate searching for apogonids within resting sites, whilst moving along transects. Data were analysed using a power analysis, taking into consideration factors such as time taken to lay and remove transects. Given the highly aggregated distribution patterns of apogonids, transects of 200m x 2m were found to be the most statistically powerful and logistically feasible sampling method and were adopted for the main study.

Visual censuses of apogonids were conducted at One Tree Reef ($23^{0}30$'S, $153^{0}67$'E), in the southern GBR, and at Lizard Island ($14^{0}40$'S, $145^{0}28$'E), in the northern GBR, Australia. One Tree Reef consists of a platform reef with a shallow, ponding lagoon surrounded by a continuous outer reef rim. Lizard Island is a high continental island with a well developed fringing reef and sheltered lagoon. Censuses were conducted between 0800 and 1700 hrs during July 1998 at One Tree Reef and during August 1998 at Lizard Island. Transects were laid down on the reef at least 5 mins prior to the commencement of surveys. Transects were censused slowly (~ 40 min per transect), allowing time to search within shelter sites (caves and branching corals).

Censuses were conducted within each of three levels of exposure at One Tree Reef (Fig. 2.1) and Lizard Island (Fig.2.2). Exposed sites were on southerly to easterly facing reefs, and thus received prevailing south-easterly trade winds. Sheltered sites were on northerly to westerly facing reefs and were generally protected from south-easterly trade winds. Lagoonal sites represented the most protected habitats at each location. Within each level of exposure, three reef zones were sampled (flat, slope and base). Within each reef zone, three replicate transects were laid randomly within each of three sites.

During censuses, all apogonids observed within transects were identified and their standard length (SL) and the microhabitat within closest proximity to each fish recorded. Fish were recorded from the "water column" microhabitat if they were located further than 30 cm from the substratum. Standard length estimates were divided into 5 mm size classes for fish < 30 mm SL, 10 mm size classes for fish 30 mm to 100 mm SL, and 20 mm size classes for fish > 100 mm SL. At regular intervals throughout the survey period, visual size estimates were checked by estimating the SL of randomly chosen apogonids of a range of species and sizes underwater. These fish were then collected with clove oil or small hand spears and placed in individual, labelled bags and measured to compare with recorded visual estimates. Biomass estimates were calculated using visual SL estimates and length to weight conversions calculated for a range of species collected from One Tree Reef and Lizard Island (Table 2.1). In the few cases where length-weight conversions were not available for a particular species, the general relationship for the genus was used.

Table 2.1: Length-weight relationships used in calculating biomass estimates from visual census data from One Tree Reef and Lizard Island.

Species	**Standard Length (mm) to Weight (gm) Conversion**	**Regression Coefficient**	**Sample Size (n)**
Apogon cyanosoma	$W = 1 \times 10^{-5}\ SL^{3.28}$	0.99	53
Apogon doederlini	$W = 1 \times 10^{-5}\ SL^{3.22}$	0.99	144
Apogon exostigma	$W = 5 \times 10^{-6}\ SL^{3.39}$	0.98	55
Apogon fragilis	$W = 4 \times 10^{-6}\ SL^{3.48}$	0.99	69
Apogon guamensis	$W = 4 \times 10^{-6}\ SL^{3.43}$	0.96	46
Apogon leptacanthus	$W = 4 \times 10^{-6}\ SL^{3.59}$	0.98	56
Archamia leai	$W = 5 \times 10^{-6}\ SL^{3.47}$	0.99	67
Cheilodipterus artus	$W = 1 \times 10^{-5}\ SL^{3.20}$	0.99	109
Cheilodipterus macrodon	$W = 6 \times 10^{-6}\ SL^{3.30}$	0.99	74
Cheilodipterus quinquilineatus	$W = 1 \times 10^{-5}\ SL^{3.20}$	0.99	165
Rhabdamia gracilis	$W = 3 \times 10^{-5}\ SL^{2.97}$	0.96	34
Apogon spp.	$W = 1 \times 10^{-5}\ SL^{3.24}$	0.99	466
Archamia spp.	$W = 8 \times 10^{-6}\ SL^{3.33}$	0.98	91

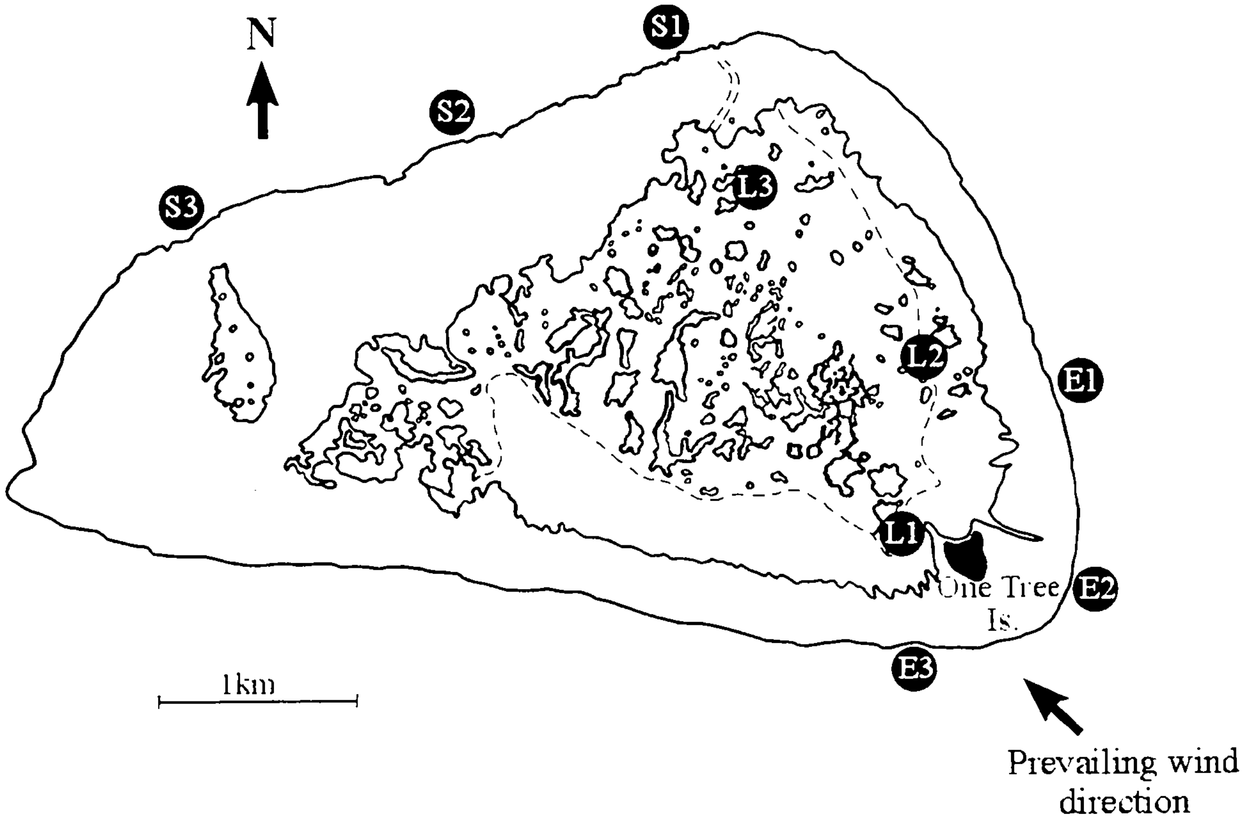


Fig. 2.1. One Tree Reef study sites. L1, L2, L3 - Lagoonal sites; S1, S2, S3 - Sheltered sites; E1, E2, E3 - Exposed sites.

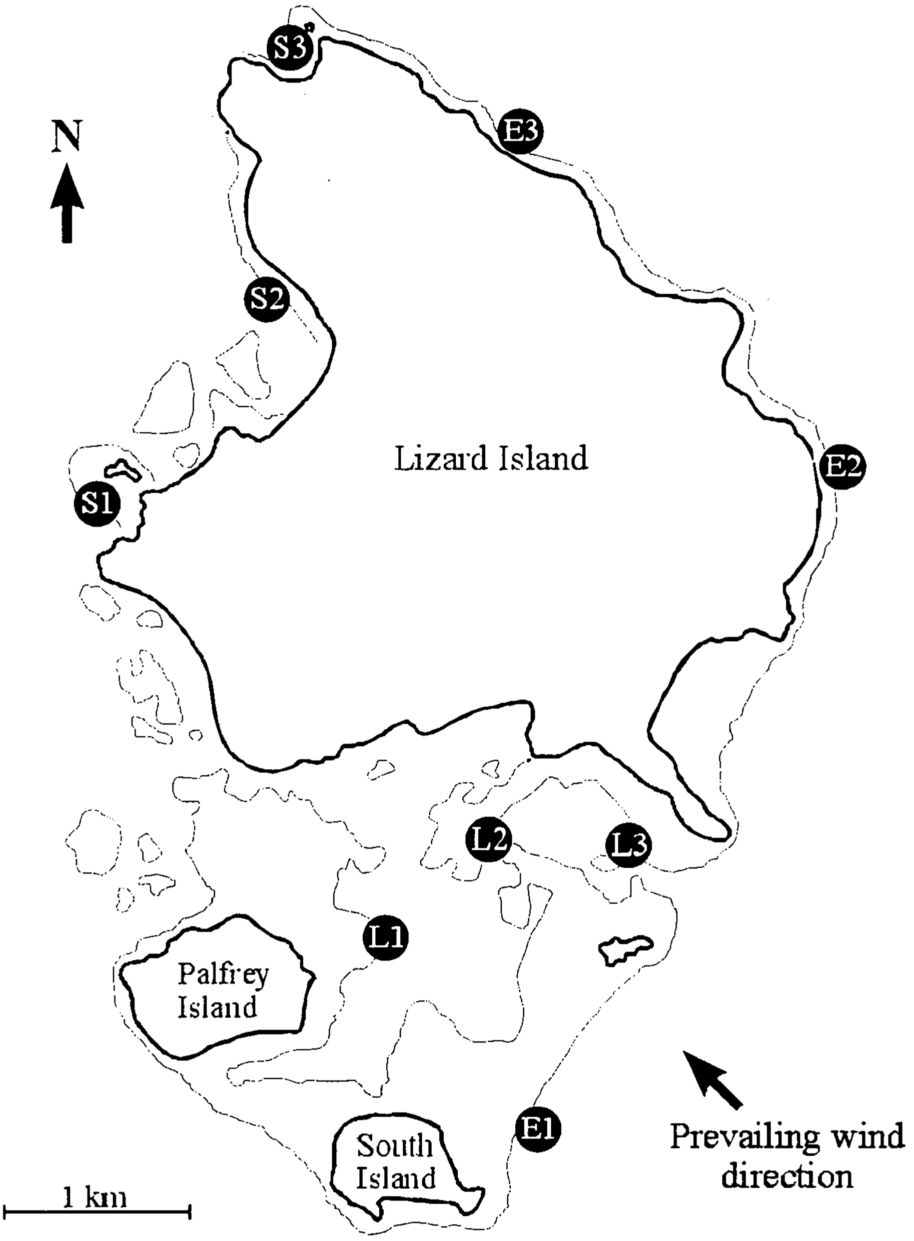


Fig. 2.2. Lizard Island study sites. L1, L2, L3 - Lagoonal sites; S1, S2, S3 - Sheltered sites; E1, E2, E3 - Exposed sites.

2.3 ANALYSES

Visually estimated size distributions of a range of apogonids were compared to their measured size distributions using chi-square tests of independence for each location. Patterns of apogonid abundance and biomass were examined separately using 3-way ANOVA's involving the fixed factors: location, exposure and reef zone. Few apogonids were ever recorded from reef flat habitats and this zone was therefore not included in the analysis. In order to increase the interpretability of ANOVA results and to enable ANOVA assumptions to be met, transects were pooled within each site and a mean value of overall apogonid abundance or biomass per site was used as a replicate in the analyses. Data were examined for normality and heteroscedasticity using Q-Q plots and residual plots. Data were then $\log_{10}(x+1)$ transformed to meet ANOVA assumptions. Significant differences found in the ANOVA were further examined using Bonferroni post-hoc multiple comparisons. The overall mean SL and mean weight of apogonids were compared between One Tree Reef and Lizard Island using one-way ANOVA's. Patterns of broad-scale habitat use (level of exposure and reef zone) were examined using Principal Component Analyses of a covariance matrix of $\log_{10}(x + 1)$ transformed data. Since no apogonids were recorded from exposed reef flats at One Tree Reef, these sites were removed from the analysis. Habitats were then grouped on bi-plots based on significant clusterings (Sandland & Young 1979) identified in a Ward's cluster analysis of Euclidean distances. Patterns of microhabitat use were also examined using Principal Component Analyses. However, to avoiding confounding the effects of location and exposure, only lagoonal sites were examined in analyses. All analyses were carried out using SPSS™ v. 9.0.

2.4 RESULTS

In total 4,514 apogonids from 3 genera and 16 species were recorded in daytime visual censuses at One Tree Reef, whilst 17,922 fish from 5 genera and 20 species were recorded from Lizard Island. There was no significant difference between the visually estimated size distributions and the measured size distributions of 94 apogonids collected from One Tree Reef (chi-squared = 2.25, df = 11, p > 0.99) (Fig. 2.3a) and 87 apogonids collected from Lizard Island (chi-squared = 2.67, df = 11, p > 0.99) (Fig. 2.3b).

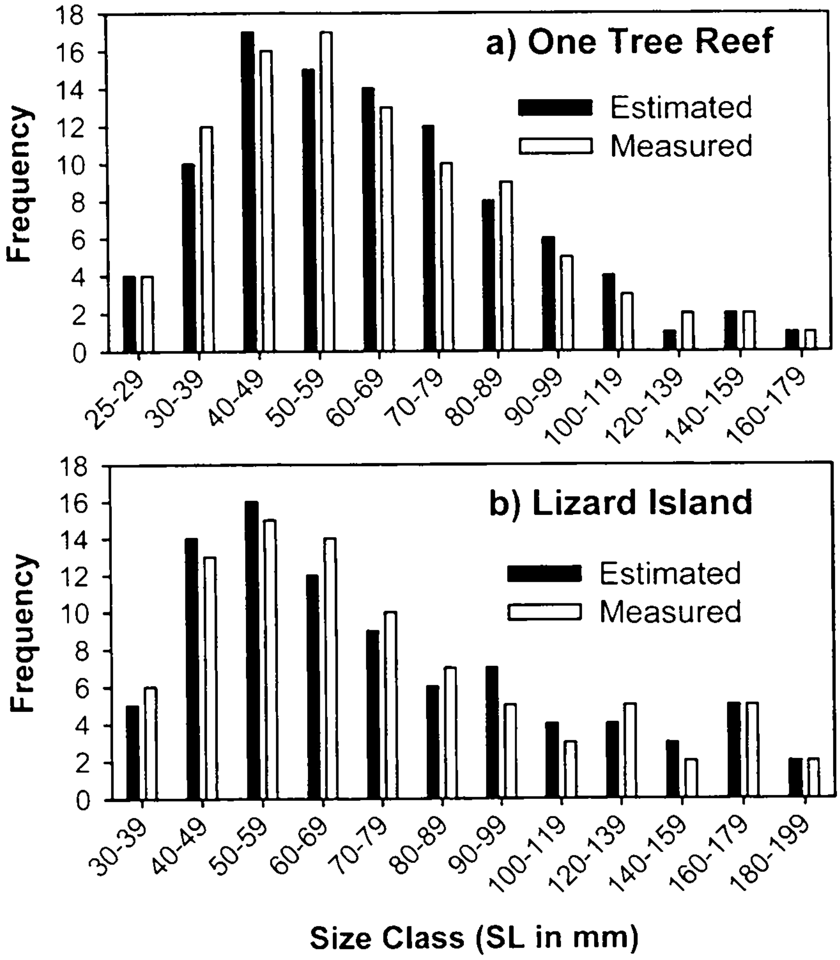


Fig. 2.3. Underwater visual standard length estimates versus laboratory measured lengths of a range of species of apogonids collected from a) One Tree Reef and b) Lizard Island.

Surveys indicated that Lizard Island contained a significantly higher abundance of apogonids per m^2 than One Tree Reef within each zone and level of exposure (ANOVA, df = 1, F = 57.196, $p < 0.001$) (Fig. 2.4a). Data also suggested a significant difference in apogonid abundance between each level of exposure within each of One Tree Reef and Lizard Island (ANOVA, df = 2, F = 137.5, $p < 0.001$) (Fig. 2.4a). At One Tree Reef, censuses at lagoonal sites recorded approximately 3 times as many apogonids as sheltered sites (Bonferroni test, $p < 0.001$) and more than 12 times as many apogonids as exposed sites (Bonferroni test, $p < 0.001$). At Lizard Island, censuses at lagoonal sites recorded approximately 4 times as many apogonids as sheltered sites (Bonferroni test, $p < 0.001$) and approximately 38 times as many apogonids as exposed sites (Bonferroni test, $p < 0.001$) (Fig. 2.4a). There was also a significant difference in the abundance of apogonids between zones within each level of exposure (ANOVA, df = 1, F = 9.595, $p < 0.01$), with the lowest numbers of apogonids recorded from reef flats in all cases, and similar numbers recorded from reef slopes and bases.

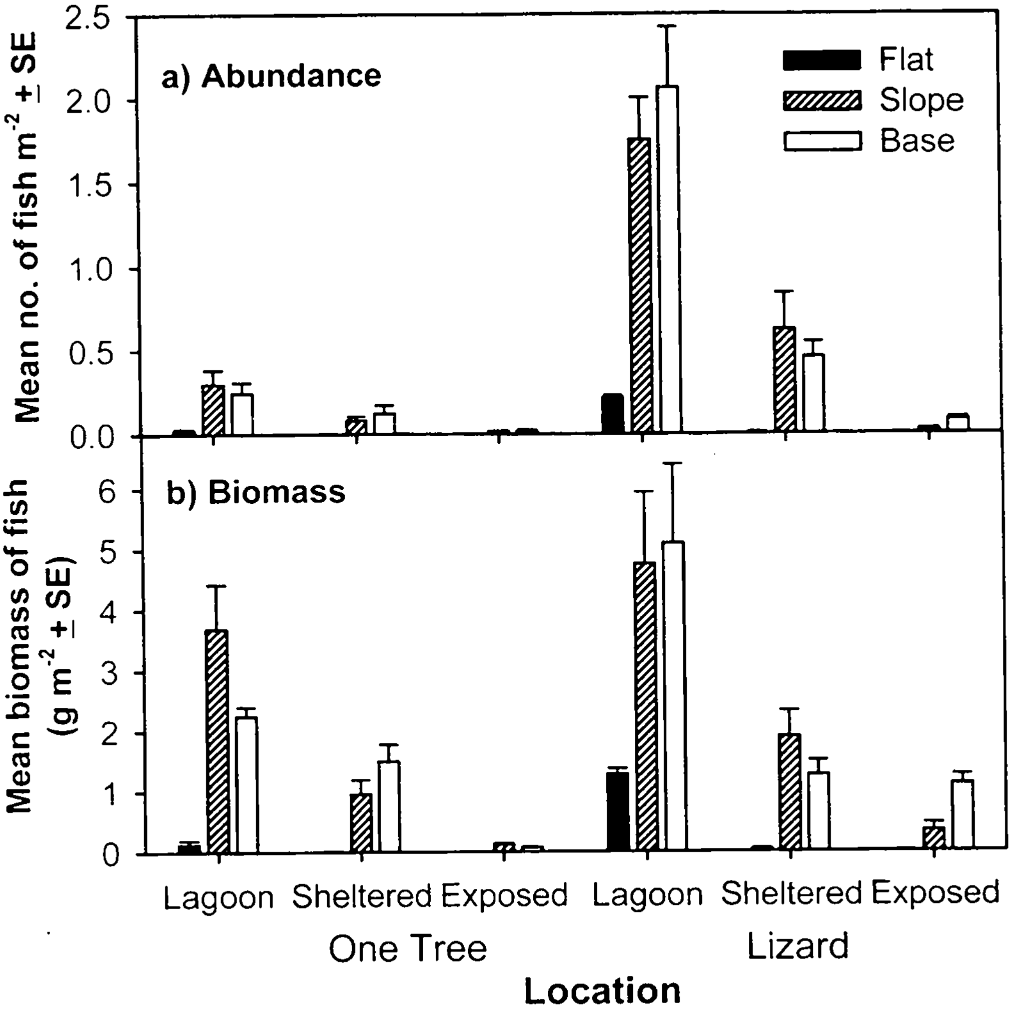


Fig. 2.4. Mean relative abundance and biomass of all apogonid species per m^2 within each level of exposure and zone at One Tree Reef and Lizard Island (n = 3 sites per habitat).

The overall mean size of apogonids at One Tree Reef (SL: 47.3 ± 0.1 mm) was significantly greater than at Lizard Island (SL: 34.4 ± 0.1 mm) (ANOVA df = 1, F = 2605 $p < 0.001$). Similarly, the mean weight of apogonids at One Tree Reef (6.6 ± 0.1 g) was also significantly greater than at Lizard Island (2.9 ± 0.1 g) (ANOVA, df = 1, F = 1526, $p < 0.001$). Patterns of apogonid biomass (Fig. 2.4b) were similar to those of abundance (Fig. 2.4a). However, an ANOVA of biomass data revealed a 3-way interaction between the factors: location, exposure and zone (ANOVA, df = 2, F = 11.905, $p < 0.001$).

A principal component analysis of within-reef habitat use by apogonids at One Tree Reef revealed a distinct grouping of sites, related to the level of wave exposure (Fig. 2.5). PC1 explained 57.0% of the variation in the data and appeared to be largely driven by absolute apogonid abundance, which was low in all exposed sites and in lagoonal and sheltered reef flat sites, and high in lagoonal and sheltered reef base and slope sites. PC2 explained 18.0% of the variation in the data and appeared to be driven by the dominance of species which were characteristic of either sheltered or lagoonal habitats. The Ward's cluster analysis identified several major groupings: exposed slope and base sites grouped together with lagoonal and sheltered flat sites. Since no apogonids were recorded from exposed flats, these sites were excluded from the analysis. Lagoonal and sheltered base and slope sites formed a second group. Probability testing (Sandland & Young 1979) of a Ward's cluster analysis of sites indicated that the groupings were statistically significant ($p < 0.0001$, Fig. 2.6).

A comparable pattern was seen at Lizard Island, where PC1 explained 62.3% of the variation in the data and appeared to be driven by overall apogonid abundance within habitats. PC2 explained 12.4% of the variation in the data and appeared to be driven by the dominance of species assemblages reflective of either lagoonal or sheltered habitats. Again, within-reef habitat use revealed two major groupings of sites, related to level of wave exposure (Fig. 2.7). The first group was composed of all exposed sites, together with all reef flats. There was, however, the inclusion of one lagoonal reef slope site and one sheltered reef slope site in this group, indicated by a Ward's cluster analysis. The second group consisted of all other lagoonal and sheltered slope and base sites. These two groups were found to be statistically significant through probability testing of a Ward's cluster analysis ($p < 0.01$, Fig. 2.8).

Most species of apogonids were found sheltering in a range of microhabitats by day. In most instances, several species of apogonid shared the same shelter site and fish often occurred at shelter sites in large schools. At One Tree Reef, apogonids were most often recorded from microhabitats consisting of caves (58%) or branching *Porites* spp. coral (19%) (mainly *P. cylindrica*). Together with other forms of branching coral, these microhabitats contained 90% of apogonids recorded in all visual censuses (Table 2.2). At Lizard Island, the highest abundances of apogonids were recorded from branching *Porites* spp. coral (40%) and caves (23%), with a significant proportion of fish, (mainly *Rhabdamia gracilis* and *Archamia* spp.) recorded from the water column (18%) (Table 2.2). Within the One Tree Reef lagoon, a PCA of apogonid microhabitat associations showed that most species of apogonids were associated with a range of microhabitats, and that microhabitat associations were generally consistent among sites (Fig. 2.9). Only one species, *Apogon guamensis,* was consistently associated with a single microhabitat, *Porites* spp. branching coral. At Lizard Island, a PCA of microhabitat associations showed a similar pattern (Fig. 2.10). Most species were broadly associated with a number of habitats. However, three species appeared to be consistently associated with one or two habitat types. *Cheilodipterus macrodon* was primarily associated with caves, *Apogon bandanensis* was only found in *Porites* spp. branching coral and *Rhabdamia gracilis* was consistently found in either branching coral or the water column at all lagoonal sites.

Table 2.2: Number of apogonids recorded in each microhabitat type at One Tree Reef and Lizard Island.

	One Tree Island		**Lizard Island**	
Habitat	**No. of fish**	**% of total**	**No. of fish**	**% of total**
Caves	2626	58%	4125	23%
Branching *Porites* spp.	866	19%	7085	40%
Branching coral, other	608	13%	2789	16%
Sand	213	5%	394	2%
Open water	186	4%	3154	18%
Rubble	10	0.2%	0	0 %
Urchin spines	3	0.07%	0	0%
Foliose coral	2	0.04%	219	1.2%
Soft coral	0	0%	156	0.9%
TOTALS	**4514**		**17922**	

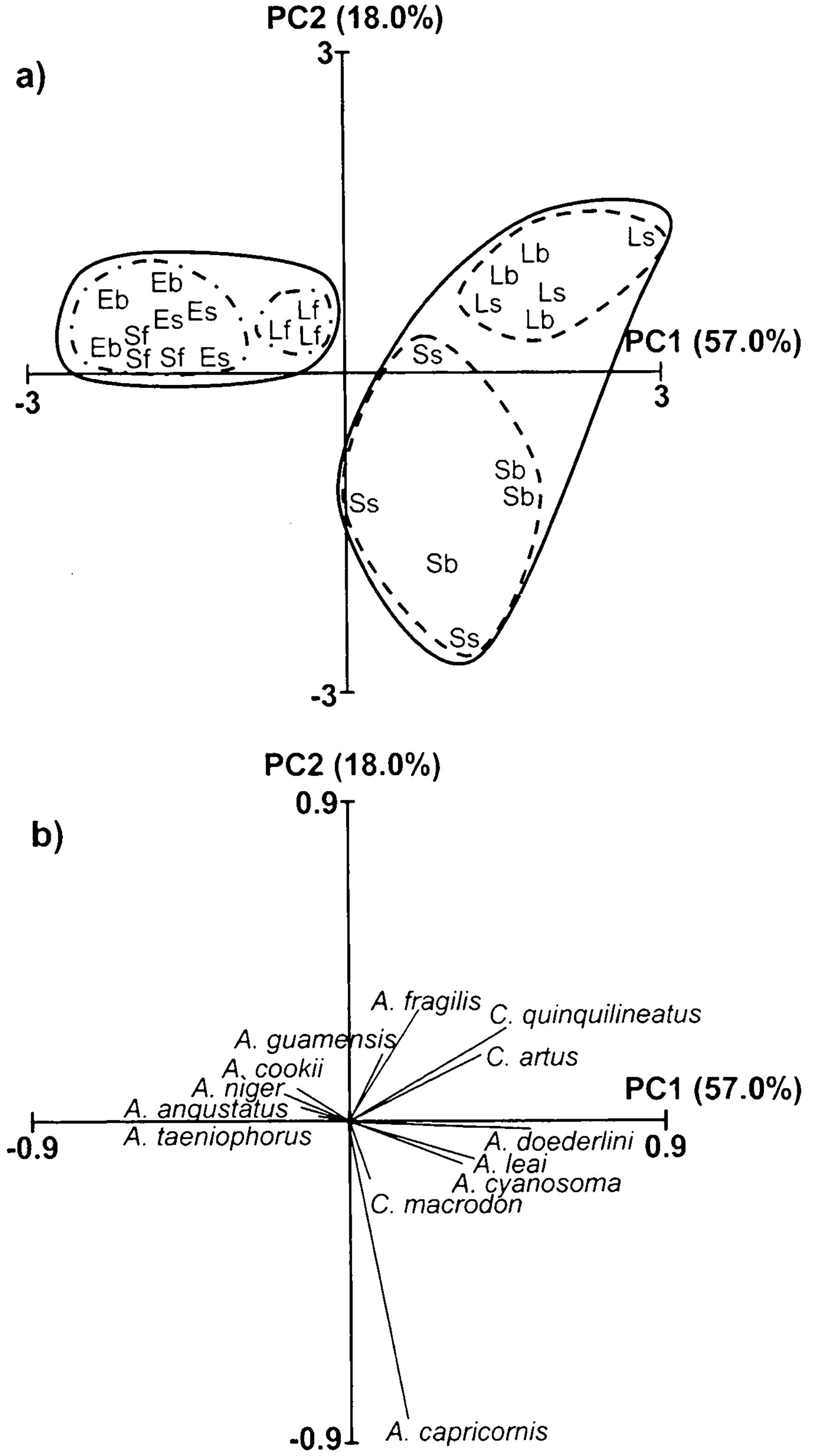


Fig. 2.5. Principal component bi-plot of habitat use by apogonids at One Tree Reef. a) Habitat eigenvalues. E - exposed, S - sheltered, L - lagoon; f - flat, s - slope, b - base. Solid line: cluster analysis split 1; Dashed line: cluster analysis split 2; Dot-dashed line: cluster analysis split 3 (for splits see Fig. 2.6). b) Species eigenvectors.

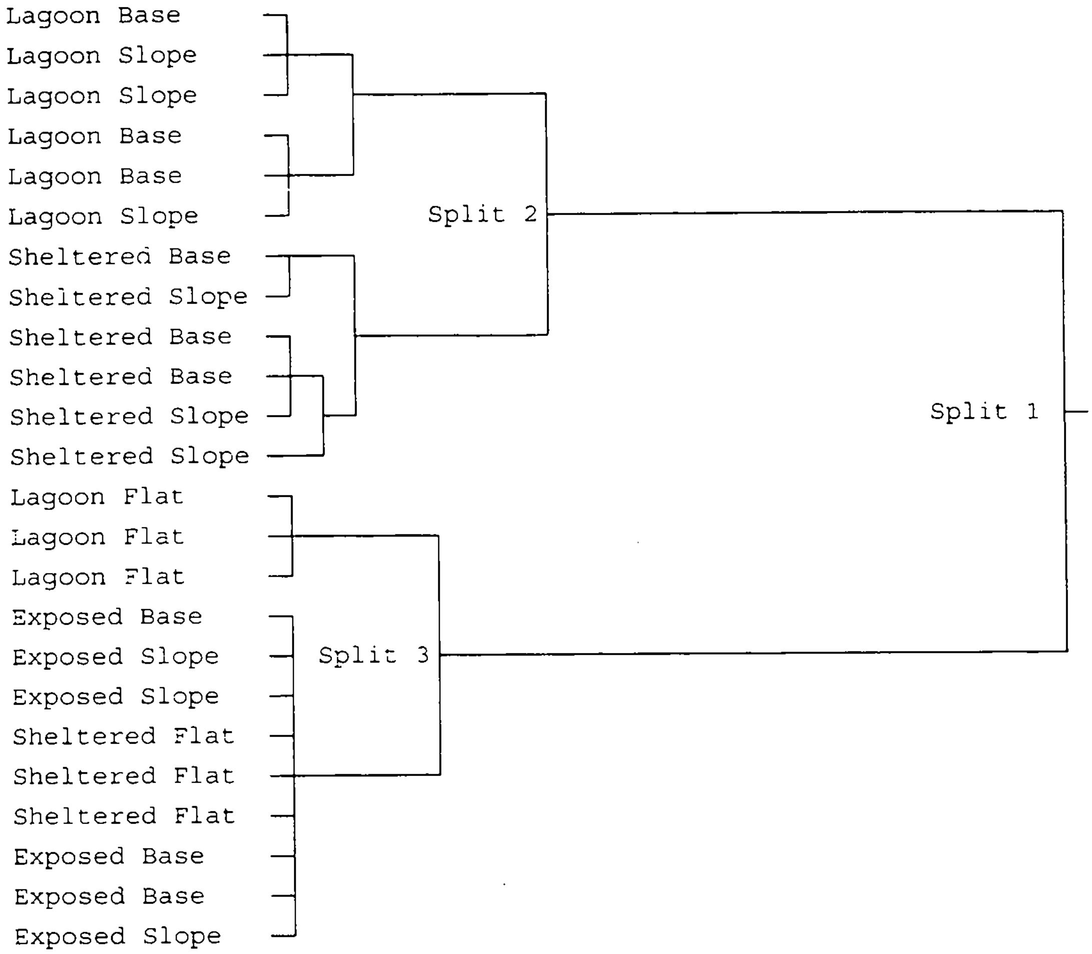


Fig. 2.6. Ward's Cluster Analysis of habitats at One Tree Reef based on apogonid species composition (n=3 sites). Probability analysis of fissions: Split 1, $p < 0.0001$; Split 2, $p < 0.01$; Split 3, $p < 0.01$; all other splits $p > 0.05$.

