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UNDERGRADUATE PROJECT REPORT

Candidate Number	35708
Project Supervisor	Martin Speight

Fish community structure on coral reef bombies on Hoga Island, south-east Sulawesi

Abstract

The diversity of fish communities is highest in coral reef ecosystems and the range of interacting processes affecting species' distributions is similarly extensive. This study describes the fish community associated with bombies off Hoga Island, south-east Sulawesi and relates spatial variation in community structure to environmental features of the habitat. Twenty reef fish families were observed, with 60% of fish counted belonging to the Pomacentridae. The most abundant species was the humbug, *Dascyllus aruanus.* Bombie size was found to be the most important variable explaining variation in fish species richness and abundance. Bombie shape and coral composition were also significant variables, but distance from the reef crest was not. A significant species-area relationship, explained by the habitat diversity hypothesis, was obtained using bombie volume as a three-dimensional expression of habitat area.

Multivariate canonical correspondence analysis found ‘bombie volume’, ‘distance from crest’ and ‘branching coral cover’ were the most important measured variables affecting community structure and showed how individual species’ distributions may vary according to particular habitat features. The results are useful for further understanding fish community dynamics and for use in local and regional management schemes.

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Introduction

The importance of coral reef ecosystems in terms of taxonomic diversity and ecological complexity is widely accepted and has been emphasized many times (e.g. Harmelin-Vivien, 2002; Knowlton and Jackson, 2001). Hence the need exists to continually contribute to our knowledge of the manifold species and interactions that occur within these ecosystems. One key group of organisms that forms part of this ecosystem is the fish, the communities of which reach their most diverse on coral reefs (Sale, 1991) and as such, exhibit remarkable degrees of spatial variation at several scales. The purpose of this study will be to quantitatively describe the structure of the fish community within one zone of one particular reef and to explain some of its variation.

The fish community can be described in terms of the number of species (richness), fish abundance (Jennings *et al*. 1996) and the community composition – i.e. which species are present or absent. The various factors that influence community structure can be classified as biological, physical (e.g. water depth, salinity, or temperature) or historical (both natural and anthropogenic disturbances) (Lecchini *et al*. 2003).

Biological processes shown to be important in affecting fish populations are competition (both intra- and inter-specific), mutualism (e.g. cleaning symbioses (Knowlton and Jackson, 2001)), predation, herbivory and larval recruitment. A debate has existed over whether recruitment is dependent on stochastic or deterministic processes (Ault and Johnson, 1998; Doherty, 2002); it is becoming clearer now that one cannot disregard either type (Morgan, 2001), but consider, for example, both random fluctuations in larval availability and non-random habitat selection by settling larvae (Ault and Johnson, 1998).

Attempting to quantify the relative importance of these processes is very difficult, often being done via mathematical modelling (e.g. Doherty, 2002), partly due to the large time-scales (years to decades) required to measure changes in these processes (Knowlton and Jackson, 2001). Many studies therefore try to relate variation in fish assemblages to measurable habitat features (Holbrook *et al*. 2002; Chabanet *et al*. 1997; Ormond *et al*. 1996; Lecchini *et al*. 2003), then link their findings to underlying biological mechanisms. For example, many authors (see Chabanet *et al.*1997) have found a positive correlation between live coral cover and the abundance of butterflyfish (Chaetodontidae), explained by the fact that most are corallivores.

Fish associate with coral for different reasons, which in turn affect community interactions:

- Adults, especially of small site-attached fish species, compete with each other to use coral branches and crevices as shelter from predators. If predation pressure is high, the availability of coral providing adequate shelter, (e.g. branching corals), will affect fish abundance by affecting mortality rates (Jones and McCormick, 2002).
- Adults may also compete for nesting and spawning sites (Ormond *et al*. 1996), which will particularly affect the population structure of species without a pelagic larval stage.
- The larvae of some species will selectively settle on coral – a process that has shown larvae to be behaviourally sophisticated. Different species show

patterns of selectivity based on different criteria (Leis and McCormick, 2002), e.g. from the presence of conspecifics to water depth.

- As a food resource, either directly (corallivores), or indirectly: carnivorous fish feed on invertebrates or smaller fish associated with the coral and herbivorous fish feed on algae growing next to the coral.
- Migratory fish may use structural features of the reef as reference points; species may have a tendency to use particular features (e.g. specific coral growth forms), resulting in an approximate correlation between a fish species' distribution and a coral's distribution.

Thus, environmental differences in the coral habitat will affect associations that fish have with it and so correlate to differences in fish community structure.

In this study, the relationship between fish community structure and habitat features was investigated in the bombie zone of Hoga Island, south-east Sulawesi. Coral reef "bombies" (Fig. 1) are patches or mounds of coral that are found in a zone in between the reef crest and seagrass zone (adjacent to the shore). They vary in size (which can be measured in terms of area or volume) from about $10cm^2$ to several $metres^2$.

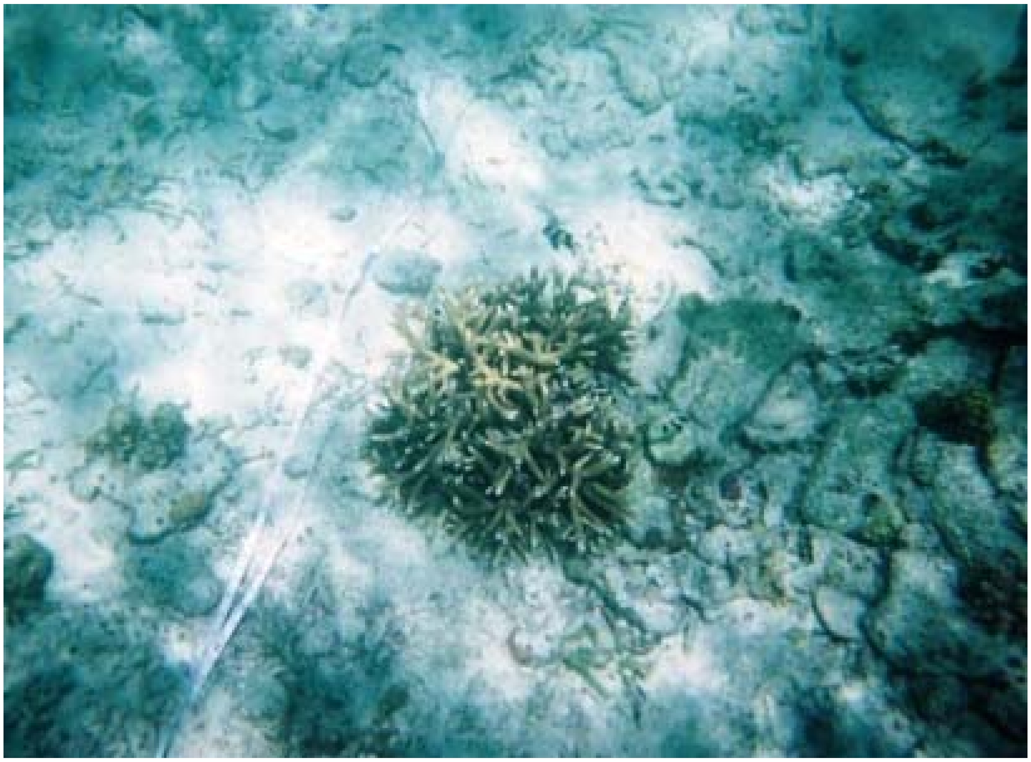

Figure 1. A small bombie, cylindrical in shape of approximately 0.3m diameter (a 1m tape measure can be seen to the left of the bombie), and composed of branching coral. Six or seven associated fish (*Dascyllus aruanus*) can be seen swimming above it.

Since bombies are coral outcrops separated by areas of sand, rubble and sea grass, one would expect fish-coral associations, and thus the fish community in the bombie zone, to differ markedly from the community found on the reef crest and slope. Studies have already found fish communities differ significantly between reef zones (Chabanet *et al*. 1997; Ormond *et al*. 1996; Ault and Johnson, 1998; Lecchini *et al*. 2003), indeed often more so than between geographically distinct coral reefs (e.g. Letourner, 1996). Therefore this study will focus on describing the fish community found within one zone, measuring environmental features of the habitat and relating differences found between bombies to spatial variation in the species richness, abundance and composition of the fish community.

Perhaps the most obvious environmental variable to use is bombie size. The species-area relationship, that larger areas contain more species, is one of the basic and universal rules seen in ecology (Rosenweig, 1995; Gotelli, 2001), most often represented by the power function $S = cA^z$, where S is species richness, A is area, c is a constant measuring the initial slope of the curve and z is a constant measuring the rate at which richness increases with area (Lomolino, 2001). As previous studies of patch reefs (e.g. Holbrook *et al*. 2001) have also shown, the diversity of the fish assemblage is expected to increase with bombie size in a curvilinear fashion. Also investigated is the effect of the location of each bombie in terms of its distance from the reef crest, thereby subdividing the bombie zone and seeing whether fish biodiversity varies according to a local geographic gradient. Again this may affect different species' distributions in different ways or not at all. For example, Lecchini *et al.*(2003) found the variable 'distance from the coast' was significant in explaining spatial variation in seven reef fish families in the Ryuku Islands, southern Japan, but did not explain variation in the family Pomacentridae. Finally, the coral composition of each bombie is examined, both in terms of the amount of live versus dead coral cover (which several studies have found has a significant affect on fish diversity (e.g. Edinger *et al*. 1998; Chabanet *et al*. 1997) and individual species' distributions (e.g. Ault and Johnson, 1998)) and the number of different coral growths forms (as a measure of habitat complexity) - previously found to be the most important factor in explaining fish community variation (e.g. Ormond *et al*. 1996).

Results from this type of study contribute to the understanding of the way fish assemblages vary in space and the influence of environmental factors. However, generalisations about the relative importance of the underlying mechanisms should rarely be made, since the results of many studies are contradictory (Morgan, 2001). Yet by relating environmental variables to community structure it is possible to predict community structure in novel locations using similar environmental measurements (e.g. Holbrook *et al*. 2001) – the basis of species distribution mapping.

At a local scale the results can be used to assess the conservation value of the bombie zone as supporting a unique fish assemblage and be used in the ongoing management scheme of the local area, part of the Wakatobi Marine National Park. Whilst extrapolation of results of small-scale studies to larger spatial scales should be done with caution (Lewis, 1998), these results could be used, for example, in a comparison with an unprotected bombie zone in the region, where anthropogenic disturbances continually occur, e.g. blast and cyanide fishing are particular concerns in eastern Indonesia (Edinger *et al*. 1998).

Methods

Study area

This study was conducted over a six-week period in July – August 2005, in the Wakatobi Marine National Park. Set up in 1996, it includes all the islands in the Tukangbesi Archipelago south east of Sulawesi (Fig. 2a), a region of the Indo-Pacific where coral reef biodiversity reaches its height. Specifically, the study site was the bombie zone between buoys 2 and 3 off the south-west shore of Hoga Island (Fig. 2b).

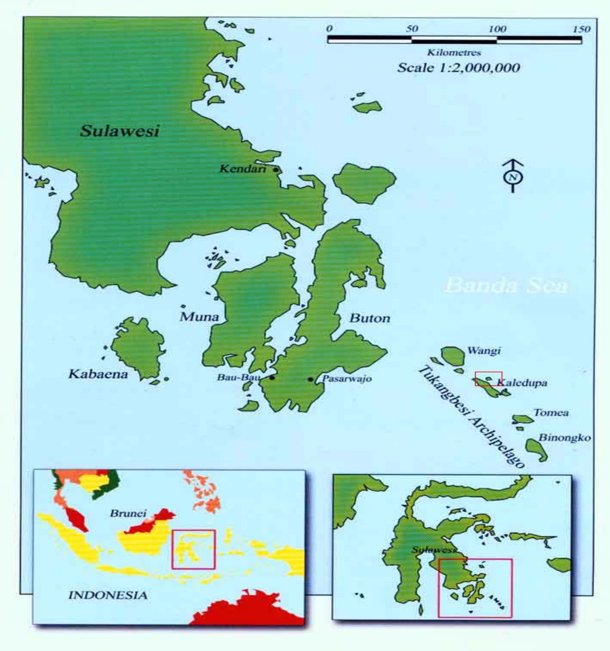

Figure 2a. Map showing the locationn of Hoga within the Tukangbesi Archipelago (red box). Smaller maps show location of Sulawesi within Indonesia (left) and the location of the Wakatobi Marine Park to the south east of Sulawesi. (courtesy of OpWall).