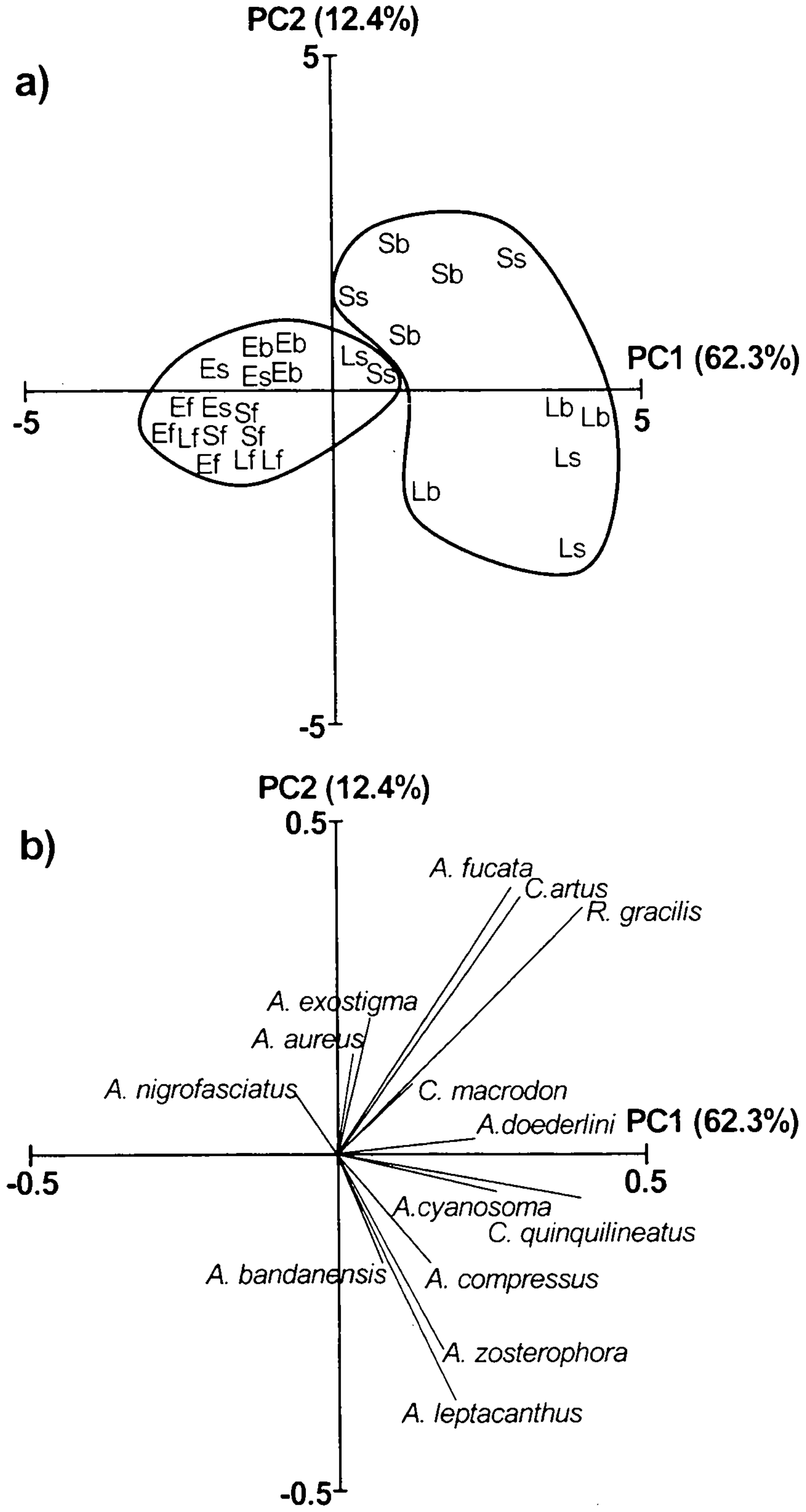


Fig. 2.7. Principal component bi-plot of habitat use by apogonids at Lizard Island. a) Habitat eigenvalues. E - exposed, S - sheltered, L - lagoon; f - flat, s - slope, b - base. Solid line: cluster analysis split 1 (for split see Fig. 2.8). b) Species eigenvectors.

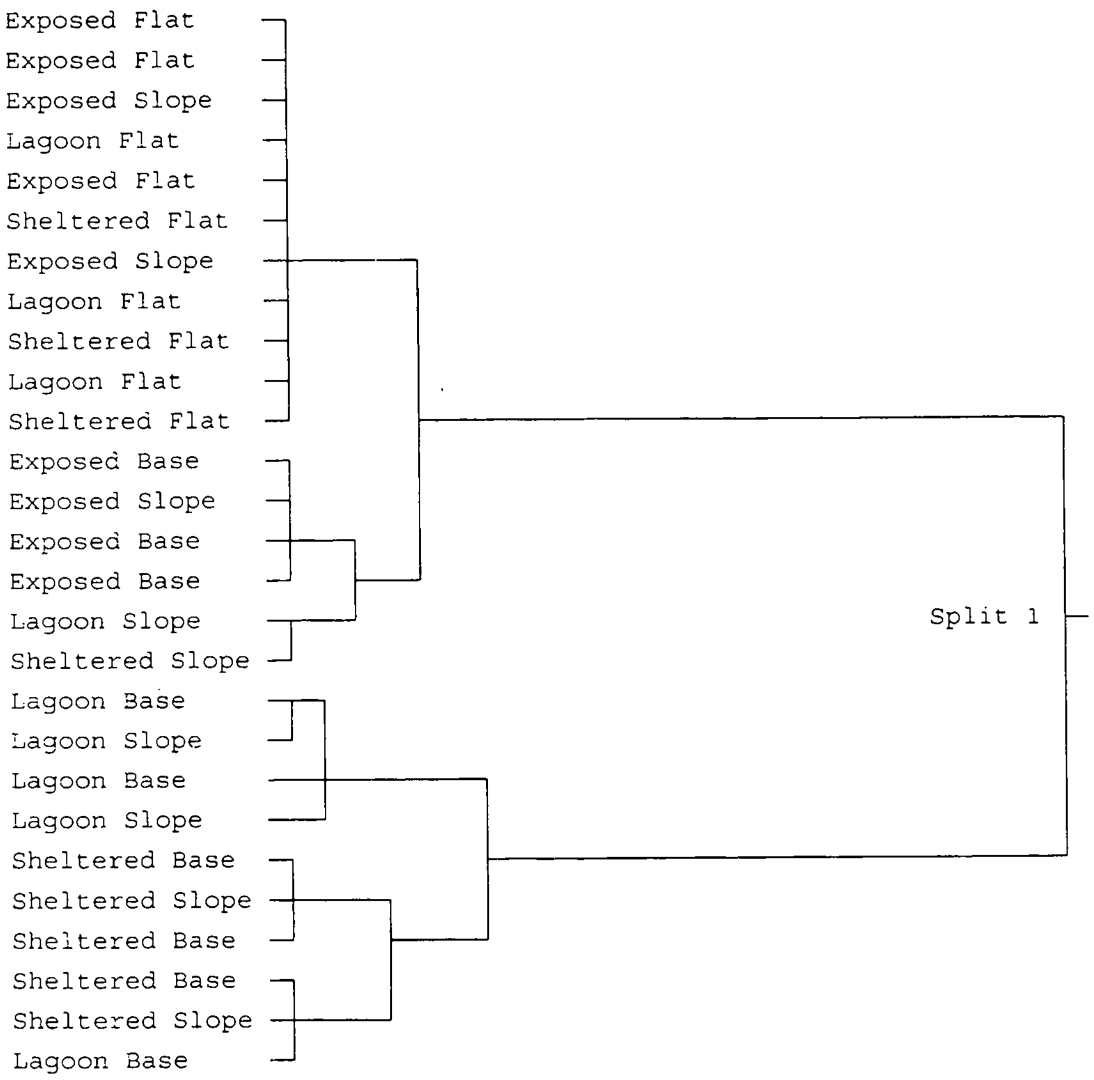


Fig. 2.8. Ward's Cluster Analysis of habitats at Lizard Island based on apogonid species composition (n = 3 sites per habitat). Probability analysis of fissions: Split 1, $p < 0.01$; all other splits $p > 0.05$.

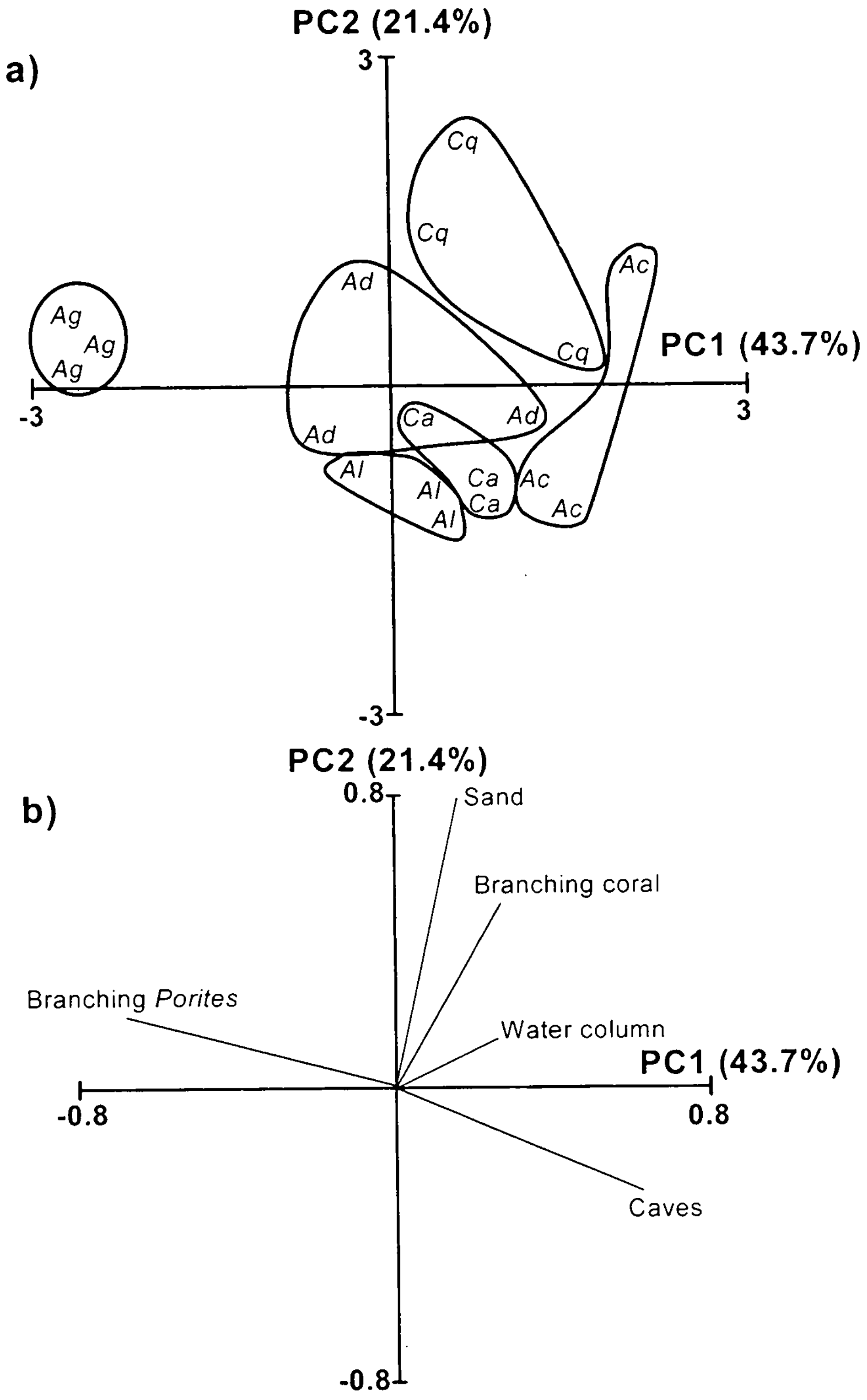


Fig. 2.9. Principal component analysis of microhabitat use by apogonids at One Tree Reef (n = 3 sites). a) Species eigenvalues. *Ac - Apogon cyanosoma, Ad - Apogon doederlini, Ag - Apogon guamensis, Al - Archamia leai, Ca - Cheilodipterus artus, Cq - Cheilodipterus quinquilineatus.* b) Microhabitat eigenvectors.

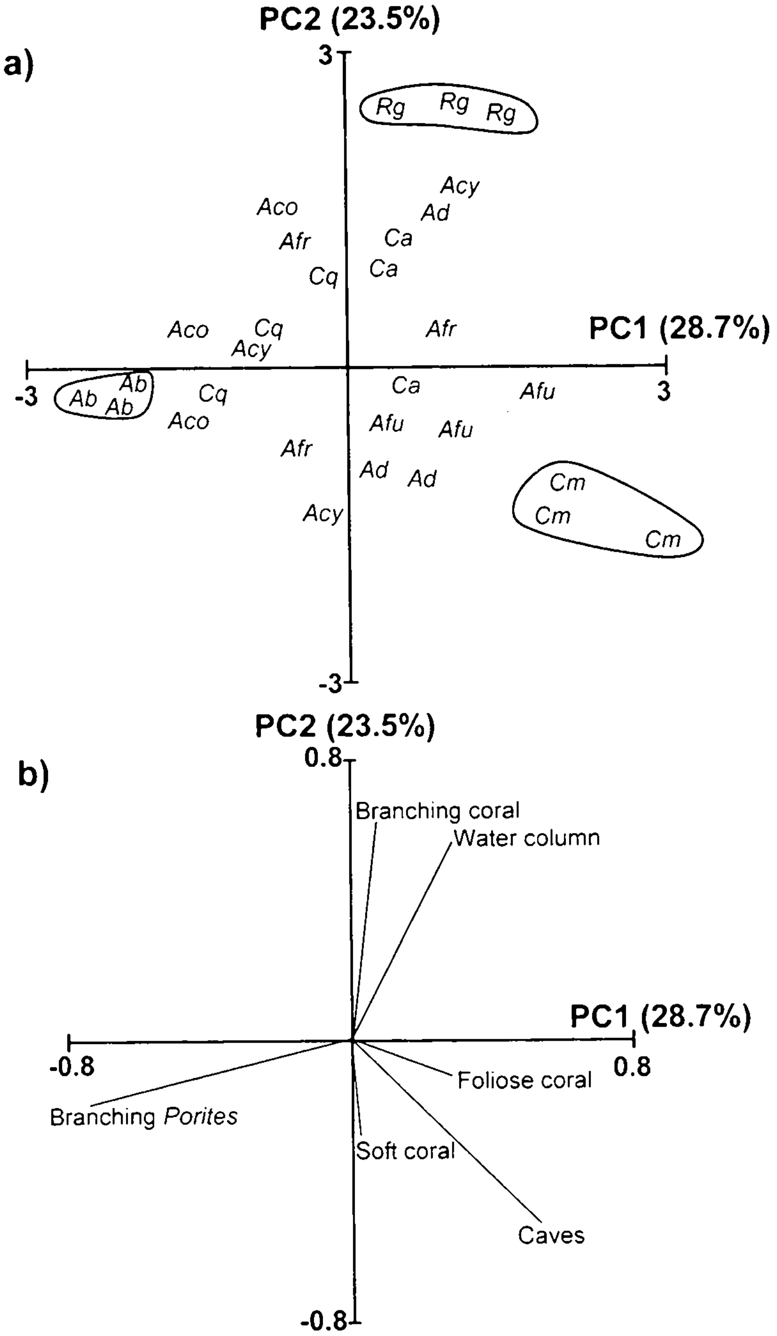


Fig. 2.10. Principal component analysis of microhabitat use by apogonids at Lizard Island (n = 3 sites). a) Species eigenvalues. *Ab - Apogon bandanensis, Aco - Apogon cookii, Acy - Apogon cyanosoma, Ad - Apogon doederlini, Afr - Apogon fragilis, Afu - Archamia fucuta, Ca - Cheilodipterus artus, Cm - Cheilodipterus macrodon, Cq - Cheilodipterus quinquilineatus, Rg – Rhabdamia gracilis.* b) Microhabitat eigenvectors.

2.5 DISCUSSION

Within-reef patterns of apogonid abundance were found to be most strongly influenced by the level of wave exposure among habitats, with peak abundances occurring in habitats subject to the least wave energy. These patterns are consistent with previous qualitative observations. Vivien (1975) noticed a general trend of higher apogonid abundance within the lagoon and back-reef habitats of Tulear, Madagascar, while Hobson and Chess (1978) found a strong correlation between apogonid abundance and water movement in the Marshall Islands. In addition, Chave (1978) found that 5 out of the 6 most common species of apogonids on Hawaiian reefs preferred calm waters.

Apogonids may show a preference for habitats with low water movement for several reasons. The underlying effect of habitat availability cannot be discounted. Exposed habitats may have a reduced availability of shelter sites such as branching corals, reducing the overall number of apogonids that could potentially use these habitats as resting sites. However, observations indicated that where suitable shelter sites were available within exposed and sheltered habitats (e.g. caves or large colonies of branching coral), they were often devoid of apogonids, whereas, comparable habitats within lagoonal sites were regularly occupied by apopogonid schools. These observations suggest that other factors may be structuring the distribution patterns of apogonids.

Apogonids may be relatively poor swimmers, and may therefore find it energetically expensive to combat the higher wave energy of exposed habitats used freely by other taxa. Although there is no data available on the swimming abilities of adult apogonids, data on immediate pre-settlement apogonids suggest that they are relatively poor swimmers compared with pre-settlement fish of other taxa (Stobutzki &

Bellwood 1997). Since censuses were conducted during the day, most apogonid species were recorded in their resting habitats. It seems likely that they would choose to rest in habitats where minimal energy is required to maintain their position. It is possible that apogonids rest in sheltered habitats in order to conserve energy, but then move into more exposed feeding habitats at night (*cf.* Gladfelter 1983, Fishelson & Sharon 1997). However, whilst apogonids have been suggested to move among reef zones within the same level of exposure to feed (e.g. Chave 1978, Fisher 1991), there is no evidence to suggest migrations of apogonids between levels of exposure to feed, as observed in other nocturnal taxa e.g. Pempheridae (Gladfelter 1979) and Holocentridae (Hobson 1972). It is more likely that apogonids rest and feed within the same level of exposure.

Peaks in apogonid abundance within the most sheltered habitats may also be related to food availability. Dietary studies indicate that the major prey items consumed by apogonids are demersal plankton (Hiatt and Strasburg 1960, Vivien 1975). These prey taxa generally reside within the substrate during the day and emerge into the water column at night (Hobson & Chess 1979). Hobson & Chess (1986) suggest that demersal plankton may be more abundant in habitats with low water movement in order to maintain their position within the reef system during emergence periods. Only one known study has attempted to quantify the abundance patterns of demersal plankton over a range of exposure levels on reefs. Alldredge & King (1977) estimated demersal plankton densities on the windward reef face and across various lagoon habitats at Lizard Island, GBR. Although Alldredge and King (1977) recorded the highest overall densities of plankton on the windward reef face outside the lagoon, the vast majority of these plankton were copepods, a group which form only a minor dietary component for apogonids (Vivien 1975). The prey taxa most commonly consumed by apogonids, (eg.

decapods, isopods and polychaetes) (Vivien 1975), were found to occur in highest abundance within lagoonal habitats (Alldredge and King 1977).

Studies of the distribution of diurnal planktivorous reef fishes also suggest abundance patterns are related to food availability. Prey consumed by diurnal planktivores is usually of oceanic origin (Hobson 1991). These prey are generally encountered in highest densities in reef habitats with high water movement, particularly exposed reef fronts (Hobson & Chess 1978, Hamner et al. 1988, Freidlander & Parrish 1998). Similarly, diurnal planktivore densities have also been found to peak in habitats with the highest degree of water movement (Hobson & Chess 1978, Thresher 1983, Parrish 1989, Freidlander & Parrish 1998). Whilst a relationship between apogonid abundance and food availability appears likely, it is still unknown whether this relationship is causative or consequential.

Apogonids were found to occur in very low densities on reef flats at all levels of exposure and where they did occur, were generally restricted to a few habitat-specific species (e.g. *A. angustatus*, *A. cookii* and *A. taeniophorus*). This may be due to the partial emergence of reef flats during spring low tides. Apogonids appear to be strongly attached to specific resting sites and may return to the same sites on a daily basis over several months to years (Kuwamura 1985, Okuda and Yanagisawa 1996, addressed in Chapter 2). It therefore appears unlikely that apogonids would use resting sites which become temporarily unavailable during certain tides. Whilst reef flats are used by many apogonid species at night for foraging (Vivien 1975, Chapter 4), these species generally reside within reef slope or base habitats by day (Chapter 4).

Patterns of apogonid biomass were similar to those of abundance, however, the overall difference between levels of exposure was less pronounced. This was due to the predominance of the largest species of apogonid, *C. macrodon*, in exposed habitats. *C.*

macrodon reaches twice the maximum size (220 mm TL, Randall et al. 1990) of other apogonid species and its presence at exposed sites disproportionately elevated biomass estimates. The average size and average weight of apogonids at One Tree Reef was considerably higher than at Lizard Island. Since censuses were conducted during winter at both sites, it was unlikely that recruitment pulses strongly influenced average size estimates. This disparity was more likely a result of species assemblage differences between One Tree Reef and Lizard Island. Many of the smallest apogonid species recorded in censuses (*Rhabdamia gracilis*, *Apogon fragilis* and *Archamia* spp.) were extremely common at Lizard Island but were rare or absent from One Tree Reef. Alternatively, latitudinal differences in fish demographics may cause differences in the maximum age and size reached at each location. A study of latitudinal gradients in the demographics of apogonids suggests that fish from higher latitudes tend to reach a larger maximum size and are generally longer-lived than conspecifics from lower latitudes (Marnane unpublished data). Therefore, apogonid populations from One Tree Reef may have a generally larger and older size and age structure than populations from Lizard Island.

Most apogonid species were found to use a broad range of resting microhabitats. In addition, many species were found sharing the same microhabitat as multi-specific schools. It appears that microhabitat type may be relatively unimportant to apogonids, providing it affords sufficient shelter from predators. It also appears that there may be limited competition for diurnal shelter sites, allowing several apogonid species to coexist within the same microhabitat. This view is consistent with the observations of Greenfield and Johnston (1990) who reported a large overlap in the resting microhabitats of apogonids from Belize and Honduras. By comparison, strong microhabitat segregation has been observed among species of apogonids when they are active at night (Chapter 3). It appears therefore, that apogonids may not compete strongly for shelter sites but may compete for foraging grounds or food resources.

Overall, this study suggests that patterns of apogonid abundance and biomass on reefs are primarily driven by the level of wave exposure among habitats. Apogonids are likely to be most important in reef processes within areas of low wave energy, particularly reef lagoons. Their high abundances suggest they are an important part of reef energetics, however, due to their mostly cryptic diurnal behaviour, apogonids remain one of the least studied of the major groups of reef fishes. This study forms the framework for later chapters by identifying the spatial scales over which to concentrate further research into the role of apogonids in reef processes.

CHAPTER 3: THE STRENGTH OF RESTING SITE FIDELITY IN APOGONIDS

3.1 INTRODUCTION

Site fidelity and homing behaviour have been documented in a range of freshwater and marine teleosts (Quinn & Brodeur 1991). On coral reefs, many fishes have been reported to hold territories, return to home sites, or display restricted movement limited to home ranges (Sale 1978a). The movement of fish with respect to these sites will have consequences for population processes such as recruitment and mortality (Sale 1978b, Jones 1991), and trophic processes, such as energy and nutrient transfer between habitats (Meyer *et al.* 1983, Parrish 1989, Bellwood 1995a). Despite the relevance of fish movement to a wide range of reef processes, most reports of movement in reef fishes have been based on incidental or casual observations. Whilst a number of studies have reported the movement patterns of a small number of known individuals (e.g. Sale 1978a, Aldenhoven 1986, Eckert 1987), few workers have quantified movement in reef fishes directly through large-scale tagging programs followed by long-term observations (Jones 1991, Frederick 1997).

Most species of apogonids are nocturnal feeders, resting by day within caves or amongst branching coral. At resting sites apogonids often form dense, multi-specific aggregations (Greenfield & Johnson 1990, Chapter 2). If apogonids feed in a range of habitats and then return to the same sites daily, they may play an active role in the transport of material between feeding grounds and resting sites. Additionally, resting schools of apogonids may concentrate energy and nutrients in the form of fish biomass and faeces at specific sites on the reef. If the same sites are used over an extended period of time, schools of apogonids may represent not only localised, but predictable resources for predators and detritivore communities.

The objective of this study was to examine the relationship between apogonids and their resting sites in three common coral reef species: *Apogon doederlini*, *Cheilodipterus artus* and *Cheilodipterus quinquilineatus*. Resting site fidelity can be examined in two ways: by either measuring the long term persistence of individuals at home sites, or by examining the drive of individuals to return to home sites after being displaced (Hartney 1996). The specific aims of this study were therefore to i) monitor the persistence of tagged apogonids at resting sites on the reef over an extended period of time, and ii) to investigate whether tagged individuals, displaced from resting sites, return to their point of initial collection.

3.2 MATERIALS AND METHODS

Study sites and tagging

This study was carried out within the One Tree Reef lagoon, southern Great Barrier Reef, Australia ($152^0 03$'E, $23^0 30$'S), between July 1997 and Nov 1999. Adult *A. doederlini*, *C. artus* and *C. quinquilineatus* were collected using the anaesthetic clove oil (Munday & Wilson 1997) and hand nets whilst using SCUBA. These species are relatively common within the One Tree Reef lagoon, occurring at densities of up to at least 25, 3 and 5 adult fish per m^2 at resting sites for *A.doederlini*, *C. artus* and *C. quinquilineatus* respectively (Chapter 5). To aid resighting tagged fish, initial densities of tagged fish were generally greater than 50% of all adult apogonids present within tag site boundaries. Fish were tagged underwater using visual fluorescent implant tags (Northwest Marine Technologies Inc., USA), injected sub-cutaneously into the dorsal musculature. Six body positions and three tag colours were used to provide uniquely identifiable tag combinations for each fish. Since apogonids are relatively translucent, sub-cutaneous tags could be easily seen by day. Tagged fish were retained in mesh-covered containers at their site of initial capture (in the case of site fidelity studies), or at release sites (in the case of displacement studies), for at least 6 hours prior to release. This allowed fish to recover from handling, tagging and anaesthesia before being exposed to any risk of predation. Any specimens which, upon visual examination, had not fully recovered after this period were excluded from the experiments. All fish received at least two tags to ensure a greater tag persistence through time.

Tag loss

Rates of tag loss were investigated in a representative range of apogonid species which were readily obtainable from Orpheus Island, central GBR (near to the James Cook University aquarium facility) and could be easily maintained in aquaria. Specimens of *Apogon compressus*, *A. cyanosoma*, *A. leptacanthus*, *Archamia fucata* and *Cheilodipterus quinquilineatus* were held in 1000 l open-air aquaria (thus exposed to sunlight in water approximately 0.5 m in depth) in a recirculating seawater system within the James Cook University research aquarium. All fish were anaesthetised before receiving at least two tags during October 1997. Tag loss was then monitored for 8 months in *A. leptacanthus* and *A. fucuta* and for 16 months in *A. compressus*, *A. cyanosoma* and *C. quinquilineatus*.

Site fidelity

Site fidelity was examined by recording the persistence of tagged fish at resting sites over 16 months. Adult *A. doederlini* (45.6 - 57.6 mm standard length, SL), *C. artus* (78.4 - 98.2 mm SL) and *C. quinquilineatus* (52.0 - 72.6 mm SL) were collected from 10 sites within the One Tree Reef lagoon during July 1997. Tag sites ranged in size from approx. 9 m^2 to 18 m^2 and consisted of a small cave or a discrete clump of branching coral (*Porites cylindrica* and *Acropora spp.*) on micro-atolls and areas of contiguous reef (Fig. 3.1). Tagged fish were released at their point of collection between 1600 and 1800 hours (day 0). On the second day at liberty, between 0800 and 1600 hrs, the positions of tagged fish at resting sites were mapped with respect to a grid of permanent markers (plastic gardening tags attached to the substratum with cable ties). Initial densities of tagged fish, (*A. doederlini* n=199, *C. artus* n=134, *C. quinquilineatus* n=213), were based on day 2 censuses to exclude fish lost due to early tagging and handling induced mortality. Tagged fish were subsequently remapped on day 9 and then at 4-monthly intervals over a period of 16 months between 0800 and 1600 hrs. An area of approximately 50 m diameter surrounding tag sites was also examined at the same time to record any tagged fish which had strayed outside tag sites (greater than 1 m from tag site grids).

Displacement experiments

In order to investigate whether site fidelity was active or passive and to infer the relative importance of resting sites to each species, adult *A. doederlini*, *C. artus* and *C. quinquilineatus* were individually tagged then displaced distances of approximately 1 km and 2 km from collection sites (Table 3.1, Fig. 3.1). To facilitate resighting tagged fish, fish were collected from habitats dominated by the coral *Porites cylindrica*. Fish were transported to release sites in 15 litre mesh-covered containers and were held underwater in these containers until released. Controls, consisting of tagged specimens being transported then re-released at collection sites, provided an estimate of tagging and handling mortality. All fish were released between 2100 and 2230 hours. Tag sites were then examined each morning between 0800 and 1100 hours for three days post-release to record the presence and return of tagged fish. Fish that were sighted on day one or day two but not resighted on subsequent days were considered to have returned and were included in cumulative totals. Release sites were also surveyed the morning following release.

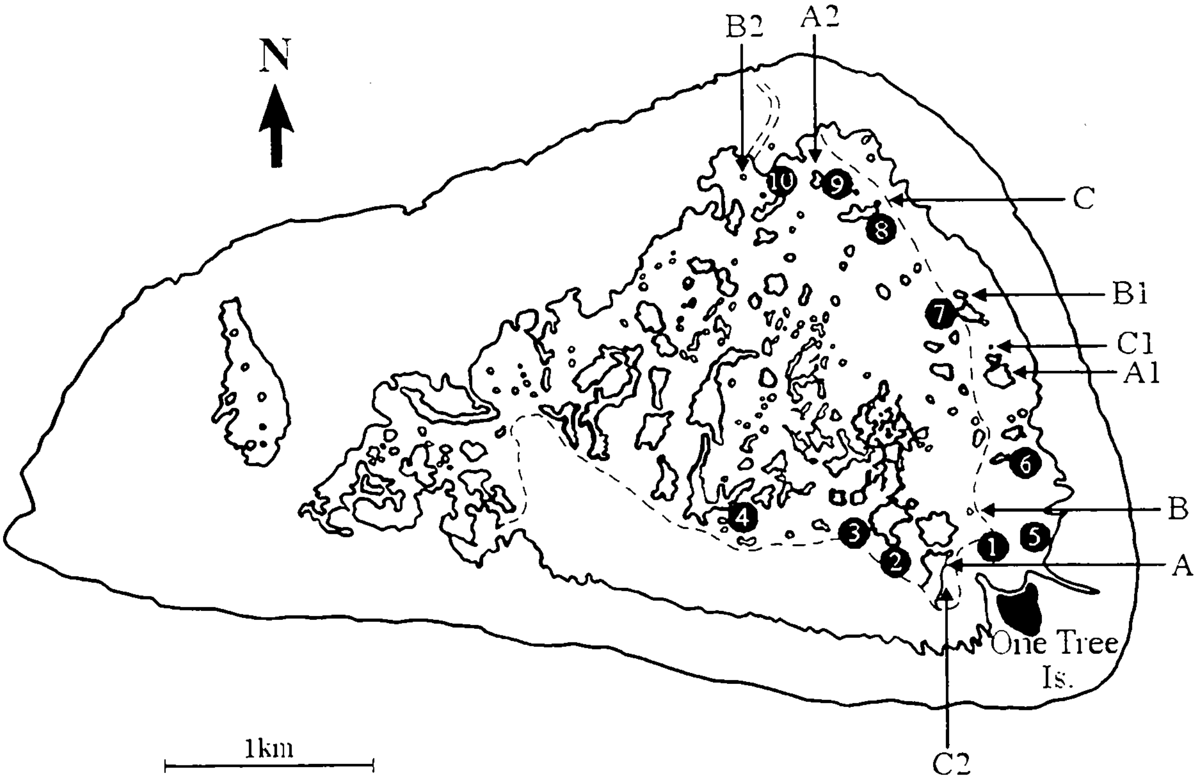


Fig. 3.1. Map of One Tree Reef Lagoon showing the location of sites used in site fidelity studies (nos. 1 to 10), and the location of collection and release site used in displacement experiments (A, B, C collection sites; A1, B1, C1 release sites at approximately 1km from collection sites; A2, B2, C2 release sites at approximately 2km from collection sites).

Table 3.1: Number of specimens tagged and released at the site of collection (control) and at distances of approximately 1 km and 2 km from collection sites.

Site	Distance displaced (km)	*C. artus* tagged (n)	*C. quinquilineatus* tagged (n)	*A. doederlini* tagged (n)
A (control)	0	15	19	23
A1	1.10	15	22	23
A2	1.97	16	19	26
B (control)	0	14	14	25
B1	1.03	15	16	25
B2	1.89	15	15	24
C (control)	0	11	16	19
C1	0.92	16	21	26
C2	2.03	17	20	27

3.3 ANALYSES

A 2-way ANOVA was used to compare the mean distance moved by tagged fish 4 months after release among species (fixed) and among sites (random). Four months represented the longest period of time after tagging that still had sufficient numbers of tagged fish remaining to permit an analysis among all species. Homoscedasticity and normality were examined using Levene's test and Q-Q plots respectively and data were $\log_{10}(x+1)$ transformed to meet assumptions. A *post-hoc* examination of significant effects was performed using Bonferroni tests. Displacement experiments were analysed using log-linear modelling of a 3x3x2x2 contingency table followed by stepwise selection (Agresti 1990) to investigate the influence of site, species and release distance on return success 3 days after displacement. Log-linear statistics quoted refer to changes in partial statistics caused by removing terms from higher order models in a hierarchical set. ANOVA, Levene's test, Q-Q plots and Bonferroni tests were carried out using SPSS™ v.9.0. Log-linear analysis was carried out using Statistica™ v.4.5.

3.4 RESULTS

Tag loss

After 8 months less than 4% of all fish held in aquaria had lost a single tag, and after 16 months less than 9% of all fish had lost a single tag (Table 3.2). None of the fish were observed to lose both tags throughout the course of the observations. After 16 months, tags had faded considerably but were still clearly identifiable. In the field, less than 10% of all tagged individuals were observed to lose a single tag over the course of experiments. Tagging was considered to have a minimal effect on fish behaviour, since many fish, both in the laboratory and field, were observed brooding eggs within 1 to 2 days of tagging.

Table 3.2: Rates of tag loss for double-tagged cardinalfishes held in aquaria for up to 16 months. (%) refers to the number of fish missing a tag out of the total number of fish still surviving after each time period. In all cases tag loss refers to the loss of 1 tag (no fish were observed to lose both tags).

		8 months		**16 months**	
Species	Specimens tagged (n)	Fish remaining	Fish missing tag	Fish remaining	Fish missing tag
A. compressus	37	31	2 (6.5%)	22	2 (9.1%)
A. cyanosoma	24	14	0	0	-
A. fucata	15	11	0	0	-
A. leptacanthus	18	12	0	0	-
C. quinquilineatus	32	25	1 (4.0%)	15	1 (6.7%)
Total	**126**	**93**	**3 (3.2%)**	**37**	**3 (8.1%)**

Site fidelity

There was a strong persistence of all three species of apogonids at resting sites over time (Fig. 3.2). However, all species showed a steady decline in the number of tagged fish remaining over time. Tagged specimens of *A. doederlini* were only recorded at resting sites for 8 months, whilst tagged *C. artus* and *C. quinquilineatus* persisted for at least 16 months. Tagged fish were recorded within an average of 36 to 79 cm of their initial resting positions over the course of the study (Fig. 3.3). There was no detectable difference among sites in the distance moved by fish after 4 months (F = 1.69, d.f. = 9, p = 0.15), however, there was a significant difference among species in the distance moved after 4 months ($F = 19.60$, d.f. = 2, $p < 0.0001$). *C. artus* showed the highest degree of movement after 4 months (mean = 78.6 cm, S.E. = 7.4), whilst *A. doederlini* (mean = 43.9 cm, S.E. = 3.7) and *C. quinquilineatus* (mean = 45.7 cm, S.E. = 2.8) showed the smallest degree of movement and were not significantly different from each other (Bonferroni test, $p = 0.98$). The results also suggest that there is no increase in the distance moved by tagged individuals from the initial tagging sites over time (Fig. 3.3).

During searches extending to a diameter of approximately 50 m around tag sites, only six individuals were ever found greater than 1 m from mapped tag sites (two *A. doederlini*, three *C. artus* and one *C. quinquilineatus*) and all of these individuals were within 5 m of initial recorded positions. These individuals were located outside tag sites during November and March surveys and three of these individuals were located in initial positions again during July surveys.

Displacement experiments

Individuals of all species displayed the ability to return over 2 km to their original tag sites in a single night after displacement (Fig. 3.4). New returns continued for at least 3 days post-release in all species, however, by the third day the mean rate of new returns had diminished to between 0% and 15% of the tagged fish resighted. The return success of tagged fish on the third day was significantly different among species ($\Delta G^2 = 16.41$, Δd.f. = 2 , $p < 0.0001$). *C. artus* had the greatest return success with 81% and 63% of tagged fish returned by the third day from distances of approximately 1 km and 2 km respectively, followed by *C. quinquilineatus* (65% and 52%) and *A. doederlini* (56% and 33%) (Fig. 3.4). Fish released at distances of approximately 1 km also had a significantly higher return success than those released at approximately 2 km ($\Delta G^2 = 12.26$, Δd.f. = 1, $p < 0.0001$). There were no significant effects of site on return success ($\Delta G^2 = 12.78$, Δd.f. = 24, $p = 0.97$), and no significant 3-way interactions involving site, species and distance released and their influence on return success ($\Delta G^2 = 0.43$, Δd.f. = 2, $p = 0.81$). No tagged fish were located at the release sites the morning after release.

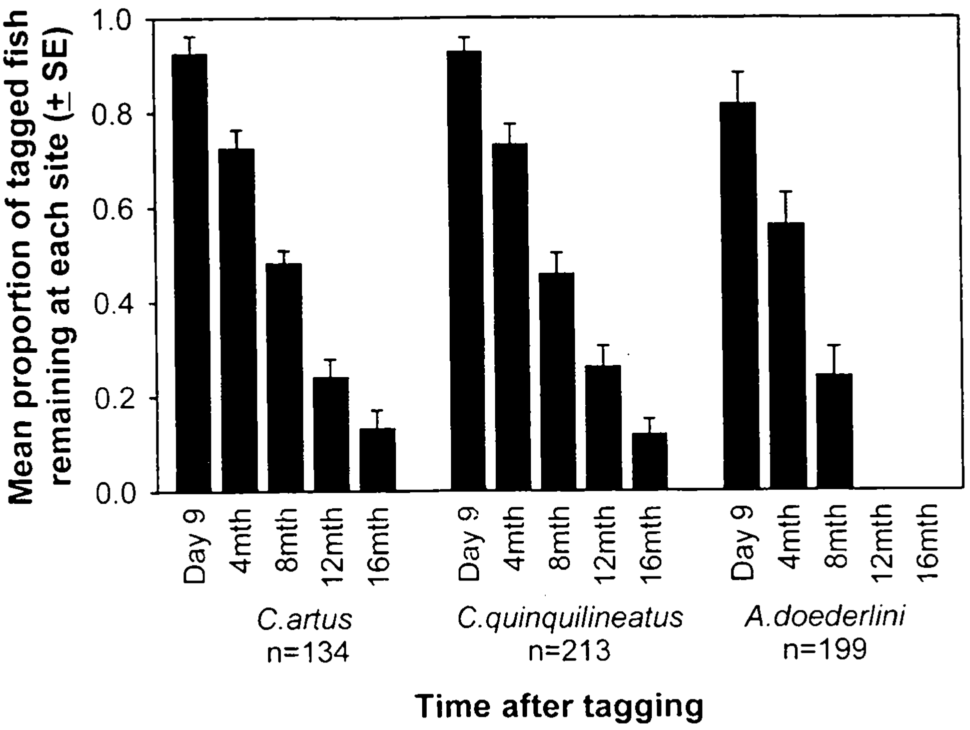


Fig. 3.2. Mean proportion of tagged fish remaining at all sites with respect to the number of fish initially tagged.

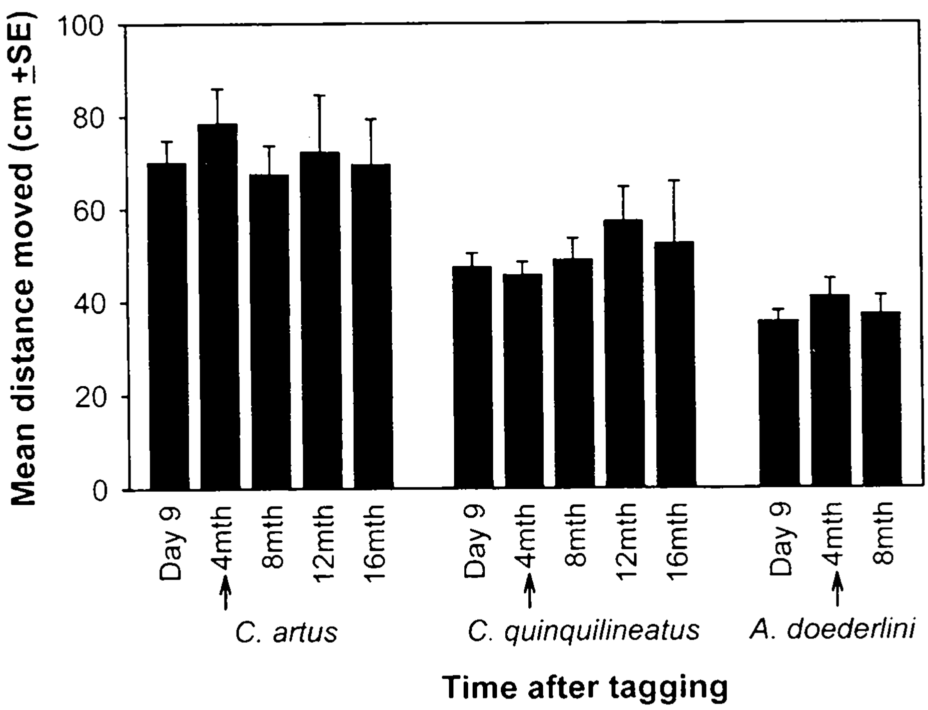


Fig. 3.3. Mean distance moved by tagged fish over time at all sites with respect to initial mapped positions.

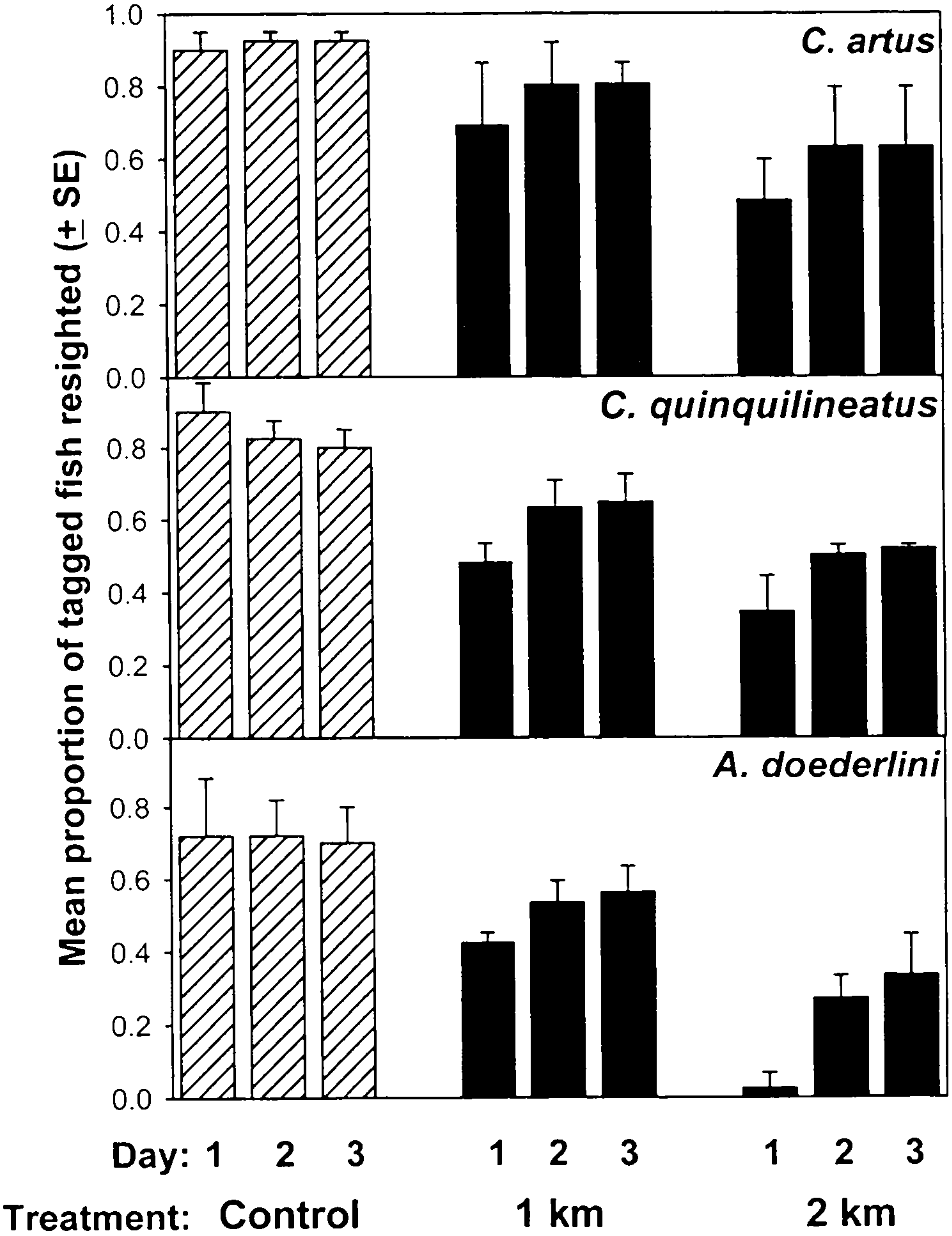


Fig. 3.4. Mean cumulative return success for each species displaced approximately 1 km and 2 km from resting sites (n = 3 sites per species).

3.5 DISCUSSION

The species of apogonids examined all demonstrated a strong relationship with their diurnal resting sites. The results suggest that apogonids may be using the same resting sites on a daily basis for a major part of their adult life. Observations were made at 4-monthly intervals and may, therefore, have missed some smaller-scale movements in between sampling periods. However, results are consistent with those of Kuwamura (1985) and Okuda & Yanagisawa (1996) who recorded strong site fidelity in apogonids from rocky reefs in Japan over periods of several weeks up to several years. In contrast, Lewis (1997), working on the Great Barrier Reef, alluded to much higher levels of movement in post-recruit apogonids, with frequent migrations between bommies within a reef. However, Lewis (1997) inferred movement rates through repeated censuses rather than direct observations of tagged individuals. Furthermore, he included a wide size range of apogonids (>15 mm SL) to infer post-recruitment movement rates. It may be that such within-reef movement is restricted to the younger phases. Finn & Kingsford (1996) suggest that juvenile apogonids display a high degree of mobility shortly after settlement followed by a more stable occupation of sites on the reef as adults. The present study focused on site fidelity only in adult apogonids (> 45.6 mm SL). Throughout this period there appears to be a high degree of site fidelity.

The steady decline in tagged fish at resting sites over time may be due to: tagging and handling mortality, selective predation upon tagged individuals, tag loss, emigration, or natural mortality. Mortality due to tagging and handling was likely to be highest soon after tagging. To allow for this, initial censuses were not conducted until 2 days post-tagging. Furthermore, mortalities of fish due to any long-term effects of tagging and handling, or due to the selective predation of tagged fish, were unlikely to be high, since the disappearance of tagged fish corresponded closely with the decline of untagged adult apogonids within tag sites (Marnane unpubl. data). Tag loss is also unlikely to be a major contributing factor, considering the low rates of tag loss observed in aquaria (less than 10% of fish were observed to lose a single tag in aquaria after 16 months). Although only one of the three focal species was included in the aquarium observations of tag loss, there was little evidence of inter-specific differences in rates of tag loss observed among the five species studied. This suggests that the low rates of tag loss observed were likely to be applicable to the three focal species used in field studies.

A strong degree of emigration from tag sites would be expected to produce a gradual increase over time in the distance tagged fish were found with respect to initial resting positions, with a steady increase of tagged fishes outside tag sites. However, the distance moved by fish was relatively consistent through time, and searches within the vicinity of tag sites found only six out of 546 individuals which had strayed more than 1 metre from tag site boundaries over the entire course of the study (all were found within 5 m of tag site grids). Emigration cannot be discounted entirely, however, as fish may have moved outside the 50 m search radius during the 4-month intervals between surveys and were therefore not observed in the following census.

Whilst the mortality of fish due to tagging and handling cannot be discounted, it seems likely that the loss of tagged fish over time is due primarily to natural mortality. The lower persistence of *A. doederlini* at resting sites through time may reflect a shorter lifespan of *A. doederlini* compared to *C. artus* and *C. quinquilineatus*. Limited aging studies suggest that lifespans of apogonids may be less than 1 to 2 years (Chrystal *et al.* 1985, Milton & Blaber 1995). Okuda *et al.* (1998) suggest that *A.doederlini* from sub-tropical waters in Japan may reach 7 years, however, this is likely to represent a different species or geographic variant to *A. doederlini* from the present study (Okuda pers. comm.). The largest *A. doederlini* collected by the author from One Tree Island (61.3 mm SL) corresponds to a <1 year old fish from Okuda *et al.*'s (1998) study.

Most apogonids exhibit little selectivity in choice of resting sites among reef habitats and depth gradients (Dale 1978, Greenfield & Johnson 1990) and often share resting sites with other apogonid species, forming large, multi-specific schools (Chave 1978, Greenfield & Johnson 1990, Chapter 2). On this basis it would be expected that apogonids could refuge in a number of suitable resting sites after their nocturnal forays. However, the displacement experiments indicated that a large proportion of fish chose to bypass many apparently suitable resting habitats (containing conspecifics), in favour of returning to their home resting sites.

For apogonids to home after displacement, the benefits of returning to resting sites must outweigh the risk involved in making the journey (Switzer 1993). Apogonids may compete for shelter sites and have a social structure that may not permit them to enter other resting sites. However, their multi-specific aggregations at resting sites would suggest that there is limited competition for daytime shelter sites (Greenfield & Johnson 1990). In addition, where apogonids had been permanently removed from resting sites, the space was not rapidly reoccupied by other adults, but was instead slowly reoccupied by juvenile apogonids (Marnane pers. obs.). Alternatively, there may be competition for nocturnal feeding grounds, and home resting sites may merely provide close access to these grounds. Homing may also be driven by the knowledge of past reproductive success at specific sites (c.f. Warner 1995). The return to a familiar environment may result in lower mortality, and may provide improved foraging efficiency when compared to foraging over unfamiliar substrata (Noda *et al.* 1994). However, schools of apogonids often had resident associated predators, such as scorpaenids and serranids. Therefore, the benefits of using such shelter sites must also outweigh the costs associated with attracting potential predators.

Homing behaviour has been observed in a number of teleost species (Quinn & Brodeur 1991), with the most well known examples being from the salmonids (Ditmann & Quinn 1996). Homing has been definitively demonstrated in only a few coral reef fishes, with displacement of tagged fishes between 100 and 700m from home sites (e.g. Bardach 1958, Ogden & Buchman 1973). However, homing in reef fishes may be more common than expected, with several incidental observations of fish returning to feeding, shelter or spawning sites over distances of hundreds of metres to several kilometres (Winn *et al.* 1964, Bellwood 1995b, Warner 1995, Samoilys 1997, Zeller 1997). The present study demonstrates homing ability in apogonids from distances of at least 2 km from resting sites. Although apogonids often move from their resting sites into a range of micro-habitats to feed (Chapter 4), Chave (1978) suggests that most species stay within metres of daytime shelter sites at night. It appears unlikely, therefore, that apogonids would have a prior mapped knowledge of areas 2 km away, and could use this knowledge to navigate back to home sites. Apogonids may therefore be using general navigational cues for homing, such as sound and/or chemical signatures of home reefs (*c.f.* Elliot *et al.* 1995, Stobutzki & Bellwood 1998). The basis and onset of this homing behaviour would be an interesting area of further investigation.

Since apogonids are often found aggregated at resting sites, the daily return of apogonids to the same resting positions over long periods of time may have localised impacts on predator distributions and detritivore communities. Apogonids form a major dietary component for many species of predatory fishes, including commercially important species (Kingsford 1992, Stewart & Jones 2001). If apogonids exhibit high mortality rates, as this study suggests, resting sites may represent localised, predictable resources for predators. This may in turn influence predator distribution patterns with respect to resting sites. In addition, if apogonids still have material in their guts when they return to resting sites, much of this material is likely to be passed on to detritivore communities as faeces. The strong fidelity of apogonids to specific resting sites on the reef may therefore represent spatially and temporally predictable resources for detritivore communities (Bray *et al.* 1981, Parrish 1989). Results of this chapter suggest that apogonids are likely to play a key role in concentrating nutrients and energy at specific sites on reefs, with the possibility of important flow-on effects for local predator and detritivore communities.

CHAPTER 4: DIET AND NOCTURNAL FORAGING IN APOGONIDS

4.1 INTRODUCTION

Nocturnal planktivores are likely to be functionally distinct from their diurnal counterparts on coral reefs (Hobson 1991). Diurnal planktivores generally feed on small prey of oceanic origin whereas nocturnal planktivores usually feed on much larger prey of reef origin (Hobson and Chess 1978, 1979). Nocturnal planktivores often migrate away from their shelter sites to forage in a range of reef and non-reef habitats (e.g. Hobson 1974, Ogden & Erlich 1977, Nagelkerken et al. 2000) while their diurnal counterparts typically feed in the water column in close proximity to the reef (Hamner et al. 1988, Hobson 1991). Although the role of diurnal planktivores in reef tropho-dynamics has received much attention, the role of nocturnal planktivores has been largely overlooked. Most nocturnal planktivores are cryptic by day and are therefore often underestimated or missed in standard daytime visual censuses of reef fish communities (Ackerman & Bellwood 2000). In addition, there have been few studies of nocturnal planktivores during their active, feeding phase, probably due to the logistical constraints of working underwater at night.

The Family Apogonidae (cardinalfishes) forms the dominant component of nocturnal planktivore assemblages on Indo-Pacific reefs (Allen 1993). By day, apogonids rest in caves or amongst branching coral, often forming dense, multi-specific aggregations (Greenfield & Johnson 1990). Apogonids have been reported to consume prey from both reef and non-reef sources, including open water, sand and seagrass habitats (Vivien 1975, Fisher 1991). They may also be significant predators of demersal plankton (Vivien 1975, Chave 1978), a trophic pathway that has received little attention on coral reefs (Parrish 1989). Apogonids have been shown to return to the same resting sites daily over extended periods of time (Kuwamura 1985, Okuda & Yanagisawa 1996, Chapter 3), and thus may play a significant role in the concentration of energy and nutrients from a range of habitats at localised, predictable sites on reefs (cf. Bray et al. 1981).

Only a handful of studies have examined the trophic biology of apogonids. Generalist diets, consisting of demersal plankton and benthic invertebrates, have been described for apogonids from the Marshall Islands (Hiatt and Strasburg 1960, Hobson & Chess 1978), Hawaii (Chave 1978) and Madagascar (Vivien 1975). However, comparable data on the feeding ecology of Indo-West Pacific apogonids are lacking. A number of studies have examined apogonid distribution patterns during the day (e.g. Vivien 1975, Dale 1978, Greenfield & Johnston 1990, Finn & Kingsford 1996), however, except for qualitative observations (e.g. Hiatt and Strasburg 1960, Livingston 1971, Chave 1978, Allen 1993), there are no published accounts of nocturnal distribution patterns.

In order to evaluate the trophic role of apogonids on reefs, it is necessary to combine dietary information with both diurnal and nocturnal distribution data. The specific objectives of this chapter, therefore, were to describe: a) foraging patterns, b) diel feeding patterns and c) diet, in seven common apogonid species from the Great Barrier Reef.

4.2 MATERIALS AND METHODS

Study site and species

This study was carried out within the One Tree Reef lagoon, southern Great Barrier Reef, Australia (152^{0}03'E, 23^{0}30'S). One Tree Reef contains a shallow lagoon (average depth, 3 to 5 m) with a well defined outer reef wall and an inner matrix of patch reefs and micro-atolls. The seven most abundant apogonid species in the lagoon were studied: *Apogon cyanosoma, Apogon doederlini, Apogon exostigma, Apogon guamensis, Archamia leai, Cheilodipterus artus,* and *Cheilodipterus quinquilineatus.* Only large juvenile and adult apogonids (>30 mm standard length) were examined owing to difficulties in identifying newly settled individuals of some species and the possibility of ontogenetic shifts in the diet (cf. Fishelson & Sharon 1997) and habitat use (Finn & Kingsford 1996) of early juveniles.

Foraging movements

The nocturnal movements of apogonids between resting and feeding sites were examined through a direct comparison of day and night distributions. Censuses were conducted over 5 days surrounding the quarter moon phase during November 1998, February 1999 and July 1999. During each of the three sampling periods five randomly placed transects were laid perpendicular to the reef at each of five micro-atolls selected randomly from a range of suitable sites. Quadrats of an estimated 8 m^2 and the water column immediately above them were surveyed at points along the transect within all reef habitats, including the reef flat, crest, slope, base and at distances of 5, 10, 20 and 30 m from the reef over the sand areas between micro-atolls (1 quadrat per habitat type). The observers remained outside the quadrat during the census. All apogonids present within the quadrat were recorded including an estimate of their standard lengths, heights above the substratum, and the nearest microhabitat type (reef, sand or water column). Specimens were recorded as being from the "water column" microhabitat if further than 30 cm from the substratum. Quadrats were surveyed between 0900 and 1500 hrs, then resurveyed the same night between 2100 hrs and 0300 hrs. Whilst the behaviour of apogonids was highly variable during crepuscular periods, observations throughout the study suggested that their behaviour was relatively consistent within the sampling periods used.

In order to reduce diver effects at night, only available moonlight was used to locate census points on the transect. Once the census points were located, quadrats and the water column immediately above them were briefly illuminated by 2 divers using 2 x 12 volt underwater halogen lights. Apogonids generally "froze" in position when illuminated. All apogonids present within the quadrat immediately upon illumination were recorded, including estimates of their standard length, nearest microhabitat type and height of individuals above the substratum. At regular periods throughout nocturnal surveys, a graduated, 1.5 m PVC pipe was used for calibrating estimated heights above the substratum. Illumination periods generally lasted a few minutes. Any specimens that entered the quadrat after initial illumination were excluded from the survey. Specimens that could not be positively identified were collected after the census. This was achieved by one diver stunning the target fish with torch-light while the second diver collected the fish using hand nets. These fish were then placed in individual, labelled bags and later identified in the laboratory.

Feeding patterns

The diel feeding patterns of each species was assessed through examination of stomach contents of fish collected at dawn and dusk. Fish were collected around dawn

(0530 and 0700 hrs) and dusk (1700 to 1830 hrs) during November 1998, February 1999 and July 1999 from at least 2 randomly chosen sites per time of day and sampling period within the lagoon. Fish were collected on SCUBA using hand nets and small hand spears. In both dawn and dusk samples, fish were collected from their resting sites. Fish were killed immediately underwater, then placed on ice within 30 mins and frozen within 2 hrs of collection. Fish were later dissected and the stomach contents removed, recording the presence of identifiable items. Identifiable material had presumably been recently consumed and had not yet undergone significant digestion.

Diet was assessed through the examination of stomach contents of specimens collected at night (2100 to 0300 hrs) during late February 1999 from 3 randomly chosen sites within the lagoon. At each site, species were collected from across the entire range of habitats in which they occurred at night. Fish were collected by scuba divers with hand nets after stunning them with torchlight. Fish were killed immediately then placed on ice within 30 mins and frozen within 2 hrs. Stomach contents were later removed, identified and placed in major taxonomic categories. The mean weight of each prey taxonomic category for each apogonid species was calculated by weighing a random sample (>10 where possible) of intact prey specimens. Mean prey item weights for each prey category were then multiplied by mean prey occurrences in the stomachs of each apogonid species to provide an estimate of the mass of material in each dietary category for each apogonid species. Combined error terms were calculated using Goodman's estimator following Bellwood (1995a):

$$\mathrm{SE}\,(\bar{x} \cdot \bar{y})^2 = \bar{x}^2 \cdot \mathrm{SE}_{\bar{y}}^{\,2} + \bar{y}^2 \cdot \mathrm{SE}_{\bar{x}}^{\,2} + \mathrm{SE}_{\bar{x}}^{\,2} \cdot \mathrm{SE}_{\bar{y}}^{\,2}$$

Where: $\bar{x}$ = mean prey item weight in each prey category; $\bar{y}$ = mean number of prey items from each prey category per individual fish; $\mathrm{SE}_{\bar{x}}$ = standard error of mean prey item weight; $\mathrm{SE}_{\bar{y}}$ = standard error of mean prey number.

4.3 ANALYSES

Data on day and night distributions of apogonids violated assumptions of homoscedasticity and normality. Distributions of each species were therefore analysed using chi-square tests of independence among the three survey periods. Distribution data were pooled among sites and habitats, where necessary, to meet chi-square assumptions. Data on the heights of apogonids above the substratum violated assumptions of homoscedasticity and were analysed using Kruskall-Wallis tests followed by post-hoc Tukey-type multiple comparisons following Zar (1984). The dietary relationships between species were examined using a principal component analysis (PCA). PCA was carried out on the correlation matrix of dietary data from Table 4.2 (before data were converted to percentages). Pearson's correlation was used to examine the relationship between height above substratum and principal component 1 scores from the principal component analysis. All analyses were carried out on SPSS™ v. 9.0.

4.4 RESULTS

Foraging movements

Surveys conducted during the day showed a restricted distribution of apogonids at resting sites, primarily on the reef slope and at the reef base (Fig. 4.1a). Although the abundance of apogonids differed at each time of year, patterns of habitat use by each species were not significantly different among the three sampling periods (all chi-squared values < critical values; $p = 0.09$ to 0.69). The three sampling periods were therefore pooled for analyses. All species were predominantly located within caves or branching coral during the day (indicated by negative heights above the substratum in Fig. 4.1a). Although there was a significant difference in mean heights above the substratum among species during the day (Kruskal-Wallis, $H = 175$, d.f. = 6, $p < 0.001$), Tukey-type multiple comparisons revealed overlapping height distributions among *C. artus*, *A. guamensis, C. quinquilineatus* and *A. doederlini* ($Q = 0.04$ to 2.91, $k = 7$, $p > 0.05$) and between *A. leai* and *A. exostigma* ($Q = 1.11$, $k = 7$, $p > 0.5$).

Night surveys showed that the majority of species foraged in different habitats to their diurnal resting sites (Fig. 4.1b). For example, *A. cyanosoma* was recorded primarily in caves in the reef base by day and occurred almost exclusively on the reef flat at night, whilst *A. doederlini* occurred on the reef slope and base by day and foraged over sand between micro-atolls at night. Furthermore, in contrast to daytime distributions, there was a strong degree of spatial separation between species at night with little overlap in horizontal distribution patterns (Fig. 4.1b). Those species that overlapped in horizontal distributions had strongly segregated positions in the water column. Mean heights above the substratum at night were significantly different among species (Kruskal-Wallis, $H = 2718$, d.f. = 6, $p < 0.001$) (Fig. 4.1b) with a post-hoc multiple comparison suggesting overlapping nocturnal vertical distributions in only *A. cyanosoma* and *A. exostigma* (Tukey-type comparison, Q = 0.41, k = 7, p > 0.5). However, these species had distinct horizontal distributions with *A. cyanosoma* occurring primarily on reef flats whilst *A. exostigma* was found almost exclusively within the reef base habitat.

Most species showed a strong link with specific microhabitat types at night (Table 4.1). *A. doederlini, A. cyanosoma* and *A. exostigma* were located above sand more than 87% of the time, whilst *A. leai* and *A. guamensis* were located in the water column 82% and 78% of the time respectively. *C. artus* and *C. quinquilineatus* did not show a strong link with any one microhabitat and were frequently located in the water column and above sand and reef microhabitats at night (Table 4.1).

Feeding patterns

In all seven species, a large proportion of individuals had identifiable material in the stomachs when collected at dawn, whereas fish collected at dusk usually had empty stomachs or small fragments of heavily digested material (Fig. 4.2). The only major exception was *A. cyanosoma*, where identifiable items were found in the stomachs of 36% of specimens collected at dusk.

All of the species examined, except for *C. artus*, consumed a wide range of prey categories (Table 4.2). The dominant taxa consumed by most species were crustaceans (mainly small decapods and decapod larvae). *C. artus* was an exception and fed almost entirely on teleosts, primarily *Spratelloides delicatulus* (Clupeidae). In all species, except *C. artus*, the source of prey was largely of reef origin (Fig. 4.3). A number of prey categories could not be confidently assigned to either reef or oceanic origin, contributing to the large unknown category in each species. The prime example of this was for *C. artus* which consumed mostly clupeids which could be assigned to either reef or oceanic origin.