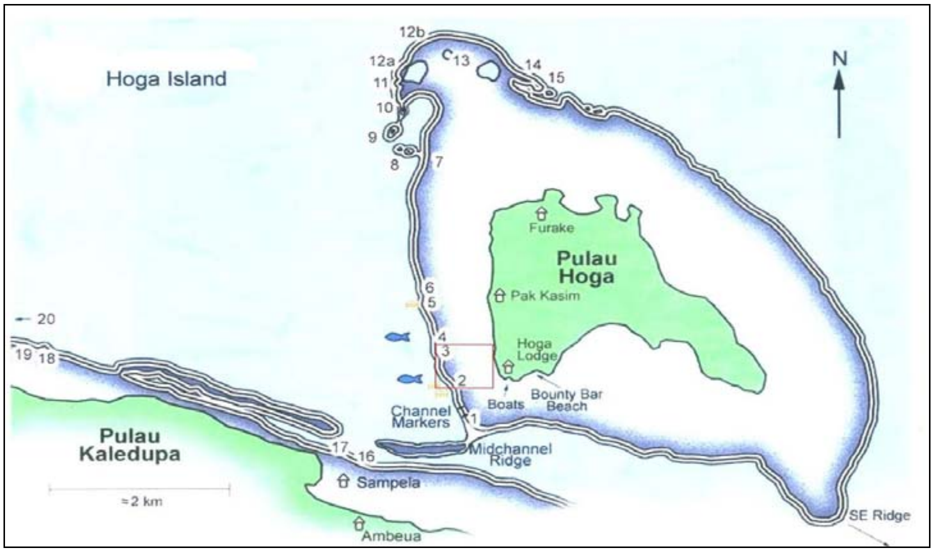

Figure 2b. Map of Hoga showing sampling area between buoy 2 and 3 (red box).

Sampling methods

All data was collected snorkelling during the two-four hour period around high tide each day, which meant water depth on the reef flat remained between 1.5m and 2.1m. This allowed four or five bombies to be sampled per day. At each bombie a visual survey of the fish assemblage was conducted, followed by measurements of environmental features.

A 1.5m by 1.5m quadrat was laid over or around each bombie to mark the area in which surveys were conducted. As fish were often scared away at the approach of a snorkeller, five minutes would be spent hovering by the bombie, being as still as possible, to allow the fish to become accustomed to human presence. The fish species present and their abundances were then recorded for twenty minutes. To be counted, a fish had to clearly interact with the bombie, e.g. feed, swim through the structure etc. Fish that swam into the sample area but passed by without stopping were not counted.

For unfamiliar fish species, a rough sketch and/or notes on defining features were made, then later looked up in a fish identification book (e.g. Allen *et al.* 2003). Whilst this method proved successful in most cases, some congeneric fish were indistinguishable from each other (Lewis, 1998), so were grouped together according to a visual description, whereas others proved impossible to identify even when observed on separate occasions - often because it was a variant from the example shown in the fish ID guide - and so were only identified to family level.

Each bombie was assigned to a size class (small, medium or large) according to its maximum length (less than ~0.5m, ~0.8-1.2m and greater than ~1.2m, respectively) and to one of three classes of approximate three-dimensional shape (cuboidal, cylindrical or triangular). The relevant dimensions of the bombie were then measured, for example, length, width and height for cuboidal bombies or diameter and height for cylindrical bombies - later used to calculate each bombie's approximate volume.

Bombies at three distances from the reef crest (50m, 70m and 90m) were sampled. Distance measurements were conducted at the start of each snorkel by swimming to the crest and using a transect tape to measure out the required distance when swimming back towards shore. Bombies at each distance were then found by swimming parallel to the crest; to save time re-measuring distances, usually bombies at only one distance were sampled per snorkel.

The coral composition of each bombie was classified according to whether it was composed of one growth form (Single) or more than one (Mixed), then the percentage cover of the following growth forms was estimated:

- Submassive
- Massive
- Branching
- Tabulate
- Foliose
- Encrusting
- Mushroom

The percentage of dead coral cover (not assigned to a particular growth form) was also recorded for bombies of mixed composition; bombies of single composition had no dead coral.

Bombies within each of the classes devised to measure size, distance and coral composition were sampled according to an orthogonal, balanced design (Table 1). The final dataset consisted of fish counts and environmental measurements for ninety bombies.

		Bombie Size			
		Small	**Medium**	**Large**	**Total**
Distance From Crest	**50m**	5s + 5m	5s + 5m	5s + 5m	30 (s+m)
	70m	5s + 5m	5s + 5m	5s + 5m	30 (s+m)
	90m	5s + 5m	5s + 5m	5s + 5m	30 (s+m)
	Total	30 (s+m)	30 (s+m)	30 (s+m)	**90 (s+m)**

Table 1, Showing the balanced, orthogonal design of the experiment. “s” stands for bombies composed of a single growth form, and “m” for bombies of mixed growth form, hence there are 45 bombies of each.

The time necessary to conduct visual surveys that accurately reflect the fish assemblage on a bombie, and how to classify bombies was decided after four preliminary snorkels. For example, during these snorkels it was seen what shapes the majority of bombies approximated to, the size range of bombies and how far along the reef flat, from crest to shore, the bombie zone started and ended.

Data analysis

The majority of analyses performed on the data were General Linear Models (GLMs) using Minitab, to test for significant differences in fish diversity across all the bombies according to the environmental variables measured. Initially only one-way ANOVAs were performed using species richness (S) and fish abundance (N) as response variables and ‘size’, ‘shape’, ‘distance from crest’ and ‘coral composition’ as categorical explanatory variables. Visual inspection of histograms of residuals and Normal probability plots from initial analyses showed that square root and $\log_{10}$ transformations needed to be applied to the species richness and abundance data respectively. Bar charts were drawn to show differences between group means, with all error bars representing standard error of the mean.

The importance of bombie size was analysed further by using ‘volume of bombie’ as an explanatory variable, which incorporates both ‘size’ and ‘shape’ (as both are used to calculate volume). This is probably a more realistic variable to use as it does not categorize bombies into arbitrary classes and being a continuous variable, the shapes of the relationships between size and richness or abundance can be described. Regression analyses were performed to model the effect of bombie volume, and the species-area relationship ($S = cA^z$) was tested using volume instead of area by taking logarithms ($\log(S) = \log(c) + z\log(A)$) and seeing how well the data fits a straight line.

More complex GLMs using more than one x-variable were run to see whether their explanatory power was improved by the inclusion of certain other variables and to test for any significant interaction terms.

Multivariate analysis was used to show relationships between bombies and fish species (Henderson, 2003). Canonical Correspondence Analysis (CCA), which allows direct relation of variation in the fish community structure to environmental variables (Ter Braak, 1986), was the technique employed, using ‘ECOM 1.37’ software.

Prior to analysis, rare species observed on fewer than five different bombies were removed as they were likely to have a disproportionate effect on the results. In order to allow canonical coefficients to be comparable to each other and remove arbitrariness in their units (Ter Braak, 1986), each value of each environmental variable was divided by its standard deviation, putting them all on the same scale.

All 90 bombies were included in the analysis and given a unique five-figure code reflecting its size, distance from crest and coral composition, e.g.:
SD501: 'S' = small, 'D5' = Distance of 50m, '01' = single coral composition (bombies numbered from 01 - 05 are of single coral composition, those from 06 – 10 are mixed).
Therefore, 'LD708' is a large bombie, 70m from the crest and of mixed coral composition.

The first run found appreciable multicollinearity due to the correlation of certain environmental variables, so variables were removed in turn to find the best combination that would explain community structure (Lecchini *et al*. 2003).

An ordination plot was produced as part of the CCA output, depicting the main patterns of variation in the community composition and how species distributions may correlate with environmental variables. Also produced are eigenvalues for each axis (representing the degree of correspondence between species and sites (Palmer, 1993)) and the amount of variance in the original data accounted for by each axis (for detailed accounts on interpreting CCA outputs see e.g. Ter Braak, 1986 or Jongman *et al*. 1995).

Results

Overall fish community structure

Over the entire period of data collection a total of 2070 fish belonging to twenty different families were counted (Table 2). Of these, 1247 fish (60.2%) were of the family Pomacentridae (damselfish), which was ten times more abundant than the next most abundant family, Labridae (127 individuals, 6.1%), (see Fig. 3). The family Pomacentridae was also the most speciose, with at least 25 different species observed, and the most widespread, with a representative of the family on every bombie sampled.

Common Name	***Species* or Family (bold)**	**Number Counted**
White Damsel	*Dischistodus perspicillatus*	70
Monarch Damsel	*Dischistodus pseudochrysopoecilus*	50
Blackvent Damsel	*Dischistodus melanotus*	8
Palespot Damsel	*Dischistodus chrysopoecilus*	4
Honeyhead Damsel	*Dischistodus prosopotaenia*	7
Humbug Dascyllus	*Dascyllus aruanus*	426
Reticulated Dascyllus	*Dascyllus reticulatus*	51
Threespot Dascyllus	*Dascyllus trimaculatus*	3
Anemonefish spp.	*Amphiprion spp.*	16
Staghorn Damsel	*Amblyglyphidodon curacao*	16
Sergeant spp.	*Abudefduf spp.*	3
Black chromis		17
Blue Chromis	*Chromis cyanea*	65
Blue-Green Chromis	*Chromis viridis*	21
Spiny Chromis	*Acanthochromis polyacanthus*	1
Other chromis spp.		38
Blue Damsel	*Pomacentrus pavo*	81
Neon Damsel	*Pomacentrus coelestis*	4
Threespot Damsel	*Pomacentrus tripunctatus*	17
Goldbelly damsel	*Pomacentrus auriventris*	2
Black damsel		164
Black, ocellated dorsal spot damsel		153
Yellow damsel		23
Yellow, ocellated dorsal spot damsel		4
Dusky Gregory	*Stegastes nigricans*	3
Other damsel spp.		54
Total Damselfish	**Pomacentridae**	**1247**
Firetail dottyback	*Labracinus cyclopthalmus*	17
Other dottyback spp.		35
Total Dottybacks	**Pseudochromidae**	**52**
Peacock Grouper	*Cephalopholis argus*	1
Grouper spp.	*Epinephelus spp*	59
Total Groupers, Anthias	**Serranidae**	**60**
Blackeye thicklip wrasse	*Hemigymnus melapterus*	4
Pinstriped wrasse	*Halichoeres melanurus*	3
Bluestreak cleaner wrasse	*Labroides dimidiatus*	13
Other wrasse spp.		107

Total Wrasse	**Labridae**	**127**
Flagtail triggerfish	*Sufflamen chrysopterus*	6
Orange-lined Triggerfish	*Balistapus undulatus*	10
Total Triggerfish	**Balistidae**	**16**
Redfin butterflyfish	*Chaetodon lunulatus*	10
Other butterflyfish spp.		25
Total Butterflyfish	**Chaetodontidae**	**35**
Bicolor Angelfish	*Centropyge bicolor*	6
Keyhole Angelfish	*Centropyge tibicen*	15
Pearl-scaled Angelfish	*Centropyge vroliki*	4
Total Angelfish	**Pomacanthidae**	**25**
Striped Monocle Bream	*Scolopsis lineatus*	8
Monocle Bream	*Scolopsis bilineatus*	99
Total Bream	**Nemipteridae**	**107**
Scorpionfish		1
Lionfish		1
Total Scorpionfish	**Scorpaenidae**	**2**
Doublebar goatfish	*Parupeneus bifasciatus*	5
Dash-Dot Goatfish	*Parupeneus barberinus*	2
Yellowstripe Goatfish	*Mulloidichthys flavolineatus*	5
Total Goatfish	**Mullidae**	**12**
Dusky Rabbitfish	*Siganus fuscescens*	1
Total Rabbitfish	**Siganidae**	**1**
Beaked leatherjacket	*Oxymonacanthus longirostris*	5
Total Filefish	**Monacanthidae**	**5**
Cardinalfish	**Apogonidae**	**119**
Squirrelfish	**Holocentridae**	**1**
Pufferfish	**Tetraodontidae**	**1**
Blenny	**Blenniidae**	**25**
Goby	**Gobidae**	**31**
Dragonet	**Callionymidae**	**5**
Surgeonfish	**Acanthuridae**	**16**
Parrotfish	**Scaridae**	**2**
Juveniles (unidentified spp.)		127
All Fish		**2070**

Table 2. A list of species/families observed and their frequency. Where a latin name is not given in the second column, identification to species level was not possible and the common name given is a description of the group rather than a species name, e.g. Black chromis is a group of fish that visually and behaviourally (as far as was observed) were indistinguishable from each other and so if not a single species, probably consists of two or three closely related species. Where '(Other)… spp.' is written this implies identification to genus/family level was possible but ambiguity (in sketches made underwater, identification books etc.) meant identification to species level was not; such groups will invariably consist of more than one species. For data analysis such groups are treated as one "species", meaning diversity estimates will be on the conservative side.