A principal component analysis of the dietary relationship between apogonids suggested a clear separation between species (Fig. 4.4a) with 56.9% of the variance explained by PC1 and PC2. Diet taxon vectors (Fig. 4.4b) indicated that PC1 was driven primarily by planktonic versus benthic taxa, whereas PC2 appeared to be driven largely by prey size. A plot of PC1 scores versus height of fish in the water column (Fig. 4.5) showed a strong correlation (Pearson's correlation, $r = -0.89$, d.f. $= 5$, $p < 0.01$), suggesting that species in similar feeding habitats have similar diets. For example, *A. leai* and *A. guamensis* are both found primarily in the water column above the reef at night (Table 4.1, Fig. 4.1b), and both feed mostly on planktonic prey taxa (Table 4.2, Fig. 4.4). By comparison, *A. doederlini* and *A. exostigma* feed close to the substratum (Table 4.1, Fig 4.1b) and both consume mostly benthic prey taxa (Table 4.2, Fig. 4.4).

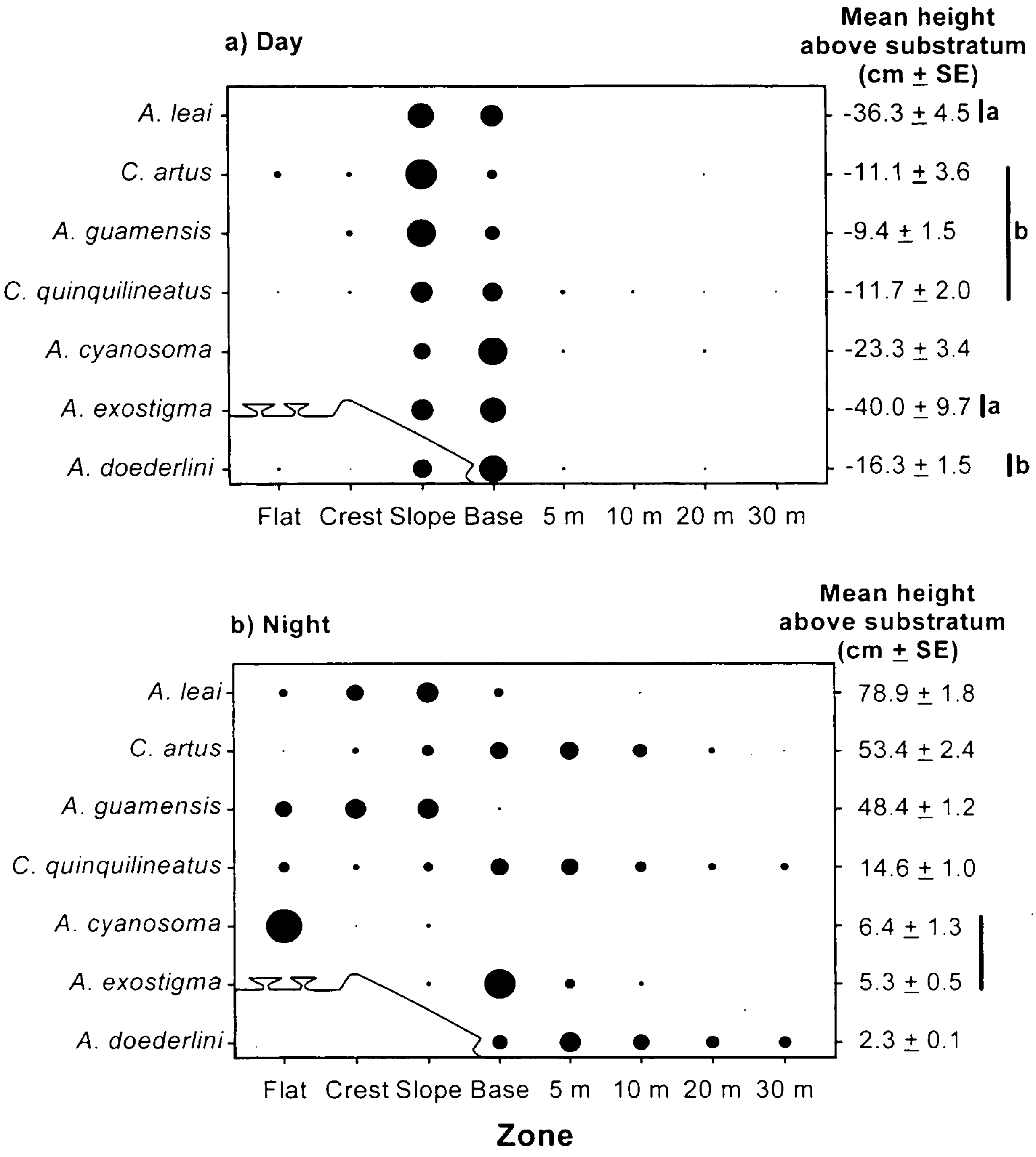


Fig. 4.1 Bubble plots of proportional habitat use by seven apogonid species during: A) Day (0900 - 1500 hrs) and B) Night (2100 - 0300 hrs). Circle areas represent the number of fish recorded from each habitat as a proportion of the total number of fish of each species recorded across all habitats (based on 75 quadrat censuses; fish sample sizes in Table 4.1). Negative heights above substratum indicate that fish were in caves

or within branching coral. Overlapping heights above substratum are indicated by vertical bars.

Table 4.1: Distribution of species with respect to microhabitat type. Data represents the percent occurrence of each species with respect to the nearest microhabitat type (within 30 cm); n = total number of fish recorded during surveys.

	Sand		Reef		Water column		n	
Species	Day	Night	Day	Night	Day	Night	Day	Night
A. cyanosoma	3%	87%	92%	12%	5%	1%	264	143
A. doederlini	5%	93%	91%	5%	4%	2%	650	1108
A. exostigma	2%	90%	98%	8%	0%	2%	54	209
A. guamensis	0%	0%	100%	22%	0%	78%	60	834
A. leai	0%	0%	98%	18%	2%	82%	164	688
C. artus	14%	15%	66%	34%	20%	51%	155	195
C. quinquilineatus	13%	29%	62%	36%	25%	35%	447	276
						TOTAL	1794	3453

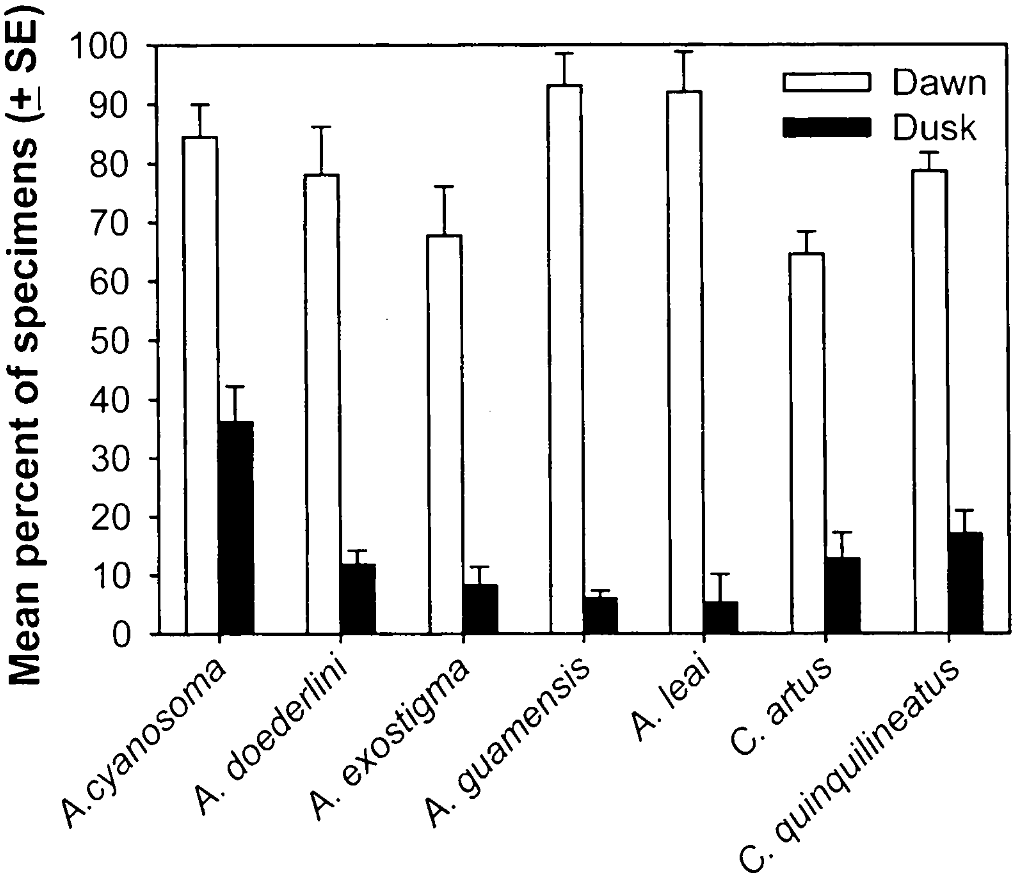


Fig. 4.2 Mean percent of specimens collected at dawn (0530 - 0700 hrs) and dusk (1700 - 1830 hrs) with identifiable prey items in their stomachs. SE values based on 3 sample periods: Nov., Feb. and July.

Table 4.2: Mean percentage composition of stomach contents of fish collected at night. Data represents mean occurrence of prey item per fish x mean prey item weight (± combined SE), converted to a percentage of mean total weight of stomach contents; n = sample size; * indicates prey categories for which mean weights were unobtainable. In such cases, values were taken from the same prey type from similar-sized apogonid species. SE in brackets.

	% Dietary contribution (±SE)																
Species	Amphipoda	Brachyuran adults	Brachyuran larvae	Caridea	Chaetognatha	Copepoda	Isopoda	Mollusca	Mysidacea	Ostracoda	Penacidae	Polychaeta	Sergestidae	Stomatopoda	Tanaidacea	Teleostei	**Total prey weight (mg)**
A. cyanosoma	5.1	0.0	0.0	22.5	0.5*	0.0	0.2	0.0	0.1*	0.3	7.8	4.0	53.7	0.5	0.3	5.0	**29.9**
n = 32	(1.8)			(3.6)	(0.1)		(0.1)		(0.1)	(0.1)	(2.9)	(0.8)	(20.9)	(0.1)	(0.2)	(2.3)	
A. doederlini	11.6	14.6	4.3	2.9	0.0	0.0	0.7	0.2	0.5	1.1	17.1	4.7	26.7	2.0	0.4	13.1	**57.1**
n = 47	(1.9)	(2.4)	(1.0)	(1.1)			(0.3)	(0.1)	(0.1)	(0.2)	(7.3)	(1.6)	(16.7)	(0.4)	(0.2)	(7.2)	
A. exostigma	0.2*	25.5	0.0	6.7	0.0	0.0	0.1	0.0	0.0	0.0	42.2	3.0	5.9	2.1	0.3	13.9	**120.0**
n = 35	(0.1)	(6.9)		(3.4)			(0.1)				(9.8)	(0.6)	(1.9)	(0.4)	(0.1)	(4.0)	
A. guamensis	2.4	3.1	56.6	2.8	0.2	0.1*	0.7	0.0	0.0	0.0	5.3	19.4	2.3	3.2	0.0	3.9	**42.1**
n = 35	(0.7)	(0.9)	(17.2)	(1.0)	(0.1)	(0.1)	(0.2)				(1.9)	(8.1)	(1.2)	(0.8)		(1.1)	
A. leai	0.4	2.0	65.1	5.4	1.3	1.3	1.2	0.0	0.1	0.5	7.3	2.4	10.4	1.8	0.0	0.7*	**18.5**
n = 36	(0.2)	(0.7)	(23.0)	(0.7)	(0.3)	(0.2)	(0.4)		(0.1)	(0.1)	(3.5)	(0.6)	(1.1)	(0.5)		(0.4)	
C. artus	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.4	0.0	0.0	0.0	0.0	88.2	**540.8**
n = 45		(0.1)									(1.8)					(20.2)	
C. quinquilineatus	0.0	11.2	0.0	3.2	0.0	0.0	0.2	0.0	0.3	0.0	46.7	1.7	6.7	0.2	0.1	29.7	**179.5**
n = 40		(3.3)		(0.3)			(0.1)		(0.1)		(14.9)	(0.6)	(3.3)	(0.1)	(0.1)	(14.9)	

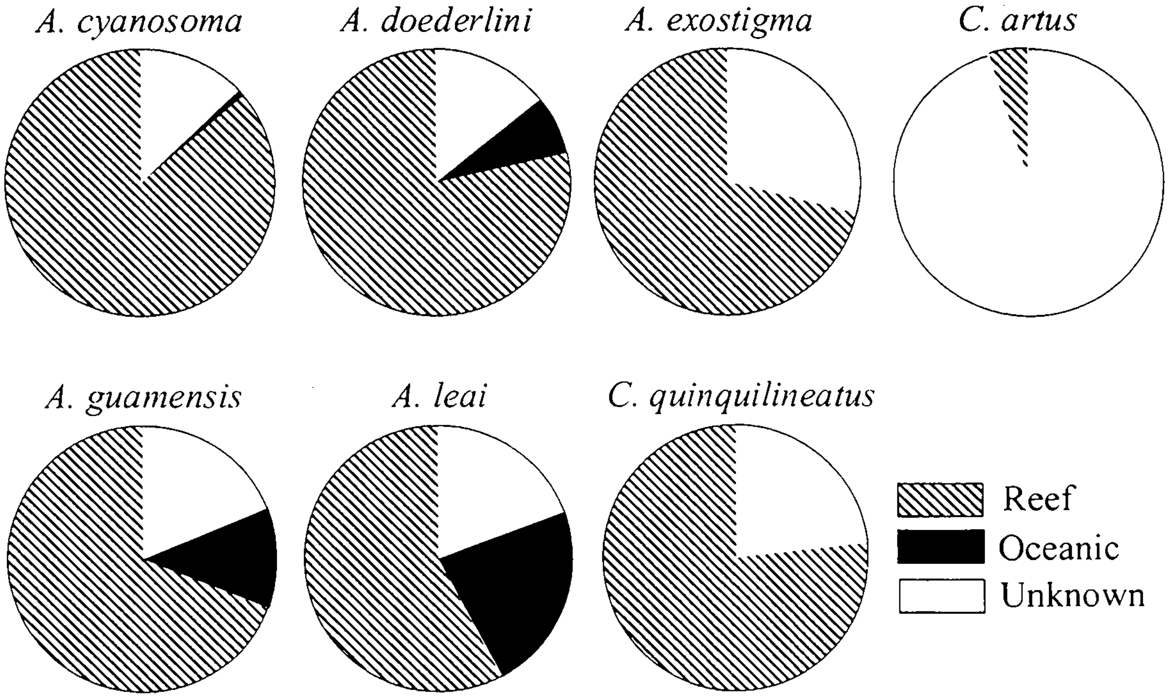


Figure 4.3 Sources of prey in the diets of apogonids. Prey of reef origin includes benthic taxa and demersal plankton. Oceanic prey includes holoplanktonic taxa and larval forms of benthic taxa. Sources of prey taxa based on available literature. Unknown category includes unidentified prey, prey for which the source was unavailable in the literature and prey which could be equally attributed to either oceanic or reef origin categories.

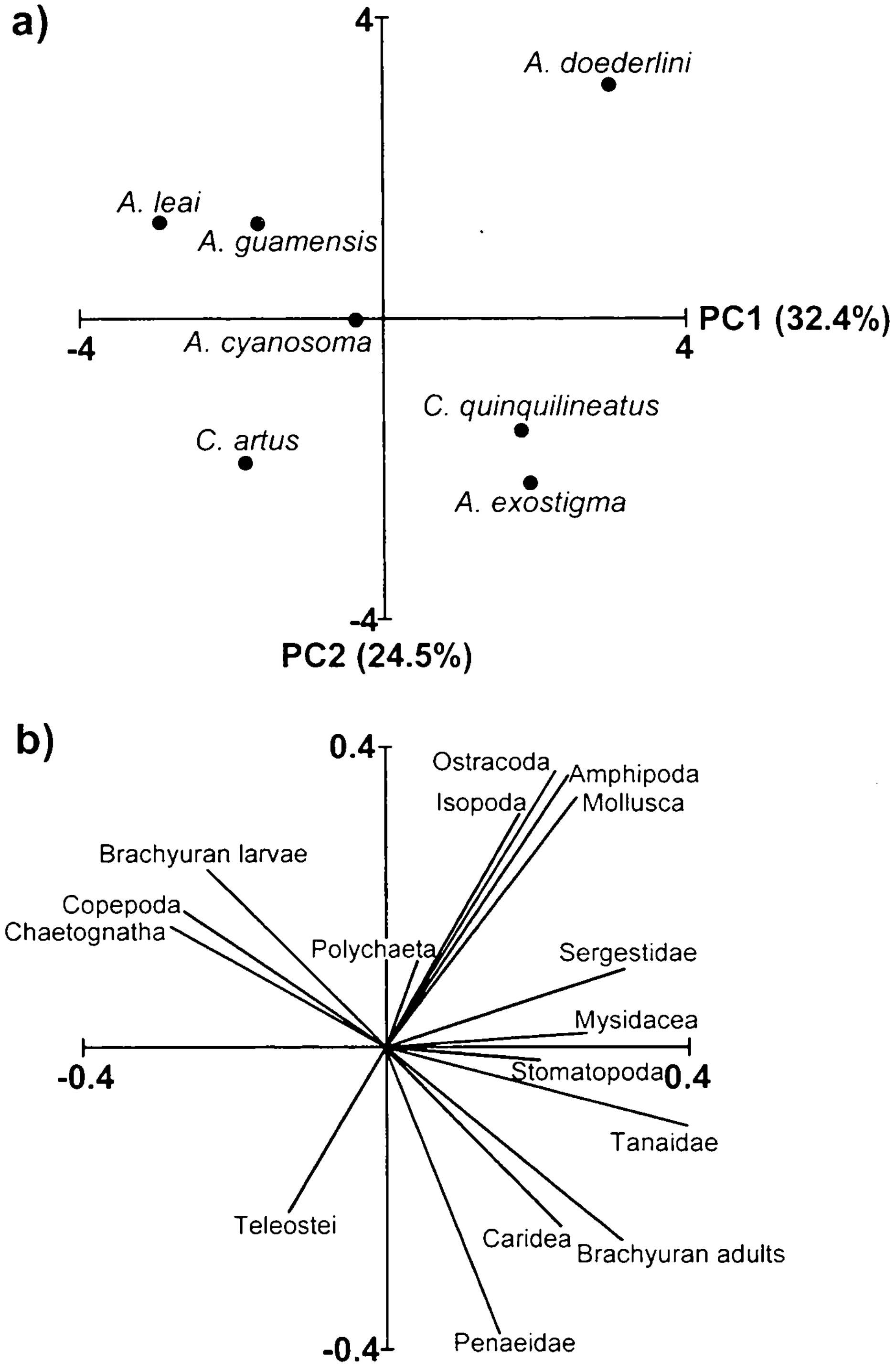


Fig. 4.4 Principal component analysis of dietary relationships, a) Species eigenvalues on principal components 1 and 2, b) Prey category eigenvectors.

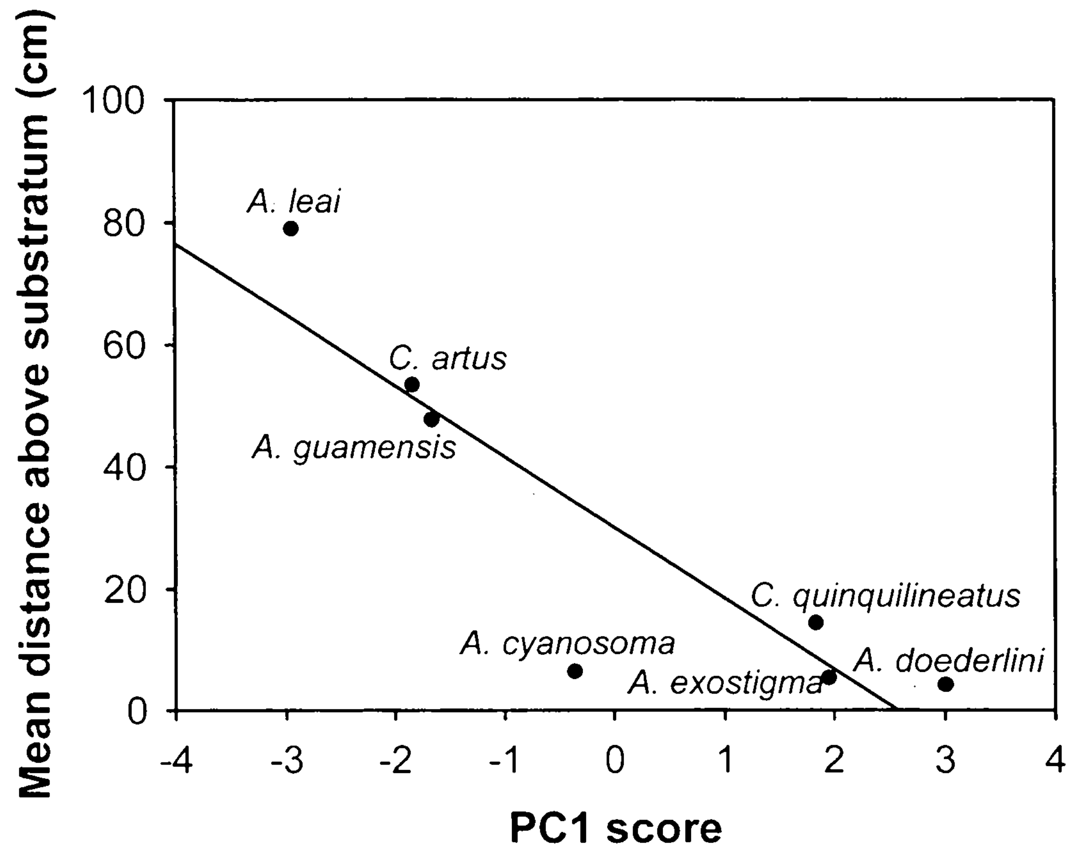


Fig. 4.5 Relationship between PC1 scores from principal component analysis (Fig. 4) and mean foraging heights of fish above the substratum at night (Fig. 2B).

4.5 DISCUSSION

Daytime habitat overlap among apogonids contrasted greatly with the marked segregation of apogonids into discrete foraging locations at night. Apogonids were found to share restricted resting habitats during the day, mainly along the slope and base of micro-atolls. This was not surprising, considering that these zones have a high degree of topographic complexity, and are therefore likely to provide the greatest protection from diurnal predators (Hixon & Beets, 1993). Species were distinctly separated during the night, both horizontally and vertically. Surprisingly, patterns of spatial segregation appeared to operate over exceptionally small scales of only tens of centimetres vertically and several metres horizontally.

Spatial niche partitioning has been reported in a number of diurnal reef fishes, across many spatial scales including microhabitat, reef zone, level of exposure and depth gradients (Williams, 1991) but has rarely been documented in nocturnal reef fishes at night. Gladfelter (1983) described spatial niche separation of eight species of holocentrids into different reef zones in the West Indies, whilst Burke (1995) described segregated habitat use of seagrass beds and sand habitats in two species of haemulids from Belize. The habitat division observed among apogonids was of a finer scale than previously observed in nocturnal fishes and was finer than that seen in most diurnal fishes. However, spatial segregation patterns were similar to those described for diurnal planktivorous fish assemblages from Enewetak Atoll (Hobson and Chess 1978), whereby the feeding positions of species within the water column were dictated largely by body morphology. It is not known if the spatial segregation observed in apogonids is due to strong habitat preference or competitive exclusion. The former might be expected, but intense aggressive interactions observed between apogonids in aquaria at night (pers. obs.) suggest that competition may play an important role.

It appears that this is the first study to quantify nocturnal distribution patterns in reef fishes using relatively unbiased survey techniques. Previous distribution studies of nocturnal reef fish have either: examined diurnal distributions only (e.g. Greenfield & Johnson 1990), used qualitative observations at night (Starck & Davis 1966, Hobson 1974, Chave 1978), or used standard visual methods with a continuous light source to census fish at night (e.g. Gladfelter 1983, Burke 1995). Surveying nocturnal fish during the day is of limited utility because they are generally inactive and their position may not reflect feeding locations (Nagelkerken et al. 2000). Surveys conducted at night with a continuous light source are likely to enhance diver biases for species that display photo-tactic responses. These biases are difficult to measure and correct. The "brief-illumination" technique used in the present study provides a quantitative alternative to previous survey methods. When moving between census points using only moonlight, fish showed little response to diver presence. Replacing the "brief illumination" with infra-red visual or video censuses may provide a useful refinement of this method.

The majority of apogonid species examined in this study appear to be primarily nocturnal in their feeding behaviour, as noted in previous studies (Vivien 1975, Chave 1978, Fishelson et al. 1997). The only possible exception to nocturnal feeding was in *A. cyanosoma* which contained identifiable prey items in the stomachs of a relatively large proportion of specimens (36%) collected at dusk. *A. cyanosoma* may supplement nocturnal feeding with diurnal or crepuscular feeding. Vivien (1975) suggested that *A. cyanosoma* may ingest some prey during the day based on gut content analysis. However, the exact time at which specimens were collected was not specified (only "day" versus "night"), which may limit resolution if crepuscular feeding was involved.

Apogonids are likely to play a role in concentrating nutrients and energy from a range of foraging habitats into localised, predictable resting sites on the reef. After a nocturnal foraging period, the majority of individuals returned to the same resting sites on the reef (Chapter 3). Data suggest that these sites are maintained on a daily basis for periods of several months to years (Kuwamura 1985, Okuda & Yanagisawa 1996, Chapter 3). At dawn most individuals still have a large quantity of material in their guts (Fig. 4.2) and, given the speed of digestion and throughput (cf. Marnane & Bellwood 1997) a significant proportion of this material is likely to be deposited at resting sites. This accrual of material, in the form of fish biomass and faeces, is likely to provide a spatially and temporally predictable resource for both predators and detritivore communities (cf. Bray et al., 1981). The most striking example of this is *A. doederlini* which feeds almost exclusively over sand areas between micro-atolls and returns to shelter sites within the reef slope and base.

A. doederlini is highly abundant within the One Tree Reef lagoon, with adult densities commonly between 10 and 20 fish per m^2 at resting sites (Marnane unpubl. data). *A. doederlini* may therefore be a key species responsible for gathering nutrients and energy from sand areas within the lagoon and concentrating these at resting sites on the reef. *A. cyanosoma* may play a similar role, moving material from foraging grounds on the reef flat to resting sites at the reef base. Apogonid faeces may be particularly important as it delivers nutrients to a localised area in a particulate rather than a suspended form, which would retain material within the reef system (i.e. within the boundary layer, cf. Baird & Atkinson 1997). Previous studies on haemulids in the Caribbean (Meyer et al. 1983) identified fish waste as a potential source of nutrients to enhance coral growth. In this respect, apogonids sheltering within corals may exhibit a symbiotic relationship, with the corals providing shelter whilst apogonids enhance local coral growth via nutrient enrichment.

Apogonids are largely generalist feeders. Dietary analysis (Table 4.2) indicated that all of the species examined, with the exception of *C. artus*, ate a wide range of organisms. *C. artus* preyed mostly upon clupeids, and is likely to be trophically similar to diurnal piscivores, such as serranids, which also feed largely on clupeids within the lagoon (Kingsford 1992). The prey consumed by the majority of apogonid species included a large proportion of benthic taxa and demersal plankton (e.g. brachyurans, sergestid shrimps, and polychaetes), whilst holoplanktonic forms such as chaetognaths and copepods represented only minor dietary components. It is possible that small, holoplanktonic prey undergo a more rapid digestion than larger benthic and demersal prey, and may therefore be under-represented in samples of stomach contents. However, even if a ten-fold difference in digestion rates was assumed, benthic taxa and demersal plankton would still dominate apogonid diets. In a trophic sense, apogonids play a functional role that is distinctly different to that of most diurnal planktivores, which generally consume oceanic plankton (Hobson & Chess 1978). Apogonids are more likely to play a role of recycling in reef systems rather than of importing nutrients and energy to reefs from open water systems (cf. Hamner et al. 1988).

Significant dietary separation was found among apogonids, despite their generalised diets. The primary axis of dietary separation was benthic versus planktonic prey and, secondarily, small versus large prey. This separation appears to be strongly linked with the position of species within the water column. Species that were high in the water column (e.g. *A. leai* and *A. guamensis*) consumed mostly small, planktonic prey whilst species that foraged low in the water column (e.g. *A. doederlini* and *A. exostigma*) consumed mostly large, benthic prey. Taxon-specific differences in the distances demersal plankton migrate vertically into the water column at night have been observed (Alldredge & King 1985) and are consistent with the observation that dietary separation in apogonids is associated with foraging location within the water column. However, the question remains as to whether the feeding preference of apogonids determines their position in the water column, or whether position in the water column dictates the availability of prey taxa.

Results from this chapter emphasise the need for data beyond gut contents and diurnal distributions if we are to understand the trophic roles of nocturnal fishes. In the case of apogonids, nocturnal behaviour appeared to be the main factor determining the functional role of each species. This study highlights the need to match methods to questions: both diurnal and nocturnal distribution data as well as dietary information are necessary to infer the trophic roles of nocturnal fishes on reefs. The high abundances and rapid turnover rates of apogonids on Indo-Pacific reefs suggest that they are important in reef tropho-dynamics. Given their strongly segregated feeding and shared resting locations, apogonids may play a key role in the transfer of nutrients between habitats and in the concentration of nutrients at specific sites on reefs.

CHAPTER 5: THE ROLE OF APOGONIDS IN THE TRANSFER OF MATERIAL TO DETRITIVORES AND PISCIVORES

5.1 INTRODUCTION

In Chapter 3, apogonids were found to display a high degree of fidelity to diurnal resting sites. A study of feeding (Chapter 4) indicated that apogonids forage in a range of habitats including sand areas in between reefs, before returning to a restricted range of resting habitats on the reef. Therefore, apogonids may be responsible for concentrating nutrients and energy from a range of habitats at localized sites on the reef. Since apogonids use the same resting sites on a daily basis for extended periods of time, the faeces deposited by resting schools may provide a predictable resource for detritivores. In addition, the biomass of apogonids at resting sites may provide an important resource for diurnal predators. In order to determine the importance of each of these resources, this chapter examines the defecation rates of apogonids and the turnover rates of apogonid biomass at resting sites.

5.1a Transfer of material to detritivores

Fish faeces generally contain enough organic material to represent a viable food source for a variety of reef fishes and invertebrates (Bailey and Robertson 1982). Fish faeces is likely to be of particular importance in situations where fish occur in high densities, such as in feeding or resting schools (Meyer & Schultz 1985). In addition, defecation by schools of fishes residing within the branches of corals or caves are likely to deliver organic carbon and nitrogen to reefs within the boundary layer, thereby reducing the net loss of nutrients from reef systems through advection by currents (Baird & Atkinson 1997). However, relatively few studies, apart from those on bioeroding reef fishes (e.g. Bardach 1961, Scoffin et al. 1980, Bellwood 1996), have examined the importance of fish faeces in reef processes (Robertson 1982).

The concentration of faeces below resting schools of fishes may have consequences for the distribution and abundance patterns of reef detritivores (Bray et al. 1981) and may have localised impacts on coral growth (Meyer at al. 1983). In addition, resting schools of fishes may act to concentrate resources from a range of habitats, such as seagrass, sand areas or open water communities, at predictable sites on the reef (Bray et al. 1981, Helfman et al. 1982). Studies which have investigated the impacts of resting schools of fishes on detritivore communities are virtually non-existent, however, two studies have suggested that resting schools of fishes have impacts on local coral growth. Meyer et al. (1983) examined nocturnal haemulids (*Haemulon flavolineatum* and *H. plumieri*) from the Caribbean which rest by day in dense schools above coral colonies. They suggested that waste excreted by resting schools of haemulids increased local coral growth rates and tissue condition (Meyer et al. 1983, Meyer & Schultz 1985). This process has also been suggested by Liberman et al. (1995) to be a factor responsible for increased growth in coral colonies containing schools of damselfish (*Dascyllus marginatus*) in the Red Sea.

Apogonids generally form dense schools at resting sites by day after feeding at night in a range of habitats (Vivien 1975, Chapter 4). Apogonids also appear to use the same resting sites on a daily basis for extended periods of time (Chapter 3). Since most apogonids return to resting sites at dawn with full guts and have empty guts by dusk (Chapter 4) any material not assimilated by fish is likely to be deposited at their resting sites in the form of faeces. The faeces produced by resting schools of apogonids may, therefore, provide a spatially and temporally predictable concentration of resources for detritivore communities and may enhance local coral growth. To investigate this possibility, this study aimed to quantify the defecation rates by schools of apogonids at resting sites and also defecation rates of apogonids over a reef-wide scale.

5.1b Transfer of material to reef piscivores

Few studies have quantified mortality rates in reef fishes past the first few months after settlement (van Rooij & Videler 1997). Our knowledge of life histories of reef fishes is therefore largely restricted to longevity estimates obtained from otolith aging studies (e.g. Choat et al. 1996, Lo et al. 1998, Meekan et al. 2001). Whilst longevity estimates do not directly mirror mortality rates in fishes, there is strong evidence to suggest that instantaneous mortality rates and the inverse of maximum longevities are closely linked (Hoenig 1983). Longevity estimates indicate that a wide range of life histories exist amongst reef fish taxa. Estimates of maximum longevities to date range from only a few months in gobies (Robertson & Kaufman 1998) to almost 70 years in acanthurids (Choat & Axe 1996), with the majority of species examined being relatively long-lived (>10 years) (Munday & Jones 1998). Virtually nothing is known of the life histories of small, cryptic reef fish taxa (Hernaman et al. 2000). However, if small, cryptic fishes are short-lived compared to other groups, their contribution to reef energy budgets may be far greater than is currently recognised. Data on turnover rates in small, cryptic fishes is therefore critical to our understanding of their role in reef processes.

Apogonids are one of the most abundant taxa of fishes on Indo-Pacific reefs (Bellwood 1996), however, due to their small size, they generally constitute a slightly lower standing biomass than other major reef fish families (Ackerman & Bellwood 2000). The role of apogonids in reef processes has therefore received little attention. However, it is not the standing biomass but the turnover rate of this biomass that is critical to reef energetics. In this respect, apogonids may provide an important food resource for diurnal predators. However, the importance of this resource is determined by the rate of turnover of apogonid populations.

Mortality rates are one of the most difficult life history parameters to accurately quantify (Russ et al. 1998). All of the methods currently available to quantify mortality rates, ranging from age-based catch curves to empirically derived mortality estimates from growth parameters, have a range of inherent assumptions and biases (King 1995). A failure to account for these problems may have a large impact on the accuracy of the mortality estimates obtained (King 1995). This study, therefore, uses three independent methods to obtain an overall estimate of turnover rates in apogonids: 1) estimates of mortality from the loss of tagged individuals over time, 2) estimates of longevity obtained through otolith aging, and 3) monitoring population dynamics through time.

5.2 MATERIALS AND METHODS

Study sites

Field studies were carried out using SCUBA within the One Tree Reef lagoon, southern Great Barrier Reef, Australia ($23^0 30'S$, $153^0 67'E$), and experimental studies were carried out at the One Tree Reef field station.

Visual censuses versus clove oil collections

The choice of study species for turnover rate studies was determined by their ability to be reliably censused using daytime visual techniques for studies of population dynamics. This was assessed through the comparison of visual censuses of apogonids within a specified area to collections of fish from the same area using the anaesthetic, clove oil (Munday and Wilson 1997). In addition, clove oil collected samples provided estimates of apogonid biomass at resting sites. Biomass estimates were then multiplied by fish defecation rates from experiments to determine the amount of faeces deposited at resting sites.

Visual and clove oil collected samples were obtained from stations placed within the two habitats most commonly used as resting sites by apogonids within the lagoon (Chapter 2). These were: caves (n=16 stations) and the branching coral, *Porites cylindrica* (n=18 stations). Stations within cave habitats consisted of a single cave ranging in size from approximately 1.2 to 6.5 m^3. *Porites cylindrica* stations consisted of a quadrat of 4 m^2 delimited by a tape around the perimeter. Both cave and *Porites cylindrica* stations were censused visually using the same intensity of sampling as used later in population dynamic censuses, recording all apogonids present. Stations were then covered with a clear, plastic, weighted sheet to minimise clove oil dispersal, and clove oil was administered in plastic 500 ml spray bottles as a solution of approximately 6:1 ethanol to clove oil. A dose of 0.5 to 1 litre of solution was administered to each station, and anaesthetised fish were collected from the station until no more fish could be found (approximately 30 mins). Fish were kept underwater in mesh-covered containers until the completion of collections, after which they were identified, measured and returned to their point of capture.

5.2a Transfer of material to detritivores

Four species of apogonids: *Apogon doederlini* (n=55), *Apogon leptacanthus* (n=45), *Cheilodipterus artus* (n=35) and *Cheilodipterus quinquilineatus* (n=59) were collected between 0415 and 0515 hrs (just prior to dawn) from sites chosen haphazardly within the One Tree Reef lagoon during September 2000. Water temperature at collection sites ranged between 21 ^{0}C and 23.5 ^{0}C. Fish were momentarily stunned with torchlight then collected using hand nets and placed in individual, sealed bags to retain any faeces expelled during transit. Both the fish and bag contents were then transferred to individual 10 litre experimental containers at the One Tree Island Field Station between 0530 and 0600 hrs. Each container was supplied with a gentle flow-through of 5 μm filtered seawater, pumped from the lagoon, which entered and exited containers near the surface to prevent the loss of faecal pellets. Each container also contained a PVC pipe shelter to reduce stress in the fish. Water in the experimental containers ranged between 21.5 and 25 ^{0}C throughout experiments and fish were exposed to a natural light regime from indirect sunlight. Faeces were collected over 12 hrs ± 1 hr (~ 0600 to 1800 hrs), corresponding to the time fish would have spent at resting sites. Faecal pellets generally remained intact and were more dense than seawater, sinking rapidly to the bottom of containers.

At the completion of experiments, fish were removed from containers and their standard lengths and wet weights were recorded. Fish were then frozen for later dissection. Faecal pellets were siphoned out of the containers onto pre-dried and pre-weighed filter papers. Samples were gently flushed with fresh water to remove salt, dried at 60^{0}C until constant weight (approx. 2 days) then weighed. Defecation rates were calculated from the regression of dry weight of faeces produced versus wet body weight.

Estimates of defecation rates for each focal species across all lagoonal reefs were obtained by multiplying faeces production rates from experiments by biomass estimates of focal species obtained from visual surveys (Chapter 2). Biomass estimates were not available for *A. leptacanthus* since they only occurred at a few discrete locations within the One Tree Reef lagoon and were not recorded during visual surveys.

Estimates of defecation rates for all apogonids within the One Tree Reef lagoon were obtained by calculating a mean defecation rate per unit body mass for all focal species and multiplying this by the mean apogonid biomass across suitable lagoonal reef habitat recorded in visual surveys (Chapter 2).

Estimates of defecation rates by apogonids at resting sites were obtained by multiplying defecation rates from experiments by estimates of apogonid biomass at resting sites obtained through clove oil collections (above). Additional sampling of *A. leptacanthus* was required since they only occurred in discrete schools within the One Tree Reef lagoon. Clove oil sampling was likely to have missed some fish, therefore biomass estimates obtained using these methods were considered to be relatively conservative. Defecation estimates for all species of apogonids at resting sites combined were obtained by calculating a mean defecation rate from the four focal species (per unit biomass) and multiplying this by the mean biomass of apogonids at resting sites (from clove oil collected samples).

5.2b Transfer of material to piscivores

Tagging studies

Individuals used in this study (except for *A. cyanosoma*) were those described in Chapter 3. However, for the purposes this chapter, initial densities were based on day 9 censuses, rather than day 2 censuses (Chapter 3) to further reduce possible confounding effects of tagging and handling induced mortality on natural mortality estimates. Adult *A. cyanosoma* (39.4 to 45.5 mm standard length, SL), *A. doederlini* (45.6 - 57.6 mm SL), *C. artus* (78.4 - 98.2 mm SL) and *C. quinquilineatus* (52.0 - 72.6 mm SL) were collected from 10 sites within the One Tree Reef lagoon during July and November 1997 using clove oil and hand nets. Fish were tagged underwater using visual fluorescent implant tags (Northwest Marine Technologies Inc., USA), injected subcutaneously into the dorsal musculature. All fish received at least two tags to ensure a greater tag persistence through time. Rates of tag loss were monitored in aquarium studies and found to be minimal over 16 months (see Chapter 3 for details of methods). Tagged fish were retained in mesh-covered containers at their site of initial capture for at least 6 hours prior to release to allow recovery from tagging and anaesthesia before being released. The first census of fish took place 9 days after initial tagging. Fish were then censused again at 4-monthly intervals over a period of 16 months. An area of ~50 m diameter surrounding tag sites was also examined during censuses to record any tagged fish which had strayed outside tag sites.

Otolith aging

Otolith analysis was used to obtain longevity estimates for all four focal species (ie. *A. cyanosoma*, *A. doederlini*, *C. artus* and *C. quinquilineatus*). Specimens were collected using hand spears or clove oil at three different times of year (March, July and November) over a two year period (July 1997 to July 1999). Otoliths of specimens were removed, cleaned in fresh water and stored dry. Otoliths from the largest 5% of specimens of each species were prepared and thin polished transverse sections of sagittal otoliths were examined.

Otoliths were prepared by bonding them to the edge of a glass microscope slide using Crystal Bond™ thermoplastic glue with the sulcus groove of the otolith perpendicular to the edge of the slide and the primordia of the otolith flush with the edge of the slide. Slides were then held vertically and ground on 1200 grit sandpaper followed by polishing on 12μm and 5μm lapping film. The glue was then reheated and otoliths were remounted with the newly-ground surface placed face down in the centre of the glass slide. Otoliths were ground until a thin section was obtained which included the primordium. Sections were then polished and reheated to cover the polished surface with a thin layer of Crystal Bond™. Counts of increments were made from the primordium to the otolith edge, primarily along the shortest axis. Increments were defined as a bipartite structure consisting of one incremental zone and one discontinuous zone (Campana and Neilson 1985). Each otolith was read on three independent occasions and if counts did not agree within a 10% margin (in the case of daily increments) or agree completely (in the case of annual increments) the otolith was discarded. Age estimates were based on the average of the three counts.

Age estimates were converted to instantaneous mortality rates (Z), to enable a comparison with tagging study estimates of mortality using Hoenig's (1983) formula. This formula predicts the relationship between mortality and longevity based on a regression for 84 species of fish:

$$\ln(Z) = 1.46 - 1.01 \ln(\text{longevity})$$

Instantaneous mortality rates (Z) estimated using both tagging and otolith aging methods were converted to percent mortality per year using the equation:

$$\text{Mortality } (\%\ \text{yr}^{-1}) = 1 - e^{-z}$$

Otolith validation

Daily ring formation was validated in otoliths of *A. cyanosoma* and *A. doederlini* and annual ring formation was validated in *C. artus* and *C. quinquilineatus* using tetracycline banding (see Fowler 1990). Fish were anaesthetised at diurnal resting sites using clove oil then injected with tetracycline hydrochloride dissolved in sterile saline (either 5 or 10 mg of tetracycline per ml saline). Fish were injected at the rate of 50 mg tetracycline per kg of fish. At the same time, fish were also injected subcutaneously in the dorsal musculature with fluorescent elastomer (Northwest Marine Technologies Inc. USA) for ease of identification and recapture. A combination of six body positions and three tag colours provided a uniquely identifiable tag code for each fish. All fish were retained underwater in mesh covered containers at their site of collection for 6 hrs prior to release, to allow recovery from anaesthesia and handling, thereby reducing losses due to predation.

A. doederlini and *A. cyanosoma* were released at collection sites and recaptured after 10 days and re-injected with tetracycline. Fish were then released for a further four months before final collection. *C. artus* and *C. quinquilineatus* were injected only once with tetracycline and left in situ for either 1 or 2 years before collection using either clove oil or small hand spears. Otoliths of tagged fish were removed, prepared as above and stored in a light-proof container in a refrigerator. Otolith sections were later examined under a HP microscope with an ultraviolet transmitted light source to fluoresce tetracycline banding. The position of tetracycline bands were then compared to the position of otolith increments observed under transmitted incandescent light. The timing of formation of otolith increments in *A. cyanosoma* and *A. doederlini* was determined by comparing the time between tagging episodes to the number of increments between two tetracycline bands. In *C.quinquilineatus* and *C. artus* the timing of increment formation was determined by comparing the time between tagging and collection with the number of increments between tetracycline bands and the otolith edge.

Population dynamics

Studies of apogonid population dynamics were carried out on five micro-atolls within the One Tree Reef lagoon (Fig. 5.1). Sites were chosen randomly from a range of similarly-sized micro-atolls with resident populations of apogonids. Micro-atolls ranged in size from approx. 30 to 40 m in diameter and were approx. 2 to 5 m in height above the lagoon floor. Censuses of all micro-atolls were carried out between 0800 and 1600 hrs, and generally lasted between 60 and 90 minutes per micro-atoll. Censuses of each micro-atoll were repeated three times at one-weekly intervals within a given time of year. A mean of these three counts was then used as an estimate of numerical abundance for a micro-atoll within a given time of year. This process was then repeated at four-monthly intervals for a period of two years, from July 1997 to July 1999.

During censuses, the entire micro-atoll was systematically surveyed, including the lagoon floor to a distance of 5 metres from the base of micro-atolls. The numerical abundance of the four focal species was recorded, including an estimate of their standard length and whether or not fish were orally brooding eggs. The minimum size at which fish were observed to brood eggs was used as an approximation for the maturational size of each species. Individuals were then categorised as: new recruits (less than or equal to 15 mm SL), juveniles (*A. cyansoma* < 40 mm SL, *A. doederlini* < 40 mm SL, *C. artus* < 65 mm SL and *C. quinquilineatus* < 50 mm SL) and adults.

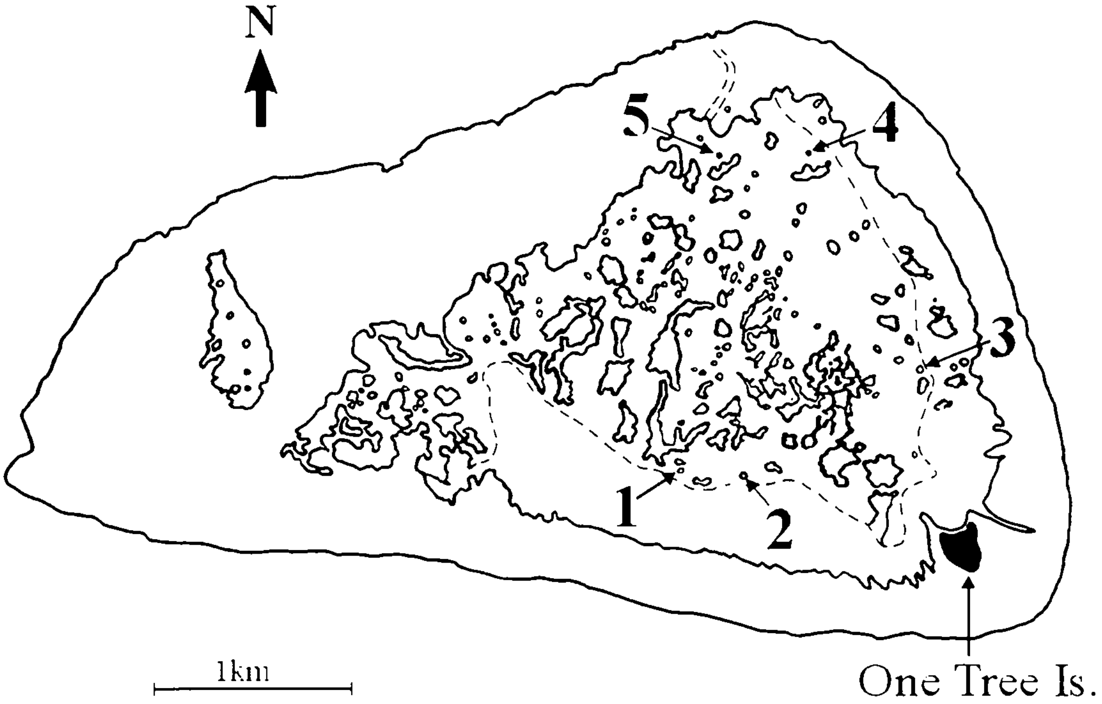


Fig. 5.1 One Tree Reef study sites used in population dynamic surveys.

5.3 ANALYSES

Visual censues and clove oil collections were compared to estimate the accuracy of visual censuses in estimating the abundance of each apogonid species. Visual censuses and clove oil collections were carried out in both cave and branching coral (*Porites cylindrica*) habitats to estimate the accuracy of visual censuses in each habitat type. This accuracy was represented as the proportion of fish collected using clove oil that were also recorded during visual censuses. Proportional data were arcsin transformed to reduce binomial error. Data were then compared between caves and *P. cylindrica* stations using a paired t-test among species. Since the accuracy of visual censuses was similar between cave and *Porites cylindrica* habitats, data from these habitats were pooled for presentation and further analysis. Pooled abundance estimates recorded in visual censuses versus clove oil collections were then compared using a paired t-test among species. In each analysis, data were examined for normality and homogeneity of variances using Q-Q plots and Levene's test.

5.3a Transfer of material to detritivores

A proportion of apogonids naturally have empty guts at dawn (Chapter 3). It would therefore be expected that as a result, some specimens would produce no faeces during the day. Therefore, fish that produced no faeces in experiments were included in calculations to produce a realistic estimate of mean faeces production rates. Rates of faecal production were compared among species using an ANOVA. Significant differences found in the ANOVA were further examined using unplanned multiple comparison procedures following Sokal & Rohlf (1995). Error terms for the weight of faeces produced per m^2 for each species were calculated from the combined standard errors of faeces production rates and apogonid biomass estimates using Goodman's estimator following Bellwood (1995a):

$$SE(\bar{x} \cdot \bar{y})^2 = \bar{x}^2 \cdot SE_{\bar{y}}^2 + \bar{y}^2 \cdot SE_{\bar{x}}^2 + SE_{\bar{x}}^2 \cdot SE_{\bar{y}}^2$$

Where: $\bar{x}$ = faeces produced per g of fish wet weight; $\bar{y}$ = biomass of fish per m^2; $SE_{\bar{x}}$ = standard error of faeces produced per g of fish wet weight; $SE_{\bar{y}}$ = standard error of biomass of fish per m^2.

5.3b Transfer of material to piscivores

Data on tagged individuals remaining over time were pooled among tag sites for each species since there were insufficient data to analyse tag sites separately. Instantaneous mortality rates were estimated based on the regression of ln (tagged fish remaining) versus time in years. Data on population dynamics were pooled among the three censuses within a given time of year. Mean values for each micro-atoll at a given time of year were then used as a replicates in analyses and presentation. Correlations between the abundance of recruits and adults through time were examined using cross-correlation analyses. Since all four species take between 3 and 6 months to grow from recruit to adult size, based on otolith aging studies (Marnane unpubl. data), a lag of one time-frame (4 months) was added to recruit data for all species in cross-correlation analyses. Significance levels used in testing cross-correlation coefficients were adjusted for multiple testing using sequential Bonferroni corrections (Rice 1989). All analyses were carried out using SPSS™ v. 10.0.

5.4 RESULTS

Visual censuses versus clove oil collections.

There was a marked difference between visual estimates of apogonid abundance and estimates obtained through clove oil collections (Fig. 5.2). A total of 543 fish from 7 species were visually censused from 34 stations, compared to a total of 836 fish from 14 species collected using clove oil from the same stations. There was no significant difference in the accuracy of visual censuses for each species between cave and *P. cylindrica* stations (Paired t-test, $p > 0.25$). Therefore, data were pooled for cave and *P. cylindrica* stations for analysis and presentation. In all species, visual estimates of abundance were significantly lower than clove oil collection estimates (Paired t-test, $p < 0.01$). The closest agreement between visual estimates and clove oil collected estimates of abundance (presented as the percent of fish collected with clove oil that were also censused visually, mean % per station ± SE) were for *C. artus*, 94 ± 3%, followed by *C. quinquilineatus* (87 ± 3%). *A. cyanosoma* (62 ± 6%) and *A. doederlini* (61 ± 5%) were censused with reasonably good precision using visual surveys, even though 40 % of fish were missed on average (Fig. 5.2).

Visual estimates of *A. leai* abundance were only 50% of clove oil collection estimates and were relatively imprecise (SE 17%). Only a small proportion of *A. exostigma* and *A. guamensis* collected using clove oil were recorded in visual censuses (4 ± 4% and 2 ± 2% respectively). In addition, seven species of apogonids were collected using clove oil but were never recorded in visual censuses: *Apogon trimaculatus* (n = 8), *Apogon kallopterus* (5), *Fowleria variegata* (5), *Apogon nigrofasciatus* (3), *Apogon coccineus* (2), *Pseudamia gelatinosa* (2) and *Fowleria marmorata* (1). Mortality, longevity and population studies will only focus on those four species that were censused with acceptable accuracy and precision using standard visual techniques (*C. artus, C. quinquilineatus, A. cyanosoma* and *A. doederlini*).

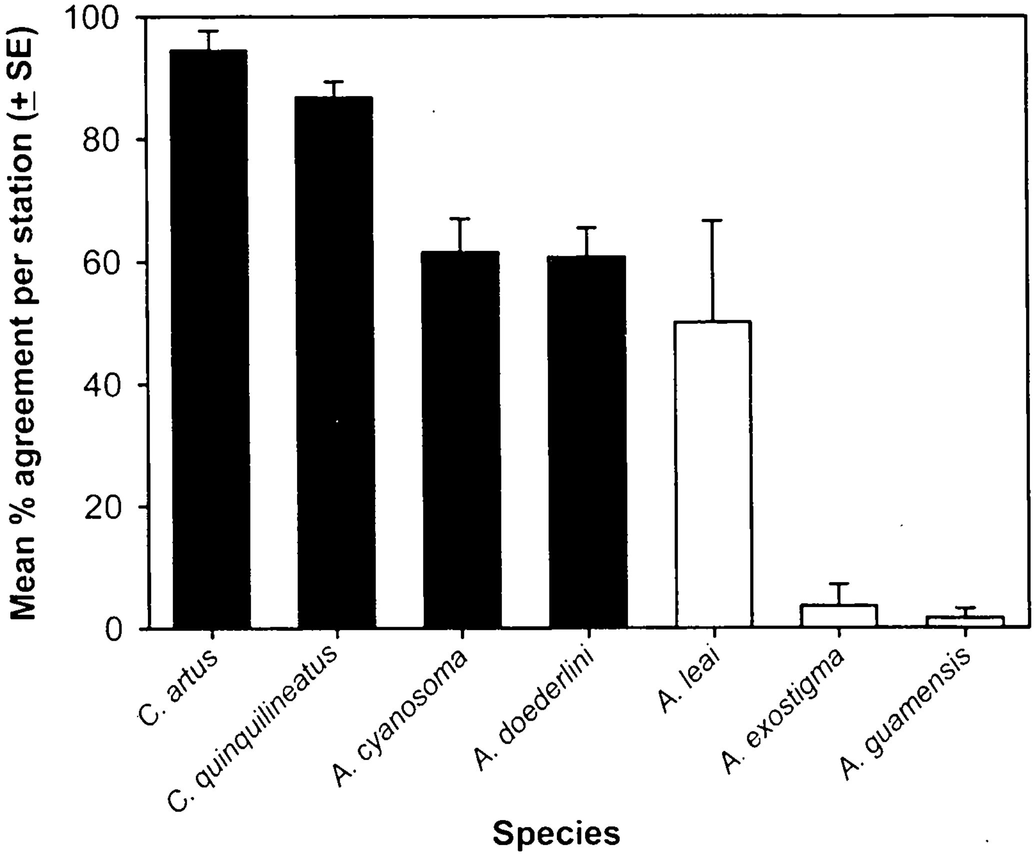


Fig. 5.2 Percent of specimens collected using clove oil that were also censused visually. Values represent mean estimates per station within cave and *Porites cylindrica* habitats combined (n = 34 stations in total). Solid bars: focal species examined in population studies.

5.4a Transfer of material to detritivores

A significant linear relationship was found between fish body weight and the dry weight of faeces produced in all four species (ANOVAS, $p < 0.001$ to 0.04) (Fig. 5.3). However, the strength of this relationship was reduced by the effect of no faeces being produced by some experimental subjects, resulting in a slightly triangular rather than linear relationship. Overall, there was a significant difference in the amount of faeces produced per unit body weight among species (ANOVA, $df = 3$, $F = 7.546$, $p < 0.001$). However, an unplanned multiple comparison of slopes revealed overlapping faeces production rates in *A. doederlini*, *A. leptacanthus* and between *A. leptacanthus* and *C. quinquilineatus*, which were all significantly greater than faeces production rates in *C. artus*. This was not a result of prolonged throughput times as all fish dissected after experiments had empty guts.

Mean defecation rates across all suitable reef habitat (reef flat, slope and base habitats) were highest in *A. doederlini* (4.2 ± 1.6 (SE) mg dry weight of faeces m^{-2} day^{-1}), followed by *C. quinquilineatus* (2.02 ± 0.54). *C.artus*, although the largest species examined, had the lowest faeces production rates (0.23 ± 0.07 mg dry faeces m^{-2} day^{-1}) (Table 5.1). *A. leptacanthus* was not recorded in visual censuses, therefore no reef-wide biomass estimates were available at One Tree Reef. The defecation rate for all species of apogonids combined, across all suitable lagoonal reef habitat was estimated to be 7.6 ± 3.2 mg dry faeces m^{-2} day^{-1} (Table 5.1). Defecation rates beneath resting schools of apogonids were highest in *A. doederlini* (432 ± 124 3 mg dry faeces m^{-2} day^{-1}), followed by *A. leptacanthus* (268 ± 57), *C. quinquilineatus* (42.7 ± 6.7), and *C. artus* (15.4 ± 3.6) (Table 5.1). The estimated defecation rate for all species of apogonids at resting sites combined was 693 ± 260 mg dry faeces m^{-2} day^{-1} (Table 5.1).

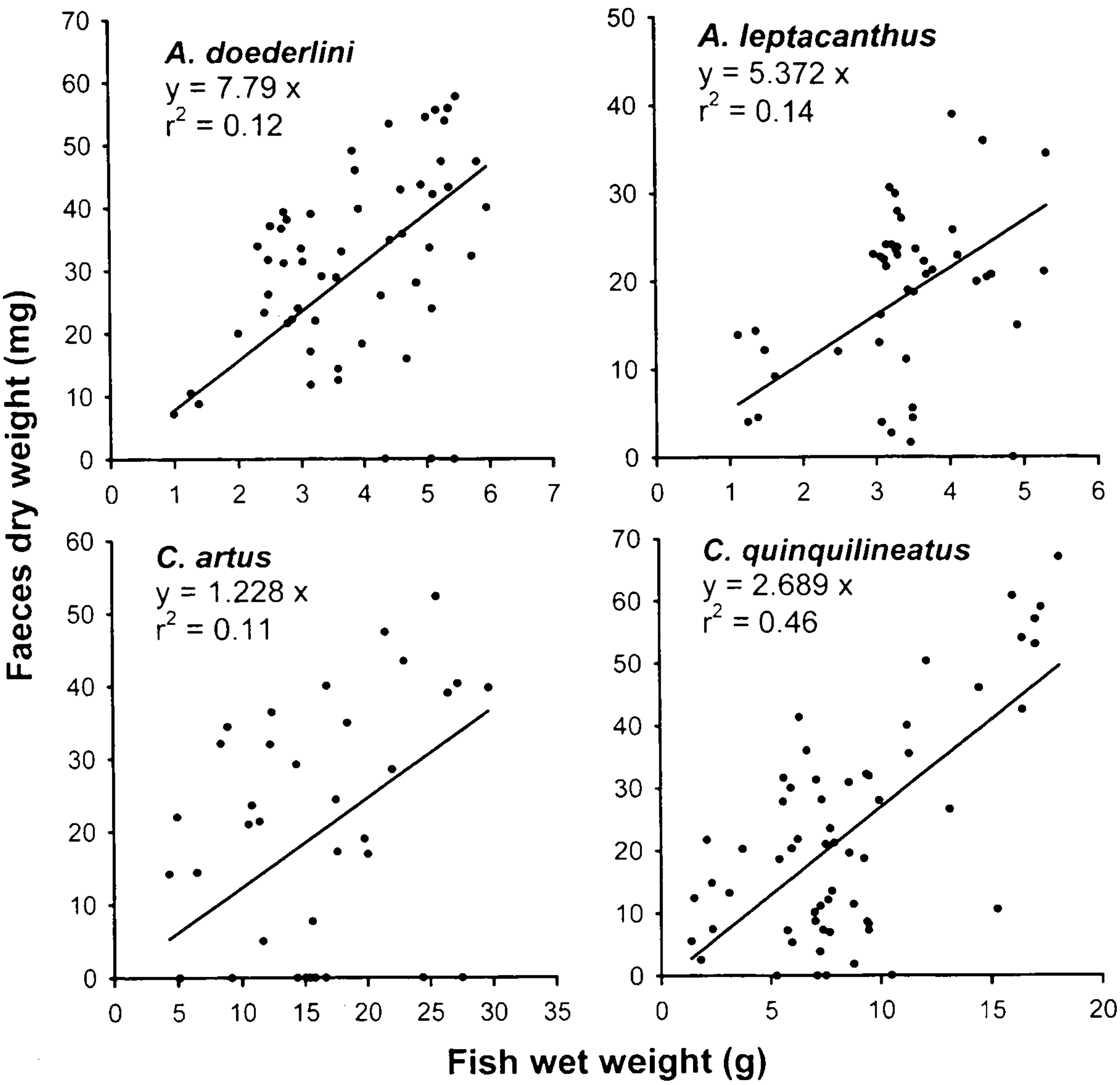


Figure 5.3 Relationship between fish weight (wet weight) and amount of faecal matter (dry weight) produced by *A. doederlini* (n = 55), *A. leptacanthus* (n = 45), *C. artus* (n = 35) and *C. quinquilineatus* (n = 59) during daylight hours (~ 0600 to 1800 hrs).

Table 5.1 Calculation of defecation rates by apogonids across all available lagoonal reef habitat and at resting sites. Fish biomass estimates are based on a) visual censuses across all lagoonal reef habitats (Chapter 1), and b) quantitative, clove oil collected samples from resting sites (Chapter 4); SE in brackets; n.a. indicates that no reef-wide biomass estimates were available for *A. leptacanthus*. Combined SE values were calculated using Goodman's estimator following Travis (1982).

Species	Faeces production rate (mg dry faeces g^{-1} fish wet wgt)	Fish biomass across lagoonal reefs ($g\ m^{-2}$)	Fish biomass at resting sites ($g\ m^{-2}$)	Faeces produced across lagoonal reefs (mg dry faeces $m^{-2}\ day^{-1}$)	Faeces produced at resting sites (mg dry faeces $m^{-2}\ day^{-1}$)
A. doederlini	7.79 (0.47)	0.55 (0.21)	57.6 (16.0)	4.2 (1.6)	432 (124)
A. leptacanthus	5.37 (0.38)	n.a.	49.7 (9.7)	n.a.	268 (57)
C. artus	1.23 (0.15)	0.19 (0.05)	12.8 (2.1)	0.23 (0.07)	15.4 (3.6)
C. quinquilineatus	2.68 (0.18)	0.75 (0.19)	15.8 (2.2)	2.0 (0.5)	42.7 (6.7)
All species	4.3 (1.5)	1.77 (0.43)	162 (24)	7.6 (3.2)	693 (260)

5.4b Transfer of material to piscivores

Tagging studies

All four species showed a rapid decline in the number of tagged fish remaining over the course of the study. Tagged specimens of *A. cyanosoma* and *A. doederlini* were only recorded at tag sites for 8 months, whilst tagged *C. artus* and *C. quinquilineatus* were observed at tag sites for at least 16 months (Fig. 5.4). There was insufficient data to analyse all tag sites separately. Therefore, the instantaneous mortality rate (Z) was calculated for each species from the combined frequency of tagged fish remaining at all sites. The highest mortality rate was recorded in *A. cyanosoma* ($Z = 3.57$, $r^2 = 0.98$), followed by *A. doederlini* ($Z = 2.26$, $r^2 = 0.99$), *C. quinquilineatus* ($Z = 1.81$, $r^2 = 0.92$) and *C. artus* ($Z = 1.52$, $r^2 = 0.97$) (Fig. 5.4). Mortality rates were approximately constant over much of the range of data in all species. However, in A. *cyanosoma* and *A.doederlini* mortality rates increased dramatically after 8 months (indicated by dotted lines in Fig. 5.4). Emigration from tag sites appeared to be minimal in all species (Chapter 3). During searches extending to a diameter of ~50 m around tag sites, only six individuals (two *A. doederlini*, three *C. artus* and one *C. quinquilineatus*) were found greater than 1 m from mapped tag sites and all of these were within 5 m of initial recorded positions. No *A. cyanosoma* were ever located greater than 1 m from tag site grids.