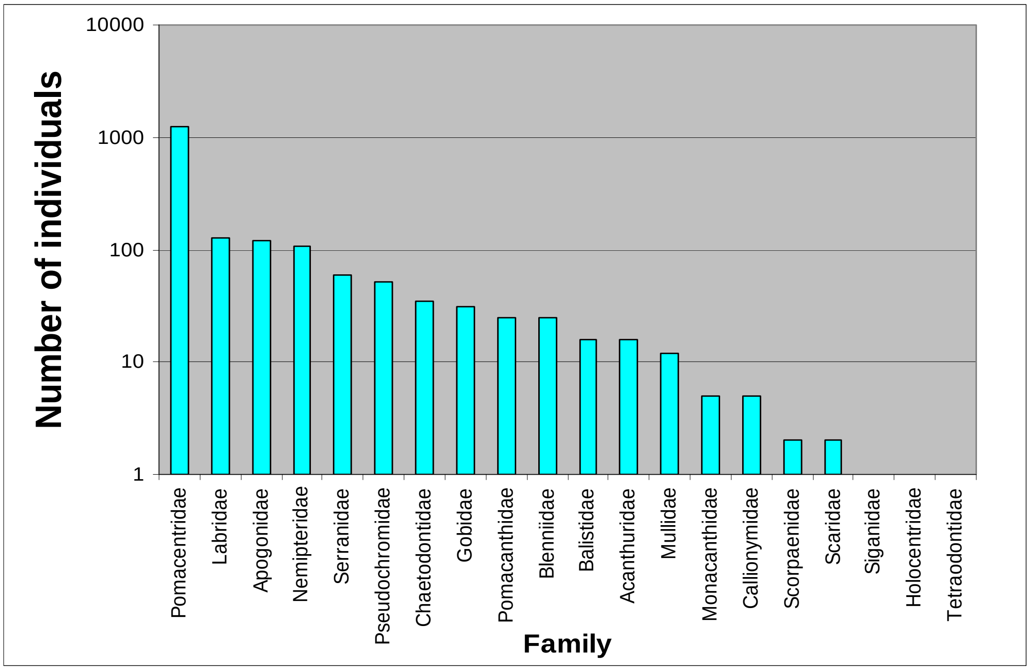

Figure 3. Total number of individuals counted in each family on all bombies.

Table 1 and figure 3 are also informative by highlighting the complete absence of certain common reef fish families, thereby indicating differences in fish communities between reef zones. Families seen in abundance on the reef slope and crest but absent from the bombies include: Lethrinidae (Emperors), Lutjanidae (Snappers), Carangidae (Jacks & Trevallys), Sphyraenidae (Barracuda), Caesionidae (Fusiliers) and Zanclidae (Moorish Idol).

The most abundant species (a fifth of fish counted) was the humbug dascyllus (*Dascyllus aruanus*), counted 426 times on 46 bombies (rank 1, Fig. 4). However the species found on the greatest number of different bombies (58) was the monocle bream (*Scolopsis bilineatus*) (see row 7, Table 3 and Fig.7). The rank-abundance plot of all fish species sampled (Fig. 4) shows a shallow reverse S-shaped curved characteristic of a log-normal distribution - the most common model used to predict species-abundance relationships (Jones *et al*. 2002). It is indicative of a species-rich community, where few species have either very high or very low abundances, and has been demonstrated for reef fish communities (Connolly *et al.* 2005).

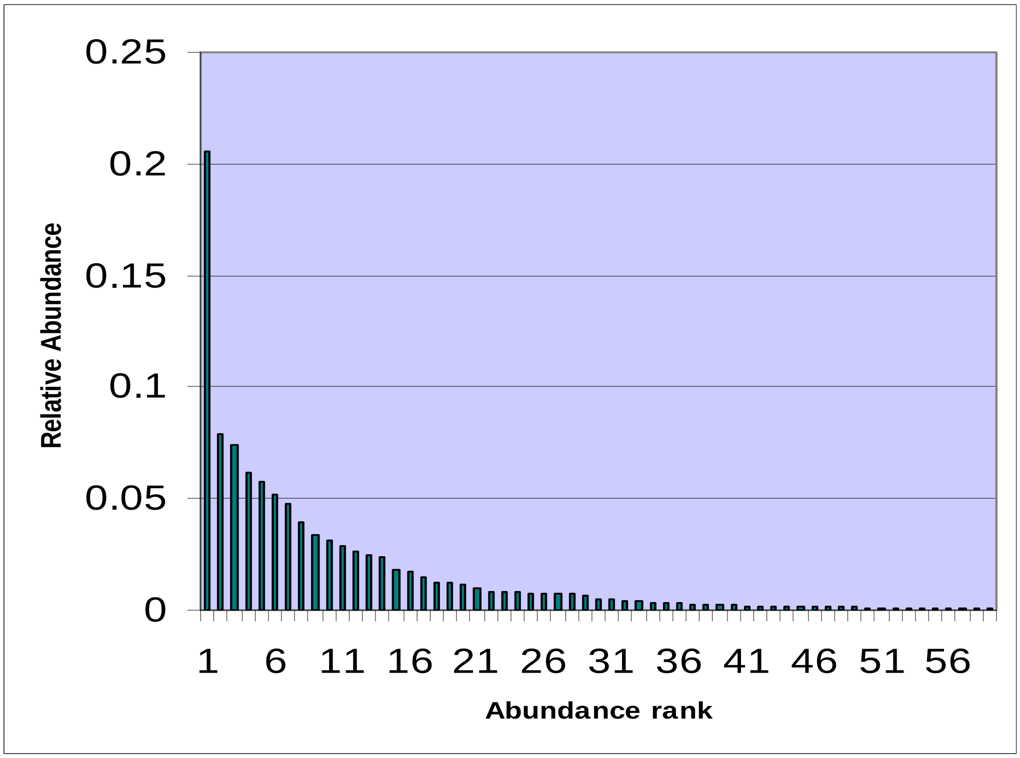

Figure 4. Rank abundance plot of relative abundance (No. of individuals per species/total no. of individuals) vs. species sequence.

Spatial variation in fish community

Among the ninety bombies sampled both the abundance of fish (N) and species richness (S) varied greatly. The average number of fish counted per bombie was 23 (range: 2 – 90), the average number of species was 8.5 (range: 2 – 20) (Fig. 5), and the two bombies with the highest and lowest abundances were also the two with the highest and least number of fish species respectively.

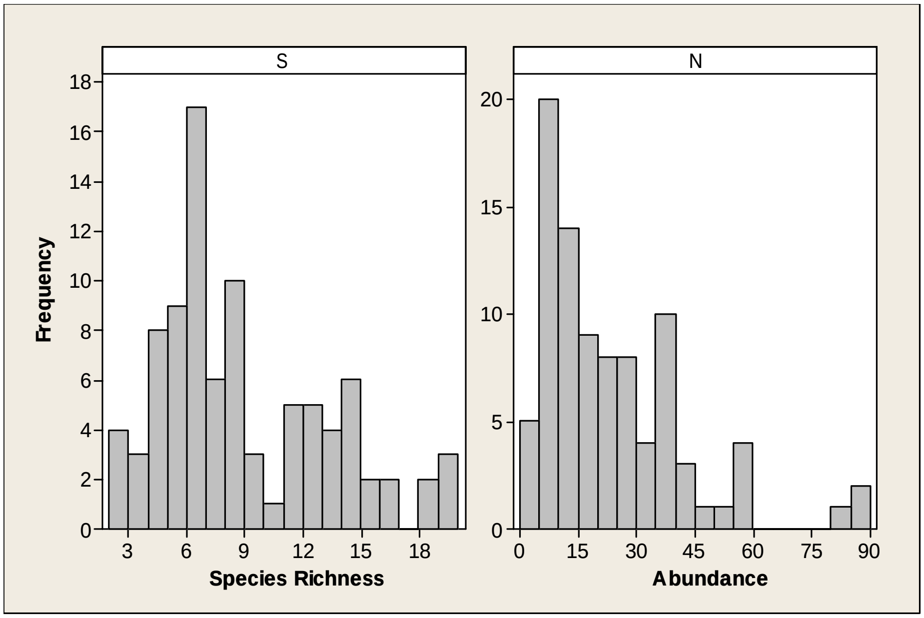

Figure 5. Frequency distributions of species richness (class width=1) and fish abundance (class width = 5) per bombie.

As expected, and suggested by the similar shapes of the graphs in figure 5, there is a correlation between species richness per bombie and fish abundance per bombie (Fig. 6), which a regression analysis showed to be highly significant (F=235.04, p<0.0005).

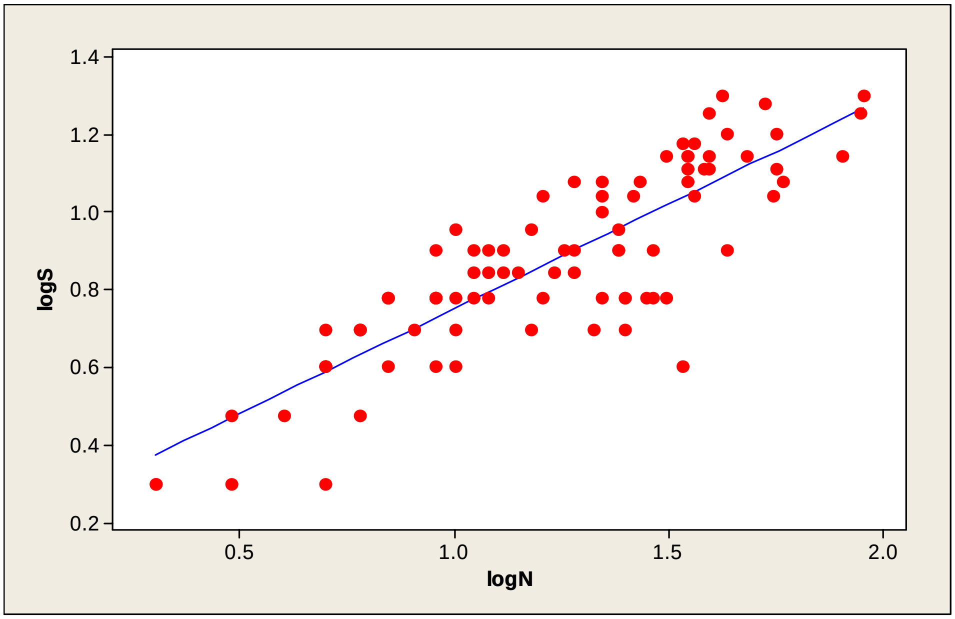

Figure 6. Regression plot of log(species richness) vs. log(fish abundance) per bombie. logS = 0.2107 + 0.5402 logN ($p<0.0005$, R^2= 72.8%).