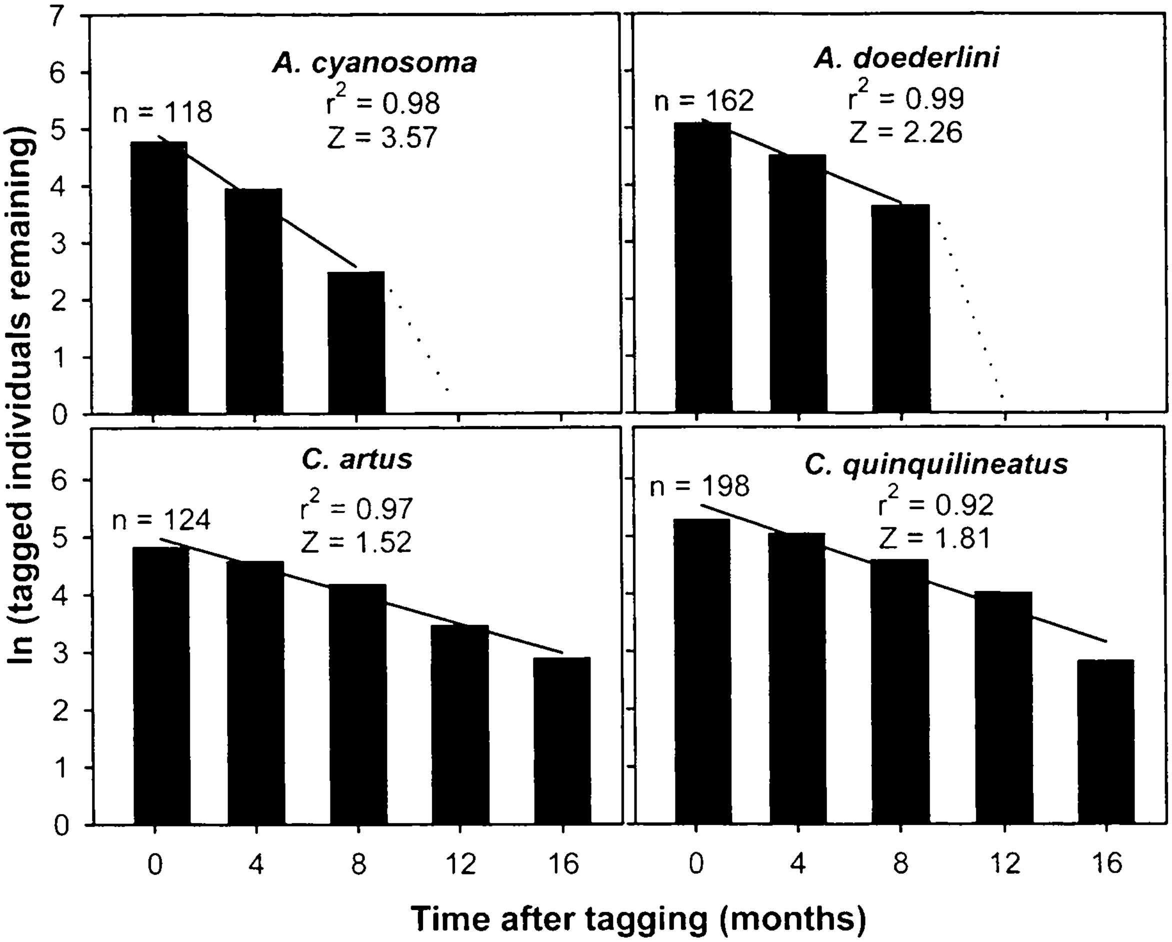


Fig. 5.4 Instantaneous mortality rate (Z) derived from the frequency of tagged fish remaining over time across all tag sites. Dotted lines for *A. cyanosoma* and *A. doederlini* indicate approximate mortality after 8 months (not included in regression).

Otolith aging

Presumed daily increments were evident in all species and, once validated, were used for age estimates in *A. cyanosoma* and *A. doederlini* (Fig. 5.5). Annual increments were used for age estimation of *C. artus* and *C. quinquilinetaus* (Fig. 5.6). All four apogonid species were relatively short-lived. The smallest and also the shortest lived species was *A. cyanosoma* where the largest 5% of specimens out of a total sample of 189 had a mean age ± 95% CI of 336 ± 32 d (max. 385 d) and a mean standard length (SL) ± 95% CI of 51.5 ± 0.8 mm (Fig. 5.7). For *A. doederlini*, of 261 specimens, the largest 5% had a mean age of 438 ± 36 d (max. 470 d) and a mean SL of 59.9 ± 0.9 mm, for *C. quinquilineatus* (n = 237) a mean maximum age of 821 ± 93 d (max. 3 yrs) and a mean maximum SL of 86.5 ± 2.1 mm, and for *C. artus* (n = 219) a mean maximum age of 962 ± 109 d (max. 3 yrs) and a mean maximum SL of 97.6 ± 3.9 mm (Fig. 5.7). A comparison of tagging estimates of mortality (method 1) versus otolith aging estimates of mortality (calculated from longevities using Hoenig's (1983) formula (method 2) revealed reasonably consistent estimates for all species (Table 5.2). The tagging method appeared to produce consistently lower estimates of mortality than the otolith aging method, however, the rank order of mortality rates among species was the same between methods. Both methods combined provided mortality rates ranging between 78.0% and 99.1% yr^{-1} for the four species examined.

Otolith validation

Injection with tetracycline hydrochloride produced fluorescent marks in the sagittal otoliths of all four species. Average counts of the number from the first to the second tetracycline marks in *A. cyanosoma* (n = 3) was 9.7 ± 0.3 (SE) (Fig. 5.8), and in *A. doederlini* (n = 6) 9.8 ± 0.4 (SE) (Fig. 5.9). Since the time between tagging events was 10 days, results indicated daily increment deposition in both species. Readings of the number of increments between tetracycline marks and the otolith edge in *C. quinquilineatus* (n = 5) and *C. artus* (n = 4) corresponded exactly to the time at liberty after tagging in all specimens (either 1 or 2 years), indicating that increments were deposited on an annual basis. Daily increments were also evident in the otoliths of *C. quinquilineatus* and *C. artus* within the first annual increment.

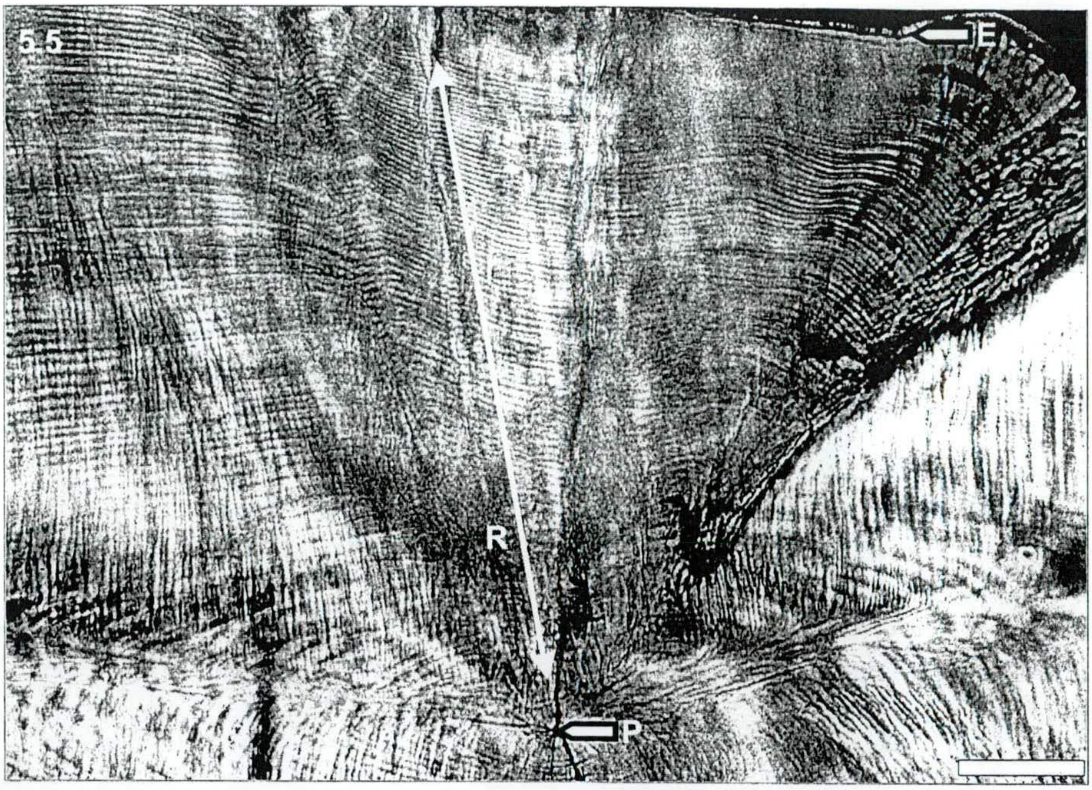


Fig. 5.5 Transverse section of a sagittal otolith of *Apogon doederlini* (age ~125 days) showing daily increment formation. P - primordium, E - otolith edge, R - primary axis along which increments were read, scalebar = 0.2 mm.

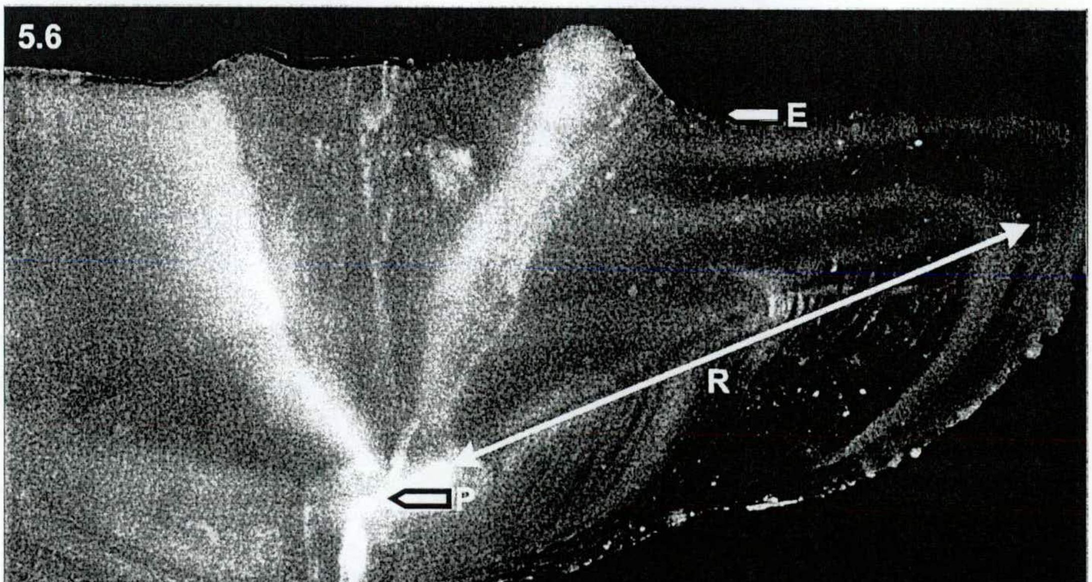


Fig. 5.6 Transverse section of a sagittal otolith of *Cheilodipterus artus* (age 2 years) showing annual increment formation. P - primordium, E - otolith edge, R - primary axis along which increments were read, scalebar = 0.4 mm.

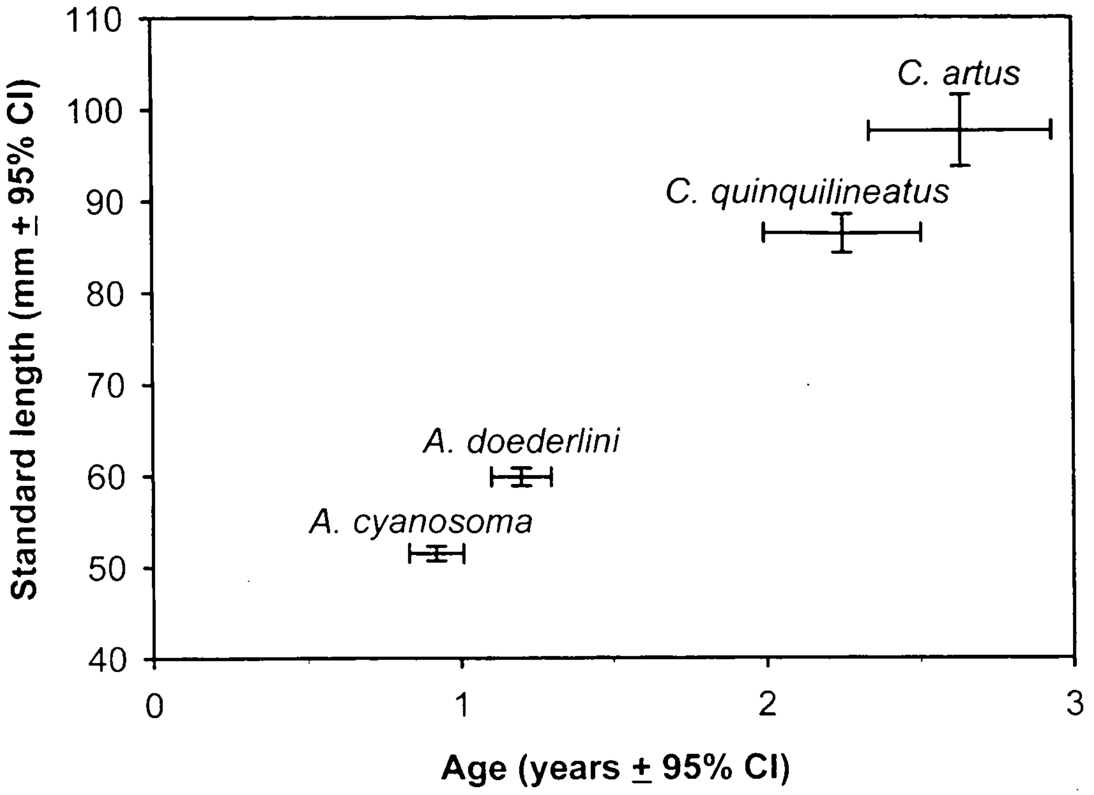
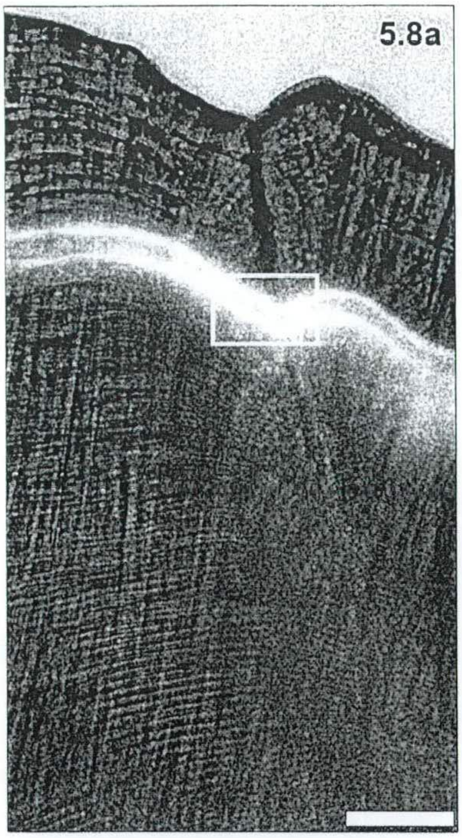


Fig. 5.7 Mean maximum size versus age for the largest 5% of all individuals collected from One Tree Reef throughout the course of the study (July 1997 to July 1999).

Table 5.2 Comparison of mortality estimates derived from the disappearance of tagged fish over time (Method 1) and derived from maximum longevities (using Hoenig's [1983] formula) of the largest 5 % of fish collected throughout the study (Method 2).

	METHOD 1: Tagging Studies		METHOD 2: Otolith Aging	
Species	Z	Mortality yr^{-1}	Z	Mortality yr^{-1}
A. cyanosoma	3.57	97.2 %	4.68	99.1 %
A. doederlini	2.26	89.6 %	3.58	97.2 %
C. quinquilineatus	1.81	83.7 %	1.90	85.0 %
C. artus	1.52	78.0 %	1.62	80.2 %



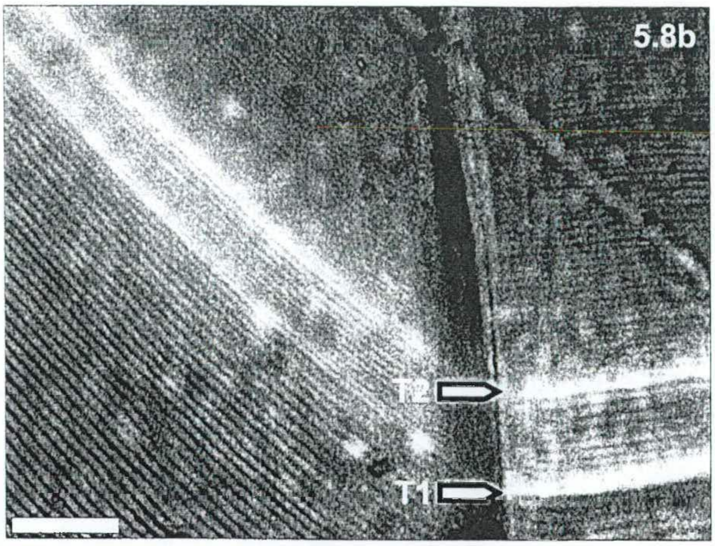
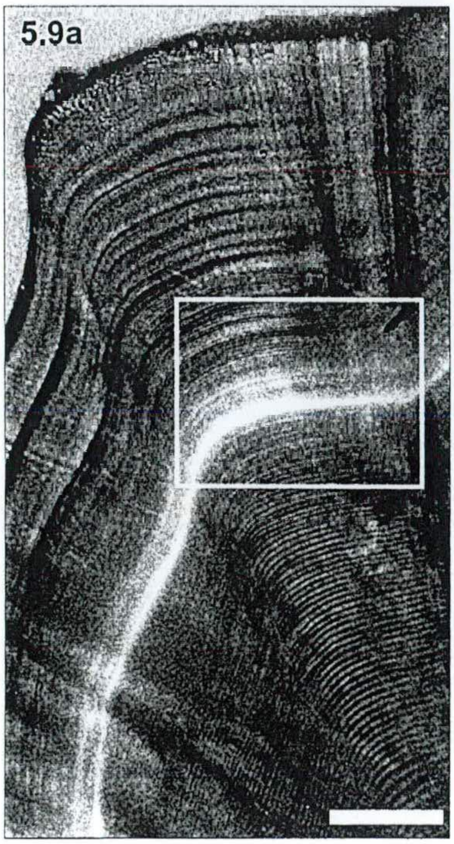


Fig. 5.8 Position of tetracycline marks in a transverse section of the sagittal otolith of *Apogon cyanosoma*. a) Position of tetracycline marks relative to otolith edge, scalebar = 0.2 mm. b) Exploded view showing daily increments between marks, scalebar = 30 μm. T1- tetracycline treatment 1 (day 1), T2 - tetracycline treatment 2 (day 10).



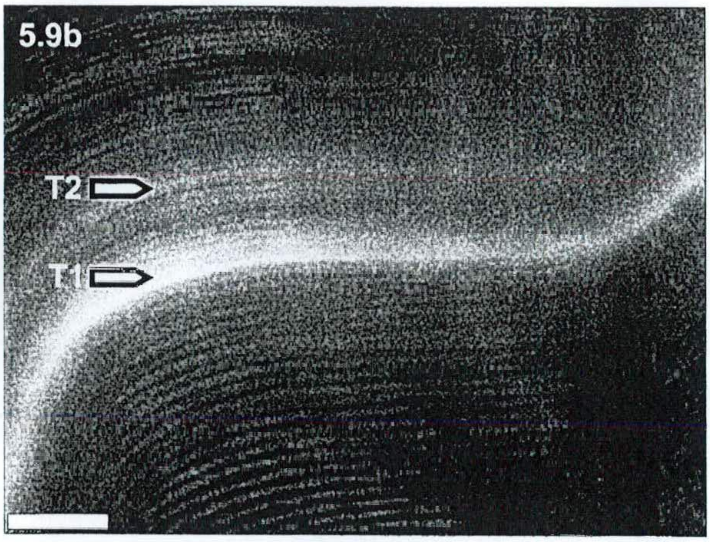


Fig. 5.9 Position of tetracycline marks in a transverse section of the sagittal otolith of *Apogon doederlini*. a) Position of tetracycline marks relative to otolith edge, scalebar = 0.2 mm. b) Exploded view showing daily increments between marks, scalebar = 50 μm. T1- tetracycline treatment 1 (day 1), T2 - tetracycline treatment 2 (day 10).

Population dynamics

Populations of all four species were found to vary widely over the two-year study period. The maximum abundances of recruits were observed during the March censuses for all species (Figs.5.10, 5.11). In *A. cyanosoma* and *A. doederlini* adult abundances were minimal during March censuses and peaked during July censuses. These two species showed the most pronounced change in adult densities throughout the year with a 5 to 20-fold increase in the density of adult fish between March and July censuses in both years (Fig. 5.10a&b). In addition, the temporal abundance patterns of recruits, time-lagged by 4 months (1 time-frame) was significantly correlated with abundances of adults in *A. cyanosoma* (cross-correlation coefficient, $r_{xy(1)} = 0.90$, $p<0.005$) and *A. doederlini* ($r_{xy(1)} = 0.88$, $p<0.005$). By comparison, *C. artus* and *C. quinquilineatus* only exhibited a maximum 2 to 4 fold change in adult densities between March and July censuses (Fig. 5.11a&b), and temporal abundance patterns of adults and recruits, time-lagged by 4 months, displayed a non-significant cross-correlation (*C. artus*: $r_{xy(1)} = 0.59$, $p>0.05$, *C. quinquilineatus* $r_{xy(1)} = 0.67$, $p>0.05$). There appeared to be only a low level of recruitment in March 1998 for all four species (Figs. 5.10, 5.11), which was evident in low adult densities during March and Nov. 1998 in *A. cyanosoma* and *A. doederlini* (Fig. 5.10a&b).

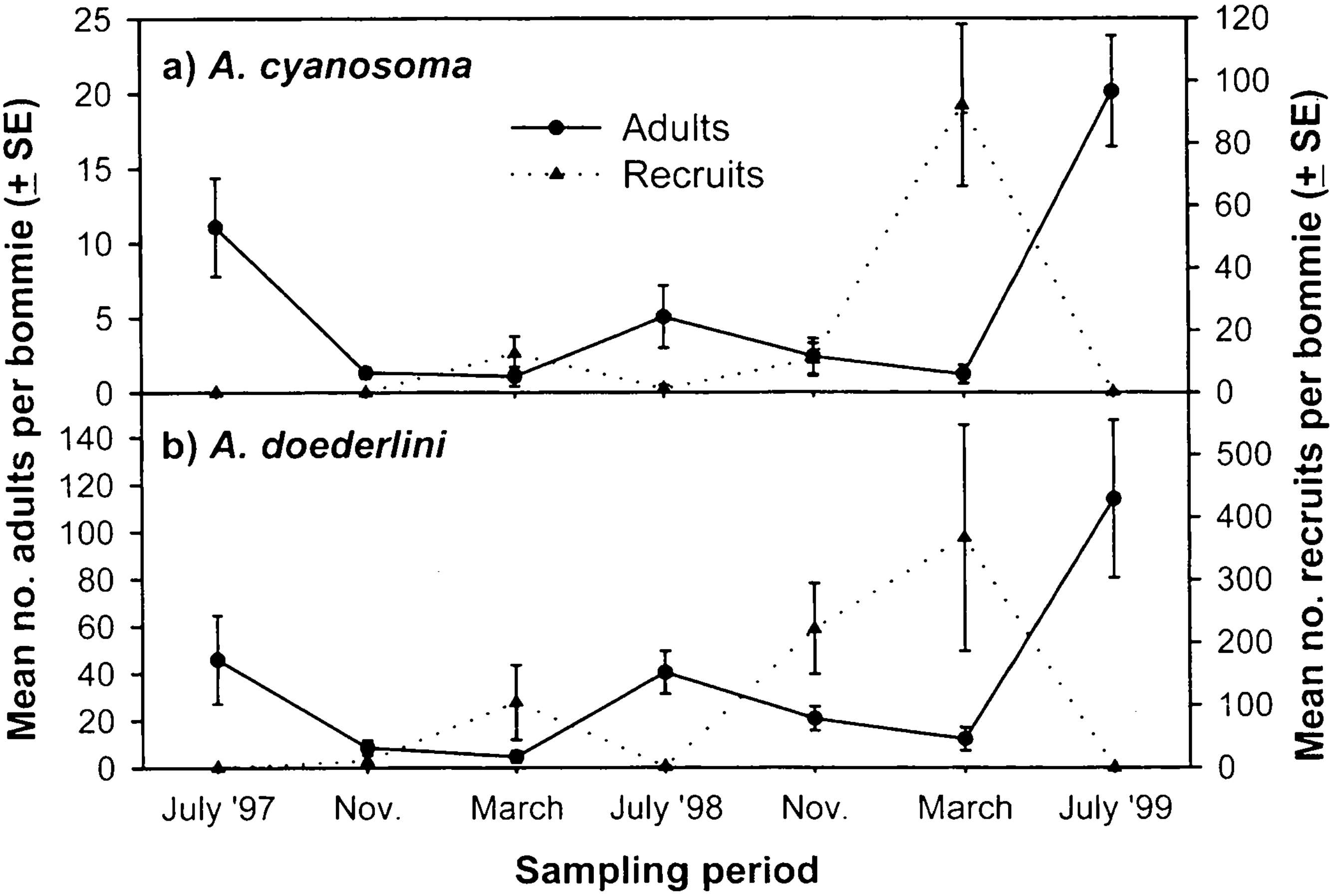


Fig. 5.10 Mean abundance of newly recruited and adult a) *A. cyanosoma* and b) *A. doederlini* censused at four-monthly intervals within the One Tree Reef Lagoon. Data points represent the mean abundance of five micro-atolls. Micro-atoll values represent the mean of 3 censuses conducted at weekly intervals within a given time of year.

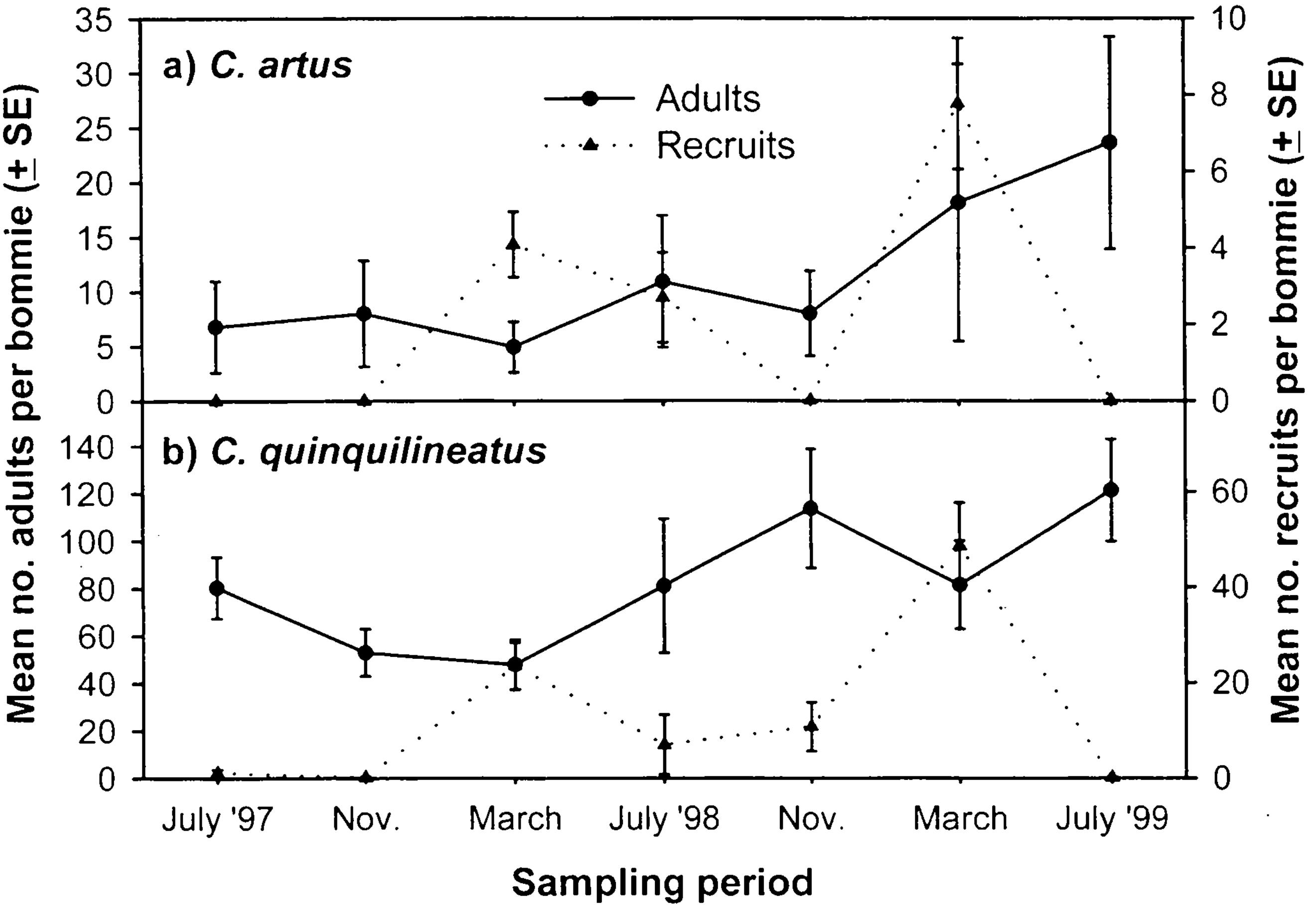


Fig. 5.11 Mean abundance of newly recruited and adult a) *C. artus* and b) *C. quinquilineatus* censused at four-monthly intervals within the One Tree Reef Lagoon. Data points represent the mean abundance of five micro-atolls. Micro-atoll values represent the mean of 3 censuses conducted at weekly intervals within a given time of year.

5.5 DISCUSSION

5.5a Transfer of material to detritivores

The relationship between fish wet weight and the dry weight of faeces produced was best described as linear. This is in accordance with the relationship between fish weight and defection described by Meyer & Schultz (1985) for Caribbean haemulids. The significance of the relationship in the present study was somewhat reduced, however, due to the inclusion of specimens in analyses that did not produce faeces. Fish that produced no faeces were excluded from calculations by Meyer & Shultz (1985a) and Bray et al. (1981). However, it was important in the present study to include these fish since an overall estimate of apogonid defecation rates on reefs was required. Since some fish naturally have empty guts at dawn (Chapter 3) presumably due to the failure to capture prey the previous night, a proportion of fish would be expected to produce no faeces at resting sites. A failure to include these fish in analyses may have resulted in an overestimate of defecation rates in the studies of Meyer & Schultz (1985) and Bray et al (1981).

There is evidence to suggest that seasonal variations occur in growth, feeding and defecation rates of coral reef fishes, with rates generally lowest during winter months (Bellwood 1995a, Jones 1991). It is highly probable that seasonal differences also occur in apogonids defecation rates at One Tree Reef. The time period sampled at One Tree Reef was during average to low water temperatures (21^0C to 23.5 ^{0}C) compared to the range of temperatures encountered throughout the study (18^0C to 30^0C), suggesting that results are likely to be an underestimate, or at the most on par with average defecation rates for the year.

The most interesting finding of this study was that estimates of defecation rates by *A. doederlini* at resting sites (432 ± 124 mg dry faeces m^{-2} day^{-1}) were of the same order of magnitude as estimates of faeces deposited by resting schools of haemulids from the Caribbean, examined by Meyer and Schultz (1985). Meyer and Schultz (1985a,b) suggest that the faeces produced by resting schools of haemulids (780 to 2700 mg dry faeces m^{-2} day^{-1}) enhanced the growth of colonies of the coral *Porites furcata*. Although faeces deposition rates for *A. doederlini* were slightly lower than those of the haemulids, *A. doederlini* usually co-inhabits resting sites with a number of other apogonid species, adding to the quantity of faeces produced. Including all species of apogonids at resting sites in calculations produced an estimate of 693 mg dry faeces m^{-2} day^{-1}, which is comparable to the lower estimates of faeces produced by haemulid schools (780 mg dry faeces m^{-2} day^{-1}; Meyer & Schultz 1985). An additional consideration is that the mean biomass of apogonids from the Lizard Island lagoon was approximately three times that of One Tree Reef (Chapter 1), suggesting that the quantity of faeces produced by resting schools of apogonids at some other locations on the GBR may be much higher than estimates for One Tree Reef.

The nutritional quality of faeces produced by apogonids is unknown, however, they consume a diet very similar to Caribbean haemulids consisting of benthic invertebrates and demersal plankton (Chapter 3, c.f. Meyer et al. 1983), suggesting the possibility that haemulid and apogonid faeces are of similar nutritional quality. If this is true, apogonids may play a similar role to haemulids through the nutrient enrichment of corals at resting sites. Meyer and Shultz (1985) suggest that much of the nitrogen and phosphorous content of faecal pellets leaches within the first 24 hrs of excretion. If these nutrients are leached within areas of low water movement, such as is the case within apogonid resting sites (Chapter 1), increased N and P may be provided for uptake by corals (Meyer & Shultz 1985b, Liberman et al. 1995).

C. artus produced by far the lowest amounts of faeces at resting sites. This was due in part to the lower abundances of *C. artus* at resting sites, but was primarily due to the lower rate of faeces production per unit body weight (1.23 mg dry faeces g^{-1} wet body wgt). *C. artus* feeds primarily on teleosts whereas *A. doederlini*, *A. leptacanthus* and *C. quinquilineatus* feed largely on demersal plankton (mostly crustaceans) (Chapter 3). Since teleosts are generally larger than demersal plankton, it is possible that they take longer to digest and the waste is not excreted by *C. artus* during the day. However, an examination of dissected *C. artus* specimens killed shortly after experiments revealed empty guts. It is more likely, therefore, that teleosts are assimilated more completely than demersal plankton, leaving little refractory material to be excreted as faeces by *C. artus*.

Apogonids have been found to return to the same resting sites on a daily basis for a major part of their adult life (Chapter 2). Therefore, the faeces produced by resting schools of apogonids is likely to represent a spatially and temporally predictable resource for detritivore communities (Bray et al 1981) and may enhance local coral growth (cf. Meyer and Schultz 1985). However, the importance of this role does not appear to be uniform across the entire family. For example, *C. artus* deposits little faeces at resting sites and may be of limited importance to detritivore communities and corals. By contrast, *A. doederlini* has a relatively high faeces input at resting sites. Interestingly, *A. doederlini* is the only apogonid species within the One Tree Reef lagoon which forages entirely over the sand areas between micro-atolls (Chapter 3). *A. doederlini* may therefore be a key species responsible for concentrating nutrients and energy from sand habitats at specific sites on the reef.

Considering the critical importance of recycling in reef systems (Hatcher 1983, Alongi 1988, Arias-Gonzalez 1997), the fate of fish faeces on reefs has received surprisingly little attention (Robertson 1982). This study forms a framework for future investigations of the importance of resting schools of fishes in the tropho-dynamics of Indo-Pacific reefs. Whilst further studies are required to determine the quality of faeces produced by apogonids, and to directly measure the impacts of apogonids on detritivore communities and coral growth, initial results suggest that the input of faeces by apogonids at resting sites is significant. In addition, since apogonids feed in a range of reef and non-reef habitats, then defecate at restricted resting sites on the reef, they are likely to be responsible for a net movement of material between habitats.

5.5b Transfer of material to piscivores

High turnover rates were exhibited in all four species of apogonids. This was evident from mortality rates, estimated from the disappearance of tagged fish over time, and also from longevity estimates derived from otolith aging. The highest turnover rates were exhibited by *A. cyanosoma* and *A. doederlini*, where few individuals appeared to survive beyond one spawning season. These results are consistent with aging studies on other apogonid species (Fisher 1991, Milton & Blaber 1995), however, it appears likely that apogonids from lower latitudes may exhibit even faster turnover rates. Milton & Blaber (1995) suggest a lifespan of only 4 to 6 months in *Rhabdamia gracilis* from the Solomon Islands, whilst Fisher (1991) suggests a maximum age of only 6 months in *Foa brachygramma* from Green Island, northern GBR. By contrast, Okuda et al. (1998) suggest that *A. deoderlini* live for up to 7 years on sub-tropical rocky reefs off Japan. The Japanese *A.doederlini*, however, is likely to be a geographical variant or a different species to *A. doederlini* from the present study (Okuda pers. comm.), and reaches almost twice the maximum size of *A. doederlini* collected from One Tree Reef. However, the largest specimen of *A. doederlini* collected from One Tree Reef corresponds to a one year old specimen of the same size from Okuda et al.'s (1998) study.

Only a few studies have examined mortality rates in unexploited reef fish populations beyond the early post-settlement stages (Russ et al. 1998). Eckert (1987) estimated mortality rates of between 4.9 % and 69.5 % for a range of wrasses species (Labridae) from the One Tree Reef lagoon. The average mortality rate (~ 30 %) for wrasses was far lower than the mortality estimates of 78 % to 99 % for apogonids in the present study. In addition, mortality estimates in Eckert's (1987) study were calculated from the disappearance of individuals from patch reefs. Since many species of labrids are known to move during ontogeny (Green 1996), mortality rates were likely to have been overestimated due to migration effects. The mortality rates observed in apogonids were similar to those estimated for the goby *Istigobius decoratus* from Lizard Island, Great Barrier Reef (Kritzer, in press). Kritzer (in press) suggests an annual mortality rate of over 99 % for *I. decoratus*, estimated from age-based catch curves.

Whilst few studies have examined mortality rates in reef fishes, there are a number of estimates of maximum longevities available for reef fishes. Most estimates have been obtained using otolith aging methods. The maximum lifespans of apogonids recorded in the present study (1 to 3 years) were lower than available estimates for most other reef fish taxa. Studies suggest that most tropical reef fish taxa are generally long-lived (>10 years; Fig. 6.2), with longevities of over 45 years in serranids (Mosse unpubl. data) and acanthurids (Choat and Axe 1996). The family Pomacentridae has received much attention in reef tropho-dynamic studies due to their high abundances and conspicuous diurnal habits (Hamner et al. 1988, Parrish 1989). Published longevity estimates for pomacentrids range from 4 to 32 years (Meekan et al. 2001), however, the majority of species examined live for more than 10 years. Therefore, whilst pomacentrids are generally more abundant than apogonids on reefs, apogonids may be turning over at faster rates and may thus play an equally important role in reef energetics.

Of the species of reef fishes reported to have similar turnover rates to those observed in apogonids, most are from the families Blenniidae and Gobiidae. Labelle and Nursall (1992) report that the blenny, *Ophioblennius atlanticus macclurei* from Barbados lives for only 3 years, whilst published longevity estimates in reef dwelling gobies range from less than one year in *Coryphopterus personatus* (Robertson & Kaufmann 1998) and *C. glaucofraenum* (Forrester 1995) from the Caribbean to 16 months in *Valencienna strigata* from French Polynesia (Reavis 1996). The Blenniidae and Gobiidae, along with Apogonidae are the most abundant reef fish taxa that are most often missed in visual surveys (Brock 1982, Bellwood 1996, Ackerman & Bellwood 2000). However, in terms of turnover rates, these taxa may be of great importance to reef energetics.

Population dynamics of apogonids appeared to directly reflect estimates of mortality and longevity for each species. In all four species, populations were highly variable over a yearly timeframe, particularly in *A. cyanosoma* and *A. doederlini*. Recruitment peaks were evident during March censuses in all species. This is in accordance with work by Finn & Kingsford (1996), who identified peaks in apogonid recruitment at One Tree Reef between January and March each year. The most interesting finding of the present study was that adult abundances also fluctuated widely over a yearly time-frame. Adult populations of the two shortest-lived species, *A. cyanosoma* and *A. doederlini*, were highly dynamic through time, fluctuating between 5 and 20-fold over a yearly timeframe. This fluctuation appeared to be in direct response to recruitment episodes, implying that there may be a large degree of recruitment limitation in *A. doederlini* and *A. cyanosoma* at One Tree Reef. This is further supported by evidence of a poor recruitment season during March 1998 translating into relatively low adult abundances in both species during July 1998 compared to other years.

Population dynamics of *A. cyanosoma* and *A. doederlini* are consistent with population dynamics observed in other short-lived species. Reavis (1997) observed 4 to 6-fold fluctuations in the adult populations of the goby *Valencienna strigata* throughout the year on Moorea Atoll, whilst Roberston & Kaufmann (1998) observed two to three-fold fluctuations in adult populations of the goby *Coryphopterus personatus* from the Caribbean. In both cases, adult abundances appeared to be responding directly to variable episodes of recruitment.

Fluctuating populations of apogonids may have flow-on effects for reef predators. Stewart and Jones (2001) suggest that reef predators may respond to seasonally fluctuating prey densities through either migration or prey switching. Evidence of strong seasonal effects on dietary composition has been reported for coral trout, (*Plectropomus leopardus*) from One Tree Reef (Kingsford 1992). *P. leopardus* was found to primarily consume clupeids during summer, when they were most abundant, with other prey taxa, including apogonids, predominating in diets during winter months (Kingsford 1992). Therefore, if short-lived species of apogonids have a poor recruitment episode in a particular year, resulting in low population densities, it appears quite likely that predators may need to migrate or switch to other prey taxa in order to satisfy energy requirements.

Adult populations of *C. artus* and *C. quinquilineatus* did not display a strong relationship with peaks in recruitment as seen in *A. cyanosoma* and *A. doederlini*. This is likely to be due to the lower mortality rates and longer lifespans of *C. artus* and *C. quinquilineatus* compared to the two smaller species. Adult abundances fluctuated only

2 to 3-fold within a yearly time frame, and the majority of this variation was within the limits of sampling error. Since *C. artus* and *C. quinquilineatus* live for more than two years, a base-level of adults is likely to persist from year to year. This "storage effect" of adults may have reduced the ability to detect the effect of recruitment pulses on adult populations in this study (Warner and Hughes 1988).

High turnover rates in apogonids suggest that they may provide an important dietary resource for reef piscivores. Apogonids are consumed by a wide range of reef fish taxa including serranids (Randall & Brock 1960, Kingsford 1992, St John et al. 2000), scorpaenids (Hiatt and Strasburg 1960) and lutjanids (Connell & Kingsford 1998). In particular, apogonids form the dominant prey item for serranids of the genus *Cephalopholis* (Stewart 1998). In the present study, *Cephalopholis* spp. were often seen in association with resting schools of apogonids and predation events were witnessed regularly. Stewart and Jones (2001) suggest that at Lizard Island in the northern Great Barrier Reef, *Cephalopholis* spp. may comprise up to 30% of the total predator abundance. If these figures are representative of other reefs, apogonids may provide a major trophic link on Indo-Pacific reefs between their primary food source, demersal plankton and higher trophic levels.

This study presents one of the first comparative evaluations of methods used to estimate turnover rates in reef fishes. In general, all three estimates of turnover rates in apogonids provided consistent findings. Tagging estimates of mortality rates were slightly lower than estimates obtained through otolith aging. This was surprising, since tagging fish is generally assumed to result in increased mortality due to tagging effects (King 1995). In addition, any migration of tagged fish away from tag sites would also be likely to result in an overestimate of mortality rate (King 1995). Apogonids appear to have very high site fidelity (Chapter 3) and migration may have been negligible in this study. It is possible that the formula used to calculate mortality from longevity estimates (Hoenig 1983) may not have been particularly reliable for short-lived species. This formula was itself based on mortality estimates from the literature, therefore, existing biases and inaccuracies were likely to be incorporated. However, the most likely explanation for the discrepancy between the two techniques was that there was a rapid decline in tagged fish remaining after 8 months in *A. cyanosoma* and *A. doederlini* which was not explained by the instantaneous rate of mortality (see dotted line, Fig. 5.4). This may have also been the case in *C. artus* and *C. quinquilineatus* after 16 months but was not measured. Taking this factor into consideration, the tagging and otolith aging methods gave remarkably consistent results.

Overall, apogonids are highly abundant and appear to be relatively short-lived compared to most other reef fish taxa, suggesting that they provide an important link between their primary food source, demersal plankton, and higher trophic levels. Since apogonid abundances vary dramatically with season, populations are likely to have a strong seasonal effect on reef processes. Apogonids have a high input to reef processes but this input is likely to be very focused. They forage widely within lagoons and deposit faeces in highest concentrations at resting sites within lagoonal reefs. They are also available to predators in highest concentrations at lagoonal resting sites. Although the input of apogonids to reef processes is focused within lagoons, this role may be of great importance to whole-reef processes.

CHAPTER 6: OVERVIEW

Nocturnal fishes are likely to be functionally distinct from their diurnal counterparts, however, to date we know little of their role in reef tropho-dynamics. On Indo-Pacific reefs apogonids form the major component of nocturnal planktivore assemblages (Hobson 1991). Apogonids are largely cryptic by day, and are hence frequently underestimated or missed in standard daytime visual surveys of reef fish assemblages (Brock 1982, Ackerman & Bellwood 2000). If apogonids play a significant role in reef processes, neglecting them from censuses of reef fish communities may have serious consequences for the accuracy of tropho-dynamic models. Therefore this thesis, examined the role of apogonids in reef processes.

The first objective of this study was to determine the spatial scale over which apogonids were likely to have the greatest influence on reef processes. In chapter 2, the highest abundance and biomass of apogonids was found on reefs with the lowest degree of exposure. In particular, apogonids were highly abundant on lagoonal reefs at both One Tree Reef and Lizard Island with abundances on these reefs 3 to 4 times greater than sheltered reefs and an order of magnitude greater than exposed reefs. Since apogonids are likely to have the most influence on reef processes within lagoons, apogonid populations within the One Tree Reef Lagoon were used as a basis for further investigations of their role in reef tropho-dynamics.

This thesis identified two major processes within the One Tree Reef lagoon in which apogonids were likely to play a significant role: 1) Within-reef transport and recycling of material, and 2) Providing a localised, predictable resource for detritivore communities and reef piscivores. This overview discusses the importance of apogonids in each of these roles relative to other reef fish taxa and reef energetic processes.

Within-reef transport and recycling of material.

Apogonids are trophically distinct from their diurnal planktivorous counterparts in two aspects: Firstly, apogonids were found to feed in habitats which differed markedly from their diurnal resting sites, which indicated a role in the net transport of material on reefs. The most common diurnal planktivores, pomacentrids, feed largely in the water column directly above their resting sites (Sale 1978a, Liberman et al. 1995), suggesting little net transport of material. Secondly, apogonids primarily consume prey of reef origin, whereas diurnal planktivores consume prey largely of oceanic origin (Hobson 1991).

The overall proportion of prey attributable to different sources was calculated by multiplying the proportion of prey taxa attributable to each sources (demersal plankton/benthic invertebrates, oceanic plankton, teleosts and unknown sources) for each species of apogonid by the relative abundance of that apogonid species (chapter 3). From these calculations, the major component of apogonid diets was demersal zooplankton and benthic invertebrates, accounting for 57% of the prey consumed (Fig. 6.1). By comparison, only 7% of prey was attributable to oceanic sources. Even if all of the unknown prey was attributable to oceanic plankton, this would still constitute a considerably smaller component (28%) than prey of reef origin (57%). This suggests a role of recycling in apogonids rather than importation of material to reefs.

Demersal plankton may be an important trophic pathway on coral reefs. The standing biomass of demersal plankton in the water column at night is estimated to be over an order of magnitude greater than the biomass of oceanic plankton over coral reefs during the day (Kingsford 1992). However, apart from a few early studies on the taxonomic composition (Alldredge & King 1977) and vertical migration behaviour (Hobson and Chess 1982) of demersal plankton, this trophic pathway has been virtually ignored in studies of reef tropho-dynamics (Parrish 1989). In particular, the turnover rates of demersal plankton are poorly known.

Efficient recycling has been recognised as a critical process in the successful function of coral reef systems (Hatcher 1983, Alongi 1988, Arias-Gonzalez 1997). It appears likely that the predation of demersal plankton by apogonids forms an important link in this process through the cycling and retention of material within reef systems. Whilst corals and other reef invertebrates are likely to be significant predators of demersal plankton (Parrish 1989), there appear to be few reef fish taxa, apart from apogonids, that actively feed on demersal plankton within the lagoon at night (Goldman & Talbot 1976, Marnane pers. obs.). Other fish taxa such as goatfishes (Mullidae) feed on interstitial communities and may consume some demersal plankton living in surface sediments during the day (McCormick 1995). However, these fish taxa are generally far less abundant than apogonids and may be restricted to feeding on only a narrow range of accessible demersal plankton during the day. Apogonids appear to be the key group of reef fishes involved in the predation of demersal plankton within lagoonal systems at night.

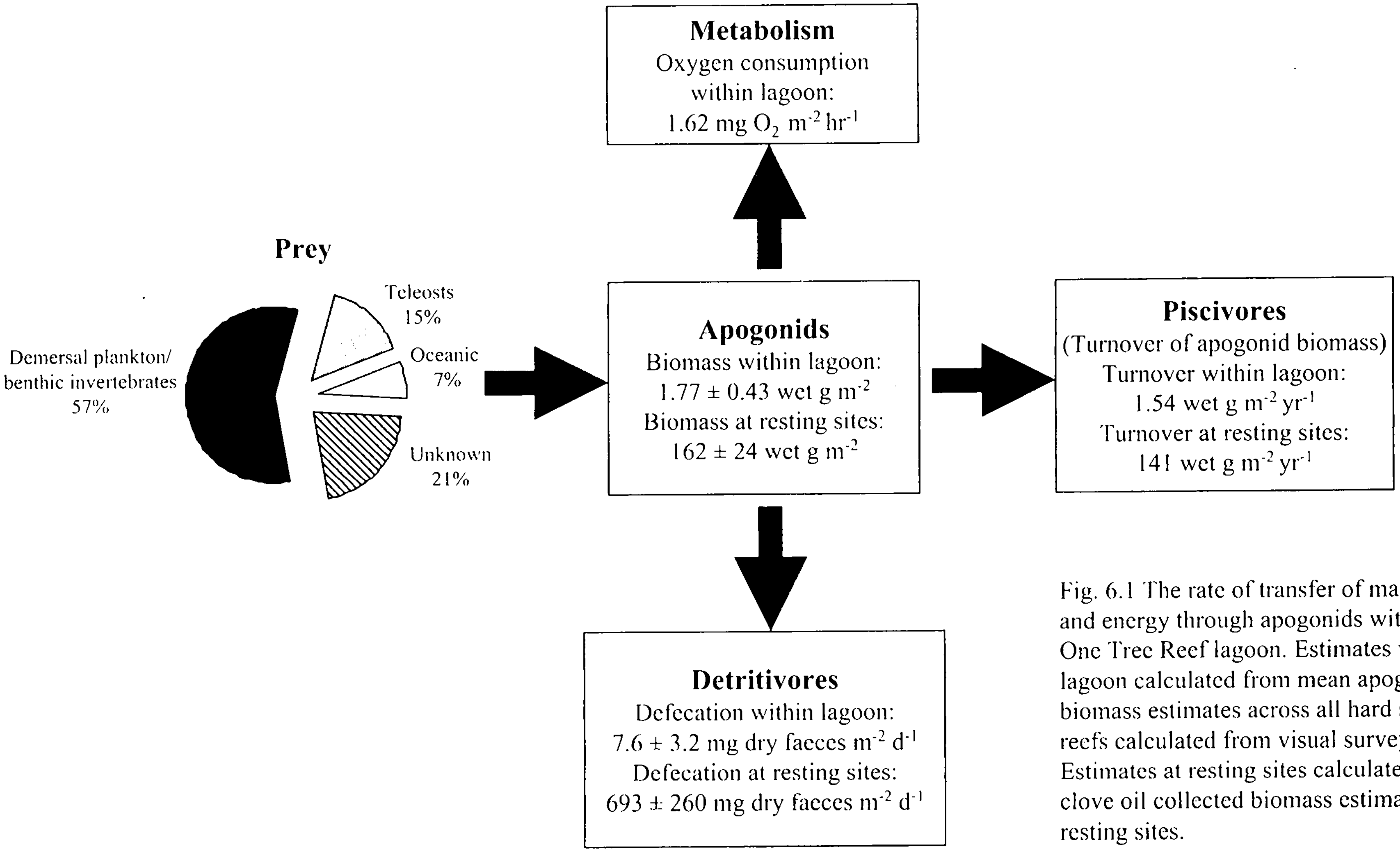


Fig. 6.1 The rate of transfer of material and energy through apogonids within the One Tree Reef lagoon. Estimates within lagoon calculated from mean apogonid biomass estimates across all hard substrate reefs calculated from visual surveys. Estimates at resting sites calculated from clove oil collected biomass estimates at resting sites.

Spatially predictable but seasonally variable resources for detritivores and piscivores

In Chapter 3 apogonids were shown to display strong fidelity to diurnal resting sites, with an indication that individuals use the same resting sites on a daily basis for a major part of their adult life. In addition, apogonids were found to form dense schools at their diurnal resting sites (Chapter 2). Therefore, energy and nutrients obtained by apogonids through feeding in a range of reef habitats are likely to be concentrated at discrete sites on the reef. This process is likely to have important consequences for detritivore communities with respect to apogonid resting sites. It was estimated that an average of 693 ± 260 mg dry faeces m^{-2} d^{-1} (Fig. 6.1) was deposited at resting sites. This is comparable to estimates of defecation rates for haemulids from the Caribbean that were found to enhance local coral growth. Further research is required into the quality of apogonid faeces and the impacts of apogonids on coral growth and detritivore communities, however, it appears that the input of faeces by apogonids at resting sites is significant.

Perhaps the most important influence of apogonids in reef systems is their role in linking demersal plankton communities with reef piscivores. The importance of apogonids for reef piscivores lies in the combination of two aspects: their standing biomass and the turnover rate of this biomass. Whilst apogonids are highly abundant on Indo-Pacific reefs (Bellwood 1996), they are generally small in size and do not appear to comprise a large proportion of the ichthyobiomass. The standing biomass of apogonids on lagoonal reefs (including reef flat, slope and base habitats) was estimated to be 18 ± 4 kg ha^{-1} at One Tree Reef and 49 ± 13 kg ha^{-1} at Lizard Island. Biomass estimates for entire reef fish assemblages range from 175 kg ha^{-1} (Goldman & Talbot

1976) to 2373 kg ha^{-1} (Williams & Hatcher 1983), with most estimates in the range of 1000 kg ha^{-1}. Based on this average, apogonid biomass may comprise around 2% to 5% of the overall fish biomass on reefs.

Goldman and Talbot (1976) estimated a total fish biomass of approximately 350 kg ha^{-1} within the One Tree Reef lagoon from explosive samples, however, over 50% of this biomass comprised large grazing fishes. When broken into trophic groups, the biomass of planktivores in Goldman and Talbot's (1976) study, (which included pomacentrids, caesionids, clupeids and labrids), only amounted to approximately 35 kg ha^{-1}. Based on this estimate, apogonids may comprise around 50% of the total planktivore biomass within the One Tree Reef lagoon. In addition, the actual biomass of apogonids is likely to be even greater since apogonid biomass estimates were calculated from visual censuses (Chapter 2) which were likely to have underestimated true abundance by at least 30 to 40% (Chapter 5). However, it must be noted that biomass estimates given for apogonids are based on the area of hard substrate within the lagoon (reef flat, slope and base habitats) and exclude sand areas between reefs. Goldman and Talbot (1976) do not indicate what proportion of their collection, if any, was taken over sand areas. Nonetheless, apogonid biomass estimates from the present study should be treated with caution when comparing with estimates for reef fish assemblages across the entire reef areas.

The standing biomass of apogonids on reefs only provides a partial indication of their significance in reef processes. More critical in reef energetics is the turnover rate of this biomass. In this respect apogonids are outstanding, with maximum longevities of between 1 and 3 years and mortality rates of between 78 and 99% yr^{-1} at One Tree Reef (chapter 5). Using a mean conservative estimate of mortality rates for apogonids within the One Tree Reef lagoon (87%; Chapter 5) and biomass estimates from visual surveys (chapter 2) and clove oil collected samples (chapter 5), this translates into a turnover rate of apogonid biomass across lagoonal reef habitats of 1.54 g m^{-2} yr^{-1} and 141 g m^{-2} yr^{-1} at resting sites (Fig. 6.1). Available longevity estimates for the eight most abundant reef fish taxa are listed in Figure 6.2. All of these families, with the exception of gobies and blennies, are relatively long-lived (average maximum longevities >10 years) (Fig. 6.2). Gobies and blennies, along with apogonids are highly abundant on reefs but often missed in visual surveys (Ackerman & Bellwood 2000). However, longevity estimates in these three taxa suggests that they may be far more important in reef tropho-dynamics than their standing biomass would suggest. Pomacentrids have received much attention for their role in reef processes (e.g. Hamner et al. 1988, Parrish 1989) and are similar in size to apogonids, however, the vast majority of pomacentrid species examined to date live for more than 10 years (Fig. 6.2). Whilst generally less abundant on reefs than pomacentrids (Bellwood 1996, Ackerman & Bellwood 2000), apogonid populations may be turning over at rates 5 to 10 times faster, providing longevity is a good approximation for mortality rates.

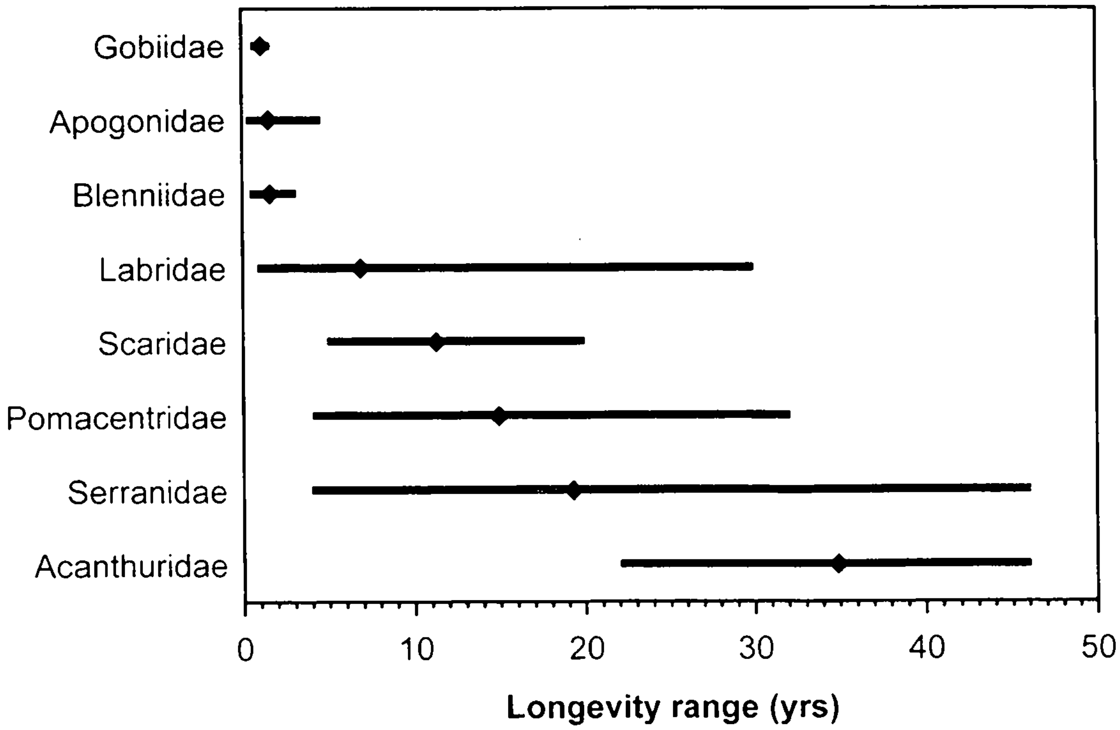


Fig. 6.2 Range of available longevity estimates (in years) for eight common reef fish families (tropical species only). ♦ = average longevity; Longevity data obtained from published and unpublished sources (Gobiidae, 4 species - Reavis 1997, Robertson & Kaufmann 1998, Forrester 1995, Kritzer, in review; Apogonidae, 11 species - Fisher 1991, Milton & Blaber 1995, present study; Blenniidae, 3 species - Labelle and Nursall 1992, SK Wilson unpubl. data; Labridae, 26 species - Warner & Hughes 1988, JL Ackerman unpubl. data; Scaridae, 7 species - Choat et al. 1996; Pomacentridae, 13 species - Fowler 1990, Doherty & Fowler 1994, Sale et al. 1994, Khoda 1996, Lo et al. 1998, Meekan et al. 2001; Serranidae, 13 species - Lo et al. 1998, Russ et al. 1998, JW Mosse unpubl. data; Acanthuridae, 9 species - Choat & Axe 1996).

Studies suggest that the average longevity of apogonid assemblages from lower latitudes may be less than apogonids from higher latitudes (Milton & Blaber 1995, Okuda 1996, Marnane unpubl. data). Since some of the focal species examined at One Tree Reef were close to the limit of their range in latitude (Kuiter 1992), longevity estimates presented may represent maximum estimates for these species on the GBR.

Apogonids from lower latitudes may be turning over at even faster rates. Longevity estimates for apogonids from Lizard Island, towards the northern end of the GBR, suggest that most species live for around one year or less (Table 6.1). The exception to this was for *C. macrodon*, found to reach at least 5 years of age. However, *C. macrodon* is more than twice the size of all other apogonid species on the GBR, reaching more than 20 cm in length (Randall et al. 1997) and may represent the upper longevitiy limit for the Family Apogonidae on the GBR. Overall, data suggests that standing biomass alone may be a poor indicator of the importance of apogonids in reef processes. It appears that there may be a large flux of energy through apogonids to higher trophic levels due to their short life-spans, and that apogonids are likely to provide an important resource for reef piscivores.

Table 6.1: Mean age and mean size of the largest 5% of apogonids of each species collected from Lizard Island during February 1997, Nov. 1997 and August 1998.

Species	**Mean age ± SE**	**Mean size ± SE**	**Total sample**
Rhabdamia gracilis	196 ± 16 days	34.3 ± 0.5 mm	81
Apogon fragilis	298 ± 23 days	32.1 ± 1.0mm	69
Apogon leptacanthus	320 ± 18 days	43.9 ± 0.3mm	106
Archamia fucata	357 ± 11 days	46.4 ± 0.9mm	87
Cheilodipterus macrodon	4.7 ± 0.6 yrs	185.1 ± 5.2 mm	74

Since most apogonids are relatively small, they may also be important in reef energetics simply due to their mass-specific metabolic demands. Small fishes have higher mass-specific metabolic rates that larger fishes (Miller 1979, Clarke & Johnston 1999), therefore, the energy consumed by apogonids on reefs may be disproportionately high relative to their standing biomass. Grazing fishes such as scarids and acanthurids comprise the greatest proportion of ichthyo-biomass at One Tree Reef (Goldman & Talbot 1976), however, most of these species are generally large and would therefore be likely to consume far less energy per unit biomass than apogonids. Using Mann's (1965) formula it is estimated that the oxygen consumption of 1 kg of scarids is approximately 110 mg hr^{-1} (comprised of 4 fish of average weight 250 g, actual mean weight = 270 g at Lizard Island; Gust et al. 2001). By comparison, the oxygen consumption of 1 kg of apogonids is approximately 270 mg hr^{-1} (345 fish, mean weight 2.9 ± 0.1 g at Lizard Island; Chapter 2). Therefore, the energy demands per unit of biomass of apogonids, on average, are likely to be 2.5 times the demands of scarids.

The oxygen consumption of apogonids within the lagoon at One Tree Reef was calculated using Mann's (1965) formula using the weight and abundance of apogonids estimated from visual surveys (Chapter 2). A minimum estimate of oxygen consumption for apogonids was 1.62 mg m^{-2} hr^{-1} across lagoonal reef habitats (Fig. 6.1). The only available estimate of oxygen consumption for reef fishes was determined for a whole reef fish assemblage at Orpheus Island, central GBR by Ackerman & Bellwood (2000). They estimate an oxygen consumption of around 15 mg m^{-2} hr^{-1} for the entire fish assemblage. Based on these estimates, it is possible that apogonids may be responsible for more than 10% of the energy flux through all reef fishes. The assemblage examined by Ackerman & Bellwood (2000) was at the upper limits of biomass estimates for reef fish assemblages (2033 kg ha^{-1}), suggesting that the estimate of the fraction of energy flux attributable to apogonids is likely to be conservative. It appears critical, therefore, to take mass-specific energy demands into account when investigating the roles of various taxa in reef energy budgets (cf. Arias-Gonzalez et al. 1997).

Future directions

This thesis forms a baseline of research into the role of apogonids in reef processes, and has identified many areas worthy of further research. Apogonids are significant predators of demersal plankton communities, however, we know little of the trophic function of demersal plankton on reefs. Further work should address the flow of energy through demersal plankton by examining trophic interactions between demersal taxa, their predators, such as apogonids, and their prey, to estimate their importance in reef energy budgets. Apogonids were also found to deposit significant amounts of faeces at resting sites. This suggests that apogonids may have an impact on detritivore communities and corals at these resting sites. Further research is required into the quality of apogonid faeces and the fate of these faeces including impacts on local coral growth and the distribution and abundance of detritivore communities.

This thesis suggests that small, cryptic reef fishes, which are commonly missed in visual surveys, may be extremely important in reef tropho-dynamics through high population turnover rates and high mass-specific metabolic rates. However, we know little of the trophic ecology and life-histories of small cryptic reef fishes. This study provides evidence of the importance of one of these taxa. Further research into the role of other major families of small, cryptic fishes, in particular the Gobiidae and Blenniidae, is essential if we are to accurately model the contribution of reef fishes to tropho-dynamic processes.