When comparing the number of bombies on which a species was observed (N_B) with the total number of individuals observed of that species (N_I), there is an overall positive correlation as one might expect. However a distinction between two groups of species emerges according to the ratio of N_B/N_I , with species in Group 1 all having a ratio greater than 0.5 and those in Group 2 less than 0.5 (Table 3). The two groupings can be seen when N_B is plotted against N_I (Fig. 7). To highlight the division, only species where at least 15 individuals have been observed are included in the scatterplot and table below.

Non-linear regression analyses showed fitting one model through the data was much less powerful ($F=13.72$, $p<0.0005$, R^2=52.3%) than fitting two curves through each group as seen in figure 7 (Group 1: $F=162.77$, $p<0.0005$, R^2=96.7%; Group 2: $F=21.32$, $p<0.0005$, R^2=79.5%).

Fish Group	No. of Bombies where present (N_B)	Number of Individuals (N_I)	N_B/N_I	Group
Scolopsis bilineatus	58	99	0.585859	1
Dischistodus perspicillatus	54	70	0.771429	1
Black damsel	50	164	0.304878	2
Labridae	50	107	0.46729	2*
Dascyllus aruanus	46	426	0.107981	2
Epinephelus spp.	46	59	0.779661	1
Black, ocellated dorsal spot damsel	39	153	0.254902	2
Pseudochromidae	35	35	1	1
Juveniles	33	127	0.259843	2
Dischistodus pseudochrysopoecilus	32	50	0.64	1
Apogonidae	27	119	0.226891	2
Gobidae	25	31	0.806452	1
Pomacentrus pavo	20	81	0.246914	2
Blenniidae	19	25	0.76	1
Chaetodontidae	17	25	0.68	1
Other damselfish	16	54	0.296296	2
Labracinus cyclopthalmus	14	17	0.823529	1
Centropyge tibicen	12	15	0.8	1
Black chromis	11	17	0.647059	1
Amblyglyphidodon curacao	11	16	0.6875	1
Yellow damsel	10	23	0.434783	2
Acanthuridae	10	16	0.625	1
Dascyllus reticulatus	9	51	0.176471	2
Amphiprion spp.	9	16	0.5625	1
Pomacentrus tripunctatus	7	17	0.411765	2
Other chromis spp.	6	38	0.157895	2
Chromis viridis	5	21	0.238095	2
Chromis cyanea	3	65	0.046154	2

Table 3. The 28 most abundant fish species/groups (for explanation of group names see Table 1 legend), and their Group assignments (Group 1 or 2) based on N_B/N_I ratio (see main text). *According to the N_B/N_I ratio, the assignment of Labridae (wrasse), strictly, should be to Group 2, but this is less clear from Figure 7, where the datapoint lies in between the clear groupings, but perhaps slightly closer to Group 1. This ambiguity arises because its N_B/N_I ratio of 0.467 is very close to the group boundary of 0.5.

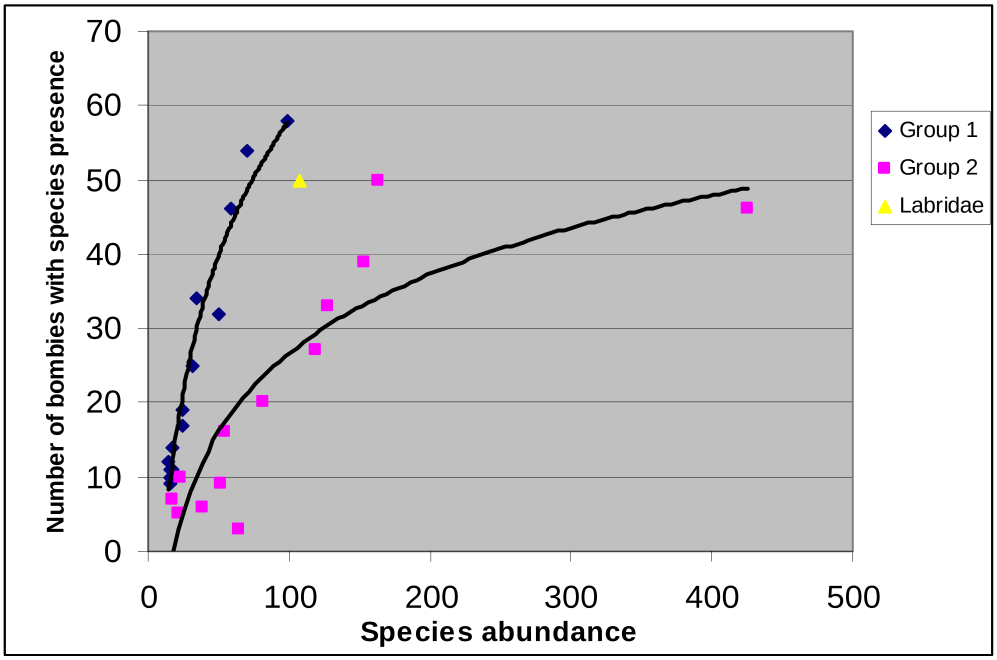

Figure 7. Plot of the number of bombies on which a species was observed against species abundance. Best fit quadratic model for Group 1: $N_B = -6.864 + 1.192\, N_I - 0.005333 N_I^{2}$, ($p<0.0005$, R^2=96.7%). For Group 2 (including Labridae): $N_B = -5.049 + 0.4063\, N_I - 0.000670\, N_I^{2}$, ($p<0.0005$, R^2=79.5%)

Species within Group 1 were seen on many more bombies than species in Group 2 with similar total abundances. For example, *Dischistodus pseudochrysopoecilus* (Group 1) was counted 50 times on 32 different bombies, whereas *Dascyllus reticulatus* (Group 2) was counted 51 times on only 9 bombies. This reflects a tendency to observe the latter species more often in groups (21 individuals on a single bombie was seen) than the former, which was never seen in groups larger than 3. With some exceptions, this is a common feature that divides the species in Group 1 from Group 2. Also Group 1 contains more species of large, more mobile fish (e.g. monocle bream, groupers, butterflyfish, surgeonfish) and Group 2 contains more examples of smaller, site-attached fish (e.g. damselfish, cardinalfish and juveniles of unidentified species).

Habitat features influencing spatial variation in fish assemblages

Bombie Size

A one-way ANOVA analysis (sqrtS=size) showed that there are significant differences between the mean fish species richness of the three bombie size classes (F=70.58, p<0.0005), with richness increasing with size (Fig. 8a). Tukey's pairwise comparison test showed the differences to be greater between large and medium bombies (b-c), and large and small bombies (a-c) (p<0.0005 for both), than between small and medium bombies (a-b) (p=0.0093).

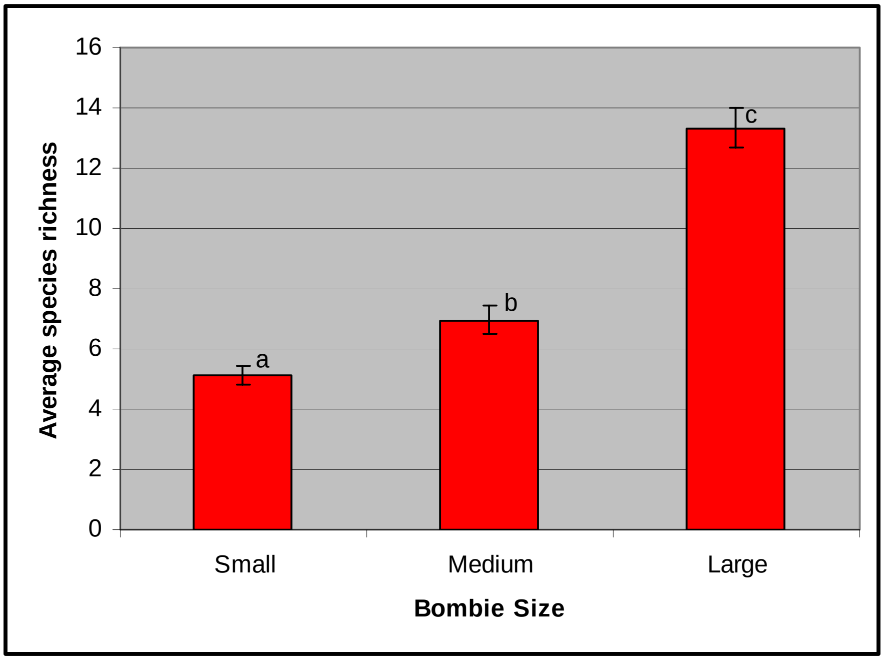

Figure 8a. A bar chart showing differences in average species diversity between bombie size classes. Different alphanumeric labels above bars represent significant differences between group means.

A one-way ANOVA analysis (logN=size) showed that size is also a significant predictor of mean fish abundance (F=40.05, p<0.0005). Again Tukey's test showed the mean abundance for each size class to be significantly different from the other two (p<0.0005) (Fig. 8b).

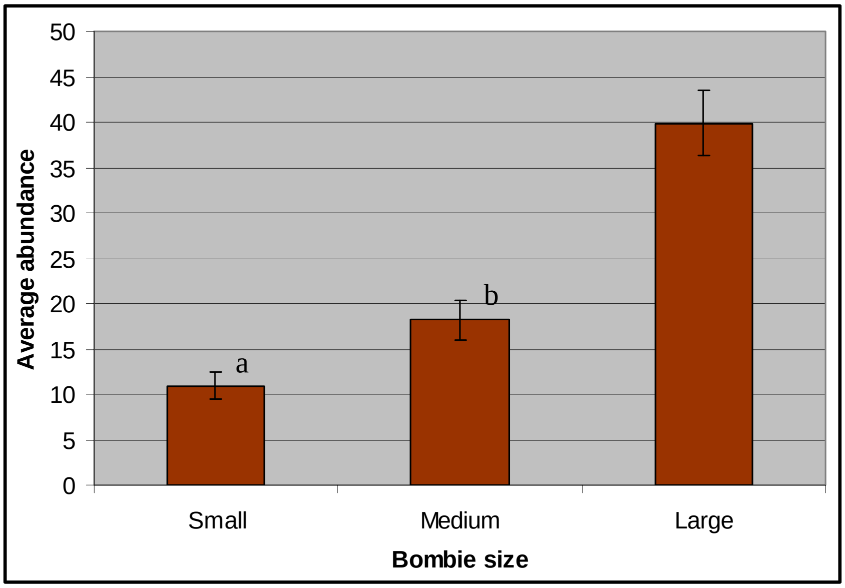

Figure 8b. A bar chart showing differences in average fish abundance between bombie size classes.

<u>Bombie Shape</u>

The effect that approximate shape had on mean fish species richness and abundance can be seen in figure 9. Both graphs show a pattern of increased mean species richness/abundance from cylindrical to cuboidal to triangular. A one-way ANOVA analysis (sqrtS=shape) proved there to be significant differences in mean species richness (F=4.75, p=0.011) supporting the pattern in figure 9a, but Tukey's test showed cuboidal and triangular bombies not to be significantly different from each other (p=0.4397). A similar ANOVA (logN=shape) with Tukey's test, also supported the pattern seen in figure 9b (F=6.15, p=0.003).

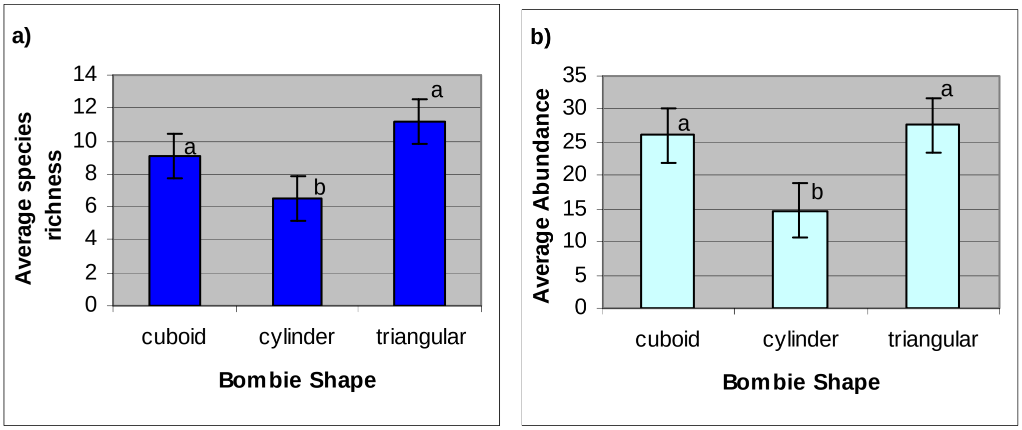

Figure 9. Bar charts showing the differences in a) average fish species richness and b) average fish abundance between bombies of different shapes. Similar labels of group means for cuboidal and triangular bombies (a) indicate they are not significantly different from each other, but both are significantly different from cylindrical bombies (b).

The fact that the difference in average abundance between cuboidal and triangular bombies is also statistically insignificant (p=0.6492), may be due to the subjectivity in classifying bombie shape: identifying cylindrical shapes was far easier than distinguishing between triangular and cuboidal shapes – also a possible reason for the relatively low number of triangular bombies identified (n=5). As such one could argue that triangular and cuboidal bombies should be classed together; on the other hand the insignificant result may not be a failing in the methodology – it may be biologically meaningful. To take an anthropomorphic view: fish may actually "see" little difference between cuboidal and triangular bombies

Bombie Volume

GLM analysis, using 'log(volume)' as a continuous explanatory variable (a measure of bombie size in three dimensions) and 'log(species richness)' as the response variable, was done to test the validity of the species-area relationship in the data. A highly significant relationship was found, ($F=98.75$, $p<0.0005$) (Fig. 10).

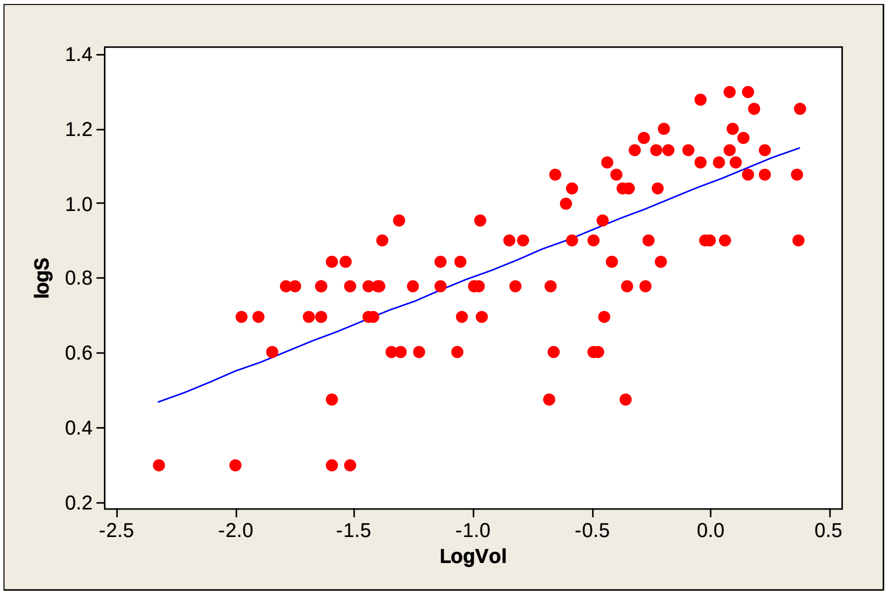

Figure 10. Plot of log(species richness) against log(volume). Fitted line equation is logS = 1.056 + 0.2534 LogVol ($p<0.0005$, $R^2 = 52.9\%$).

Therefore the species-area relationship ($S=cA^z$) is accepted as being applicable to bombies and their associated fish assemblages, with the following best-fit power function: $S = 11.37(A)^{0.2534}$. ('A' in this case referring to bombie volume).

A similar analysis with 'Log(Abundance)' as the response variable, also showed a significant positive correlation with volume ($F=55.3$, $p<0.0005$). The large degree of scatter around the model (compare figure 11 with figure 10) and low R^2 value indicate that the relationship is not tight: a lot of variation in fish abundance remains unexplained.

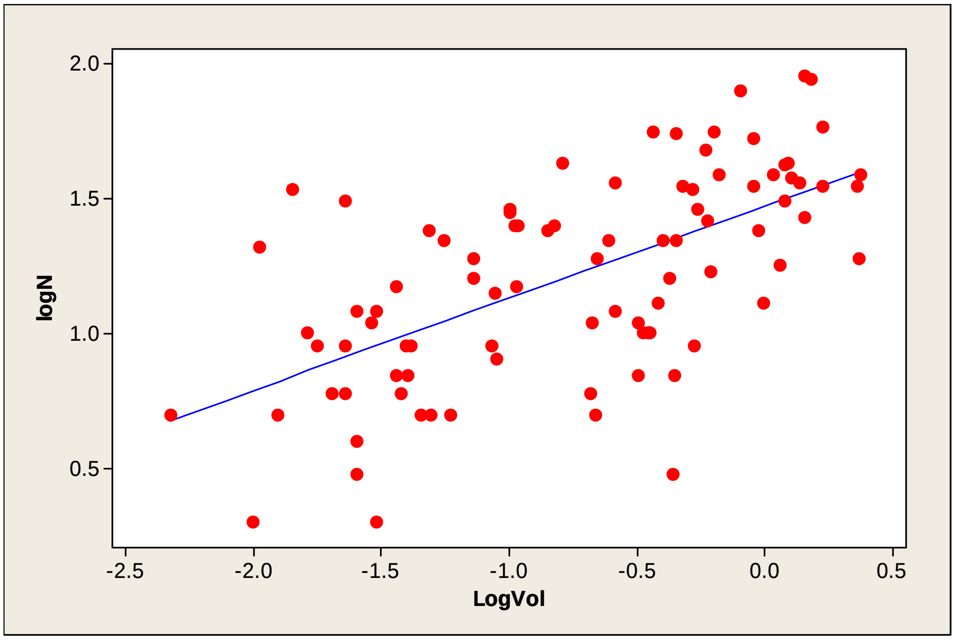

Figure 11. Plot of log(abundance) against log(volume). Fitted line equation is of logN = 1.470 + 0.3419 LogVol ($p<0.0005$, $R^2 = 38.6\%$).

Distance of bombie from reef crest

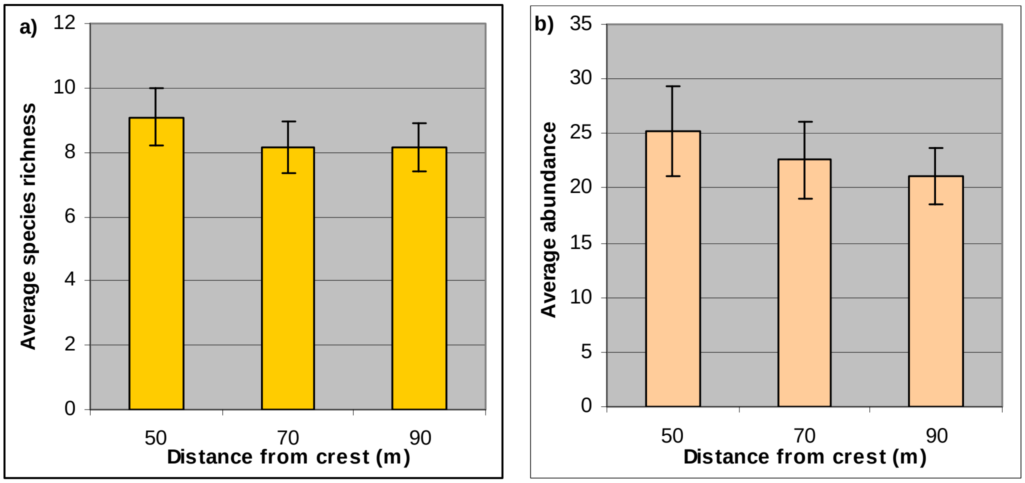

Figure 12. Bar charts showing differences in a) average fish species richness and b) average fish abundance between bombies found at three different distances from the reef crest.

Figure 12a shows that the differences in average fish species richness between bombies at different distances from the crest are small, though it does show a trend of decreasing species richness with increasing distance. The relationship between species richness and distance was shown not to be significant by a one-way ANOVA, (F=0.39, p=0.676). The same pattern can be seen for average fish abundance (Fig. 12b) and again, an insignificant result is achieved by an ANOVA (F=0.17, p=0.848). Therefore one would conclude that the distance of a bombie from the crest has no effect on the fish community in terms of species richness or abundance.

Further GLM analyses treating ‘distance from crest’ as a continuous rather than a categorical explanatory variable were carried out because of the decreasing trends in species richness and abundance from 50m to 90m seen in figure 12, which may be significant, but have been overlooked by simply comparing the group means of the bombies at the three distances. As expected the F-ratios increased, but were still not significant, so the conclusions about ‘distance’ remained unchanged.

Coral composition of bombies

The relationships between coral composition and average fish species richness (Fig. 13a) and average fish abundance (Fig. 13b) were shown to be significant by one-way ANOVAs (F=4.31, p=0.041 and F=4.62, p=0.042 respectively). A GLM which also includes ‘size’ as an explanatory variable, results in coral composition having a much more significant effect on both species richness (F=12.01, p=0.001) and abundance (F=7.85, p=0.007). This is because ‘size’ accounts for much of the noise present in the previous analyses, reducing the Error Mean Square (unexplained variation) and producing larger F-ratios. So, one can conclude that coral composition is a significant variable: bombies of mixed coral composition have on average more fish and more species than bombies of a single coral growth form.

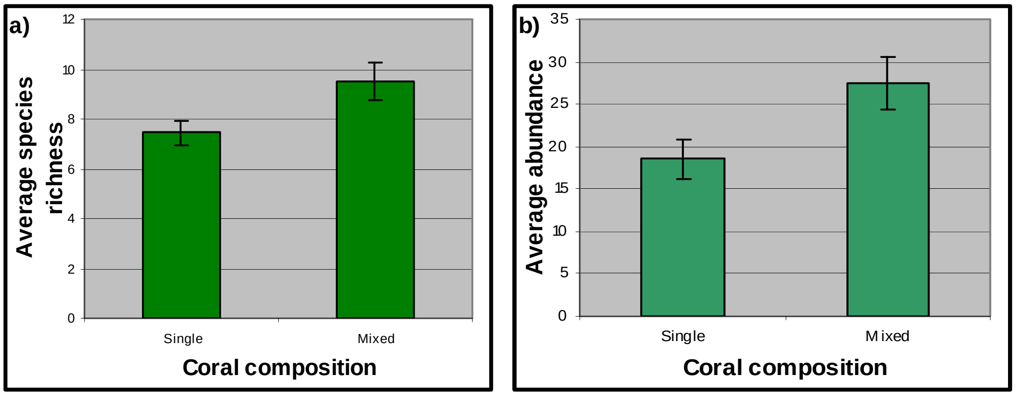

Figure 13. Bar chart showing the difference in a) average fish species richness and b) average fish abundance between bombies of a single coral growth form and those composed of more than one growth form.

Higher order analyses that included all the explanatory variables so far examined, were conducted to test for any interactions, but no significant interactions were found. Thus the way bombie size, in terms of area or volume, influences fish species richness or abundance on bombies is unaffected by coral composition and vice-versa.

Dead coral cover

For those bombies of mixed coral composition (45 out of 90 bombies), figure 14a shows how fish species richness varies with dead coral cover, and figure 14b shows how abundance varies. Both graphs show a similar pattern of decreasing richness/abundance with increasing dead coral cover. Unsurprisingly, the models fitted account for little of the variance in S or N, as seen by the low R^2 values.