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Site fidelity and homing behaviour in coral reef cardinalfishes

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Diet and nocturnal foraging in cardinalfishes (Apogonidae) at One Tree Reef, Great Barrier Reef, Australia

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ABSTRACT: Cardinalfishes (family Apogonidae) form a major component of nocturnal planktivore assemblages on coral reefs. In order to assess their trophic role on reefs, we examined diet, diel feeding behaviour and nocturnal foraging in 7 species in the lagoon at One Tree Reef, Great Barrier Reef, Australia. Between 64 and 93% of fish collected at dawn had identifiable material in the stomach compared with 5 to 36% of fish collected at dusk, suggesting that all 7 species were predominantly nocturnal feeders. The movement of apogonids between resting sites and feeding grounds was examined using day and night visual surveys. Apogonids shared restricted resting habitats by day but moved into a range of habitats at night. Species were spatially segregated at night, both horizontally and vertically in the water column. Most species had generalised diets containing primarily demersal plankton and benthic invertebrates, suggesting a role in recycling rather than importation of nutrients and energy on reefs. Dietary differences among species appeared to be driven largely by their feeding positions in the water column at night. Since apogonids feed in a range of habitats, then return to restricted resting sites during the day, they are likely to play an important role in concentrating nutrients and energy on reefs, providing localised and predictable resources for both predators and detritivore communities.

KEY WORDS: Apogonidae · Cardinalfishes · Coral reef · Feeding · Habitat use · Movement

INTRODUCTION

Nocturnal planktivores are functionally distinct from their diurnal counterparts on coral reefs (Hobson 1991). Diurnal planktivores generally feed on small prey of oceanic origin (Hobson & Chess 1978) whereas nocturnal planktivores usually feed on much larger prey (Hobson & Chess 1978) of reef origin (Hobson & Chess 1979). Nocturnal planktivores often migrate away from their shelter sites to forage in a range of reef and non-reef habitats (e.g. Hobson 1974, Ogden & Ehrlich 1977, Nagelkerken et al. 2000) while their diurnal counterparts typically feed in the water column in close proximity to the reef (Hobson 1991). Although the role of diurnal planktivores in reef trophodynamics has received much attention, the role of nocturnal planktivores has been largely overlooked. Most nocturnal planktivores are cryptic by day and are therefore often underestimated or missed in standard daytime visual censuses of reef fish communities (Ackerman & Bellwood 2000). In addition, there have been few studies of nocturnal planktivores during their active, feeding phase, probably due to the logistical constraints of working underwater at night.

The family Apogonidae (cardinalfishes) forms the dominant component of nocturnal planktivore assemblages on Indo-Pacific reefs (Allen 1993), commonly ranking second to third highest of all reef fish families in terms of both abundance and species diversity (Bellwood 1996). Apogonids are small (generally <10 cm), mostly nocturnal predators of plankton, fish and ben-

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thic invertebrates (Vivien 1975). By day, apogonids rest in caves or amongst branching coral, often forming dense, multi-specific aggregations (Greenfield & Johnson 1990). Apogonids consume prey from both reef and non-reef sources, including open water, sand and seagrass habitats (Vivien 1975). They are also significant predators of demersal plankton (Vivien 1975, Chave 1978), a trophic pathway that has received little attention on coral reefs (Parrish 1989). Apogonids may return to the same resting sites daily over extended periods of time (Kuwamura 1985, Okuda & Yanagisawa 1996, Marnane 2000), and thus may play a significant role in the concentration of energy and nutrients at localised, predictable sites on reefs (cf. Bray et al. 1981).

Despite their prominence on reefs, apogonids remain one of the least studied of the major families of reef fishes. A generalist diet, consisting mostly of demersal plankton and benthic invertebrates has been described for apogonids from the Marshall Islands (Hiatt & Strasburg 1960, Hobson & Chess 1978), Hawaii (Chave 1978) and Madagascar (Vivien 1975). However, comparable data on the feeding ecology of Indo-West Pacific apogonids are lacking. A number of studies have examined apogonid distribution patterns during the day (e.g. Vivien 1975, Dale 1978, Greenfield & Johnston 1990, Finn & Kingsford 1996); however, except for qualitative observations (e.g. Hiatt & Strasburg 1960, Livingston 1971, Chave 1978, Allen 1993), there are no published accounts of nocturnal distribution patterns. In order to evaluate the trophic role of apogonids on reefs, it is necessary to combine dietary information with both diurnal and nocturnal distribution data. The specific objectives of this study, therefore, were to describe: (1) foraging patterns, (2) diel feeding patterns, and (3) diet, in 7 common apogonid species from the Great Barrier Reef.

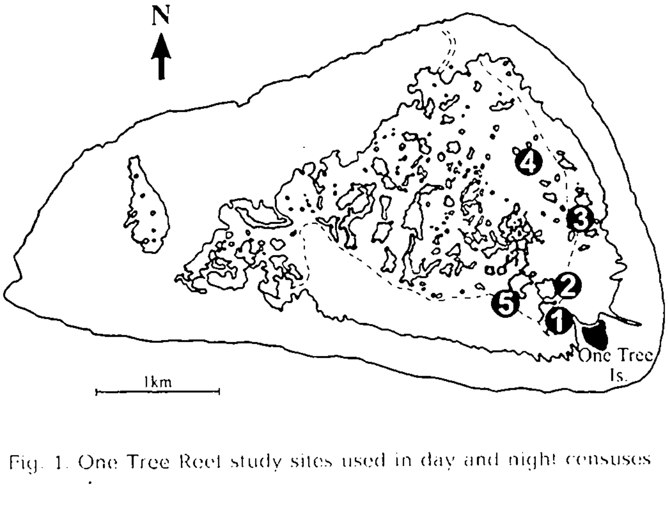

Fig. 1. One Tree Reef study sites used in day and night censuses

MATERIALS AND METHODS

Study site and species. This study was carried out within the One Tree Reef lagoon, southern Great Barrier Reef, Australia (152° 03' E, 23° 30' S). One Tree Reef contains a shallow lagoon (average depth = 3 to 5 m) with a well-defined outer reef wall and an inner matrix of patch reefs and micro-atolls (Fig. 1). The 7 most abundant apogonid species in the lagoon were studied: *Apogon cyanosoma*, *Apogon doederlini*, *Apogon exostigma*, *Apogon guamensis*, *Archamia leai*, *Cheilodipterus artus* and *Cheilodipterus quinquilineatus*. Only large juvenile and adult apogonids (>30 mm standard length) were examined owing to difficulties in identifying newly settled individuals of some species and the possibility of ontogenetic shifts in the diet (cf. Fishelson & Sharon 1997) and habitat use (Finn & Kingsford 1996) of early juveniles.

Foraging movements. The nocturnal movements of apogonids between resting and feeding sites were examined through a direct comparison of day and night distributions. Censuses were conducted over 5 d surrounding the quarter moon phase during November 1998, February 1999 and July 1999. During each of the 3 sampling periods 5 randomly placed transects were laid perpendicular to the reef at each of 5 micro-atolls selected randomly from a range of suitable sites (Fig. 1). Quadrats of an estimated $8\ m^2$ and the water column immediately above them were surveyed at points along the transect within all reef habitats, including the reef flat, crest, slope, base and at distances of 5, 10, 20 and 30 m from the reef over the sand areas between micro-atolls (1 quadrat per habitat type). The observers remained outside the quadrat during the census. All apogonids present within the quadrat were recorded including an estimate of their standard lengths, heights above the substratum, and the nearest microhabitat type (reef, sand or water column). Specimens were recorded as being from the 'water column' microhabitat if further than 30 cm from the substratum. Quadrats were surveyed between 09:00 and 15:00 h, then resurveyed the same night between 21:00 and 03:00 h.

In order to reduce diver effects at night, only available moonlight was used to locate census points on the transect. Once the census points were located, quadrats and the water column immediately above them were briefly illuminated by 2 divers using 2 × 12 V underwater halogen lights. Apogonids generally 'froze' in position when illuminated. All apogonids present within the quadrat immediately upon illumination were recorded, including estimates of their standard length, height above the substratum and nearest microhabitat type. Illumination periods generally lasted a few minutes. Any specimens that entered the quadrat after initial illumination were excluded from the survey. Specimens which could not be positively identified were collected after the census. This was achieved by one diver stunning the target fish with torch-light while the second diver collected the fish using hand nets. These fish were then placed in individual, labelled bags and later identified in the laboratory.

Feeding patterns. The diel feeding patterns of each species were assessed through examination of stomach contents of fish collected at dawn and dusk. Fish were collected around dawn (05:30 to 07:00 h) and dusk (17:00 to 18:30 h) during November 1998, February 1999 and July 1999 from at least 2 randomly chosen sites per time of day and sampling period within the lagoon. Fish were collected on SCUBA using hand nets and small hand spears. In both dawn and dusk samples, fish were collected from their resting sites. Fish were immediately killed underwater, then placed on ice within 30 min and frozen within 2 h of collection. Fish were later dissected and the stomach contents removed, recording the presence of identifiable items. Identifiable material had presumably been recently consumed and had not yet undergone significant digestion.

Diet was assessed through the examination of stomach contents of specimens collected at night (21:00 to 03:00 h) during late February 1999 from 3 randomly chosen sites within the lagoon. At each site, species were collected from across the entire range of habitats in which they occurred at night. Fish were collected by scuba divers with hand nets after stunning them with torchlight. Fish were killed immediately then placed on ice within 30 min and frozen within 2 h. Stomach contents were later removed, identified and placed in major taxonomic categories. The mean weight of each prey taxonomic category for each apogonid species was calculated by weighing a random sample (>10 where possible) of intact prey specimens. Mean prey item weights for each prey category were then multiplied by mean prey occurrences in the stomachs of each apogonid species to provide an estimate of the mass of material in each dietary category for each apogonid species. Combined error terms were calculated using Goodman's estimator, following Travis (1982):

$$\mathrm{SE}\,(\bar{x} \times \bar{y})^2 = \bar{x}^2 \times \mathrm{SE}_{\bar{y}}^{\,2} + \bar{y}^2 \times \mathrm{SE}_{\bar{x}}^{\,2} + \mathrm{SE}_{x}^{\,2} \times \mathrm{SE}_{y}^{\,2}$$

where $\bar{x}$ = mean prey item weight in each prey category; $\bar{y}$ = mean number of prey items from each prey category per individual fish; $\mathrm{SE}_{\bar{x}}$ = standard error of mean prey item weight; SE_{y} = standard error of mean prey number.

Statistical analyses. Data on day and night distributions of apogonids violated assumptions of homoscedasticity and normality. Distributions of each species were therefore analysed using chi-square tests of independence among the 3 survey periods. Distribution data were pooled among sites and habitats where necessary to meet chi-square assumptions. Data on the heights of apogonids above the substratum violated assumptions of homoscedasticity and were analysed using Kruskal-Wallis tests followed by post-hoc Tukey-type multiple comparisons, following Zar (1984). The dietary relationships between species were examined using principle components analysis (PCA). PCA was carried out on the correlation matrix of dietary data (see Table 2) before they were converted to percentages. Pearson's correlation was used to examine the relationship between height above substratum and principle component 1 scores from the principle component analysis. All analyses were carried out on SPSS v. 9.0 (SPSS Inc., Chicago, IL).

RESULTS

Foraging movements

Surveys conducted during the day showed a restricted distribution of apogonids at resting sites, primarily on the reef slope and at the reef base (Fig. 2A). Although the abundance of apogonids differed at each time of year, patterns of habitat use by each species were not significantly different among the 3 sampling periods (all chi-squared values < critical values; p = 0.09 to 0.69). The 3 sampling periods were therefore pooled for analyses. All species were predominantly located within caves or branching coral (indicated by negative heights above the substratum in Fig. 2A). Although there was a significant difference in mean heights above the substratum among species during the day (Kruskal-Wallis, H = 175, df = 6, $p < 0.001$), Tukey-type multiple comparisons revealed overlapping height distributions among *Apogon doederlini*, *A. exostigma*, *A. guamensis*, and *Archamia leai* (Q = 0.04 to 2.91, k = 7, $p > 0.05$) and between *Cheilodipterus artus* and *C. quinquilineatus* (Q = 1.11, k = 7, $p > 0.5$).

Night surveys showed that the majority of species foraged in different habitats to their diurnal resting sites (Fig. 2B). For example, *Apogon cyanosoma* was recorded primarily in caves in the reef base by day and occurred almost exclusively on the reef flat at night, whilst *A. doederlini* occurred on the reef slope and base by day and foraged over sand between microatolls at night. Furthermore, in contrast to daytime distributions, there was a strong degree of spatial separation between species at night, with little overlap in

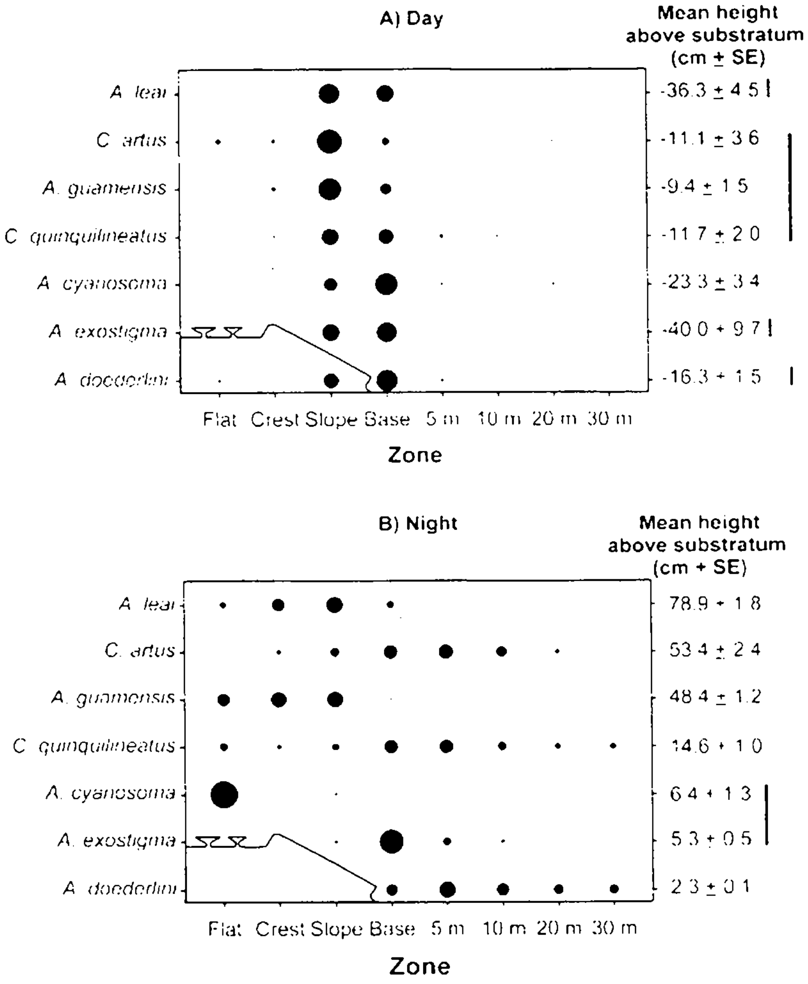

Fig. 2. Bubble plots of proportional habitat use by 7 apogonid species during (A) day (09:00–15:00 h) and (B) night (21:00–03:00 h). Circle areas represent the number of fish recorded from each habitat as a proportion of the total number of fish of each species recorded across all habitats (based on 75 quadrat censuses; fish sample sizes in Table 1). Negative heights above substratum indicate that fish were in caves or within branching coral. Overlapping mean heights above substratum among species are indicated by bars

either horizontal or vertical distribution patterns (Fig. 2B). Mean heights above the substratum at night were significantly different among species (Kruskal-Wallis, $H = 2718$, df = 6, $p < 0.001$) (Fig. 2B) with a post-hoc multiple comparison suggesting overlapping nocturnal vertical distributions in only *A. cyanosoma* and *A. exostigma* (Tukey-type comparison, $Q = 0.41$, $k = 7$, $p > 0.5$). In addition, most species showed a strong link with specific microhabitat types at night (Table 1). *A. doederleini*, *A. cyanosoma* and *A. exostigma* were located above sand more than 87% of the time, whilst *Archamia leai* and *Apogon guamensis* were located in the water column 82% and 78% of the time respectively. *Cheilodipterus artus* and *C. quinquilineatus* did not show a strong link with any one microhabitat and were frequently located in the water column and above sand and reef microhabitats at night (Table 1).

Feeding patterns

In all 7 species, a large proportion of individuals had identifiable material in the stomachs when collected at dawn, whereas fish collected at dusk usually had empty stomachs or small fragments of heavily digested material (Fig. 3). The only major exception was *Apogon cyanosoma*, where identifiable items were found in the stomachs of 36% of specimens collected at dusk.

Table 1. Distribution of species with respect to microhabitat type. Data represent the percent occurrence of each species with respect to the nearest microhabitat type (within 30 cm). n = total number of fish recorded during surveys

Species	Sand (%)		Reef (%)		Water column (%)		n	
	Day	Night	Day	Night	Day	Night	Day	Night
Apogon cyanosoma	3	87	92	12	5	1	264	143
Apogon doederleini	5	93	91	5	4	2	650	1108
Apogon exostigma	2	90	98	8	0	2	54	209
Apogon guamensis	0	0	100	22	0	78	60	834
Archamia leai	0	0	98	18	2	82	164	688
Cheilodipterus artus	14	15	66	34	20	51	155	195
Cheilodipterus quinquilineatus	13	29	62	36	25	35	447	276
						Total	1794	3453

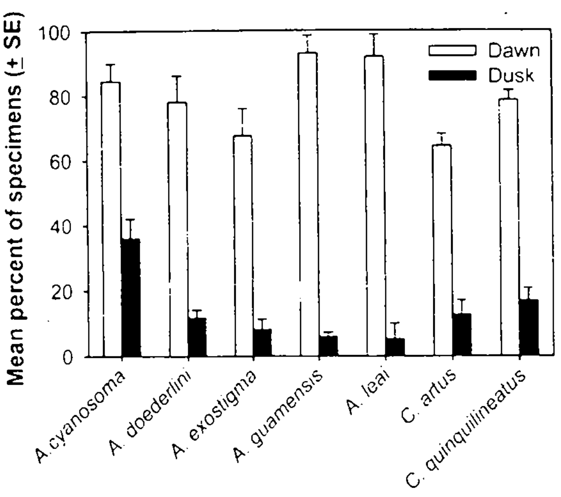

Fig. 3. Mean percent of specimens collected at dawn (05:30–07:00 hr) and dusk (17:00–18:30 hr) with identifiable prey items in their stomachs. SE values based on 3 sample periods: November, February and July

All of the species examined, except for *Cheilodipterus artus*, consumed a wide range of prey categories (Table 2). The dominant taxa consumed by most species were crustaceans (mainly small decapods and decapod larvae). *C. artus* was an exception and fed almost entirely on teleosts, primarily *Spratelloides delicatulus* (Clupeidae). Principle components analysis of the dietary relationship between apogonids suggested a clear separation between species (Fig. 4A) with 56.9 % of the variance accounted for by PC1 and PC2. Diet taxon vectors (Fig. 4B) indicated that PC1 was driven primarily by planktonic versus benthic taxa, whereas PC2 appeared to be driven largely by prey size. A plot of PC1 scores versus height of fish in the water column (Fig. 5) showed a strong correlation (Pearson's correlation, r = –0.89, df = 5, p < 0.01), suggesting that species in similar feeding habitats have similar diets. For example, *Apogon doederlini* and *A. guamensis* are both found primarily in the water column above the reef at night (Table 1, Fig. 2B), and both feed mostly on planktonic prey taxa (Table 2, Fig. 4). By comparison, *A. doederlini* and *A. exostigma* feed close to the substrate (Table 1, Fig 2B) and both consume mostly benthic prey taxa (Table 2, Fig. 4).

DISCUSSION

Daytime habitat overlap among apogonids contrasted greatly with the marked segregation of apogonids into discrete foraging locations at night. Apogonids were found to share restricted resting habitats during the day, mainly along the slope and base of micro-atolls. This was not surprising, considering that

Table 2. Mean percentage composition of stomach contents of fish collected at night. Data represent mean occurrence of prey item per fish × mean prey item weight (± combined SE), converted to a percentage of mean total weight of stomach contents; n = sample size; *Prey categories for which mean weights were unobtainable. In such cases, values were taken from the same prey type from similar-sized apogonid species. SE in brackets

Species	Amphipoda	Brachyuran adults	Brachyuran larvae	Caridea	Chaetognatha	Copepoda	Isopoda	Mollusca	Mysidacea	Ostracoda	Penaeidae	Polychaeta	Sergestidae	Stomatopoda	Tanaidacea	Teleostei	Mean total weight (mg)
A. cyanosoma n = 32	5.1 (1.8)	0.0	0.0	22.5 (3.6)	0.5* (0.1)	0.0	0.2 (0.1)	0.0	0.1* (0.1)	0.3 (0.1)	7.8 (2.9)	4.0 (0.8)	53.7 (20.9)	0.5 (0.1)	0.3 (0.2)	5.0 (2.3)	**29.9**
A. doederlini n = 47	11.6 (1.9)	14.6 (2.4)	4.3 (1.0)	2.9 (1.1)	0.0	0.0	0.7 (0.3)	0.2 (0.1)	0.5 (0.1)	1.1 (0.2)	17.1 (7.3)	4.7 (1.6)	26.7 (16.7)	2.0 (0.4)	0.4 (0.2)	13.1 (7.2)	**57.1**
A. exostigma n = 35	0.2* (0.1)	25.5 (6.9)	0.0	6.7 (3.4)	0.0	0.0	0.1 (0.1)	0.0	0.0	0.0	42.2 (9.8)	3.0 (0.6)	5.9 (1.9)	2.1 (0.4)	0.3 (0.1)	13.9 (4.0)	**120.0**
A. guamensis n = 35	2.4 (0.7)	3.1 (0.9)	56.6 (17.2)	2.8 (1.0)	0.2 (0.1)	0.1* (0.1)	0.7 (0.2)	0.0	0.0	0.0	5.3 (1.9)	19.4 (8.1)	2.3 (1.2)	3.2 (0.8)	0.0	3.9 (1.1)	**42.1**
A. leai n = 36	0.4 (0.2)	2.0 (0.7)	65.1 (23.0)	5.4 (0.7)	1.3 (0.3)	1.3 (0.2)	1.2 (0.4)	0.0	0.1 (0.1)	0.5 (0.1)	7.3 (3.5)	2.4 (0.6)	10.4 (1.1)	1.8 (0.5)	0.0	0.7* (0.4)	**18.5**
C. artus n = 45	0.0	0.4 (0.1)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.4 (1.8)	0.0	0.0	0.0	0.0	88.2 (20.2)	**540.8**
C. quinquilineatus n = 40	0.0	11.2 (3.3)	0.0	3.2 (0.3)	0.0	0.0	0.2 (0.1)	0.0	0.3 (0.1)	0.0	46.7 (14.9)	1.7 (0.6)	6.7 (3.3)	0.2 (0.1)	0.1 (0.1)	29.7 (14.9)	**179.5**

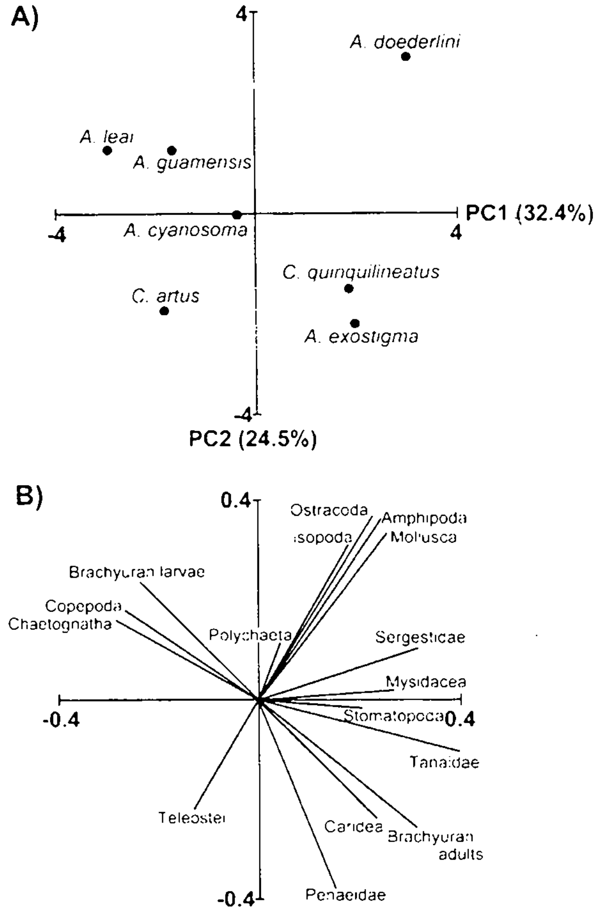

Fig. 4. Principle components analysis of dietary relationships: (A) species eigenvalues on principle components 1 and 2, (B) prey category eigenvectors

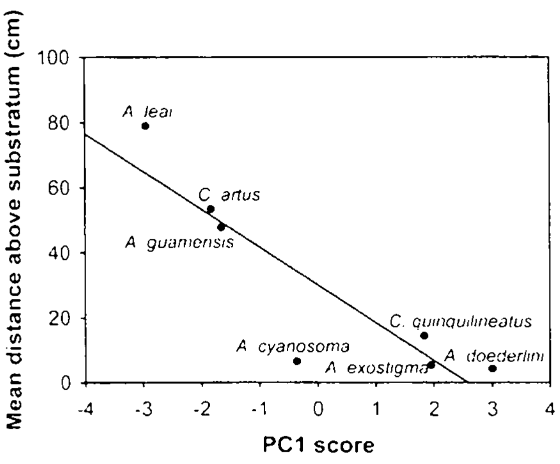

Fig. 5. Relationship between PC1 scores (see Fig. 4) and mean foraging heights of fish above the substratum at night (see Fig. 2B)

these zones have a high degree of topographic complexity, and are therefore likely to provide the greatest protection from diurnal predators (Hixon & Beets 1993). Species were distinctly separated during the night, both horizontally and vertically. Surprisingly, patterns of spatial segregation appeared to operate over scales of O(10 cm) vertically and O(1 m) horizontally.

Spatial niche partitioning has been reported in a number of diurnal reef fishes, across many spatial scales including microhabitat, reef zone, level of exposure and depth gradients (Williams 1991) but has rarely been documented in nocturnal reef fishes at night. Gladfelter (1983) described spatial niche separation of 8 species of holocentrids into different reef zones in the West Indies. Burke (1995) described segregated habitat use of seagrass beds and sand habitats in 2 species of haemulids from Belize. The habitat division observed among apogonids was of a finer scale than previously observed in nocturnal fishes and was finer than that seen in most diurnal fishes. It is not known if this is due to strong habitat preference or competitive exclusion. The former might be expected, but intense aggressive interactions observed between apogonids in aquaria at night (pers. obs.) suggest that competition may play an important role.

To our knowledge, this is the first study to quantify nocturnal distribution patterns in reef fishes using relatively unbiased survey techniques. Previous distribution studies of nocturnal reef fish have either: examined diurnal distributions only (e.g. Greenfield & Johnson 1990), used qualitative observations at night (Starck & Davis 1966, Hobson 1974, Chave 1978), or used standard visual methods with a continuous light source to census fish at night (e.g. Gladfelter 1983, Burke 1995). Surveying nocturnal fish during the day is of limited utility because they are generally inactive and their position may not reflect feeding locations (Nagelkerken et al. 2000). Surveys conducted at night with a continuous light source are likely to enhance diver biases for species which display photo responses. These biases are difficult to measure and correct. The 'brief-illumination' technique used in the present study provides a quantitative alternative to previous survey methods. When moving between census points using only moonlight, fish showed little response to diver presence. Replacing the 'brief illumination' with infrared visual or video censuses may provide a useful refinement of this method.

The majority of apogonid species examined in this study appear to be primarily nocturnal in their feeding behaviour, as noted in previous studies (Vivien 1975, Chave 1978, Fishelson et al. 1997). The only possible exception to nocturnal feeding was in *Apogon cyanosoma*, which contained identifiable prey items in the stomachs of a relatively large proportion (36%) of specimens collected at dusk. *A. cyanosoma* may supplement nocturnal feeding with diurnal or crepuscular feeding. Vivien (1975) suggests that *A. cyanosoma* may ingest some prey during the day based on gut content analysis. However, the exact time at which specimens were collected was not specified (only 'day' versus 'night'), which may limit resolution if crepuscular feeding was involved.

Apogonids are likely to play a role in concentrating nutrients and energy from a range of foraging habitats into localised, predictable resting sites on the reef. After a nocturnal foraging period, the majority of individuals returned to the same resting sites on the reef (Marnane 2000). Data suggest that these sites are maintained on a daily basis for periods of several months to years (Kuwamura 1985, Okuda & Yanagisawa 1996, Marnane 2000). At dawn most individuals still have a large quantity of material in their guts (Fig. 3) and a significant proportion of this material is likely to be deposited at resting sites. This accrual of material, in the form of fish biomass and faeces, is likely to provide a spatially and temporally predictable resource for predators and detritivore communities (cf. Bray et al. 1981). The most striking example of this is *Apogon doederlini* which feeds almost exclusively over sand areas between micro-atolls and returns to shelter sites within the reef slope and base.

Apogon doederlini is highly abundant within the One Tree Reef lagoon, with adult densities commonly between 10 and 20 fish per m^2 at resting sites (M.J.M. unpubl. data). *A. doederlini* may therefore be a key species responsible for gathering nutrients and energy from sand areas within the lagoon and concentrating these at resting sites on the reef. *A. cyanosoma* may play a similar role, moving material from foraging grounds on the reef flat to resting sites at the reef base. Apogonid faeces may be particularly important as it delivers nutrients to a localised area in a particulate rather than a suspended form, which would retain material within the reef system (i.e. within the boundary layer) (cf. Baird & Atkinson 1997). Previous studies on haemulids in the Caribbean (Meyer et al. 1983) identified fish waste as a potential source of nutrients to enhance coral growth. In this respect, apogonids sheltering within corals may exhibit a symbiotic relationship, with the corals providing shelter whilst apogonids enhance local coral growth via nutrient enrichment.

Apogonids are largely generalist feeders. Dietary analysis (Table 2) indicated that all of the species examined, with the exception of *Cheilodipterus artus*, ate a wide range of organisms. *C. artus* preyed mostly upon clupeids, and is likely to be trophically similar to diurnal piscivores such as serranids, which also feed largely on clupeids within the lagoon (Kingsford 1992). The prey consumed by the majority of apogonid species included a large proportion of benthic taxa and demersal plankton (e.g. brachyurans, sergestid shrimps, and polychaetes), whilst holoplanktonic forms such as chaetognaths and copepods represented only minor dietary components. It is possible that small, holoplanktonic prey undergo a more rapid digestion than larger benthic and demersal prey, and may therefore be under-represented in samples of stomach contents. However, even if a 10-fold difference in digestion rates was assumed, benthic taxa and demersal plankton would still dominate apogonid diets. In a trophic sense, apogonids play a functional role that is distinctly different to that of most diurnal planktivores, which generally consume oceanic plankton (Hobson & Chess 1978). Apogonids are more likely to play a role of recycling in reef systems rather than of importing nutrients and energy to reefs from open water systems (cf. Hamner et al. 1988).

Some dietary separation was found among apogonids, despite their generalised diets. Dietary separation was primarily benthic versus planktonic prey and secondarily small versus large prey. This separation appears to be strongly linked with the position of species within the water column. Species that were high in the water column (e.g. *Archamia leai* and *Apogon guamensis*) consumed mostly small, planktonic prey whilst species that foraged low in the water column (e.g. *A. doederlini* and *A. exostigma*) consumed mostly large, benthic prey. Taxon-specific differences in the distances demersal plankton migrate vertically into the water column at night have been observed (Alldredge & King 1985), supporting the conclusion that dietary separation in apogonids is associated with the species foraging locations within the water column. However, the question remains as to whether the feeding preference of apogonids determines their position in the water column or whether position in the water column dictates the availability of prey taxa.

The present study emphasises the need for data beyond gut contents and diurnal distributions if we are to understand the trophic roles of nocturnal fishes. In the case of apogonids, nocturnal behaviour appeared to be the main factor determining the functional role of each species. This study highlights the need to match methods to questions: both diurnal and nocturnal distribution data as well as dietary information are necessary to infer the trophic roles of nocturnal fishes on reefs. The high abundances and rapid turnover rates of apogonids on Indo-Pacific reefs suggests that they are important in reef tropho-dynamics. Given their strongly segregated feeding and shared resting locations, apogonids may play a key role in the transfer of nutrients between habitats and in the concentration of nutrients at specific sites on reefs.

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