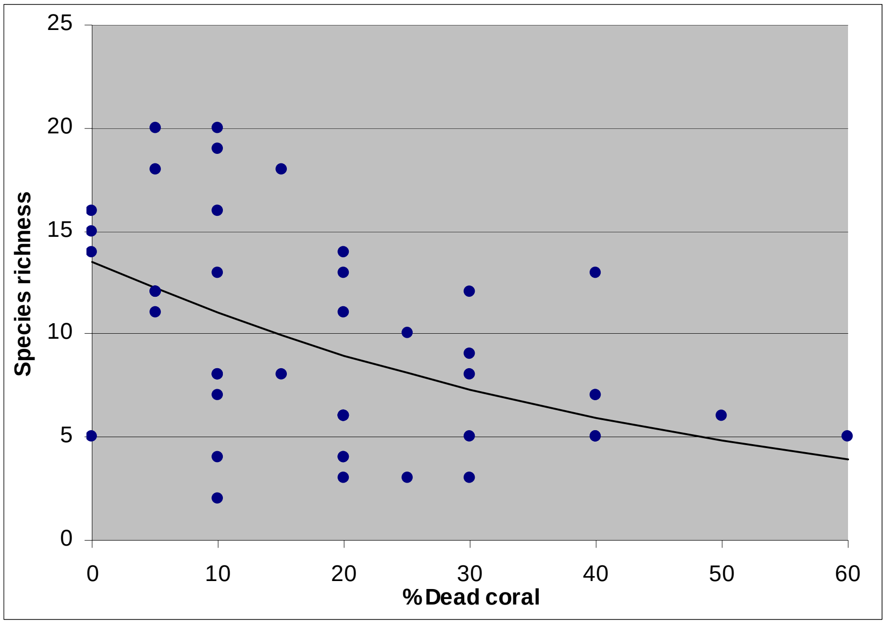

Figure14a. Plot of fish species richness against percentage dead coral cover per bombie. Best fit curve $y=13.535 \times 0.9797^{x}$ ($p<0.01$, $R^2=23\%$).

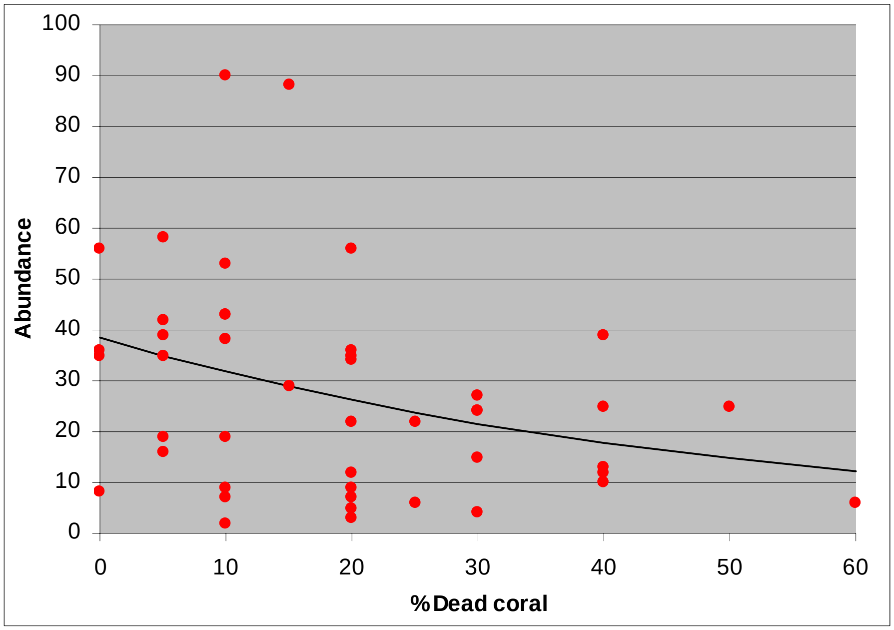

Figure 14b. Plot of fish abundance against percentage dead coral cover per bombie. Best fit curve: $y=38.41 \times 0.981^{x}$ ($p<0.05$, $R^2=12\%$).

Spatial variation in fish community composition

Spatial variation in the 33 fish groups listed in Table 4 was analysed using CCA to try and relate their distributions to measured environmental features of the bombies. All groups included in the analysis were observed on at least 5 different bombies.

Common Name	***Species* or Family**	**Abbreviation**
White Damsel	*Dischistodus perspicillatus*	WhDam
Monarch Damsel	*Dischistodus pseudochrysopoecilus*	MoDam
Blackvent Damsel	*Dischistodus melanotus*	BvDam
Humbug Dascyllus	*Dascyllus aruanus*	HDasc
Reticulated Dascyllus	*Dascyllus reticulatus*	RDasc
Anemonefish spp.	*Amphiprion spp.*	Anem
Staghorn Damsel	*Amblyglyphidodon curacao*	StDam
Black chromis		BkChr
Blue-Green Chromis	*Chromis viridis*	BgChr
Other chromis spp.		chr-sp
Blue Damsel	*Pomacentrus pavo*	BlDam
Threespot Damsel	*Pomacentrus tripunctatus*	ThDam
Black damsel		Bkdam
Black, ocellated dorsal spot damsel		Bocdam
Yellow damsel		Yldam
Other damsel spp.		Damsp
Firetail dottyback	*Labracinus cyclopthalmus*	FDott
Other dottyback spp.		Dottsp
Grouper spp.	*Epinephelus spp*	Group
Bluestreak cleaner wrasse	*Labroides dimidiatus*	BClWr
Other wrasse spp.		Wrasp
Orange-lined Triggerfish	*Balistapus undulatus*	OTrig
Cardinalfish	Apogonidae	Card
Redfin butterflyfish	*Chaetodon lunulatus*	RfBut
Other butterflyfish spp.		Butsp
Bicolor Angelfish	*Centropyge bicolor*	BiAng
Keyhole Angelfish	*Centropyge tibicen*	KyAng
Striped Monocle Bream	*Scolopsis lineatus*	SMoBr
Monocle Bream	*Scolopsis bilineatus*	MoBr
Blenny	Blenniidae	Blenn
Goby	Gobidae	Goby
Juveniles (unidentified spp.)		Juvsp
Surgeonfish	Acanthuridae	Surgf

Table 4. Fish species used in CCA. Abbreviations in column 3, based on names in column 1, were used to facilitate interpretation of the CCA output.

From 15 environmental variables used initially, the following nine were used in the final analysis (abbreviations in brackets): distance from crest (Dist), bombie volume (Vol), cuboidal shape (Cub), mixed coral composition (Mix), submassive growth form (Sub), massive (Mass), branching (Brch), encrusting (Encr) and foliose (Fol). Using these variables, the problem of multicollinearity was solved.

Size classes were not used because, unsurprisingly, they were closely correlated with volume. ‘Cuboidal shape’ and ‘Mixed coral composition’ are binary variables, where the value “1” means a bombie is cuboidal in shape or of mixed coral composition, and the value “0” means the bombie is cylindrical in shape or of single coral composition. Variables relating to individual coral growth forms are continuous (values represent percentage cover on a bombie). The forms ‘mushroom’ and ‘tabulate’ were found so infrequently, even then as a small fraction of total coral cover, that they were highly correlated with one or other of the other growth forms and so were excluded.

The CCA output shows that 21.18% of the variance in community structure was explained by the nine canonical axes, of which approximately half (10.71%) was explained by the first two axes (Table 5). Correlations of environmental variables to these two axes show that the most significant factors measured that explain variance are bombie volume, distance from crest and branching coral cover.

The low eigenvalues (row 1, Table 5) show correspondence between species and bombies is low - a result produced when several species’ optimal distributions are found outside the sites sampled, indicating the gradients of the measured environmental variables are too short (Palmer, 1993), but the CCA still works well.

Canonical Axis	1	2	3	4	5	6	7	8	9
Canonical Eigenvalues	0.233	0.1384	0.0981	0.0883	0.07108	0.0351	0.03224	0.0207	0.01755
% variance explained	6.716	3.991	2.831	2.545	2.049	1.012	0.9293	0.5977	0.506
Cumulative % variance	6.716	10.71	13.54	16.08	18.13	19.14	20.07	20.67	21.18
Correlations of variables to axes									
Volume	-0.752	-0.1667							
Distance	-0.0672	-0.4211							
Branching	0.3166	-0.4274							

Table 5. Eigenvalues for the nine canonical axes and % variance explained. Correlations are only shown for the environmental variables that have the highest correlations to the first two axes.

Figures 15 and 16 show the ordination plots of species and sites respectively, along the first two canonical axes. Both show the widest spread of points along the first (horizontal) axis, which explains 6.716% of the variation in community structure (Table 5). The arrow for ‘volume’ is longest, meaning species’ distributions differ most along this gradient (Ter Braak, 1986), and is closest to parallel with the first axis indicating it has the highest correlation to it. The arrows for ‘distance’ and ‘branching’ are nearly perpendicular to that of ‘volume’, indicating the variables are uncorrelated to ‘volume’ and are the most highly correlated to the second (vertical) axis (bottom two rows of Table 5). The arrows representing ‘foliose’ and ‘mixed’ are shortest, indicative of the fact that these variables have the shortest gradients along which species and sites can be ordered. ‘Mixed’, for example, is a binary variable so the gradient is very short (two values) and therefore not much use in explaining variation in individual species’ distributions.

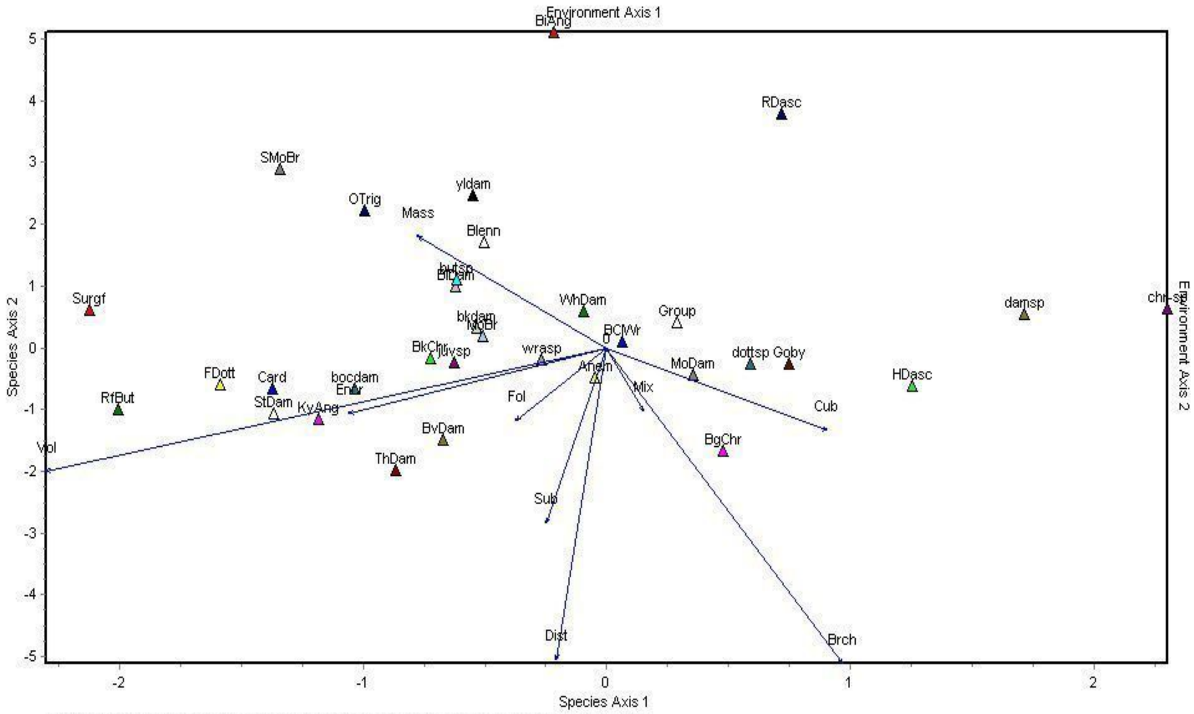

Figure 15. Ordination plot showing species (triangles) and environmental variables (arrows)

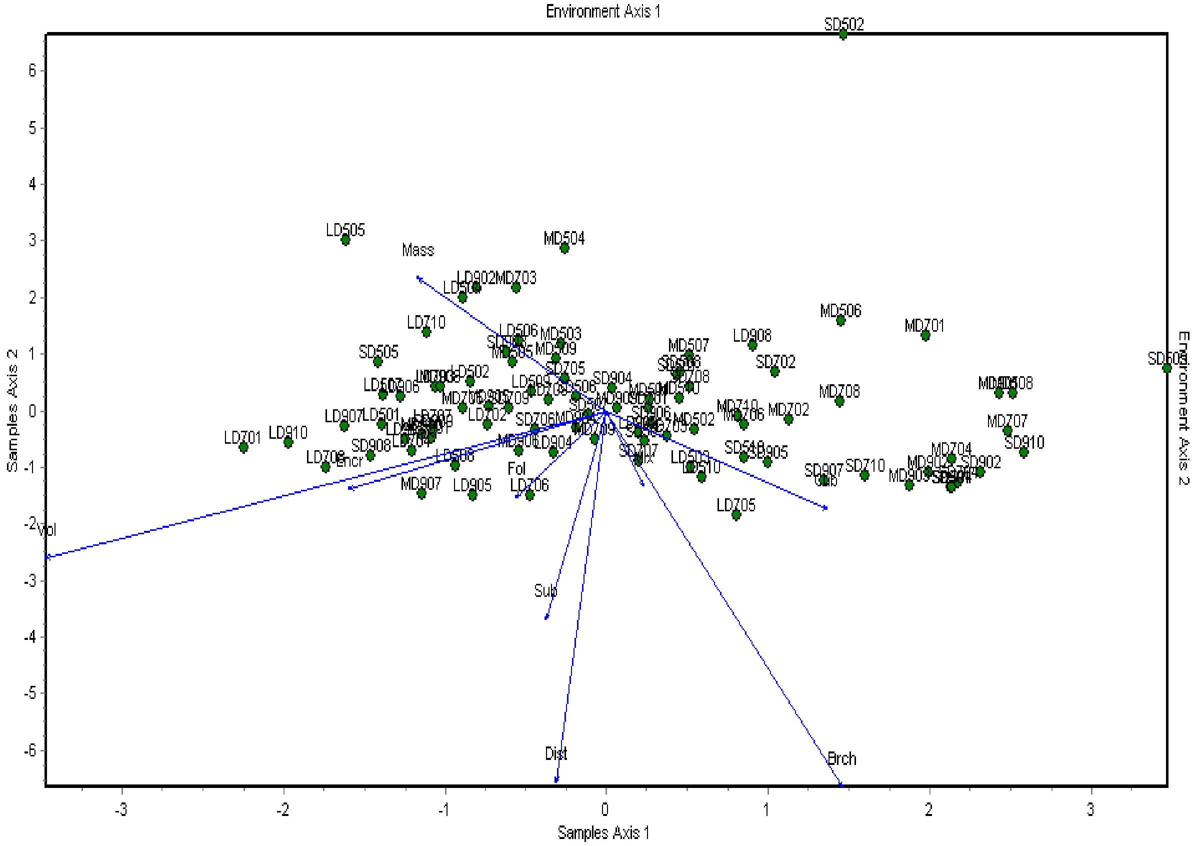

Figure 15. Ordination plot showing bombies (circles) and environmental variables (arrows)

The position of a species point along an environmental axis indicates the approximate centre of a species' distribution along that gradient. For example, the gradient 'volume' runs approximately from right (smaller bombies) to left (larger bombies) (Fig. 16), and according to figure 15, those fish found on the left-hand side e.g. surgeonfish (Acanthuridae), redfin butterflyfish (*Chaetodon lunulatus)* and firetail dottybacks (*Labracinus cyclopthalmus*) associate mainly with bombies of large volume, whereas *Chromis* spp., humbugs (*Dascyllus aruanus)* and other damselfish associate more with small bombies.

Species appearing to have strong associations with other important environmental variables ('distance' and 'branching') include the bicolor angelfish (*Centropyge bicolor*), which associates with bombies closer to the crest (see fig. 15). This inference is supported by the raw data, which shows they were seen only on bombies 50m from the crest, except for one individual observed at 70m.

Blue-green chromis (*Chromis viridis*) and *D. aruanus* are the two species found most often associated with bombies that have high branching coral cover (Fig. 15). This inference is crucial in explaining spatial variation in the *D. aruanus* population and, due to humbugs' dominance in terms of abundance, in the fish community. Therefore a GLM analysis was performed to look for a significant relationship between *D. aruanus* abundance (y-variable) and branching coral cover (x-variable). To correct for non-normality and non-homogeneity of variance the x-variable was arcsine transformed, and the y-variable was square-root transformed. A significant positive correlation was found (F=12.45, p=0.001), which no other x-variable analysed had, supporting the conclusion that branching coral cover is the major environmental variable explaining spatial variation in *D. aruanus*.

Discussion

Whilst no data was collected from outside the bombie zone with which to compare the bombie fish community to, the paucity in the data of certain ‘typical’ reef fishes and the dominance of the Pomacentridae in terms of species richness and abundance, highlights the difference in community structure that can occur between zones of the same reef. On Reunion Island, Letourner (1996) found there to be a ‘spatial continuum’ of fish communities moving between zones and proposes two non-exclusive hypotheses to explain this: i) fish are sensitive to the hydrodynamic gradient that exists between the reef front and flat and ii) that the organization of the fish communities is closely related to substratum variables. Both these hypotheses may apply here, especially when the families involved are considered. Families absent from the bombie zone generally contain species of large, fast swimming fish found in deep water by the reef slope (e.g.Caesionidae) or in open water (e.g. Sphyraenidae; Carangidae). The bombie zone is therefore too shallow for many of these species and environmental features of the substratum will play little role in determining their spatial distributions. On the other hand, the Pomacentridae generally consist of smaller fish species, often territorial and aggressive (e.g. *Dischistodus perspicillatus*, *Dascyllus aruanus*) (Allen, 1991), and so will be more influenced by habitat characteristics (Chabanet *et al*. 1997, Ormond *et al*. 1996).

The overwhelming abundance of Pomacentrid species cannot be explained with certainty, especially since they do not usually account for such a large proportion of fish counted in most studies. An exception is one conducted in the Ryuku Islands by Lecchini *et al.* (2003), who found them in even higher abundances (87% of individuals) and hypothesised that habitat degradation and overfishing negatively affected larger species but not Pomacentrids. That is unlikely to be the main reason here since the reef around Hoga has been little affected by such impacts. A contributing factor may be a limitation in the sampling method: since fish had to clearly interact with bombies to be recorded in the data, more mobile species often swam through the sample area without being recorded despite being present within the bombie zone (and maybe interacting with bombies intermittently). On the other hand, all Pomacentrids that swam into the sample area invariably spent a significant proportion of the sample time interacting with the bombie. This is a reflection of the fact that the majority of Pomacentridae are small, site-attached species.

In terms of spatial variation within the bombie zone, a pattern could be seen based on the spread of individual species among bombies (the ratio N_B/N_I). It emphasized the difference between smaller, site-attached fish such as the Pomacentridae and Apogonidae, especially those often found in schools (low N_B/N_I ratios, assigned to Group 2) and larger fish, often solitary or in pairs, that had less restricted ranges such as the Nemipteridae, Chaetodontidae and Serranidae (high N_B/N_I ratios, assigned to Group 1). Fish in group 2 were more likely to be found in groups on fewer bombies rather than evenly spread because their distributions are likely to be determined by habitat criteria (e.g. branching coral to provide refuges from predation), which not all bombies will fulfil, and because they are less likely to cross open spaces between bombies where they are more vulnerable to predators. Fish in group 1 are more transiently associated with bombies and so less “discriminatory”. Group 1 fish may be more likely to associate with bombies for food which the majority of bombies will provide to one degree or another (e.g Chaetodontidae are corallivores, Serranidae feed on smaller fish associated with bombies). Being larger and more mobile they are likely to be continually moving around within or between zones, and so their distributions are more evenly spread across the bombies sampled.

Bombie size was the most important variable measured when it came to explaining variation in species richness and fish abundance among bombies, with the species-area relationship best described by a curve with a *z*-value of 0.2534. There are few studies of species-area relationships in fish systems in the literature; however Chittaro (2002) also found a similar *z*-value of 0.24 for a patch reef system. Terrestrial system studies have used a variety of methods and produced a range of *z*-values, typically 0.1 to 0.2 for mainland areas and 0.25 to 0.35 for island situations (Rosenzweig, 1995). The reason for this difference can be accounted for by the equilibrium model of island biogeography (MacArthur and Wilson, 1967) which says that the number of species on an island represents a balance between immigration from a mainland "source pool" of species (affected by distance from the mainland) and extinction of resident species (affected by island area). Mainland curves do not depend on these factors and so the differences in species richness between different-sized mainland divisions will not be as great as between islands of equivalent size, hence the gradients of mainland curves will be shallower. If this theory is applied to bombies, the *z*-value of 0.2534, at lower end of the range typical for islands, would signify that immigrations and extinctions are occurring at faster rates than a more isolated island system with a higher *z*-value. This is supported by observations of fish, particularly mobile species, continually moving between bombies.

In explaining the species-area relationship found, the island biogeography theory says species richness on bombies should decrease with distance from the source pool (the reef crest). Though a slight trend was seen, it was not significant, even when bombie size had been accounted for. Furthermore the assumption of constant density of fish populations (Gotelli, 2001) does not hold, with abundances of individual fish species often not increasing in proportion to bombie size.

Different, but not mutually exclusive, explanations for the species-area relationship include the ‘passive-sampling’ process: if bombies are considered as ‘targets’ and fish species or individuals as ‘darts’ tossed randomly at them (Gotelli, 2001), larger targets would be expected to accumulate more darts simply by chance. Thus larger bombies will accumulate a more species-rich and abundant fish assemblage. This is probably an accurate model for some fish-bombie associations, but correlations of species’ distributions with environmental variables and the significance of variables apart from size in predicting species richness, contest it in many cases.

The habitat diversity hypothesis usually explains the majority of species-area relationships (Rosenzweig, 1995) and is equally applicable in this study, in which bombies of larger volumes have a wider variety of substratum features and environmental gradients. There are potentially several ways to measure habitat diversity with respect to bombies; the one used in this study, which looks at coral growth forms, reflects the topographic complexity and coral diversity of the habitat – both of which account for fish community variation (Edinger *et al*. 1998, Letourner, 1996). Indeed, Ormond *et al.* (1996), looking at the correlation between eleven habitat variables and the richness and abundance of 21 damselfish species in the Red Sea, found ‘the strongest relationship that between the number of hard coral growth forms and the number of damselfish species present’. In this study, the significance of the variable ‘coral composition’ supports these findings and gives credence to the habitat diversity hypothesis.

Several reasons can be hypothesised for larger bombies having more diverse fish assemblages under the habitat diversity hypothesis. They provide a wider array of nest sites or refuges, which reduces both intra- and interspecific competition for living space (Jones and McCormick, 2002), particularly among site-attached fish, compared to small bombies where limited shelter availability leads to competitive exclusion. As a food resource for corallivorous fish, large bombies will attract more individuals simply because they have more coral, and more species as they are more likely to be able to provide for species with more specialist diets. Furthermore, the corallivores themselves can contribute to maintaining habitat diversity (thus maintaining fish diversity), by predating rapidly growing coral species (Knowlton and Jackson, 2001). Correlations between large bombies and corallivores were observed: of 35 Chaetodonts counted in the study, 29 were associated with large bombies and the other 6 with medium-sized bombies. Similarly, carnivorous fish that prey on smaller fish are more likely to encounter larger, more diverse food sources associated with larger, more diverse bombies. For example, 17 individuals of *Labracinus cyclopthalmus,* (which feeds on small fish and invertebrates) were observed, all on large bombies that were of mixed coral composition and had a large number of associated damselfish (from 14 to 59). Large bombies may also contain more populations of recruitment-limited species (Harmelin-Vivien, 2002). For fish whose larvae settle in certain habitats preferentially, e.g. due to the presence of live branching corals (Lewis, 1998), large, diverse habitats will fulfil the selection criteria of more species more often than smaller, less diverse habitats. Again, this may affect adult populations of site-attached species more, since post-settlement migrations to more suitable habitats are less likely, especially when this involves crossing exposed areas between bombies. For species in which selective settlement does not occur and recruitment is largely stochastic, larvae are still more likely to settle on large bombies because of passive-sampling.

The multivariate analysis of community composition, like the univariate analyses, showed that bombie size was the most important environmental variable measured in accounting for variation in species' spatial distributions. Some species' distributions varied according to 'distance from crest' - previously found to be insignificant - which highlights the fact that only looking at community-level characteristics such as abundance and species richness may overlook the significance of some variables in explaining individual species' spatial variation. Although the CCA did not test for significant relationships between species and environmental variables, correlations seen in the ordination diagram can be selected for further analysis or study in the field. For example, the association between *Dascyllus aruanas* and branching coral was considered to be particularly useful in understanding community structure, so was tested and the relationship found to be significant.

However, for the majority of species obvious correlations with environmental variables were not revealed; along with the low percentage variance accounted for by the canonical axes (21%), this can be largely explained by the fact that fish community dynamics are influenced by many random, interacting factors. Therefore a large proportion of the unexplained variance is due to variables not included in this study, which include physical factors such as salinity, hydrodynamic gradients etc, other habitat variables such as coral species distributions, distance between bombies, algal cover etc, biological and historical factors (see introduction) and higher order interactions between variables. A proportion of the unexplained variation is also ‘pure spatial variation’ (Lecchini *et al.* 2003). This may be of importance in explaining the lack of species correlations with bombies particularly for more mobile species. Their movements will often not be targeted towards bombies (associations may follow the passive-sampling process), so their observed distributions will be random with respect to environmental variables, and perhaps often random with respect to biological factors.

As expected from a study carried out in a coral reef ecosystem the fish community observed was found to be very diverse, but with clear patterns of spatial variation. At least sixty different species (largely Pomacentridae) were observed in the bombie zone, but this is far below the true number of species present, since almost half of the individuals observed (1025/2070) were not identified to species level. The data collected showed that a log-normal distribution best models the species-abundance relationships, supporting a classic hypothesis of community structure: several randomly varying environmental factors interacting with more typical density-dependent factors to affect population dynamics (Connolly *et al.* 2005). In this study, habitat size and diversity were key environmental factors.

This study also demonstrated how univariate and multivariate analysis can complement each other to provide a more detailed understanding of community structure. To extend this knowledge at a local scale similar studies could be done at different sites around the island, to give a better idea of the effect of currents, wind etc. on the fish community. At a regional scale, studies could be conducted in bombie zones of nearby reefs and compared with each other. From a conservation perspective, it would then also be useful to compare the results to reefs that are outside protected areas and discover whether the well-documented effects of disturbances on coral reefs affect bombie fish communities in a similar manner.

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Project Management Report

The first stage of the project, the planning and background, went according to plan with no major changes to what I had anticipated. Since the data collection involved planning an overseas expedition, a lot of time was necessary to organise the trip as well as plan the project itself, yet there was little time pressure at this point because I made the decision to go on the expedition over eight months in advance. I started the literature review at this stage and continued it for nearly the entire course of the project; I predicted this would happen, as each stage of the project, especially the write-up, would throw up questions previously not addressed or thought of.

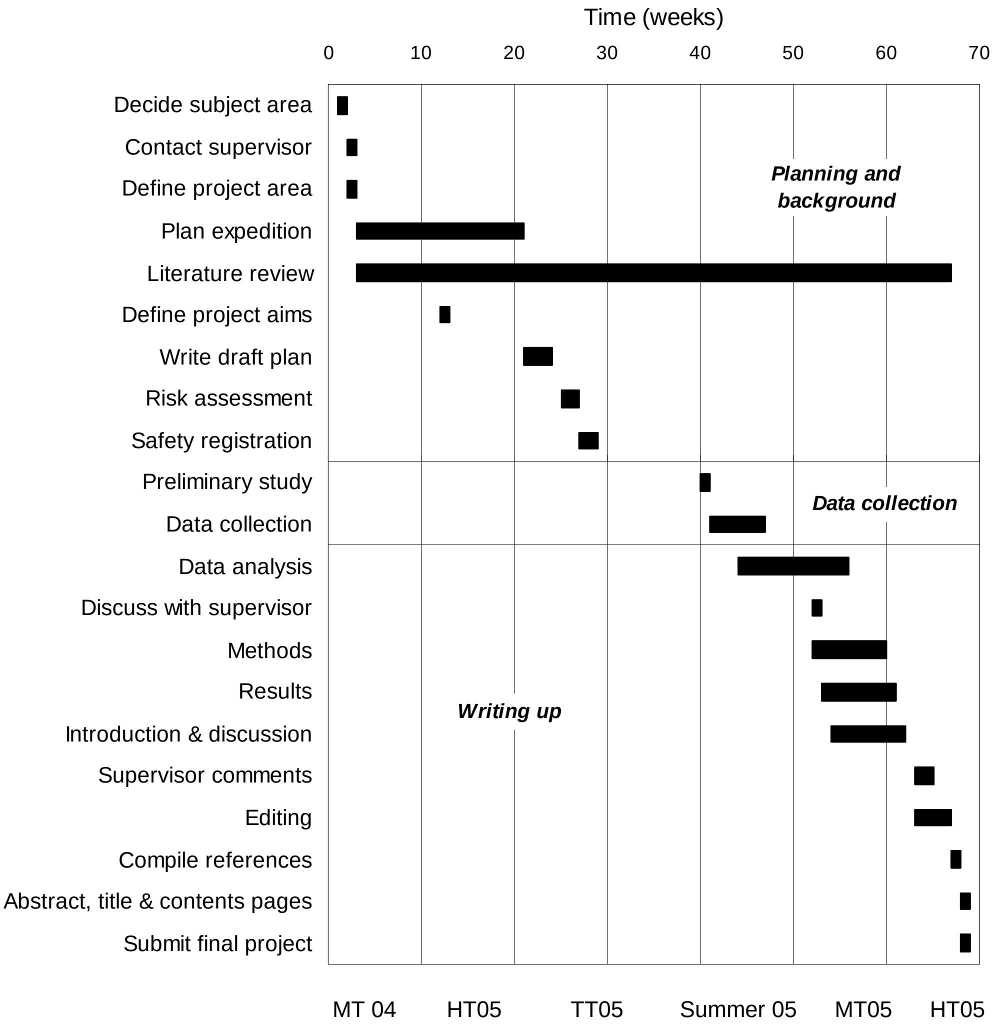
Careful planning was necessary since the data collection was being conducted in Indonesia over a six-week period. Operation Wallacea, with whom I went on the expedition, had advised that four weeks would be sufficient to collect enough data for an undergraduate dissertation, but I allowed extra weeks so there would be less time pressure and to permit me to collect more than a sufficient amount data, and in case any unforeseen mishaps occurred.

Once on Hoga Island, preliminary studies and data collection went as planned. No mishaps occurred beyond missing two days due to slight illness. Indeed I was able to collect data from more bombies than I had originally intended because on some days the high tides allowed me to stay out snorkelling for longer than usual. I was able to do some initial statistical analyses and planning of the write-up towards the end of the trip as I had hoped. This meant I had some basic analyses and graphs to discuss with my supervisor when I returned to Oxford.

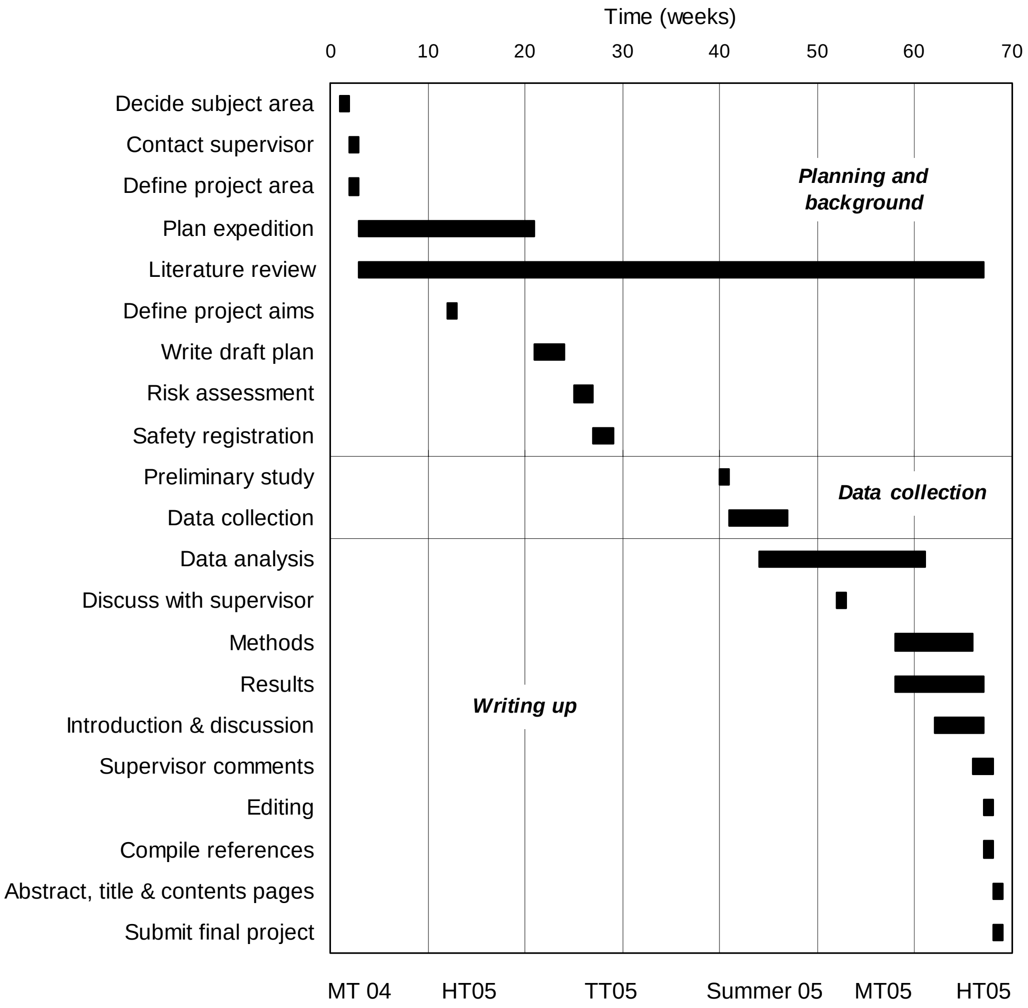
The major changes to my expected progress occurred because the data analysis that I did back in Oxford took longer than I had anticipated. This was partly because I had collected more data than planned, which took time to organise in spreadsheets and format for use in Minitab and ECOM, and partly because it took a few weeks to understand CCA and learn to use ECOM proficiently. I had to read quite a few extra papers on how CCA works and how to interpret the output that the software package produced. Furthermore, I carried out more univariate analyses than I thought I would do initially, for example some unanticipated analyses were performed after seeing the results obtained from the multivariate statistics.

Therefore the writing up of the project did not start until the end of Michaelmas term and proceeded through the vacation and into Hilary term. It meant that a first draft was not produced until the end of third week in Hilary, instead of at the start of Hilary as I had expected. However the first draft required fewer changes than I had originally thought it would, hence the time necessary to edit the project after showing it to my supervisor was shorter (1-2 weeks instead of 3-4 weeks) than expected.

Overall, the progress of my project went well. The planning and data collection stages ran almost exactly as anticipated and I encountered no major problems at all. The writing up stage was set back slightly due to the time taken to do all the data analysis, but the project itself did not suffer because of it. Enough time was allowed for such an occurrence and the project was completed and submitted within the deadline.



Gantt chart 1 – Expected progress of project.



Gantt chart 2 – Actual progress of project.